

Georgia Journal of Science

Volume 77 No. 2 *Scholarly Contributions from the Membership and Others*

Article 14

2019

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Marque'l K. Gould

Valdosta State University, marquel.gould@gmail.com

Adam J. Nienow

Marine Microalgae Research Associates, nienow.adam@gmail.com

Anastasia V. F. Nienow

Marine Microalgae Research Associates, sputnik2057@gmail.com

James A. Nienow

Valdosta State University, jnienow@valdosta.edu

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Recommended Citation

Gould, Marque'l K.; Nienow, Adam J.; Nienow, Anastasia V. F.; and Nienow, James A. (2019) "Short Term Effects of Hurricane Irma on the Phytoplankton of Lake Louise, Georgia, USA," *Georgia Journal of Science*, Vol. 77, No. 2, Article 14.

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Acknowledgements

This work was funded, in part, by Marine Microalgae Research Associates LLC, Valdosta GA, and by grants to JAN from the Major Equipment Scientific Equipment Funding Pool at Valdosta State University.

SHORT TERM EFFECTS OF HURRICANE IRMA ON THE PHYTOPLANKTON OF LAKE LOUISE, GEORGIA, USA

Marque'l K. Gould, Valdosta State University, Valdosta, Georgia
Adam J. Nienow, Marine Microalgae Research Associates, Valdosta, Georgia
Anastasia V. F. Nienow, Marine Microalgae Research Associates,
Valdosta, Georgia
James A. Nienow, Valdosta State University, Valdosta, Georgia
(jnienow@valdosta.edu)

ABSTRACT

Natural disturbances such as fires and severe storms can have profound impacts on the hydrology and ecology of inland waters, potentially altering the structure and function of the ecosystem for extended periods of time. Studies of the initial impacts are, however, uncommon. Here we report on the short-term impacts of Hurricane Irma in the structure of the phytoplankton association in Lake Louise, a small blackwater lake in southern Georgia. Irma hit the region on September 11, 2017, with tropical storm force winds. The event corresponded to a period during which we were conducting routine weekly monitoring of environmental conditions in the lake. Parameters monitored included temperature, dissolved oxygen, conductivity, and light from the surface to a depth of 6 m. Chlorophyll concentrations and the structure of the phytoplankton were also determined at 1 m intervals from the surface to a depth of 5 m. An increase in the overall abundance of phytoplankton in the upper meter of the lake and a decrease in the abundance of phytoplankton deeper in the water column were observed immediately after Hurricane Irma. These decreases were followed by a bloom involving several species of cyanobacteria beginning about four weeks after the passage of the hurricane. Signatures of the passage of the hurricane were erased in early December as cooler temperatures created isothermal conditions in the lake.

Keywords: Hurricane Irma, hurricane impacts, Lake Louise, phytoplankton

INTRODUCTION

Aquatic ecosystems are in a constant state of flux as the biotic components respond to changes in the abiotic conditions and to each other. Some of these changes, the seasonal changes in temperate lakes, for example, are relatively predictable, following a set pattern year after year. In other cases, such as long-term changes in the climate or extended periods of nutrient loading, the response may not be predictable with full certainty, but because both the change in abiotic conditions and the response of the biotic community occur over extended periods of time, it is possible to establish monitoring programs and identify trends in the community. In contrast, natural disturbances, especially tropical cyclones (hurricanes, tropical storms, and tropical depressions), are acute, stochastic events with low probability. They do not follow a predictable seasonal progression, and the severe impacts occur over a relatively brief period of time, too short to establish a meaningful environmental monitoring program. Yet natural disturbances can have profound impacts on the hydrology and ecology of inland waters, potentially altering the

