PROF. KARL E. HAVENS (Orcid ID : 0000-0002-3267-4355)

DR. JOHN R BEAVER (Orcid ID : 0000-0003-0091-2387)

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Recovery of Plankton from Hurricane Impacts in a Large Shallow Lake

Gaohua Ji[1, 2], Karl Havens[1, *], John Beaver[3] and Therese East[4]

[1] *Florida Sea Grant College Program and University of Florida Institute of Food and Agricultural Sciences, Gainesville, Florida, USA 32611*

[2] *College of Fisheries and Life Science, Shanghai Ocean University, Nanhui New City, Shanghai, P.R. China, 201306*

3 BSA Environmental Services, Beachwood, OH, USA

4 South Florida Water Management District, West Palm Beach, FL, USA

* *Corresponding author email khavens@ufl.edu*

Summary

1. We quantified recovery of plankton in a large subtropical shallow lake from the catastrophic impacts of three successive major hurricanes. This assessment was possible because hurricanes passed directly over the lake amid an ongoing long-term sampling program that included nearly all components of the plankton, from bacteria to crustacean zooplankton.

2. We compared attributes of plankton five years after the hurricanes to a pre-hurricane period and to a period immediately after the storms. We evaluated both community level properties (biomass, biomass ratios, diversity, and dominance of major plankton groups) and species-level properties (species absolute and relative biomass) at four sites in the lake representing different ecological zones.

3. The hurricanes strongly affected water quality and plankton community structure. The lake experienced a regime shift, losing its submerged aquatic vegetation and becoming homogenous and turbid at all sampled sites.

4. Five years after the storms, chemical and physical condition recovered across the lake, with a few exceptions. Between 35 and 93 plankton species were lost at the sampling sites, with greatest losses in the phytoplankton. Relative species biomass displayed substantive changes too. *Daphnia ambigua* did not recover at three of the sites, *Polyarthra vulgaris* greatly increased lake-wide, and at a central pelagic site, there was a total loss of heterotrophic nano-flagellates and a much higher biomass of diatoms than before the hurricanes, despite recovery of irradiance, depth, nutrient levels and other attributes.

5. Most community-level properties were resilient, returning to pre-hurricane conditions of total biomass, ratios of autotrophs to heterotrophs and ratios of protozoa to metazoa. This likely happened because of species compensation in the biodiverse community. The exception was at a central pelagic site, where the higher-order properties did not recover and nearly 50 percent of species were lost.

6. The community resilience, despite a regime shift, may have occurred because of a controlled lowering of water levels in the lake for flood protection, which led to regrowth of lost submerged aquatic vegetation (SAV) and migration of mud sediments back towards mid-lake.

7. In this lake and others with a history of high nutrient inputs, shallow depth and flocculent sediments, resilience may be low unless counter-acting forces are able to push the system back after a regime shift.

Key words: disturbance, recovery, resilience, regime shift, shallow lakes, tropical cyclones, plankton

Introduction

Catastrophic disturbances have large effects on the species that comprise biological communities, in terms of changes in their relative biomass, and in some instances a complete loss of taxa (e.g., Keller & Yan 1998; Supp & Ernest, 2014; Wu et al., 2015; Yang et al., 2017). During recovery from a major disturbance, the re-establishment of species is highly variable and depends on the extent of physical alteration of the environment, species growth rates, competition, predation and other factors (Martin et al., 2013; Duarte et al., 2015). While the full complement of species may not recover after a disturbance, community-level properties (e.g., total biomass) may fully recover because of compensation, i.e., remaining species take on the role of those that have been lost (Frost et al., 1995; Supp & Ernest, 2014; Connell & Ghedini, 2015). The extent of compensation in a community relates to the number of species. This concept originated decades ago, and it has been borne out in hundreds of case studies (e.g., de Mazancoourt et al., 2013; Duarte et al., 2005; Oliver et al., 2015). Plankton communities are highly diverse, containing hundreds of species, and as such may be at the extreme end of high resilience. The degree of community recovery also can vary among different areas of an ecosystem because of the idiosyncratic factors mentioned above (Hillebrand & Utz, 2015).

Communities do not always recover, because catastrophic impacts can be so destabilizing that they cause regime shifts (Scheffer et al., 2001), which sometimes are irreversible unless another counter-acting impact occurs. Communities in disturbed ecosystems, for example lakes with high rates of nutrient loading that have altered structure and function, are generally less resilient. As such, shallow nutrient-enriched lakes, such as Lake Okeechobee, are more prone to regime shifts (Carpenter, 2003).

Tropical cyclones can be an extreme disturbance event and can have both short-term and multi-year effects on water quality and plankton, when they affect lakes. There are two well-documented examples: Lake Okeechobee in the southeast USA (Havens et al., 2016) and Lake Taihu in southeast China (Zhu et al., 2014). Tropical cyclones have affected these lakes in recent years and caused major changes in ecosystem structure and function (Havens et al., 2011; Zhu et al., 2014; Havens et al., 2016).

The eyewalls of three major hurricanes passed directly over Lake Okeechobee in 2004 (Hurricanes Frances and Jeanne) and 2005 (Hurricane Wilma). The wind velocities during those hurricanes, measured at mid-lake meteorological stations, were 87, 108 and 120 km h^{-1}, respectively. This created large waves, wind-seiches and water currents that re-suspended an estimated 2.1, 0.7 and 1.4 million metric tons of mud sediment into the water column, and distributed it lake-wide (Jin et al., 2011). Thousands of hectares of submerged aquatic vegetation (SAV) also were uprooted. The back-to-back hurricanes resulted in 5-fold increases in suspended solids, and increased dissolved inorganic N (DIN) and soluble reactive P (SRP; Havens et al., 2011). Biomass of bacteria and flagellates was reduced, phytoplankton growth was suppressed due to light limitation, and there was a shift from nitrogen (N)-fixing cyanobacteria to diatoms (Beaver et al., 2013). Biomass of crustacean zooplankton increased, possibly due to less predation by sight-feeding fish (Rogers & Allen 2008). After the first two hurricanes, there was a short-lasting relaxation of light limitation, as solids settled from the water column, and this led to a massive lake-wide bloom of *Microcystis aeruginosa* (Havens et al., 2016). The third hurricane, in fall 2005, immediately caused the bloom to dissipate and it did not re-occur.

While there is substantive documentation of short-term responses of shallow lakes to tropical cyclones, there is no literature regarding long-term recovery dynamics. There are case studies about recovery of other ecosystems from perturbation, including coral reefs (Roff et al., 2015) and wetlands (Means et al., 2017), and studies documenting plankton recovery from other disturbances, notably nutrient enrichment and reduction (Jeppesen et al., 2007; Wu et al., 2015; Yang et al., 2017). However, we can glean just limited insight from those studies regarding the resilience of plankton from a sudden catastrophic event such as a major hurricane strike.

To quantify the recovery of plankton in Lake Okeechobee from hurricane disturbance we used a unique long-term plankton dataset that included taxonomic and biomass data for bacteria, flagellates, ciliates, phytoplankton, rotifers and crustacean zooplankton. The hurricanes hit the lake at approximately the mid-point of the 12-year monitoring program to collect those data. We predicted that the plankton would lose species, and that most of them would recover because of their short generation times and capacity to re-enter the community from connected places such as the lake's littoral zone. We further predicted that high-level properties, including total biomass, ratio of autotrophs to heterotrophs and ratio of protozoa to metazoan, would fully recover in the species-rich arena via species compensation. Our expectation that any sort of major recovery could occur, despite the intensity of the disturbance and a regime shift (Havens et al., 2011; Beaver et al., 2013), was based on knowledge that managed low water levels occurred in the years after the hurricanes. This resulted in shallow water in areas that had lost SAV. It also led to transport of fine particulates back towards the center of the lake.

