Hurricane effects on the planktonic food web of a large subtropical lake

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Hurricanes Frances and Jeanne passed over Lake Okeechobee, Florida, in September 2004 and Hurricane Wilma in October 2005. The storms created large waves, strong currents, high wind seiches and uplifted over 3 million metric tons (collectively) of sediments into the water column. Suspended solid concentrations increased five-fold and there were substantial changes in the plankton. Unlike previously documented effects of hurricanes in the open ocean and estuaries, where increased nitrogen inputs stimulate primary productivity, the hurricanes resulted in substantial reductions in biomass of bacteria, phytoplankton and phototrophic nanoflagellates, both in pelagic and near-shore habitats. Increases in macro-zooplankton biomass were observed in both habitats. There were sustained large increases in dissolved inorganic nitrogen and phosphorus in the water column after the hurricanes, coincident with large declines in mean irradiance in the mixed layer. Further, results from laboratory bioassays that exposed the phytoplankton to nutrient additions and a controlled light gradient indicate that the community shifted from being frequently nitrogen limited to most commonly light limited after the storms. The results confirm that the major driver of plankton food-web dynamics in this system is light availability, and that the primary mechanism of change caused by hurricanes is an accentuation of light limitation via greatly increased sediment re-suspension. There additionally was evidence of food-web-mediated effects where the loss of submerged vegetation and increased turbidity reduced the density and efficiency of visually feeding fishes, leading to a significant increase in biomass of macro-zooplankton.

KEYWORDS: plankton; hurricanes; light limitation; shallow lakes

INTRODUCTION

Hurricanes can profoundly affect the structure and function of plankton communities, as documented in recent studies conducted primarily in the open ocean and estuaries. In the ocean, hurricanes can generate turbulent mixing that entrains nutrients from deeper waters, stimulating phytoplankton production. They also can disperse heterogeneous patches of higher plankton biomass associated with eddies, leaving a more homogeneous distribution of primary and secondary productivity. Such effects were observed off the Bahamas and in the central Gulf of Mexico following the passage of Hurricane Katrina in 2005 (Gierach *et al.*, 2009a,b). Nutrient upwelling also was identified as the cause of phytoplankton blooms in the Chesapeake Bay after Hurricane Isabel in 2003 (Roman *et al.*, 2005). In coastal systems, the addition of limiting nutrients in flood pulses associated with heavy rains from land-

falling hurricanes also can stimulate phytoplankton production and in some cases result in changes in phytoplankton taxonomic composition. Flood pulse effects of hurricanes have been documented in Pensacola Bay, Florida (Hagy et al., 2006), Guana Tolomato Matanzas Estuary, Florida (Dix et al., 2008) and Pamlico Sound, North Carolina (Peierls et al., 2003). In general, it has been suggested that estuaries are relatively resilient in that nutrient concentrations, transparency and phytoplankton biomass typically return to pre-storm levels within months after hurricanes (e.g. in the Pensacola Bay example and many others); however, Peierls et al. (Peierls et al., 2003) noted that changes in phytoplankton taxonomic composition may persist for multiple years. Residence time of the system determines in part the duration of the impacts (Murrell et al., 2007).

Only a few studies have examined responses of other components of the plankton to hurricanes. Zhang and Wang (Zhang and Wang, 2000) observed that the biomass of ciliated protozoa was significantly reduced in the Bohai Sea, China following a hurricane in 1998, but were unable to identify the cause. Roman et al. (Roman et al., 2005) observed that the abundance of calanoid copepods increased after Hurricane Isabel passed over Chesapeake Bay in 2003, and that this subsequently led to increased recruitment of larval fish. This was considered to be a resource-driven response, because hurricane-related water and nutrient inputs to the Bay led to wide-spread increases in phytoplankton biomass. Most recently, in a modeling study, Gierach et al. (Gierach et al., 2009b) examined potential effects of Hurricane Katrina (2005) on plankton size structure in the Gulf of Mexico. They concluded that the hurricane resulted in increased absolute and relative biomass of large phytoplankton due to nutrient injection from deeper water, and changes in the spatial distribution of both micro- and macro-zooplankton.

All of these studies have involved coastal and marine systems, where interactions between sediment and water are generally less pronounced than in shallow lakes, and only in the case of Pamlico Sound was there a short period of potential light limitation of phytoplankton production associated with re-suspension of sediments and reduced underwater irradiance (Peierls et al., 2003). In large shallow lakes, where wind-driven waves can re-suspend flocculent bottom sediments into the water (Douglas et al., 2002), the effects of hurricanes are expected to be markedly different and more prolonged.

We previously have examined effects of a low-intensity hurricane on Lake Okeechobee, but only from the perspective of water chemistry and submerged aquatic vegetation (Havens et al., 2001, 2007a).When a hurricane affected the lake in 1999, wind-driven waves

and currents uplifted sediments into the water column, significantly increased turbidity and nutrient concentrations, and reduced underwater irradiance (Havens et al., 2001; Abtew and Iricanin, 2008).

Irradiance is a major controlling factor of plankton dynamics in shallow mixed lakes (Reynolds, 1993; Aldridge et al., 1995; Phlips et al., 1995; Rucker et al., 1997). Thus, hurricanes are expected to have major effects on the plankton, altering the manner in which carbon is partitioned among the various trophic guilds and potentially changing resource availability for fishes and fundamental properties such as photosynthesis/respiration (P/R) ratio and the ratio of consumers to decomposers. Yet to date, there have been no quantitative analyses of these effects, simply because there has not been a major hurricane coincident with an ongoing plankton assessment of sufficient temporal duration to measure responses.

A detailed assessment of plankton composition and functional properties, including nutrient and light limitation, started at Lake Okeechobee in 2000, largely to evaluate system recovery from the 1999 hurricane as well as response to a rapid draw-down in the water level (Havens et al., 2001). This evolved into a comprehensive long-term plankton monitoring program that encompassed a period when the lake was affected by three strong hurricanes. Data from that program allowed for a detailed comparison of conditions using multiple years of data and testing predictions of hurricane effects on shallow subtropical lakes.

Knowing that underwater light availability is a major driver of seasonal dynamics in lakes of this type (shallow, subtropical and subject to seasonally variable wind-driven sediment re-suspension), we predicted that following major hurricanes, there would be a reduction in the relative biomass of phytoplankton, phototrophic flagellates, the ratio of producers to consumers and decomposers, as a result of severe light limitation caused by re-suspended sediments; and increased biomass of large zooplankton, as increased turbidity releases the animals from the typically high predation pressure by visually feeding fish in subtropical lakes (Jeppesen et al., 2007).