structure and function of the ecosystem for extended periods of time (Turner et al. 2003; Peierls et al. 2003; Ji et al. 2018). One way around this problem is to establish long-term monitoring programs. These are typically established to look for long-term trends in specific ecosystems, but are able to capture immediate impacts of disturbances (Turner et al. 2003). For example, monitoring programs established in Lake Okeechobee, Florida, in the 1970s allowed the short- and long-term impacts of hurricanes Irene, in 1999 (Havens et al. 2001), Charley, Frances, Ivan, and Jeanne, in 2004, and Wilma, in 2005, to be analyzed in some detail (James et al. 2008; Havens et al. 2011; Ji et al. 2018). Similar programs aided in capturing the impacts of Hurricane Ivan, in 2004, on Pensacola Bay, Florida (Hagy et al. 2006) and tropical cyclone Irene, in 2011, on a system of lakes in the northeastern United States (Klug et al. 2012). Peierls and his colleagues, lacking a long-term monitoring program, were unable to capture the immediate impacts of three successive hurricanes near Pamlico Sound, North Carolina; they were, however, able to establish a program after the fact and capture the long-term impacts of the hurricanes (Bales 2003; Peierls et al. 2003).

The establishment of long-term monitoring programs is expensive both in terms of equipment and supplies and in labor, and most such efforts are reserved for larger systems of regional importance, such as those cited previously. As a consequence, reports of the impacts of major storms and hurricanes on smaller bodies of water are rare, even from regions where hurricanes are relatively common. Here, we report on one such case.

Lake Louise, Georgia, like much of the southeastern United States, is subject to periodic hurricanes. Oxygen isotope anomalies in the latewood cellulose of pine trees suggest that hurricanes influenced tree growth in the vicinity of Lake Louise at least 47 times between 1750 and 1940, and another 21 times between 1940 and 1990, with most of the latter storms corroborated by hurricane tracks and local measurements of rainfall (Miller et al. 2006). Unfortunately, oxygen isotope anomalies track precipitation and not wind speed, so it is not always clear how close the hurricanes came to Lake Louise and what additional impacts they may have had; storms tracking 400 km away can influence precipitation at Lake Louise enough to cause an isotope anomaly in the latewood, while some closer storms may not (Miller et al. 2006). More direct evidence of the long-term impacts can be seen in the sediment core analyzed by Tepper and Hyatt (2011). They found a 9-cm thick layer of silt and plant debris in a section of the core dated to approximately 1800. They attribute this layer to the hurricane season of 1780, which included three major Atlantic hurricanes, including one of the deadliest on record (Tepper and Hyatt 2011). In this case the hurricanes may have had such an impact on the lake ecosystem that they influenced the development of the system for the next 150 years (Tepper and Hyatt 2011). More recently, the centers of six storms with tropical storm force winds or greater have passed within 50 km of Lake Louise since 1990: Allison in 1995, Josephine in 1996, Jeanne in 2004, Alberto in 2006, Hermine in 2016, and Irma in 2017 (NOAA 2019). The last of these, Irma, is the subject of this report. In February 2017, we began a weekly sampling program in Lake Louise in order to acquire updated baseline data for a proposed undergraduate research course scheduled for the summer of 2018. Sampling continued almost without interruption until December 2017. This fortuitous set of circumstances allowed us to capture some of the immediate impacts of the hurricane on both the physical environment and the structure of the phytoplankton.

MATERIAL & METHODS

The Study Site

Lake Louise ($30^{\circ} 43.5' N$, $83^{\circ} 15.5' W$) is located about 15 km south of Valdosta, Georgia (Figure 1); it is an important component of the Lake Louise Field Station maintained by Valdosta State University (Riggs et al. 2010). The 76.9 ha field station encompasses three major vegetation systems: the Atlantic Coastal Plain Streamhead Seepage Swamp, Pocosin, and Baygall; the Gulf and Atlantic Coastal Plain Swamp System; and the Southern Atlantic Coastal Plain Wet Pine and Savanna and Flatwoods (Riggs et al 2010). While only one of these, the Streamhead Seepage Swamp, Pocosin, and Baygall system, is in direct contact with the lake (Riggs et al. 2010), all three contribute to a forested environment giving the lake a degree of shelter from surface winds.



Figure 1. Lake Louise, Georgia. Top. Satellite image of the region, showing the position of Lake Louise relative to Valdosta. Bottom left. Satellite image of Lake Louise. Images courtesy of Landsat/Copernicus ©2019 Google. Bottom right. A view of the lake showing the surrounding trees.