Methods

Study Site

Lake Okeechobee, located at 26^{o}58'N, 80^{o}50'W, is the largest lake in the southeastern USA (1,730 km^2). It is very shallow (mean depth 2.7 m, maximum depth 5 m) and nearly always completely mixed (Rodusky et al., 2005). Approximately 30% of the lake is a littoral zone with emergent vegetation, and the pelagic zone has four ecologically distinct zones (Phlips et al., 1993). The northern and central pelagic zones have high concentrations of nutrients, are underlain by flocculent mud sediments and the phytoplankton often is limited by light. A major difference between the north and central zones is that in the north, there is higher phytoplankton biomass, because this zone is in the immediate proximity of inflows from the largely agricultural watershed. Light limitation is somewhat less common than in the central zone of the lake. A near-shore zone extends along the west and south edges of the lake, is adjacent to a marsh of emergent plants, and overlies sand and peat sediments. It has lower turbidity and nutrient concentrations, and in years when water levels are low, has benthic macro-algae and SAV. A fourth zone is an ecotone. It is a crescent-shaped zone between the central and near-shore zones and is a place where there often is both optimal nutrient and light availability to fuel cyanobacteria blooms (Phlips et al., 1993).

We used data from four long-term sampling sites of the South Florida Water Management District, with one sites in each of the ecological zones. The sites (Figure 1) are N (north pelagic), C (central pelagic), W (west, in the transition zone) and S (south, in the near-shore zone).

Water Quality Sampling and Analysis

As with other studies of rare stochastic events, we took advantage of a pre-existing sampling program as the source of data. That program was designed to identify long-term trends, not to quantify effects of hurricanes. Hence, the sampling frequency of plankton was monthly or quarterly, which we know is not frequent enough to detect short-lasting changes or rare species. Yet for the purpose of our study, where we looked just at long-term changes in multi-year periods, the low frequency of sampling was adequate.

Samples were collected from January 2000 to July 2012. Afterwards, many plankton components were eliminated from the program by the agency that oversees the long-term monitoring. Sampling was approximately monthly before August 2002 and was reduced to quarterly intervals thereafter.

At each sampling site, depth was measured with a weighted and calibrated nylon line and transparency was measured with a 20 cm black and white Secchi disk (SD). Temperature was measured at approximately 0.5 m below the water surface, where samples also were collected for analysis of color, total suspended solids (TSS), Chl-*a*, ammonium (NH_4), nitrate (NO_3), nitrite (NO_2), TP, TN and SRP. Nutrients were analyzed following standard USEPA protocols including the use of reference standards and blanks. All samples were filtered through Whatman GF/F filters before analysis (USEPA, 1979; SFWMD, 2002). Chl-*a* samples were also processed following the standard USEPA method and analyzed by a spectrophotometer, with and without correction for phaeophytin, until December 2010, after which the samples were analyzed by high performance liquid chromatography (HPLC). Samples with over-lapping measurements by the two techniques for approximately one year indicated no significant difference in results.

For multi-variate statistical analyses involving the plankton, we used the paired (plankton and water quality) quarterly data. However, for a comparison of water quality conditions before the hurricanes, immediately after the hurricanes and in a recovery period (see below), we used monthly data from a separate long-term monitoring program of the same state agency, collected at the same locations and analyzed with the same methods, in order to have a larger sample size.

Plankton sampling, counting and calculations

Samples were collected synchronously for analysis of crustacean zooplankton, rotifers, ciliates, phytoplankton, nano-flagellates and bacteria. Typically sampling began at near 0800 and was complete by 1200 on the same day, with different routes being taken between stations over the period of record. Crustacean zooplankton was sampled at each site by taking vertical tows through the water column from 0.5 m off the sediments, using a 153 μm mesh 30-cm diameter conical net. Retained animals were rinsed into amber plastic bottles and preserved on-site with chilled sucrose-formalin. Rotifers and nauplii were sampled with a 3 cm diameter integrating tube. 20 L of water was collected from the entire water column, mixed in a plastic carboy, poured through a 35 μm plankton net and the retained animals were preserved as above. Another integrated sample was taken for ciliates, phytoplankton, flagellates and bacteria. Phytoplankton was preserved with Lugol's solution; bacteria and ciliates were preserved with 0.2 μm-filtered formalin and flagellates were preserved with cacodylate-buffered glutaraldehyde. All the samples had final fixative concentrations of 15%.

We determined the biomass, number of species and Shannon-Wiener diversity index (H) for each plankton group. Microscopic analyses of plankton were done by counting at least 400 individuals in order to achieve counting accuracies of 90% (Lund et al., 1958). The same laboratory (BSA Environmental Services, Ohio, USA) processed all the samples from the long-term program. Macro-zooplankton was counted at ×100 magnification. Population densities were estimated from counts as numbers per L, based on the volume of water sampled by the net and assuming 100% sampling efficiency. At least 10 individuals of each species were measured in each sample, and dry weights were calculated using published length-weight relationships (McCauley, 1984). Dry weights were converted to wet weights and then to units of carbon (C) biomass as 0.075 pg C pg^{-1} wet weight (Latja & Salonen, 1978), assuming that dry weight is 10% of wet weight (Pace & Orcutt, 1981). Rotifers, nauplii and ciliates were quantified on a per mL basis using the inverted microscope method (Lund et al., 1958) and a 24-hour settling time. Organisms were identified to species or lowest practical taxonomic level and enumerated at ×600 magnification according to Beaver & Crisman (1989). As with the crustaceans, at least 10 individual rotifers, nauplii and ciliates were measured (each species in each sample) for their lengths and widths to determine biovolumes of ciliates and dry weights of nauplii and rotifers (McCauley, 1984). Ciliate C biomass then was estimated at 0.11 pg C μm^{-3} (Rocha & Duncan, 1985); while C biomass of rotifers and nauplii was calculated as 0.075 pg C pg^{-1} wet weight, as was done for crustaceans (Latja & Salonen, 1978).

Phytoplankton was counted and the biovolume and C biomass determined in the same manner as was done for ciliates. Phototrophic and heterotrophic nano-flagellates (PNF, HNF) were enumerated by the epifluorescent method of Caron (1983), after staining cells with Primulin on 0.8 μm Nucleopore filters. Biovolumes were calculated by measuring cells and approximating size from regular geometric forms. Counts were converted to C biomass as 0.10 pg C μm^{-3} (Borsheim et al., 1987). Bacteria were stained with acriflavine (Bergström, Heinänen & Salonen, 1986) on 0.2 mm black Nucleopore filters before counting with an epifluorescent microscope at ×1000. Cell volumes were determined based on measurements of dimensions with an ocular micrometer and C biomass was calculated as 0.106 pg C μm^{-3} (Nagata, 1986).

Data Analysis

The historical sampling period was divided into three parts – pre-hurricane (January 2000 to January 2003), hurricane (September 2004 to November 2006) and recovery (January 2009 to July 2012). The main aim of this paper is to compare the pre-hurricane plankton community structure and abiotic conditions to the recovery period, given that other papers have presented in detail the short-term response to the tropical cyclones (e.g., Havens et al., 2011; Beaver et al., 2013; Zhu et al., 2014). However, we include some hurricane data for context. The pre-hurricane and recovery periods each include 3 years of data, and the recovery period does not begin until 5 years after the last hurricane. The hurricane period covers the time from onset of the first hurricane until one year after the last hurricane.

The initial data analysis included constructing notched box plots in order to compare the major physical and chemical characteristics between pre-hurricane, post-hurricane and recovery periods. Where the notches of two compared plots (interval between the UCI and LCI, which are the upper and lower 95% confidence interval of the medians), do not overlap in the plot, the medians are considered to be significantly different at a 95% confidence level (McGill et al., 1978; Chambers et al., 1983).