Study site and recent hurricane history

Lake Okeechobee is a eutrophic subtropical lake on the southern peninsula of Florida at 27°00′N latitude and 80°50′W longitude. The lake has a surface area of 1800 km^2 and a mean depth of 2.7 m. It originated during oceanic recession in the late Pleistocene (Gleason and Stone, 1975). Characteristics of Lake Okeechobee are similar to other large lowland lakes in

Europe, North America and Asia (Havens *et al.*, 2007a) in regard to nutrient enrichment, agricultural development of the surrounding watershed and sediments that are susceptible to periodic re-suspension events driven by seasonal winds and storms.

Earlier studies have identified distinct ecological regions in Lake Okeechobee (Phlips *et al.*, 1993). A deeper pelagic region extends to the base of a man-made levee along the north and east shorelines, and in this region phytoplankton are the only primary producers. A shallower 'near-shore' region occurs on a higher elevation shelf from the northwest to the south, and it supports phytoplankton, benthic algae and vascular plants. The two lake regions also differ in sediment type, with the pelagic region being underlain by mud and the near-shore region having variable sediments comprised of sand, peat, rock or mud (Fisher *et al.*, 2001).

Phlips *et al.* (Phlips *et al.*, 1993) and Aldridge *et al.* (Aldridge *et al.*, 1995) studied the seasonal dynamics of light and nutrient limitation of phytoplankton, and found that in the pelagic region, light is most often limiting, especially during winter, when rainfall is relatively low but wind velocities are high. Wind reduces light availability by suspending fine mud bottom sediments into the water column. In contrast, nitrogen sometimes is limiting in the pelagic region during summer, when wind velocities are lower and there is reduced sediment re-suspension. In the near-shore region, nitrogen limitation may persist year-round if water levels are sufficiently low to prevent transport of fine sediments from the pelagic region, or light limitation may develop in the winter when water levels are high and there is lake-wide transport of solids by wind and currents (Havens *et al.*, 2007a).

Lake Okeechobee was affected by Hurricane Irene in October 1999 and then again by Hurricanes Frances and Jeanne on 5 and 24 September 2004 (Fig. 1). In October 2005, Hurricane Wilma, the strongest of the storms, passed just south of the lake. Maximum wind velocities during the storms, measured at a mid-lake meteorological station, were 87, 108, 120 and 126 km h^{-1}, respectively. Hurricanes Frances, Jeanne and Wilma produced large wind seiches and generated waves that uplifted $6-12$ cm of mud into the water column, based on analysis of sediment profiles obtained before and after the hurricanes using ^{201}Pb methodology (James *et al.*, 2008). Estimated amounts of sediment entrained into the water during those three major storms were 2.1, 0.7 and 1.4 million metric tons, respectively, resulting in total suspended solid concentrations increasing from below 50 to as high as 200 mg L^{-1} in the water column (Abtew and Iricanin,
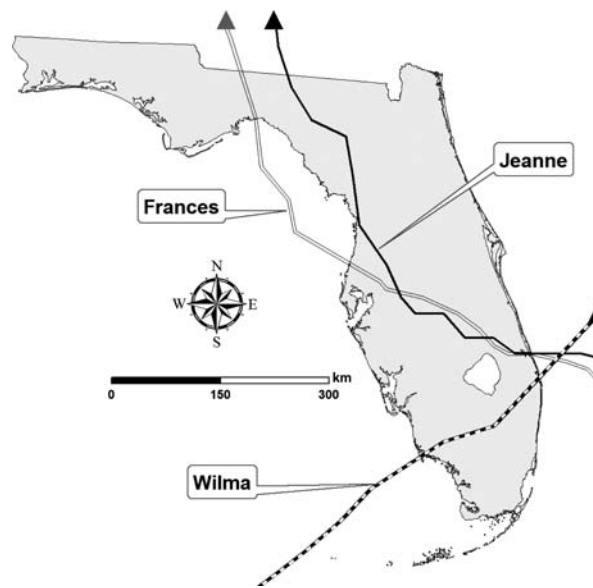

Fig. 1. Tracks of Hurricanes Frances (5 September 2004), Jeanne (24 September 2004) and Wilma (24 October 2005) as they passed over the Florida peninsula.

2008). Prior modeling studies have indicated that the fine sediments in this lake can remain in the water column for several months after re-suspension (Jin and Ji, 2001).

METHOD

Sampling locations and collection methods

Long-term sampling of plankton in Lake Okeechobee by the South Florida Water Management District (SFWMD) has been ongoing since 1996. However, only in January 2000 did that sampling begin to include components of the plankton other than phytoplankton and zooplankton and only until early 2007 was sampling maintained at a sufficient number of stations (Fig. 2) to characterize both the pelagic and near-shore regions. Here we examine pre- and post-hurricane data relative to Hurricanes Frances, Jeanne and Wilma. We also consider the brief period (two sampling events) of post-hurricane data from Hurricane Irene, in order to quantify the magnitude of impacts to the plankton. Examination of selected water quality data post 2007 also provides insight into recovery of the lake many years after the major storms.

At each of the five sampling stations, depth was measured with a weighted and calibrated nylon line and transparency was determined using a 20 cm Secchi disk. Physical and chemical parameters (temperature,
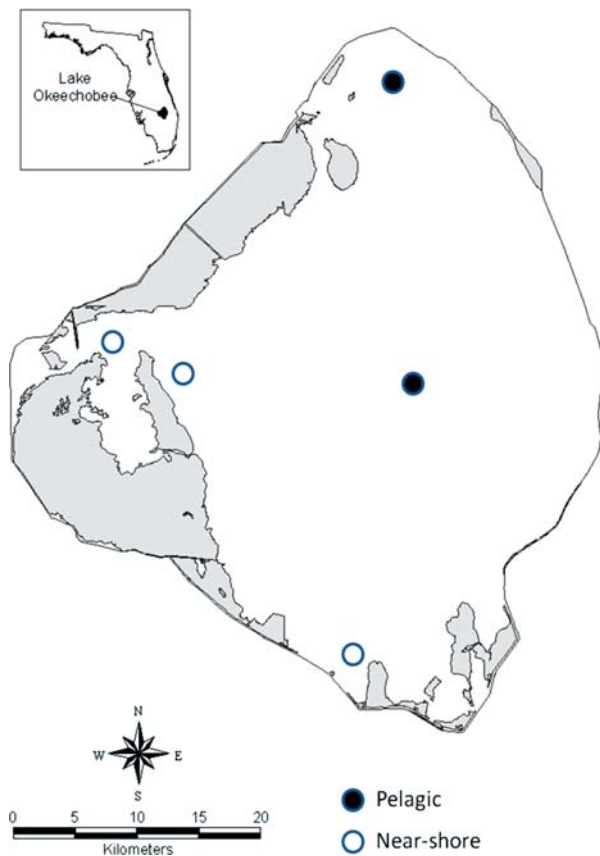
Fig. 2. Map of Lake Okeechobee with locations of the two pelagic and thee near-shore sampling stations. The shaded area is emergent wetland and the inset map indicates location of the lake in Florida, USA.