The lake itself has a surface area of about 5.7 ha, with a maximum depth of about 6.4 m (Tepper and Hyatt 2011). The lake apparently formed through the dissolution of the underlying limestone, i.e. through sinkhole collapse, about 9,500 years ago (Tepper and

Hyatt 2011; Watts 1971). Currently, Lake Louise receives most of its water either directly from rainfall, or by seepage from the surrounding soils. Because of the high organic content of the surrounding soils, the water seeping into the lake is enriched with tannic acid and humic substances (Tepper and Hyatt 2011). As a result, the waters of the lake are the color of weak tea and the lake is often referred to as a “blackwater lake” (Riggs et al. 2010; Tepper and Hyatt 2011).

Sampling programs in 2003–2005, 2009, and 2015 (unpublished data), demonstrated the impacts of the dark color of the water on the physical and chemical characteristics and biology of the lake. Most of the solar radiation is absorbed in the upper 1–2 m of the lake; typically less than 0.1% of the incident solar radiation reaches a depth of 2.5 m. This leads to a thermally stratified lake, with stratification beginning by mid-March and continuing until mid- to late-November; during the winter, the lake alternates between stratified and isothermal states depending on weather patterns. The epilimnion can reach temperatures in excess of 30 °C during the summer, while temperatures in the bottom waters remain below 16 °C. In addition, the low rates of photosynthesis in response to the low light levels leads to oxygen concentrations of less than 1 mg/L at depths greater than 2.0 m.

Environmental Sampling

The lake was sampled weekly from February 10, 2017, through December 9, 2017. All measurements were taken between 10:00 am and 12:00 noon, near a post marking the deepest point of the lake—the site of the sediment core collected by Tepper and Hyatt (2011).

Temperature (°C), dissolved oxygen (mg/L), and specific conductivity (mS/cm) were recorded at 10-cm intervals for the first 2 m, and 50-cm intervals thereafter, to a depth of 6 m using a YSI Pro2030 (YSI, Inc., Yellow Springs, Ohio). Photosynthetically active radiation (PAR, $\mu\text{mol photons/m}^2/\text{s}$) was recorded at 10-cm intervals to a depth of 2 m using a spherical quantum sensor (LI-COR SPQA) attached to a LI-1400 recorder (LI-COR, Inc., Lincoln, Nebraska); simultaneous measurements of the incident light were made with a LI-COR quantum sensor (LI-190) attached to the same recorder.

Whole water samples (2 L) were collected from the surface and from depths 1 m, 2 m, 3 m, 4 m, and 5 m using a 1.5-L Kessler bottle. These were transported to the laboratory for further processing; initial processing was completed within 3 hours of collection. An additional 50-mL aliquot from each depth was fixed immediately with 1 mL of Lugol’s iodine for subsequent analysis using imaging flow cytometry. A net plankton sample was collected using a 25- μm mesh net dropped from the surface to the bottom and towed back to the surface.

Pigment Analysis

Replicate 250 to 500 mL subsamples of the whole water samples were filtered onto glass fiber filters with a nominal pore size of 0.7 μm ; the volume filtered depended on the concentration of microorganisms in the water sample. The filters were stored at $-80\text{ }^\circ\text{C}$ for 24 to 48 hours, at which point the filters were extracted overnight in 90% acetone at 4 °C. Extracts were then centrifuged and scanned between 350 and 800 nm against a 90% acetone blank using a PerkinElmer Lambda 35 UV/VIS spectrometer (PerkinElmer, Waltham, Massachusetts). The concentrations of chlorophylls *a*, *b*, and *c* ($\mu\text{g/L}$) were

calculated from the spectra using the trichroic equations of Jeffrey and Humphrey (1975). Calculated values less than 0.0 $\mu\text{g/L}$ were set to 0.0 $\mu\text{g/L}$ for further analysis.