We evaluated changes in plankton biomass and taxonomic structure in two ways at each sampling site. First, we examined the data from the three periods, looking just at high-level properties: total C biomass, total biomass of major taxonomic groups, and biomass ratios of autotrophs to heterotrophs, protozoa to metazoa, and phytoplankton to zooplankton. Differences in the biomass of main groups and the ratios of functional groups among the three periods were detected by a Kruskal–Wallis non-parametric test. If $p<0.05$, then Mann–Whitney U tests were implemented to identify the differences between pre-hurricane and hurricane or recovery period, using nonparametric tests in IBM SPSS Statistics 24. Then we performed PCA for cladocerans, copepods, rotifers, ciliates and phytoplankton, focusing on the biomass of dominant (>5% of total in more than two samples) species. Our aim was to determine whether the recovered species composition was similar to the pre-hurricane composition. The PCA was performed using Canoco 4.5 (Ter Braak & Smilauer, 2002). The raw mean-centered data were used in the PCA. Because the data in each of the three periods was collected quarterly, we do not expect any issues with temporal auto-correlation. Further, the comparisons in the PCA are just between three periods, and there is no attempt to establish time series where temporal auto-correlation might be of concern. Ellipses of 95% confidence were superimposed on the PCA plots to visualize differences between the three groups, using package ‘car’ in R (Fox & Weisberg, 2011). To avoid subjective judgments, two-dimensional Kolmogorov-Smirnov tests (Peacock, 1983) were applied to detect differences between the three groups of points on PCA plots, using MATLAB R2015b.

Results

Water quality

The hurricanes caused large changes in all abiotic parameters at the four sampling sites (Figure 2), with the exception of water temperature. In addition to wind effects, the storms produced heavy rainfall and runoff to the lake and this resulted in increased water depths. Waves and currents entrained sediments. As a result, TSS doubled ratios of SD to total depth declined, and concentrations of DIN, SRP, TN and TP increased. Chl-*a* concentrations decreased after the hurricanes, with the exception of a short-lasting cyanobacteria bloom before the third storm. Five years after the last hurricane almost all of the water quality parameters had recovered to pre-hurricane conditions, with the exception of continued lower Chl-*a* at the central site and lower TN concentration at both the central and south sites ($p<0.05$).

Plankton community recovery

The response of plankton, at a coarse level of resolution, was similar to water quality. The total plankton C biomass substantially declined during the hurricane period at all of the sites, as did biomass of phytoplankton, bacteria and flagellates. The total biomass recovered within 5 years, to pre-hurricane concentrations, at the south and north sites (Table 1). Total biomass also increased at the west site, but not to pre-hurricane concentrations. At the central site, total biomass declined in the recovery period. The relative proportion of C biomass of major taxonomic groups also changed during the hurricanes, with more crustacean zooplankton (mainly calanoids) and less phytoplankton and bacteria, but five years later most sites recovered to pre-hurricane conditions (Figure 3a).

When the C biomass of major plankton groups was ordinated with PCA, distinct patterns emerged (Figure 4a). The centers of 95% confidence ellipses of pre-hurricane and recovery periods are close to each other and separated strongly from the centers of ellipses for the hurricane period, suggesting recovery. The north and south sites recovered to a greater extent than the central and west sites ($p<0.05$).

Other high-level community properties were also affected by the hurricanes but then recovered five years later to pre-hurricane conditions, including: the C biomass ratios of zooplankton to phytoplankton, autotrophs to heterotrophs, and protozoa to metazoa (**Table 2**). The ratio of zooplankton to phytoplankton C biomass increased during the hurricane period because of increasing C biomass of copepods, and then decreased five years after the hurricanes.

Plankton species changes

The total number of plankton species was greatly reduced during the hurricane period compared to the pre-hurricane period, at all four sampling sites (Table 3). While the numbers of species increased in the recovery period, they did not reach the pre-hurricane levels. At the four sites, this long-term reduction in number of species was 93 (Central), 80 (West), 35 (South) and 59 (North). These 'lost' species may still have been present in the lake but at densities below the limits of detection by our sampling and counting methods. A large percentage of species were found only during the pre-hurricane period or only during the recovery period (Table 4), providing further evidence of the magnitude of the community restructuring in terms of taxonomic composition.

The change in plankton taxonomic structure was mainly due to a loss of phytoplankton species and by a large change in the composition of rotifer species from pre-hurricane to recovery periods. Ciliates and crustaceans had similar species richness in the pre-hurricane and recovery periods. The average number of species per sample also decreased during the hurricane period, but returned to a level not significantly different from the pre-hurricane period in the west and north sites. The number of phytoplankton species per sample did not recover, however rotifers and ciliates rebounded to a higher level than in the pre-hurricane period. The numbers of copepod and cladoceran species also recovered. The Shannon-Wiener index changed in a manner that was similar to species richness. Higher values occurred for rotifers and ciliates in the recovery period, and values were low for phytoplankton compared to the pre-hurricane period.

The hurricane immediately led to dominance by meroplanktonic diatoms and a near a complete loss of cyanobacteria (Figure 3b), the only exception being the short-lasting *M. aeruginosa* bloom in 2005. Cyanobacteria regained their typical long-term dominance in the phytoplankton five years after the hurricanes, especially at the west, south and north sites. However, at the species level, there were large differences in the relative C biomass amongst cyanobacteria between the pre-hurricane and recovery periods. The 95% confidence ellipses in the PCA results summarize the differences in taxonomic structure in the recovery period compared to the other periods (Figure 4b).

Although there are no data on taxonomic structure of bacteria and flagellates, those plankton groups also displayed changes in C biomass between the three periods, with evidence of impact and then recovery (Table 1). Further, greater relative biomass of cocci bacteria and phototrophic nano-flagellates occurred in the recovery period than in the pre-hurricane period (Figure 3c). The PCA plots indicate this lack of complete recovery, as the 95% confidence ellipses do not overlap, particularly at the central sampling site (Figure 4c).

Ciliates responded differently at the four sampling sites (Table 1). Their C biomass decreased right after the hurricanes at the central, north and west sites, but not in the south. Five years after the hurricanes, in the recovery period, the C biomass of ciliates was not significantly different from that measured in the pre-hurricane period. *Tintinnidium fluviatile* (Choreotrichida) was the species with highest C biomass (Figure 3d). Its relative biomass among ciliates decreased immediately after the hurricanes and then increased except at the central site. *Codonella cratera*, which also belongs to the Choreotrichida, attained a relatively higher proportion of the ciliate C biomass immediately after the hurricanes, and remained higher in the recovery period except at the south site. Although the dominant species during the recovery period were similar to those during the pre-hurricane period, their relative C biomasses changed. Thus, the ciliate community did not display a recovery at the taxonomic level. In the PCA plots based on ciliate species C biomass (Figure 4d) the centers of 95% confidence ellipses are far apart for the pre-hurricane and recovery periods at three sites, particularly at the central site while it recovered at the south site. In relative terms, rotifer C biomass varied more between the three sampling periods than did the biomass of any other plankton group, although it accounted for just a small part of the total C biomass. At all of the sites, rotifer biomass was low in the pre-hurricane and hurricane periods (Table 1). There was a lake-wide increase in rotifer biomass five years after the storms, with the largest increases at the west and south sites with or near submerged plants. The smallest increases were at the deeper north and central sites. The dominant species also changed. *Keratella quadrata*, *K. cochlearis*, *Conochilus unlcornis*, *Brachionus havanaensis* and *Euchlanis dilatata* lost their dominance, and *Polyarthra vulgaris* and other species became the dominant ones during the recovery period (Figure 3e). The species changes also are evident in the PCA plots (Figure 4e). The rotifer samples taken during the recovery period scatter far away from the samples taken during the pre-hurricane period and none of the four sites recovered.

The C biomass of copepods increased during the hurricane period, while cladocerans had a spatially variable response (Table 1). Only a few of the changes were significant. Biomass generally returned to pre-hurricane conditions five years after the storms, however, the biomass of copepods was lower than in the pre-hurricane period. Likewise, the biomass of cladocerans was lower than in the pre-hurricane period but not significant at most sites because of high variation in the data. The cladoceran assemblage tended to be more diverse in the recovery period than in the pre-hurricane period, with the exception of the central site (Figure 3f). *Daphnia lumholtzi* and *Bosmina longirostris* were found more after the hurricanes than before. *D. ambigua* was greatly reduced at the south, north and west sites. Although *Arctodiaptomus dorsalis* and *Mesocyclops edax* remained as the dominant species, there was an increase in the relative C biomass of nauplii, calanoid copepodids and cyclopoid copepodids in the recovery period, when they made up more than 50% of the total copepod C biomass (Figure 3g). The PCA plots revealed differences in taxonomic composition among the three periods (Figure 4f). Most of the crustacean zooplankton samples taken during the recovery period are separated from the pre-hurricane period, and the centers of the 95% confidence ellipses are at disparate locations in the PCA 1 vs. 2 plot. This indicates that in general the crustacean zooplankton did not recover its taxonomic composition.