dissolved oxygen, pH, redox potential and conductivity) were measured at surface, mid-depth and 50 cm off the lake bottom with a YSI multi-parameter sonde. Samples from the same sites were collected for analysis of ammonia (NH_4), nitrate (NO_3), nitrite (NO_2) and soluble reactive phosphorus (SRP) and were obtained in a separate long-term sampling program (at the same locations and temporal frequency) performed by the SFWMD. Nutrients were analyzed following standard USEPA protocols, including the recommended use of reference standards and blanks. All samples were filtered through Whatman GF/F filters before analysis (USEPA, 1979; SFWMD, 2002).

Plankton sampling, counting and calculations

The following plankton components were examined: macro-zooplankton, micro-zooplankton (rotifers and nauplii), ciliates, heterotrophic nanoflagellates, photo-trophic nanoflagellates, bacteria and phytoplankton.

The macro-zooplankton (cladocerans, adult copepods and copepodids) was sampled at each site with three vertical tows through the water column with a 30-cm diameter conical plankton net with a mesh size of 153 μm. Animals retained by each tow were rinsed into an amber plastic bottle and preserved with chilled sucrose-formalin solution. Micro-zooplankton (rotifers and nauplii) was sampled with a 3 cm diameter integrated sampler. Approximately 20 L of water from the entire water column, except for the bottom 50 cm, was collected in a polyethylene carboy. Microzooplankton then was filtered by pouring the 20 L water sample through a 35 μm mesh plankton net and the retained animals were preserved as above. Another integrated sample of whole water was collected for microscopic analysis of bacteria, flagellates, ciliates and phytoplankton. Bacteria and ciliate samples were preserved with 0.2 μm filtered formalin. Flagellates were preserved with cacodylate-buffered glutaraldehyde, and phytoplankton was preserved with Lugol's solution. In all cases, final concentrations of fixatives were ∼15%.

All microscopic enumerations were done by counting at least 400 individuals in order to achieve counting accuracies of 90% (Lund et al., 1958). To optimize comparability of data with contemporary studies, all calculations of C biomass from counts were performed according to the methods used by Auer et al. (Auer et al., 2004) and Havens et al. (Havens et al., 2007b). Bacteria were stained with acriflavine (Bergström et al., 1986) on 0.2 μm black Nucleopore filters prior to counting with an epifluorescence microscope at ×1000 magnification. Cell volumes were determined based on measurements of dimensions with an ocular micrometer, and C biomass was calculated with the conversion constant of 0.106 pg C μm^{-3} (Nagata, 1986).

Photo-trophic and heterotrophic nanoflagellates were enumerated by the epifluorescence method of Caron (Caron, 1983), which involves staining cells with Primulin on 0.8 μm Nucleopore filters. Biovolumes were calculated from measurements of cells approximated to regular geometric shapes. Counts were converted to biomass using the factor 0.10 pg C μm^{-3} (Borsheim and Bratbak, 1987). Micro-phytoplankton, ciliates, nauplii and rotifers were counted with an inverted microscope technique (Lund et al., 1958) and a 24 h settling time. The biovolume of individual phytoplankton cells (μm^{-3}), including those in colonies and filaments, and the biovolume of ciliates, were determined by measuring dimensions and then calculating volumes of similarly shaped regular geometric shapes. Biomass of phytoplankton was calculated using the factor 0.11 pg C μm^{-3} (Rocha and Duncan, 1985),

which is the same conversion factor used for ciliates (Turley *et al.*, 1986). Dry weights for nauplii and rotifers were determined using published length−weight relationships (McCauley, 1984). Rotifer and nauplii biomass was determined using the factor 0.075 pg C pg^{-1} wet weight (Latja and Salonen, 1978), assuming that wet weight is equal to 10 times the calculated dry weight (Pace and Orcutt, 1981).

Macro-zooplankton was counted at ×100 magnification. Population densities were estimated from the counts as numbers per liter, based on the volume of water sampled by the net and assuming 100% sampling efficiency. Dry weights were calculated and converted to wet weight and then to carbon biomass in the same manner used for rotifers and nauplii.

We calculated the biomass-weighted mean length of zooplankton in the two regions for pre-hurricane and post-hurricane periods (as a possible indicator of changes in fish predation pressure); however, there were no significant differences because a particular species of copepod (*Arctodiaptomus dorsalis*) was extremely dominant in all samples.

Nutrient and light bioassays

Laboratory bioassays were performed to determine factors limiting phytoplankton growth [light, nitrogen (N), phosphorus (P) or N + P] following the methods described in East and Sharfstein (East and Sharfstein, 2006). An integrated water sample was collected at the same north, central, south and west sites in the lake where the plankton sampling occurred (the western bay site was not included in the assays). The water was transported to the laboratory inside 20-L polycarbonate carboys covered with a tarpaulin and allowed to equilibrate in the dark overnight at 25°C. Triplicate 150 ml aliquots of water and associated phytoplankton from the lake were placed into 60 250 ml screw-cap glass Erlenmeyer flasks for the bioassays. Light treatments included five levels of PAR irradiance (12 h light/12 h dark cycle): 240, 115, 48, 23 and 12 μmol m^{-2} s^{-1}, with 240 μmol m^{-2} s^{-1} representing the average maximum daily near-surface irradiance previously measured in the lake (Phlips *et al.*, 1997). At each irradiance level, four nutrient treatments were added to individual flasks: 400 μg N L^{-1}, 40 μg P L^{-1}, 400 μg N L^{-1} plus 40 μg P L^{-1} and a control (no additions). Enrichment levels were selected to match those used in earlier bioassay studies on the lake (Aldridge *et al.*, 1995; Phlips *et al.*, 1997) and to follow recommendations of Schelske (Schelske, 1984). Flasks were thoroughly mixed daily and before sampling. Changes in algal biomass were determined by measuring *in vivo* fluorescence (IVF) at time zero and after 48 h (both at the end of a dark exposure cycle). A nutrient was considered limiting when IVF increased significantly in an enriched treatment but not in the control as determined by ANOVA. Light was considered limiting when a significant light gradient response was documented and no response to nutrient enrichment occurred under the optimal irradiance.

Underwater irradiance

Phlips *et al.* (Phlips *et al.*, 1995) identified that the degree of light limitation of phytoplankton in Lake Okeechobee is best predicted from estimates of I_m, which they calculated according to Stefan *et al.* (Stefan *et al.*, 1976) as $I_m = [I_o/(K_t)(Z_m)][1 - e^{-[(Kt)(Zm)]}]$: where I_o is mean daily surface PAR irradiance, K_t the light extinction coefficient (m^{-1}) and Z_m the depth of the mixed layer, which was assumed to be equal to total depth. I_m is more useful than Secchi transparency in this regard because it takes into consideration seasonal variation in incident PAR, in addition to attenuation in the water column. Although we did not have underwater irradiance data to calculate K_t for the pre- and post-hurricane periods, we approximated light extinction from the relationship Secchi $= 1.7/K_t$ (Wetzel, 1983; Kratzer *et al.*, 2003), and assuming that I_o follows a seasonal pattern identified by Oswald and Gataas (Oswald and Gataas, 1957) for this region of Florida, we calculated I_m. We compared mean values of I_m in the pelagic and littoral zone before compared to after the hurricanes, and we also examined the correlation between I_m and phytoplankton biomass for the entire data set.

Statistical analyses

Plankton and water quality data were natural log transformed before performing statistical analyses, in order to normalize the skewed data. To test for hurricane effects, we performed one-way ANOVAs to compare means from two distinct periods—pre-hurricane (July 2000 to August 2001), and post-hurricane (September 2001 to January 2007), for the two lake regions. We additionally include January and April 2000 as post-hurricane data, because, as noted, this period reflects the lingering impacts of Hurricane Irene (Havens *et al.*, 2001). We also provide representative data from 2008 to 2009, to indicate the degree to which physical and chemical attributes of the pelagic and near-shore region had returned to pre-hurricane levels 3 years after the storms.

We did not account for seasonal dynamics in this study due to irregular sampling. As a result, the statistical analyses are conservative given that in each time period there is variation in the data that might be due in part by seasonal changes in light and nutrient limitation (Aldridge *et al.*, 1995) and changes in depth that influence the degree of benthic–pelagic coupling (James and Havens, 2005; Havens *et al.*, 2007a).

RESULTS

Physical and chemical conditions and limiting factors

Water depths varied from below 3 m during the pre-hurricane period to over 4 m in the post-hurricane period. Secchi transparencies ranged from a maximum of 60 cm to a minimum of 10 cm (Fig. 3a). There was a significant reduction in transparency from 30 cm before the hurricanes, to an average of 15 cm afterwards (Table I). In the near-shore region, water depths varied from below 2 m to near 4 m, and transparencies ranged from over 1 m to below 0.1 m (Fig. 3b). Transparencies here were also significantly reduced, from 53 cm before to 26 cm after the hurricanes (Table I).

In the pelagic region, mean concentrations of dissolved inorganic N (DIN = sum of NO_3, NO_2 and NH_4) and SRP were 212 and 42 μg L^{-1}, respectively, before the hurricanes. Both DIN and SRP concentrations increased substantially following the hurricanes, with DIN exceeding 800 μg L^{-1} and averaging 465 μg L^{-1} and SRP exceeding 80 μg L^{-1} and averaging 70 μg L^{-1}. DIN concentrations declined in early 2007; however, SRP concentrations remained elevated to the end of the study period. Post-hurricane increases in mean pelagic DIN and SRP concentrations were both statistically significant (Table I). In the near-shore region, concentrations of DIN and SRP were relatively low in the pre-hurricane periods. DIN was depleted to below detection limits in summer 2002, 2003 and 2004. Immediately after the hurricanes, DIN and SRP concentrations increased to levels very similar to those observed in the pelagic region and then displayed similar temporal dynamics until the end of the study period (Fig. 3c and d). Post-hurricane increases in mean near-shore DIN and SRP concentrations were both statistically significant.

There was a consistently higher occurrence of light limitation in the pelagic region than in the near-shore region. On average, light was limiting in the pelagic region 60% of the time before and 78% of the time after the hurricanes (Table I). In the near-shore region, light was limiting 17% of the time before and 42% after the hurricanes (Table I). Consistent with these results, I_m in the pelagic region declined from 1.2 $\pm$ 0.1 mole photons day^{-1} before the hurricanes to 0.5 $\pm$ 0.2 mol photons day^{-1} afterwards, and the corresponding decline in the near-shore region was from 3.9 $\pm$ 0.5 to 2.0 $\pm$ 0.5 mole photons day^{-1}.

Plankton biomass and composition

The 7-year pattern of plankton biomass in the pelagic and near-shore regions (Fig. 4a and b) indicates considerable and sometimes asynchronous variation (i.e. maxima are coincident for the two regions in 2000, 2002 and 2003, but do not coincide in time in 2004 or 2005). Phytoplankton account for most of the plankton biomass until 2005, after which, bacteria and macro-zooplankton are the predominant plankton components.

Total plankton biomass was reduced by over 50% in the post-hurricane period, in both the pelagic and near-shore regions (Fig. 5a and b). These reductions were due to significant declines in the biomass of phytoplankton, bacteria and photo-trophic nanoflagellates (Fig. 5c and d, Table I). In both the pelagic and near-shore regions, there were significant increases in macro-zooplankton biomass following the hurricanes. Three plankton components (heterotrophic nano-flagellates, ciliates and micro-zooplankton) were consistently unaffected by the hurricanes in the pelagic and near-shore regions. When considered in the context of trophic groups (Fig. 5e and f), the post-hurricane changes are particularly evident, with relative biomass of producers dropping from near 60% to below 30% in the pelagic region, and from around 80% to below 50% in the near-shore region.