Discussion

Overview

Three consecutive hurricanes had catastrophic effects on Lake Okeechobee, pushing the lake into an alternative state (Havens et al., 2011; Beaver et al., 2013) *sensu* Scheffer et al. (1993). Here we documented a recovery of plankton that many of the expected properties observed in prior studies conducted on other ecosystems ranging from coral reefs (Roff et al., 2015) to estuaries (Duarte et al. 2015), soil communities (Means et al., 2017) and lakes responding to reductions in nutrient input (Wu et al., 2015). The plankton at three of the four sites in Lake Okeechobee were resilient, in that their species composition changed yet they retained most of their community-level properties. The site that did not recover, in the central pelagic zone, lost nearly 50% of its plankton species. Our prediction that most of the plankton species would recover after five years, because of short generation times and capacity to re-enter the community from connected places such as the lake's littoral zone was not supported. However, we did find that a greater percentage of species recovered at sites near that littoral refuge.

Lake-wide, the extensive loss of phytoplankton species and appearance of 'new' rotifer species may have been a function of subtle changes in environmental conditions, competition, predation or even parasitism and cannot be explained with the data in hand. The ensuing discussion does not heavily focus on why certain species were replaced by others, and instead considers community-level properties, spatial variation in resilience, and recovery from a regime shift.

Tropical cyclones as catastrophes for shallow lakes

Tropical cyclones are a common and catastrophic disturbance of lakes occurring in lowland areas of the subtropics near oceans and seas. Shallow lakes are particularly sensitive to these events because they lie in areas with flat topography, so that even if a lake is not large, there can be a long wind fetch over adjacent land onto the lake surface. Because shallow lakes also tend to occur at the lower end of drainage basins, they can receive an influx of nutrient-rich water after intense rain events that usually accompany cyclones. Finally, because of the close interaction between sediments and water column, a moderately strong cyclone can transform a lake or parts of a lake from clear water with SAV to highly turbid water with very little primary productivity, even in the plankton (Havens et al., 2016). The potential for such a regime shift is high (Carpenter, 2003) and depending on circumstances it may be irreversible.

Despite the potential impact of tropical cyclones on some of the world's largest lakes (Havens et al., 2016), studies of resilience of the full community from impacts of tropical cyclones are non-existent. Long-term data from before and after events are rare, and the storms are not predictable in time or location of impact.

Recovery of the phytoplankton

Nutrient availability and underwater irradiance are primary factors limiting phytoplankton production in subtropical lakes, where intense fish predation precludes top-down control by zooplankton grazers (Jeppesen et al., 2007; Havens & Beaver 2011). In Lake Okeechobee, the resuspension of muddy bottom sediments is the major factor controlling underwater irradiance in the north and central zones, while phytoplankton can also attenuate light in the transition and near-shore zones (Phlips et al., 1993). Submerged aquatic vegetation and periphyton also can affect irradiance by competing with and reducing phytoplankton biomass in the near-shore zone (Havens 2003). Previous studies revealed that the physical entrainment of millions of metric tons of muddy sediment into the water column was a major impact of the Florida hurricanes (Havens et al., 2001, 2011; Beaver et al., 2013; Havens et al., 2016). It led to reduced light availability for primary production and raised concentrations of DIN and SRP to very high levels that later fueled cyanobacterial harmful algal blooms.

When turbid, light-limited conditions disappeared five years after the hurricanes, phytoplankton C biomass and Chl-*a* recovered to pre-hurricane levels in the near-shore zone. However, in the central pelagic zone the phytoplankton biomass remained low, coincident with the largest reduction in number of species at any of the four sampling sites. The low biomass also coincided with a lower concentration of N than before the storms. Earlier studies have demonstrated that N is the nutrient that most often limits phytoplankton productivity in Okeechobee (Aldridge et al., 1995; Phlips et al., 1997), and that N may be of equal importance to P in controlling cyanobacterial harmful algal blooms (CyanoHABs) in general (Paerl et al., 2016).

In the one other study to examine the response of a large shallow lake to tropical cyclones (Zhu et al., 2014), Lake Taihu displayed almost immediate blooms *Microcystis* coincident with sediment resuspension and elevated nutrient concentrations. Based on reviewing the results of that study and others conducted on Taihu (Qin et al., 2007), two major differences between the lakes are: the nature of sediments, and role of mero-plankton. The central pelagic zone of Okeechobee has flocculent mud sediments with a high amount of fine inorganic material (Aumen & Wetzel 1995). When the lake is affected by wind and waves, resuspension of this material results in elevated levels of DIN and SRP, but also extreme and long-lasting extreme low underwater irradiance (Havens et al., 2011). The central area of Lake Taihu has sand sediment, and the northern area has dense mero-plankton (Zhu et al., 2014). Thus, wind and wave-driven resuspension in Taihu immediately brings cyanobacteria into an environment with abundant nutrients and adequate light for bloom formation. Indeed, the nature of sediment material may be the most important factor determining short-term response dynamics of shallow lakes to cyclones. In the longer-term (years), both lakes responded in a similar manner. Lake Okeechobee also had a large bloom after hurricane impacts, comprised of the same *Microcystis* species as in Taihu, but it was delayed by 10 months due to light limitation, and it was suppressed by a third hurricane (Havens et al., 2016).

Recovery of the protozoa

While less is known about the factors controlling biomass of protozoa in subtropical lakes (grazing vs. bacterial biomass vs. POC, for example), their responses generally matched what we observed in the phytoplankton and were again consistent with the prediction about recovery of high-level properties and a change in taxonomic composition. The ratio of protozoan to metazoan biomass recovered to pre-hurricane levels as did the total biomass of ciliates. Flagellates recovered, except that heterotrophic forms were nearly absent at the central pelagic site in the recovery period. The taxonomic composition of the ciliate assemblage was very different in the recovery period than in the period before the hurricanes. This might reflect a change in the composition of bacteria or flagellate taxa, because ciliates are quite specific in their food selection. However, we do not have data to test that hypothesis. While less-often studied than phytoplankton and metazoan zooplankton, protozoa play a critical role in energy transfer in pelagic food webs, particularly in highly eutrophic lakes (Beaver & Crisman 1989; Work et al., 2005).

Recovery of the zooplankton

Immediately after the hurricanes, cladocerans declined while copepods increased, even though phytoplankton and other food resources were reduced in biomass. A study of the response of the lake's fish assemblage to the hurricanes (Rogers & Allen 2008) provides a possible explanation: there was an increased dominance by zooplanktivores after the storm. Fish predation is considered a reason for the scarcity of cladocerans during summer months in Florida lakes, as well as in other lakes in the subtropics (Jeppesen et al., 2007; Havens et al., 2015). The dominant copepod in the lake, *Arctodiaptomus dorsalis*, is the most common crustacean in Florida (Bays & Crisman 1983; Crisman et al., 1995; Beaver & Havens 1996) and it has the ability to undertake rapid escape maneuvers to escape fish (Havens & Beaver, 2011). It also is possible that high abiotic turbidity immediately following the hurricane increased the reaction distance of sight-feeding fish and that this further favored the copepods. While we have no data on the longer-term changes in fish biomass or taxonomic composition, several attributes of the crustacean zooplankton are consistent with continued effects of fish predation in the recovery period. Those attributes include: (1) reduced crustacean biomass; (2) increased rotifer biomass; (3) lack of recovery of *D. ambigua* except at the turbid central pelagic site; (4) increased ratio of immature to adult copepods; and (5) high percentage of nauplii in total copepod biomass at the south and west sites compared to the central site.