DISCUSSION

Previous studies of plankton communities in lakes have identified variation with season, between years and among lakes along trophic gradients (Gaedke and Straile, 1994; Auer *et al.*, 2004; Work *et al.*, 2005; Havens *et al.*, 2007b). However, no prior study has comprehensively examined how a catastrophic climatic event, such as a hurricane, influences plankton composition. Because many large shallow lakes occur in lowland regions of the sub-tropics that are impacted by hurricanes, quantitative information is important to understand long-term dynamics of plankton, as it relates to changes in nutrient, sediment and water loading, and the value of management options such as sediment
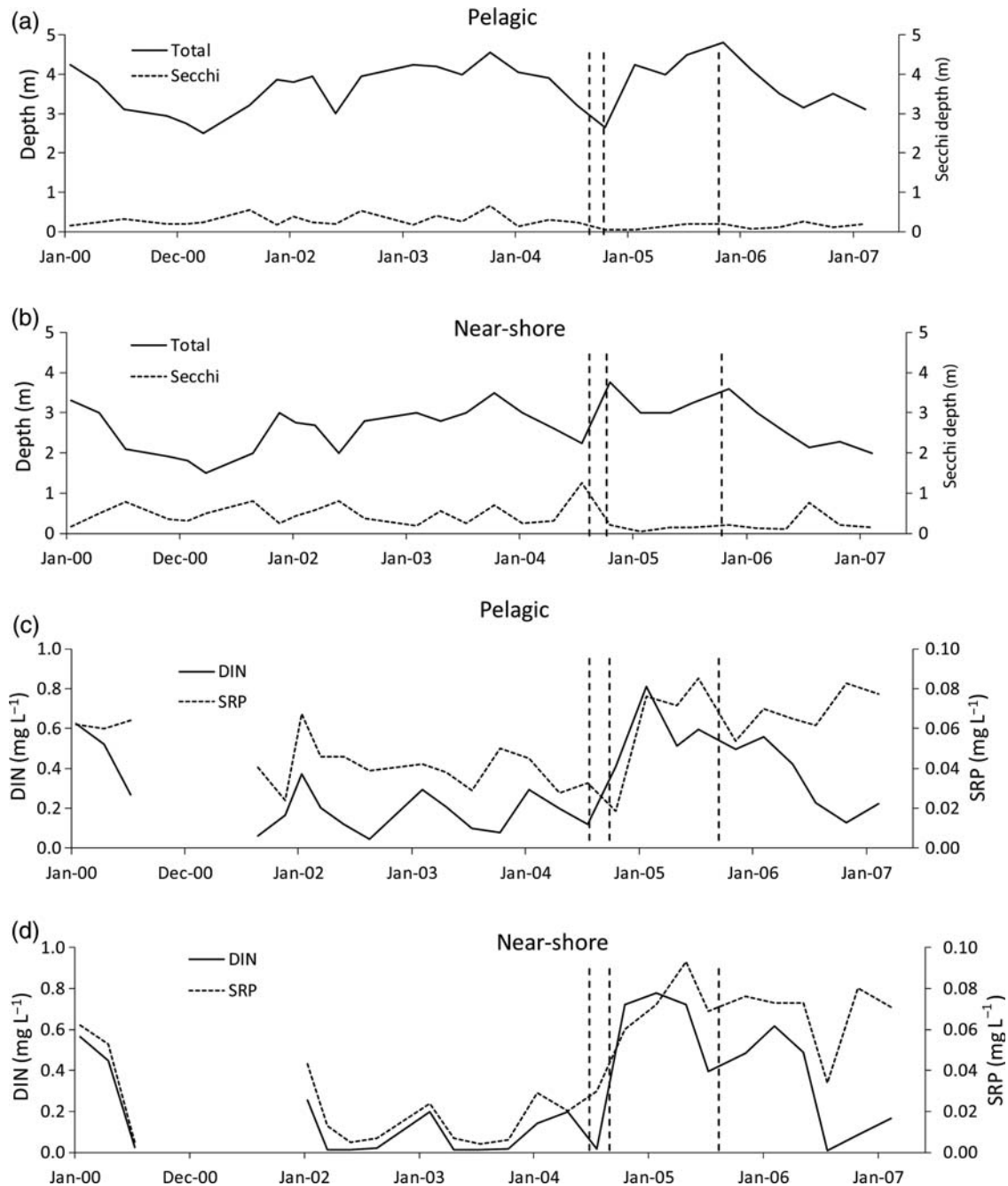
Fig. 3. Seven-year time series of physical and chemical attributes for the pelagic and near-shore regions: (**a** and **b**) total and Secchi depths; and (**c** and **d**) concentrations of DIN and SRP. There is an 18-month data gap early in the period of record when analysis of these attributes was not performed. The vertical lines indicate the approximate time when the three hurricanes occurred.

removal. In this study, we filled that information gap with a comprehensive analysis of plankton responses to three successive hurricanes experienced by Lake Okeechobee over a short period of time.

Phlips *et al.* (Phlips *et al.*, 1995) previously examined seasonal and spatial variation in light availability and phytoplankton biomass (measured as chlorophyll *a*) in

Lake Okeechobee based on sampling bimonthly at 84 locations over a 4-year period when there was no hurricane activity in the vicinity of the lake. They found that the biomass of phytoplankton was consistently higher at near-shore sites than pelagic sites, and that the latter regions displayed a more pronounced reduction in phytoplankton during the winter. These changes

Table I: Pre-hurricane versus post-hurricane means (± 1 SE) of plankton biomass and selected physical and chemical attributes of the water in the pelagic versus near-shore regions of Lake Okeechobee

Attribute	Pre-Hurricane	Post-Hurricane
Pelagic zone		
BACT	52 ± 9	21 ± 6
HNF	9 ± 2	9 ± 1
PNF	19 ± 4	7 ± 2
PHYTO	280 ± 44	69 ± 32
CIL	51 ± 10	49 ± 10
MICZ	2 ± 1	4 ± 2
MACZ	60 ± 8	90 ± 16
Secchi (cm)	30 ± 3	15 ± 2
DIN (μg L^{-1})	212 ± 30	465 ± 47
SRP (μg L^{-1})	42 ± 3	70 ± 3
I_m (m)	1.2 ± 0.1	0.5 ± 0.1
LIMIT	60%	78%
Near-shore zone		
BACT	34 ± 5	19 ± 6
HNF	8 ± 1	4 ± 1
PNF	23 ± 4	5 ± 1
PHYTO	538 ± 53	162 ± 30
CIL	58 ± 11	54 ± 7
MICZ	3 ± 1	3 ± 1
MACZ	39 ± 7	87 ± 16
Secchi (cm)	53 ± 3	26 ± 4
DIN (μg L^{-1})	139 ± 29	428 ± 45
SRP (μg L^{-1})	25 ± 4	71 ± 4
I_m (m)	3.9 ± 0.5	2.0 ± 0.5
Limit (%)	17	42

Numbers in bold indicate differences between the two time periods that are significant at $P < 0.05$ based on a one-way ANOVA. BACT, bacteria; HNF, heterotrophic nanoflagellates; PNF, phototrophic nanoflagellates; PHYTO, phytoplankton; CIL, ciliates; MICZ, micro-zooplankton (rotifers and nauplii); MACZ, macro-zooplankton (adult copepods, copepodids and cladocerans); ALL, all plankton. Plankton data have units of μg C L^{-1}. Limit, % of phytoplankton bioassay experiments indicating limitation by light and as noted, those assays were not conducted at the western-most bay station.

corresponded directly with changes in underwater light availability estimated as mean irradiance in the mixed layer (I_m), which is controlled in part by seasonal changes in daily incident PAR, but more significantly by changes in light-attenuating seston (re-suspended sediment particles) in the water column. Because the central region of the lake is underlain by unconsolidated mud sediments (Fisher et al., 2001), while the near-shore region has sand, rock or peat, the pelagic region is more subject to seasonal light limitation that coincides with normal increases in wind velocities during the winter (Aldridge et al., 1995; Havens, 1995; Jin and Ji, 2001; Havens et al., 2007a). A similar pattern has been observed in other shallow lakes in the tropics. For example, Erikson (Erikson, 1999) found that in polymictic Lake Xolotlan, Nicaragua, the major factor influencing the net growth of phytoplankton is the ratio of

photic to mixed depth; net growth was reduced in winter coincident with increased winter season winds and greater sediment re-suspension. East and Sharfstein (East and Sharfstein, 2006) developed a hierarchical decision model that predicted light limitation versus nitrogen limitation in Lake Okeechobee with 70–85% accuracy, the major determinant being the ratio of Secchi to total depth. Similarly Phlips et al. (Phlips et al., 1995) were able to explain 44% of the seasonal variation in chlorophyll *a* using I_m in the pelagic region and 73% of the seasonal variation in the near-shore region. Based on these prior results, we expected light limitation to be a major driver of changes in food-web structure following hurricane impacts to Lake Okeechobee.

Response to hurricanes: phytoplankton

There are various potential effects of hurricanes on phytoplankton, which can be related to changes in water depth, the degree of sediment re-suspension, other wind stress effects and increased water runoff from high rainfall. In oceanic regions, the major influence of hurricanes is entrainment of limiting nutrients from deeper waters, leading to increased biomass of phytoplankton and their consumers (Gierach et al., 2009a,b). In estuaries, the major documented influence is related to increased nitrogen export from watersheds, once again stimulating the development of phytoplankton (Peierls et al., 2003; Dix et al., 2008). Large lakes certainly experience effects associated with increased inputs of water, nutrients and carbon. However, in systems such as Okeechobee, where sediments play a major role in underwater light attenuation (Havens, 1995), the physical entrainment of fine sediment into the water column and subsequent reduction in light availability for primary production overwhelm other hurricane-related effects. Even the weaker hurricane (Hurricane Irene), which passed south of Lake Okeechobee in October 1999, had a major influence on limnological conditions (Havens et al., 2001). It generated bottom current velocities in excess of 100 cm s^{-1} and uplifted sediments to a degree that Secchi depth was reduced from 40 to 20 cm, and total suspended solids increased from 15 to 90 mg L^{-1}. Several months passed before there was a noticeable increase in transparency after that event, and at the time it was suggested (Havens et al., 2001) that if a major hurricane were to pass directly over the lake, it could have 'severe and long-lasting' effects on the structure and function of the ecosystem, as we have documented here.

After Hurricanes Frances, Jeanne and Wilma affected Lake Okeechobee in 2004 and 2005, fundamental changes in water chemistry and plankton persisted in
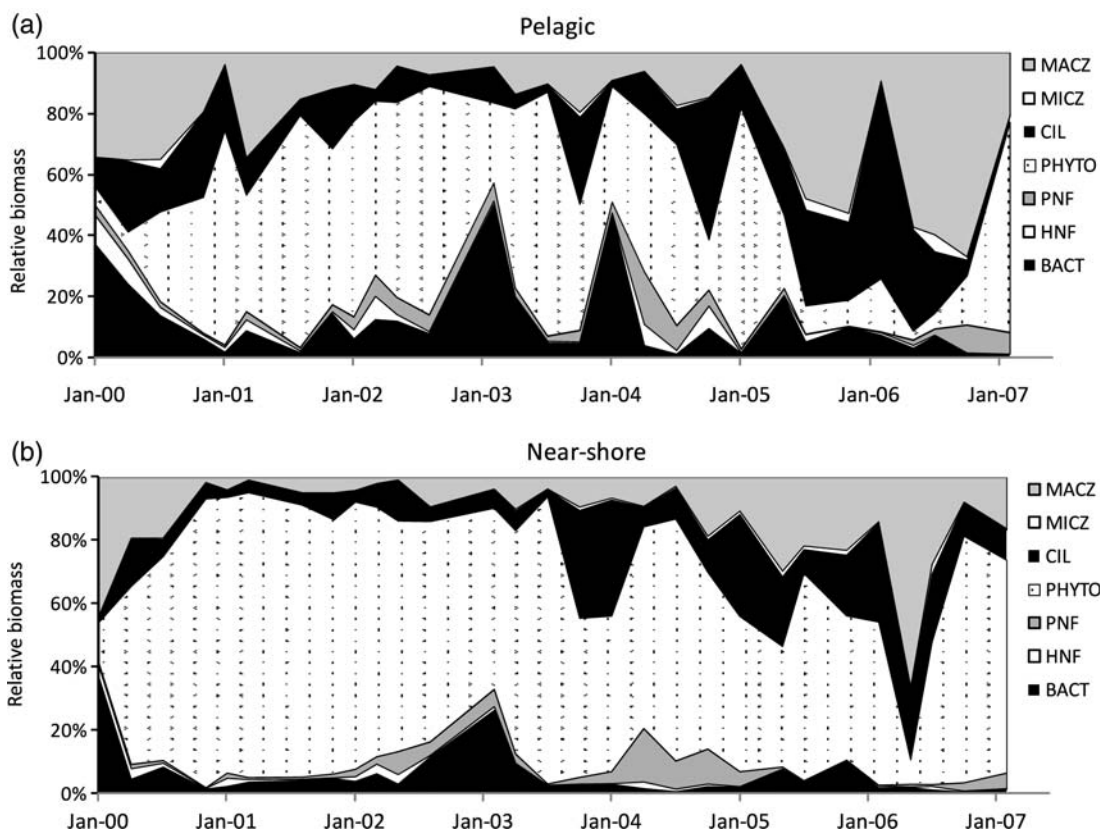
Fig. 4. Seven-year time series of relative C biomass in seven plankton components for the pelagic and near-shore regions. MACZ, macro-zooplankton; MICZ, micro-zooplankton; CIL, ciliates; PHYTO, phytoplankton; PNF, phototrophic nanoflagellates; HNF, heterotrophic nanoflagellates; BACT, bacteria.

both the pelagic and near-shore regions for over a year (James *et al.*, 2008). A four-fold reduction in phytoplankton biomass coincided with extremely low Secchi transparencies, two- to three-fold increases in DIN and SRP, and more frequent light limitation. An analysis of phytoplankton taxonomic data (James *et al.*, 2008) demonstrated that there also was a shift from cyanobacteria to diatom dominance. These changes are nearly identical to those observed seasonally by Phlips *et al.* (Phlips *et al.*, 1997) in a year-long study that examined the coincidence of plankton and water quality attributes and processes, such as N-fixation. From January to March, they found a consistently low biovolume of cyanobacteria, elevated DIN and bioassay-inferred light limitation.