Spatial variation of recovery

Because the extent and nature of recovery are dependent on many attributes of the ecosystem, they can be highly variable and not predictable. This tendency for recovery from a catastrophe to be unpredictable (Duarte et al., 2015) is well-documented in the literature, and it can happen within the confines of an ecosystem. From satellite imagery, the entire pelagic region of Lake Okeechobee that we studied appears to be a homogeneous expanse of water. However, past research has shown that there are distinct zones that vary in sediment type, depth, irradiance, presence vs. absence of SAV and composition of the plankton (Aumen & Wetzel, 1995). We predicted that because of this heterogeneity, the plankton at the four sites would not display the same recovery characteristics – and not have the same resilience. The results bore out this prediction.

The central pelagic site displayed the lowest resilience, in terms of a lack of recovery of the biomass of total plankton, phytoplankton, bacteria and flagellates. At the central site, we also observed that just 48% of the species recovered, compared to 67%, 84% and 72% of species recovering at the west, south and north sites. The highest recovery at the south (near-shore) site and lowest recovery at the central site might relate to their distances from the littoral zone. The littoral zone may have served as a place that protected plankton species during the impact from the storms, and distance might explain why the central zone has did not regain its species, even after five years. This hypothesis is plausible because when water level is low in this lake, as in the recovery period, a prevailing counter-clockwise circulation gyre in the pelagic zone (Jin et al., 2007) does not extend into the near-shore zone, essentially keeping the central pelagic zone isolated.

Recovery following a regime shift

When lakes and other ecosystems switch to an alternative state (Sheffer, 1989), also referred to in the literature as a regime shift (Carpenter, 2003), there are major changes in biological structure and function. Prior disturbances, such as nutrient enrichment, can lower ecosystem resilience and facilitate regime shifts (Dakos et al., 2015), which then may occur suddenly when there is perturbation by some force such as a hurricane. Lake Okeechobee was perfectly poised for a regime shift prior because decades of agricultural activity in the watershed (Flaig & Havens, 1995) has led to a massive quantity of nutrient-rich organic mud covering over 40% of the pelagic lake bottom (Fisher et al., 2001). Surface sediments are mixed into the water column by wind and waves during even common thunderstorms (Jin et al., 2007) and as a result, the central pelagic zone is often turbid, has low mean irradiance in the mixed layer, and has light-limited phytoplankton (Aldridge et al., 1995). Had water levels remained high in Lake Okeechobee in years after the hurricane, we suspect that the lake would have remained in a turbid state, as happened in the late 1990's during a period of high water with only limited SAV (Havens et al., 2000). Fortuitously, the dike that surrounds Lake Okeechobee was deemed unsafe by the US Army Corps of Engineers, and they implemented a new flood control schedule to regulate water levels (USACE, 2008). The result was increased outflows of water from the lake via locks, gates and canals, and a substantial lowering of water level. This served as a second ‘impact’ to the ecosystem that allowed the SAV to re-establish its former spatial extent (37,000 ha before the hurricanes, <8,000 ha after the hurricanes, and 40,000 ha in the recovery period, SFWMD, unpublished data). It is likely that the low water level also allowed sediment to migrate back toward the center of the lake, as has been observed in past shallow periods (Havens et al., 2001).

This study allowed us to characterize for the first time how the plankton of a shallow eutrophic lake recovered from a catastrophic hurricane effects. We also discerned that recovery of certain community attributes such as total biomass, ratio of autotrophs to heterotrophs and ratio of producers to consumers were resilient because of the diverse plankton assemblage that allowed compensation by species that survived to fill roles of species that were lost. In the one location where recovery did not happen, there was a loss of nearly 50 percent of species. The findings are consistent with theoretical research and case studies in recent decades dealing with community resilience (Loreau & de Mazancourt, 2013; Connell & Ghedini, 2015; Oliver et al., 2015), and indicate that factors affecting resilience in terrestrial and other aquatic systems apply to the highly diverse plankton of lakes. We also observed that in a seemingly homogeneous pelagic zone, differences in depth, underwater irradiance, sediment type and presence vs. absence of SAV influenced resilience and the recovery of community properties, including species diversity. Finally, we found that a second major perturbation (lowering of water level) was sufficient to reverse a regime shift brought on by hurricanes, and we conclude that shallow nutrient-enriched systems such as Okeechobee are not resilient without such counter-acting measures.

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Table 1 Plankton biomass at the four sampling sites during the three periods: pre-hurricane (Pre), hurricane (Hurri) and post-hurricane (Rec) in Lake Okeechobee. (means ± one standard error (bootstrapped), µg C L^{-1}). Bold font means there is significant difference (p<0.05) between PRE, HURRI and REC periods based on Mann–Whitney U test. Total is the total biomass of all plankton groups.

		Total	Phytoplankton	Bacteria	Flagellates	Ciliates	Rotifers	Cladocera	Copepoda
Center	Pre	275.6±26.7	66.9±13.6	68.9±9.9	30.0±5.7	18.8±4.4	0.17±0.05	5.31±1.47	90.8±12.7
	Hurri	**157.1±35.5**	**28.0±23.6**	**8.02±1.64**	**9.24±2.45**	15.0±4.4	0.19±0.11	**2.85±2.24**	89.3±30.0
	Rec	**146.5±19.1**	**18.1±2.9**	**4.52±0.85**	**6.86±1.70**	14.3±1.2	1.36±0.59	3.96±1.24	**47.0±7.0**
West	Pre	364.3±47.9	212.7±47.1	54.5±17.5	29.2±7.0	15.7±3.6	0.76±0.16	2.96±1.12	48.5±9.4
	Hurri	**144.8±21.0**	**49.0±18.9**	**9.52±2.33**	**11.8±7.2**	11.3±3.9	0.77±0.31	1.83±0.76	60.6±12.8
	Rec	**257.1±71.0**	179.1±72.4	26.8±4.5	13.0±3.1	**21.1±3.8**	**7.14±1.86**	0.23±0.04	**9.79±1.33**
South	Pre	235.8±25.1	115.4±25.6	45.4±6.9	32.3±8.2	13.4±2.6	0.64±0.16	1.2±0.43	25.1±5.4
	Hurri	183.6±62.2	41.7±13.0	**11.9±4.8**	**6.45±3.45**	24.9±8.5	0.36±0.14	1.6±0.73	**95.5±57.4**
	Rec	213.8±41.4	117.5±33.7	37.9±8.9	16.7±5.3	15.9±3.2	**9.67±4.74**	0.51±0.33	9.76±2.36
North	Pre	300.7±35.0	129.2±32.0	42.0±5.7	26.4±4.3	18.9±3.1	0.46±0.09	5.19±1.3	75.2±8.8
	Hurri	**134.4±32.9**	**9.88±2.32**	**16.5±4.0**	**7.33±2.88**	8.66±2.21	0.28±0.12	2.27±0.95	92.4±27.7

	Rec	243.6±36.7	101.9±25.7	56.6±15.2	**22.3±10.6**	15.7±2.3	**3.07±1.21**	**1.72±0.63**	**34.8±8.6**

Table 2 C biomass ratios of functional plankton groups in the four sampling sites during the three periods: pre-hurricane (PRE), hurricane (HURRI) and post-hurricane (REC) in Lake Okeechobee. (means ± one standard error (bootstrapped). Bold font means there is significant difference ($p<0.05$) between PRE, HURRI and REC period based on Mann–Whitney U test.