The coincident decline of phytoplankton biomass and I_m after the hurricanes further reinforces the concept of coupling between abiotic turbidity, underwater irradiance and phytoplankton growth, as does a significant positive correlation between phytoplankton biomass and I_m in the full data set ($r = 0.45$, $P < 0.001$, $n = 143$). This positive relationship is unusual in the context of what typically occurs in deeper lakes, where phytoplankton play a major role in attenuating light

(e.g. Carlson, 1977), but is consistent with results from other shallow light-limited lakes, including Lake Chapala, Mexico (Limon *et al.*, 1989) and Lakes Bold and Alexandrina, Australia (Oliver, 1981; Geddes, 1984).

Response to hurricanes: zooplankton

One response of plankton that is not as readily explained with the available data is the significant increase in absolute and relative biomass of macro-zooplankton after the hurricanes. The increase may be a result of random variability in the time series, or it could be a response to conditions more favorable to growth, survival and/or reproduction of the calanoid copepod *Arctodiaptomus dorsalis*, which accounted for nearly 95% of the macro-zooplankton biomass change. This species is an omnivore and is known to be the primary consumer of phytoplankton in Lake Okeechobee (Work and Havens, 2003). The aforementioned change in algal composition (cyanobacteria → diatoms) may have resulted in better nutritional quality of food for the copepods. It also is possible that we may

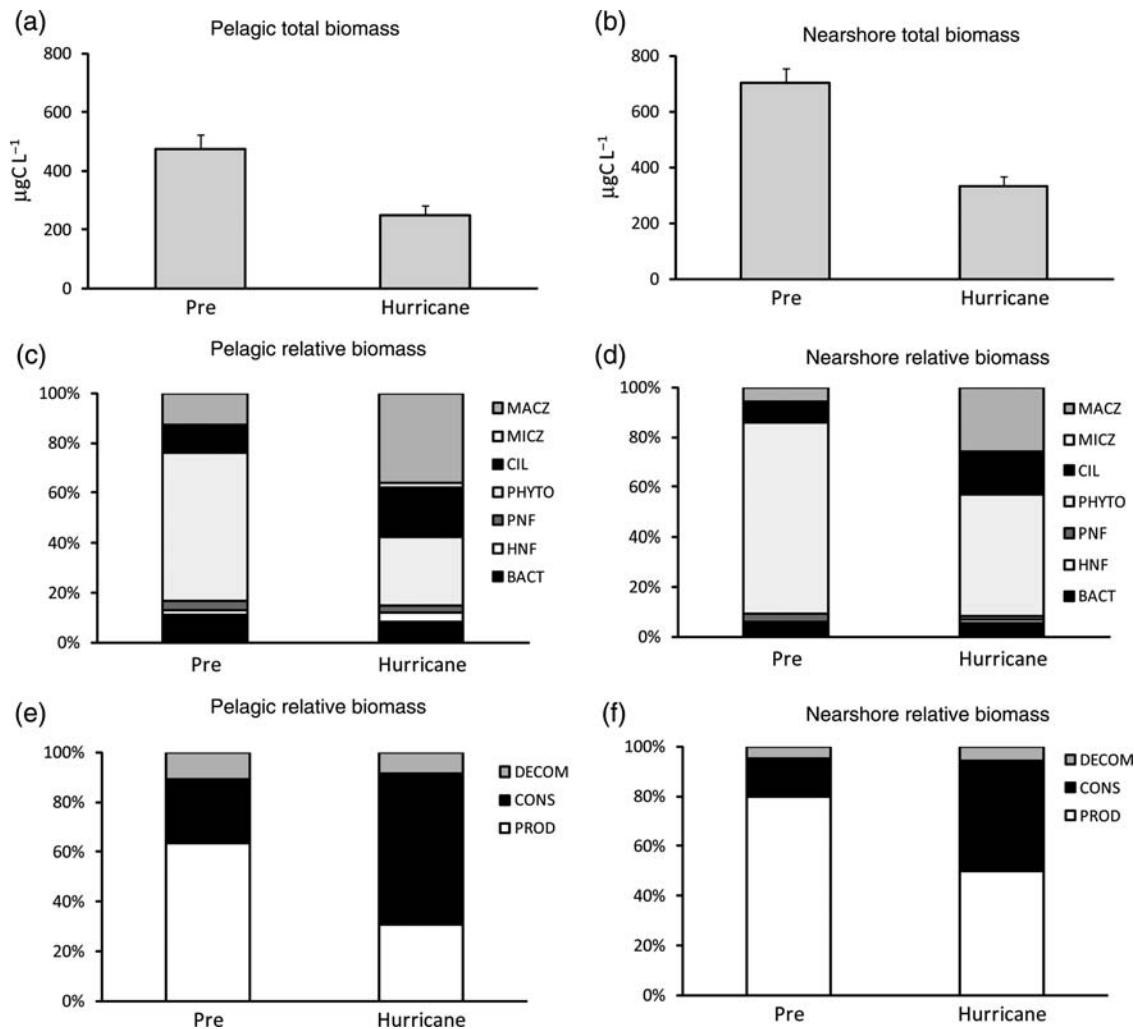**Fig. 5.** Changes in plankton biomass comparing pre-hurricane and post-hurricane periods as defined in the text: (**a** and **b**) pelagic and near-shore total biomass means with standard errors, (**c** and **d**) pelagic and near-shore relative biomass as broken out into components in Fig. 3, and (**e** and **f**) pelagic and near-shore relative biomass of decomposers (DECOM), consumers (CONS) and primary producers (PROD).

not have accounted for all available food resources. For example, Gliwicz (Gliwicz, 1986) noted that bacteria may adsorb onto sediment particles, which then may be grazed by zooplankton. We have no data from this lake regarding sediment-associated bacteria; however, we observed large numbers of bacteria on particles associated with colored inflows which may have served as an additional food source for calanoid copepods.

The increase in macro-zooplankton might also be related to a reduction in fish predation after the hurricanes. Earlier studies have pointed to fish predation as a major factor controlling macro-zooplankton biomass in Florida lakes (Havens et al., 2009) as seems to be the case in other shallow subtropical lakes (Jeppesen et al., 2007; Meerhoff et al., 2007). In an earlier study on Lake Okeechobee, Havens et al. (Havens et al., 2007c)

concluded that increased fish predation coincided with increased submerged aquatic vegetation, which increased water transparency and survival of juvenile fish, both of which contributed to an observed decline of cladocerans in the near-shore region after the 2000–2001 period of low water. Although the latter study did not show a concomitant decrease in *A. dorsalis* biomass, the extreme conditions of the post-hurricane period may have yielded more widespread reduction in grazing pressure. Most of the submerged vegetation in the near-shore region was uprooted and did not recover in the post-hurricane period considered here (James et al., 2008), and densities of planktivorous fish were greatly reduced in the near-shore region, based on results of block-netting done before and after the hurricanes (Rogers and Allen, 2008). Further, the increased

turbidity may have reduced the reaction distance of visually feeding fish (Vinyard and O'Brien, 1976; Miner and Stein, 1993), further releasing the copepods from predation.

Response to hurricanes: microbial food web

The microbial food web (MFW) plays an important role in C transfer in Lake Okeechobee, with much of the C transfer to zooplankton coming from bacteria (Work *et al.*, 2005). Likewise, protozoa account for over 80% of the biomass of all grazers in the planktonic food web (Havens *et al.*, 2007b). In the present study, hurricanes had significant effects on two components of the MFW, bacteria and photo-trophic nanoflagellates. Both were significantly reduced after the storms, coincident with the large decline in biomass of phytoplankton. Our methodology did not differentiate suspended bacteria from bacteria on larger particles originating from colored inflows which would largely be unavailable to suspension feeders.

A number of factors may control biomass of bacteria in a lake's water column, including temperature (Felip *et al.*, 1996), predation (Pace and Cole, 1994) and resource limitation (White *et al.*, 1991; Pace and Cole, 1994). An early paradigm regarding resources was that a major source of labile organic carbon for bacteria is derived from recent photosynthesis of phytoplankton (Bird and Kalff, 1984; Cole *et al.*, 1988). However, it also has been shown that refractory dissolved organic carbon (DOC) from allochthonous sources can, under certain environmental conditions, provide labile carbon to fuel bacterial productivity (Bano *et al.*, 1997).

There are two possible explanations for reduced bacteria in Lake Okeechobee after the hurricanes. First, it may simply reflect a reduced C supply from phytoplankton, consistent with the model of Cole *et al.* (Cole *et al.*, 1988). Or, it might be that the reduced transparency disrupted photo-oxidation of DOC, so that C was less available for bacterial uptake. The decline in bacteria is not readily explained based on increased grazing pressure, because the biomass of bacterial grazers (heterotrophic nanoflagellates, ciliates and microzooplankton) were unaffected by the hurricanes. While there was a significant increase in biomass of macrozooplankton, this was almost exclusively due to *A. dorsalis*, which is not considered a major consumer of bacteria (Work and Havens, 2003). Large cladoceran grazers that are known to significantly affect bacterial populations do not occur in Lake Okeechobee.

The lack of significant response of ciliates, the major protozoan grazer in this lake, to hurricanes also is not readily explained. However, it is consistent with prior seasonal data where ciliate biomass did not significantly vary. Beaver *et al.* (Beaver *et al.*, 1988) demonstrated that the ciliate populations of subtropical lakes influenced by organic color did not display significant correlations with bacterial abundance and ascribed the lack of coherence between the populations to timing of thermal stratification and the presence of mixotrophic ciliate taxa which are not solely depend on bacteria as a food resource. Moreover, our methodology did not account for bacteria cells attached to larger particles which are largely unavailable to filter-feeding ciliate taxa.

Recovery

We also can provide insight into the recovery from hurricane impacts. The impacts of Hurricane Irene (October 1999) attenuated quickly, with turbid light-limited conditions lasting only until July 2001 (Fig. 3). In that case, recovery was fast due to a rapid decline in water level that exposed tens of thousands of hectares of shoreline, allowed organic sediments to oxidize and was followed by wide-spread growth of submerged aquatic vegetation (Havens *et al.*, 2001). The effects of Hurricanes Jeanne, Frances and Wilma lasted for more than a year, but again the system recovered when lower water levels occurred in a drought that began in late 2006. Subsequent to the substantial declines in water level was the recovery of over 10 000 hectares of submerged aquatic vegetation in 2008 and 2009 (SFWMD, unpublished data). The 2008–09 biennial means of Secchi depth and concentrations of DIN and SRP averaged 55 ± 20 cm, $84 \pm 86\ \mu g\ L^{-1}$ and $25 \pm 23\ \mu g\ L^{-1}$ in the near-shore region, respectively. Recovery also occurred in the pelagic region, where the biennial means for Secchi depth, DIN and SRP were 33 ± 17 cm, $210 \pm 146\ \mu g\ L^{-1}$ and $47 \pm 17\ \mu g\ L^{-1}$.

We consider it likely that if water levels remain high for multiple years after a major hurricane affects Lake Okeechobee or another similar large shallow lake, the ecosystem would not recover this fast, as compensatory responses such as recovery of submerged aquatic vegetation, will be delayed. This prediction could be tested by studying a future event with that particular scenario. This underscores the need for continued comprehensive long-term water quality and ecological assessment.

Summary

Subtropical and tropical lakes are periodically impacted by hurricanes that generate sustained wind velocities much greater than the normal range of wind speeds experienced by these ecosystems. This study provides the first insight into how hurricanes can influence the

planktonic food web of large shallow lakes. In most respects, the nature of these influences is similar but more extreme than typical seasonal wind events. Sediment re-suspension, reduced water clarity and consequent declines in the abundance of phytoplankton and some heterotrophic components are predictable seasonal responses to wind-induced sediment re-suspension on Lake Okeechobee, and hurricane-force winds elicit a more magnified and persistent response from these same parameters. Additional effects may have occurred because the hurricanes caused widespread removal of submerged vegetation, collapse of fisheries and redistribution of mud sediments from the pelagic to near-shore regions (James *et al.*, 2008; Rogers and Allen, 2008). Those effects may have influenced near-shore and pelagic plankton communities through multiple direct and indirect pathways not quantified here. Yet clearly the pronounced reduction in light availability was the major driver of observed responses. The effect is longer lasting than has been observed in estuaries, because unlike estuaries, fine suspended sediment material remains in the water column for a long period of time in a closed shallow lake system without substantive flushing.

ACKNOWLEDGEMENTS

FUNDING

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