Site	Ratios	PRE	HURRI	REC
Central	Zooplankton/Phytoplankton	11.64±5.93	77.5±67.63	3.98±1.03
	Autotrophs/Heterotrophs	0.54±0.11	0.67±0.5	0.31±0.05
	Protozoa/Metazoa	3.39±0.62	9.68±8.27	2.52±0.59
West	Zooplankton/Phytoplankton	3.58±1.77	**10.63±6.27**	0.32±0.14
	Autotrophs/Heterotrophs	3.1±0.82	**0.86±0.32**	4.14±1.99
	Protozoa/Metazoa	22.18±7.78	**2.5±1.16**	19.09±7.44
South	Zooplankton/Phytoplankton	2.24±1.17	**10.51±6.32**	0.16±0.09
	Autotrophs/Heterotrophs	2.46±0.63	**0.75±0.26**	2.31±0.61
	Protozoa/Metazoa	45.53±14.17	**3.24±0.98**	18.13±4.48
North	Zooplankton/Phytoplankton	3.81±1.09	**12.94±4.37**	2.45±1.41
	Autotrophs/Heterotrophs	1.32±0.57	**0.19±0.09**	1.91±0.76
	Protozoa/Metazoa	4.28±1.13	**0.9±0.33**	**9.93±2.89**

Table 3 Species richness and Shannon-Wiener index (*H*) in four sampling sites during the three periods: pre-hurricane (PRE), hurricane (HURRI) and post-hurricane (REC) in Lake Okeechobee. No *H* values were calculated for crustaceans because of too few species. (means ± one standard error (bootstrapped). Bold font = significant difference *(p*<0.05) between PRE, HURRI and REC periods based on Mann–Whitney U test.

	Cladocerans	Copepods	Rotifers	Ciliates	Phytoplankton	Total

		Per sample	Total	Per sample	Total	Per sample	Total	*H*	Per sample	Total	*H*	Per sample	Total	*H*	Per sample	Total
Central	PRE	1.9	5	2.5	3	2.9	9	0.72	2.7	7	0.49	24.7	156	2.05	34.5	180
	HURRI	1.7	3	**3.6**[a]	4	2.3	8	**0.40**	3.0	7	0.62	**8.4**	35	**1.31**	**19.0**	57
	REC	1.7	2	2.6	4	**5.8**	24	0.98	**5.2**	10	**1.16**	**10.5**	47	**1.43**	**25.5**	87
West	PRE	2.0	7	2.3	4	3.5	13	0.89	4.5	13	0.97	36.2	204	2.27	48.5	241
	HURRI	**3.1**	8	**3.9**	5	**5.6**	16	1.04	4.1	11	0.83	**14.9**	62	**1.45**	**31.6**	102
	REC	**3.2**	9	2.8	4	**12.5**	39	**1.56**	**6.7**	11	1.06	**23.8**	98	**1.96**	49.0	161
South	PRE	1.8	8	2.3	4	3.7	12	0.91	3.7	12	0.76	30.3	182	2.20	41.7	218
	HURRI	**3.1**	5	**4.2**	6	**5.4**	17	0.83	3.9	9	0.78	**16.0**	65	**1.86**	**32.0**	102
	REC	3.4	10	2.4	4	**13.7**	51	**1.56**	**6.2**	11	1.04	**24.1**	107	1.97	**49.3**	183
North	PRE	2.2	6	2.7	4	3.2	11	0.77	3.8	12	0.76	28.1	181	2.06	39.9	214
	HURRI	2.1	5	**3.3**	5	4.1	13	0.73	3.9	7	0.86	**10.2**	48	**1.60**	**22.1**	78
	REC	2.6	9	2.6	4	**9.1**	35	**1.31**	**6.9**	10	**1.20**	22.8	97	1.79	43.7	155

Table 4 Species in each of the major plankton groups that were found only in the pre-hurricane period or only in the recovery period, vs. species found at both times. The final column indicates the percent of species in the recovery period that are 'new' to the plankton samples, i.e., observed for the first time.

Group	Site	Found only in Pre	Found only in Rec	Found in both Pre and Rec	Percentage found only after recovery
Phytoplankton	South	112	37	70	35%
	North	114	30	67	31%
	West	136	30	68	31%
	Center	127	18	29	38%
Rotifers	South	3	42	9	82%
	North	4	28	7	80%
	West	3	29	10	74%
	Center	4	19	5	79%
Ciliates	South	3	2	9	18%
	North	3	1	9	10%
	West	2	0	11	0%
	Center	0	3	7	30%
Cladocerans	South	2	4	6	40%
	North	0	3	6	33%
	West	1	3	6	33%
	Center	3	0	2	0%
Copepods	South	1	1	3	25%
	North	1	1	3	25%
	West	1	1	3	25%
	Center	0	1	3	25%

Figure captions

Figure 1 Map of Lake Okeechobee, USA with locations of the four sampling sites and the names of the three pelagic zones (Jan. 2000-Jul. 2014). The shaded area is the littoral zone.

Figure 2 Selected physical and chemical attributes of the water during pre-hurricane (PRE), hurricane (HURRI) and post-hurricane (REC) periods at the four sampling sites in Lake Okeechobee. TEM: water temperature, Depth: water depth, SD: transparency measured by Secchi disk, TSS: total suspended solids, DIN: dissolved inorganic nitrogen, SRP: soluble reactive phosphorus, Chl-a: chlorophyll a, TN: total nitrogen, TP: total phosphorus. UCI: upper 95% confidence interval, LCI: lower 95% confidence interval.

Figure 3 Relative biomass of main plankton groups and dominant species in each group during pre-hurricane (PRE), hurricane (HURRI) and post-hurricane (REC) in the four sampling sites.

Figure 4 Bi-plots showing the samples from the three periods (PRE: pre-hurricane (black hollow circles), HURRI: hurricane (green cross), and REC: recovery (red triangles)) in the first two PCA ordination axis, with the 95% confidence ellipses, centers of the ellipses (solid circles) and main taxonomic groups or species (arrows), in the four sampling sites of Lake Okeechobee. Species names are abbreviated. Italic bold font of HURRI or REC means that there is significant difference between points of PRE, HURRI and REC periods based on the two-dimensional Kolmogorov-Smirnov tests. Rows in the figure correspond to taxonomic groups: a – all plankton, b – phytoplankton, c – bacteria, d – ciliates, e – rotifers, f – crustaceans.

Figure 1

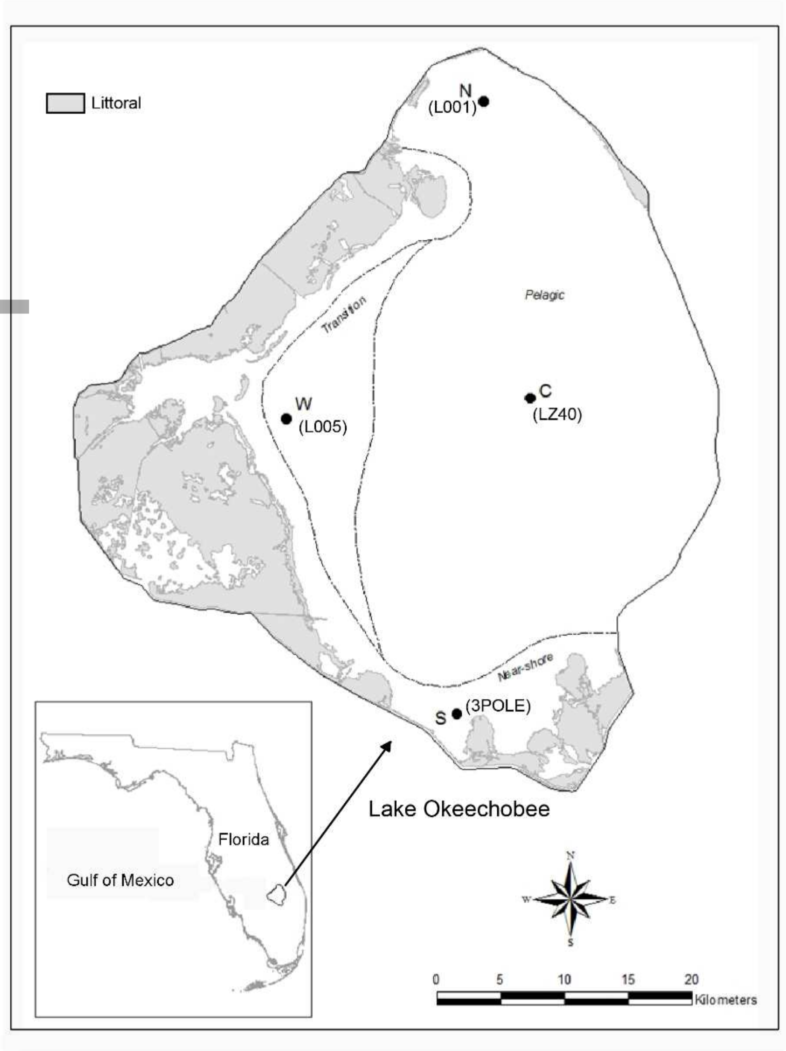
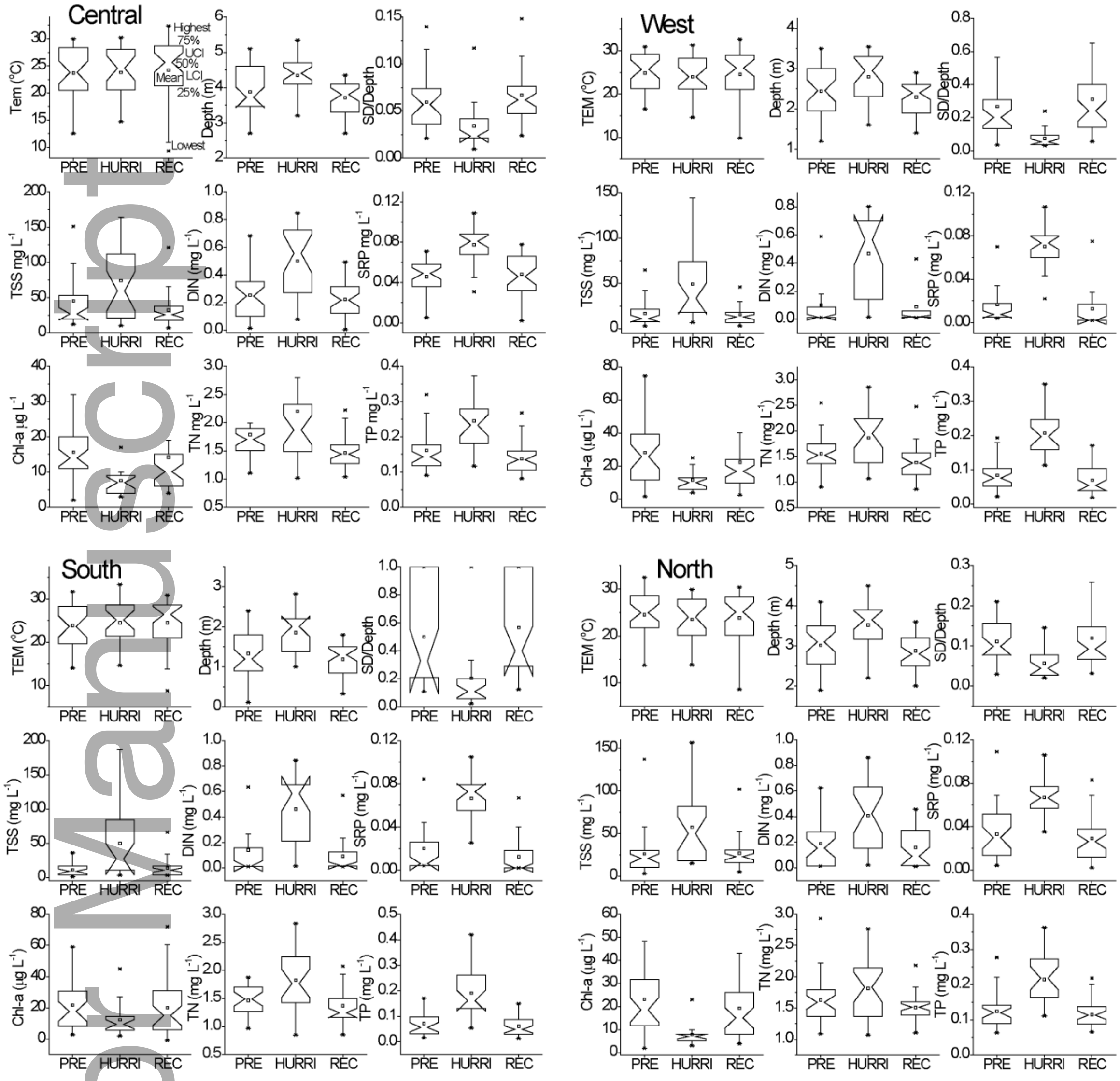

Littoral
N
(L001)
Pelagic
Transition
W
(L005)
C
(LZ40)
Near-shore
S
(3POLE)
Lake Okeechobee
Florida
Gulf of Mexico
N
W
E
S
0
5
10
15
20
Kilometers

Figure 2



Central
West
South
North
Tem (°C)
TEM (°C)
Depth (m)
SD/Depth
TSS mg L^{-1}
TSS (mg L^{-1})
DIN (mg L^{-1})
SRP mg L^{-1}
SRP (mg L^{-1})
Chl-a μg L^{-1}
Chl-a (μg L^{-1})
TN mg L^{-1}
TN (mg L^{-1})
TP mg L^{-1}
TP (mg L^{-1})
PRE
HURRI
REC
Highest
75%
UCI
50%
Mean
LCI
25%
Lowest

Figure 3

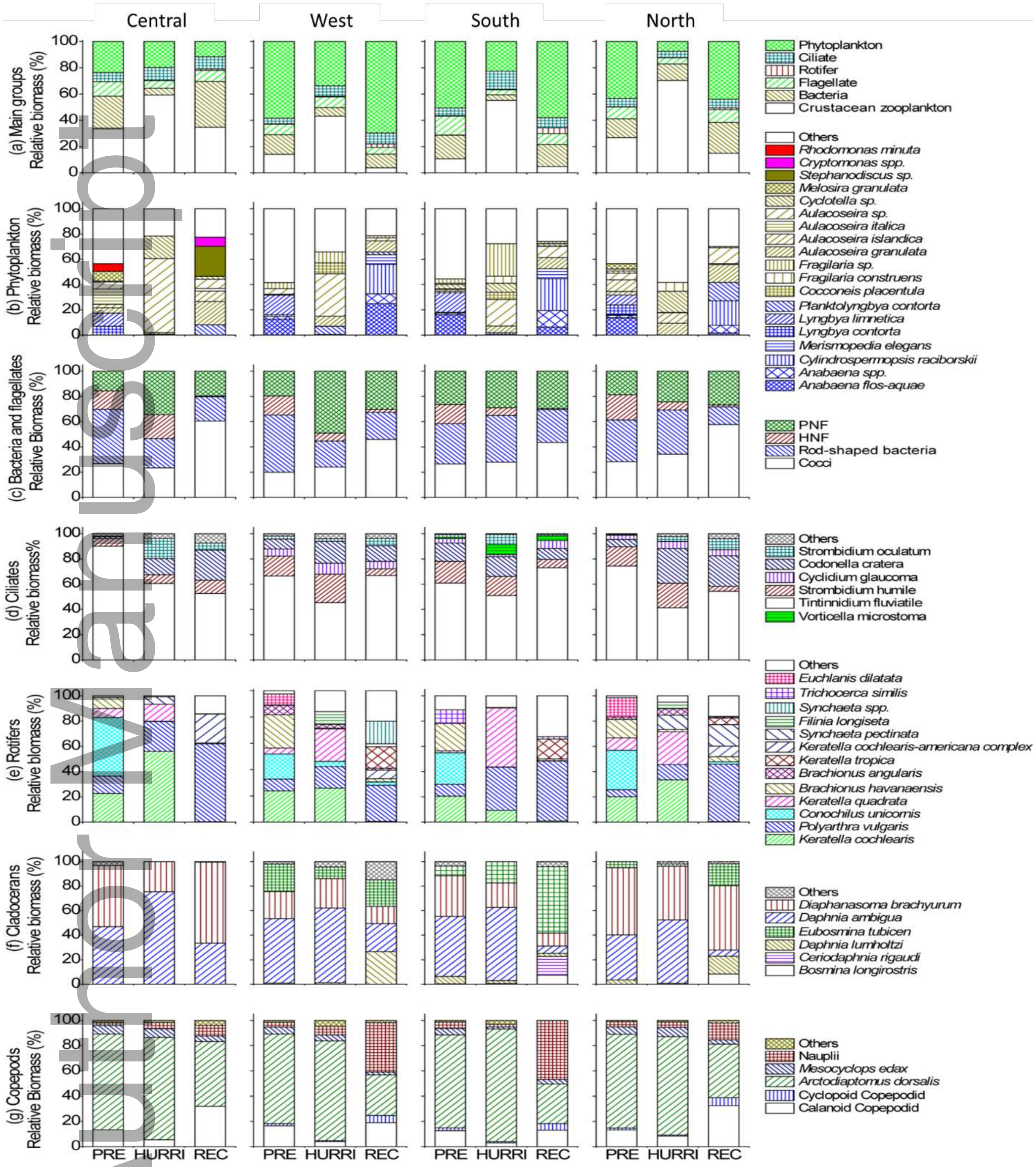
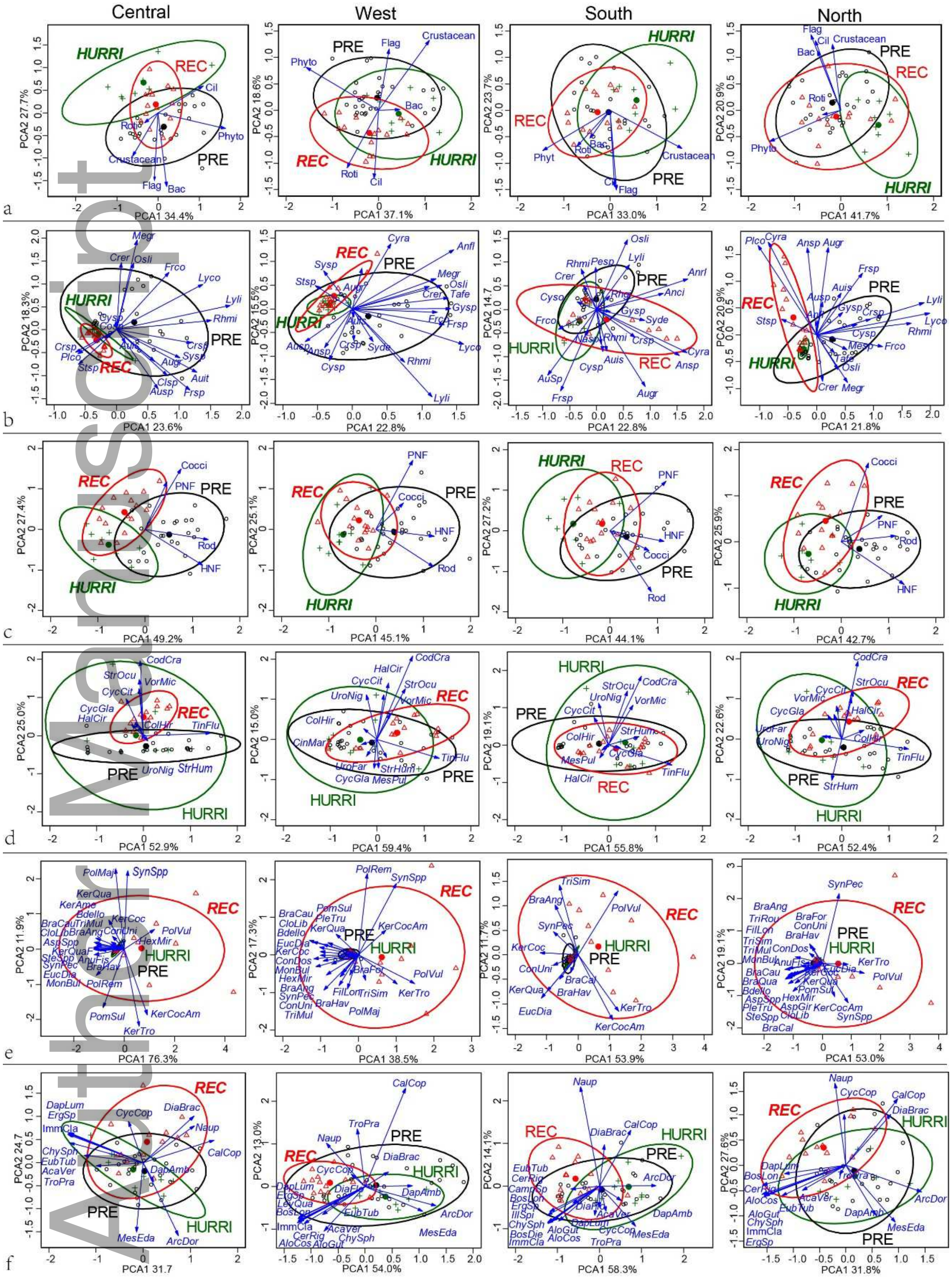

Central
West
South
North
(a) Main groups Relative biomass (%)
Phytoplankton
Ciliate
Rotifer
Flagellate
Bacteria
Crustacean zooplankton
(b) Phytoplankton Relative biomass (%)
Others
Rhodomonas minuta
Cryptomonas spp.
Stephanodiscus sp.
Melosira granulata
Cyclotella sp.
Aulacoseira sp.
Aulacoseira italica
Aulacoseira islandica
Aulacoseira granulata
Fragilaria sp.
Fragilaria construens
Cocconeis placentula
Planktolyngbya contorta
Lyngbya limnetica
Lyngbya contorta
Merismopedia elegans
Cylindrospermopsis raciborskii
Anabaena spp.
Anabaena flos-aquae
(c) Bacteria and flagellates Relative Biomass (%)
PNF
HNF
Rod-shaped bacteria
Cocci
(d) Ciliates Relative biomass%
Others
Strombidium oculatum
Codonella cratera
Cyclidium glaucoma
Strombidium humile
Tintinnidium fluviatile
Vorticella microstoma
(e) Rotifers Relative biomass (%)
Others
Euchlanis dilatata
Trichocerca similis
Synchaeta spp.
Filinia longiseta
Synchaeta pectinata
Keratella cochlearis-americana complex
Keratella tropica
Brachionus angularis
Brachionus havanaensis
Keratella quadrata
Conochilus unicornis
Polyarthra vulgaris
Keratella cochlearis
(f) Cladocerans Relative biomass (%)
Others
Diaphanasoma brachyurum
Daphnia ambigua
Eubosmina tubicen
Daphnia lumholtzi
Ceriodaphnia rigaudi
Bosmina longirostris
(g) Copepods Relative Biomass (%)
Others
Nauplii
Mesocyclops edax
Arctodiaptomus dorsalis
Cyclopoid Copepodid
Calanoid Copepodid
0
20
40
60
80
100
PRE
HURRI
REC

Figure 4


Central
West
South
North
a
PCA1 34.4%
PCA2 27.7%
PCA1 37.1%
PCA2 18.6%
PCA1 33.0%
PCA2 23.7%
PCA1 41.7%
PCA2 20.9%
b
PCA1 23.6%
PCA2 18.3%
PCA1 22.8%
PCA2 15.5%
PCA1 22.8%
PCA2 14.7
PCA1 21.8%
PCA2 20.9%
c
PCA1 49.2%
PCA2 27.4%
PCA1 45.1%
PCA2 25.1%
PCA1 44.1%
PCA2 27.2%
PCA1 42.7%
PCA2 25.9%
d
PCA1 52.9%
PCA2 25.0%
PCA1 59.4%
PCA2 15.0%
PCA1 55.8%
PCA2 19.1%
PCA1 52.4%
PCA2 22.6%
e
PCA1 76.3%
PCA2 11.9%
PCA1 38.5%
PCA2 17.3%
PCA1 53.9%
PCA2 11.7%
PCA1 53.0%
PCA2 19.1%
f
PCA1 31.7
PCA2 24.7
PCA1 54.0%
PCA2 13.0%
PCA1 58.3%
PCA2 14.1%
PCA1 31.8%
PCA2 27.6%
PRE
REC
HURRI