Light Microscopy

Net plankton samples were observed using an Olympus BX60 microscope equipped with differential interference contrast optics (Olympus, Tokyo, Japan) and a Canon EOS Rebel digital camera (Canon, Tokyo, Japan) configured for remote viewing using Entangle 0.7.1 software (developed by D. Berrangé). Common forms were photographed and identified to the lowest possible taxonomic category using Wehr et al. (2015) as a general resource for phototrophic microorganisms, Komárek & Anagnostidis (1998, 2005) and Komárek (2013) for cyanobacteria, and Dillard (1989a, 1989b, 1990, 1991a, 1991b, 1993, 2000, 2007) for eukaryotic algae.

Imaging Flow Cytometry

Subsamples of each Lugol's-fixed sample were analyzed using a FlowCam (Fluid Imaging Technologies, Scarborough, Maine) imaging flow cytometer. This instrument counts the number of particles flowing past the sensor and images all particles greater than a user-defined lower bound. The images can then be used to classify the particles according to shape. Each sample was analyzed twice, once using a 4 \times objective lens, and again using a 10 \times objective lens. When using the 4 \times objective, 5 mL subsamples were prefiltered using 243- μm mesh nylon netting before loading into the system and particles greater than 12 μm in diameter were imaged. When using the 10 \times objective, 2.5 mL subsamples were prefiltered using 100- μm mesh nylon netting and particles greater than 4 μm in diameter were imaged. These differences in prefiltration and imaging parameters lead to slight differences in the concentration of particles in the sample when using the two lenses.

Optical filters were constructed for each lens using the saved images and VisualSpreadsheet software accompanying the instrument. The optical filters can be used to sort images into categories based on up to 30 parameters defining the shape, size, and color of the object imaged. The filters were based on image libraries chosen to encompass the range of forms observed over the entire sampling period, a total of 38 image libraries and filters for the 4 \times objective and 46 image libraries and filters for the 10 \times objective. These accounted for $94.71 \pm 2.31\%$ of the particles counted in each sample using the 4 \times objective and $99.16 \pm 0.32\%$ of the particles counted with the 10 \times objective over the period extending from August 5, 2017 to October 23, 2017. Particle counts associated with optical filters representing sediment particles, animal parts, and nonphotosynthetic microorganisms were discarded, as were counts associated with optical filters comprising less than 1% of any sample collected between August 5 and October 23, leaving 10 categories for the 4 \times objective and 18 categories for the 10 \times objective. Finally, results for filters that appeared to represent different aspects or growth forms (colony sizes and filament lengths) of the same taxon when viewed with the 10 \times objective were lumped together. This reduced dataset with 11 categories was used as the basis for statistical comparisons between samples.

The image libraries associated with each category were compared with the light microscopy images of the net plankton samples. In many cases, this allowed us to associate a generic or species name with a particular image library. In other cases, this was not possible and more general names (e.g., loose colonies) were used.

Graphical and Statistical Analysis

Contour plots of environmental parameters, chlorophyll concentrations, and phytoplankton density were constructed using Surfer 13 (Golden Software LLC, Golden, Colorado). Pie charts showing the composition of each sample were constructed using Microsoft Excel 14 (Microsoft Corporation, Seattle, Washington). Calculations associated with the statistical analyses were also performed in Microsoft Excel 14.

RESULTS

Plots of environmental parameters (temperature, dissolved oxygen, and specific conductivity) for the period August 5, 2017 to October 14, 2017 can be seen in Figures 2, 3, and 4, respectively. All three show the pattern typical of Lake Louise prior to September 11: a stable, stratified system, with sharply higher temperature and oxygen concentrations and lower conductivity in the upper 2 m of the water column. Between September 9 and September 16, the period when Irma passed over the region, there was a distinct break in the pattern. The 25 °C isotherm shifted upward from a depth of just below 2 m to a depth of about 1 m, while the depth of the 20 °C isotherm remained relatively constant (Figure 2). This finding suggests that the storm caused warm surface waters to mix with cooler bottom waters, but only to a depth of about 3 m. This is corroborated by the oxygen profiles (Figure 3) and the conductivity profiles (Figure 4). In the case of oxygen, there was a short-lived spike of oxygenated water reaching a depth of 2–2.5 m at the time of the hurricane. With respect to specific conductivity, low conductivity water (0.05 mS/cm) reached depths of greater than 3 m; waters with conductivity lower than 0.04 mS/cm are

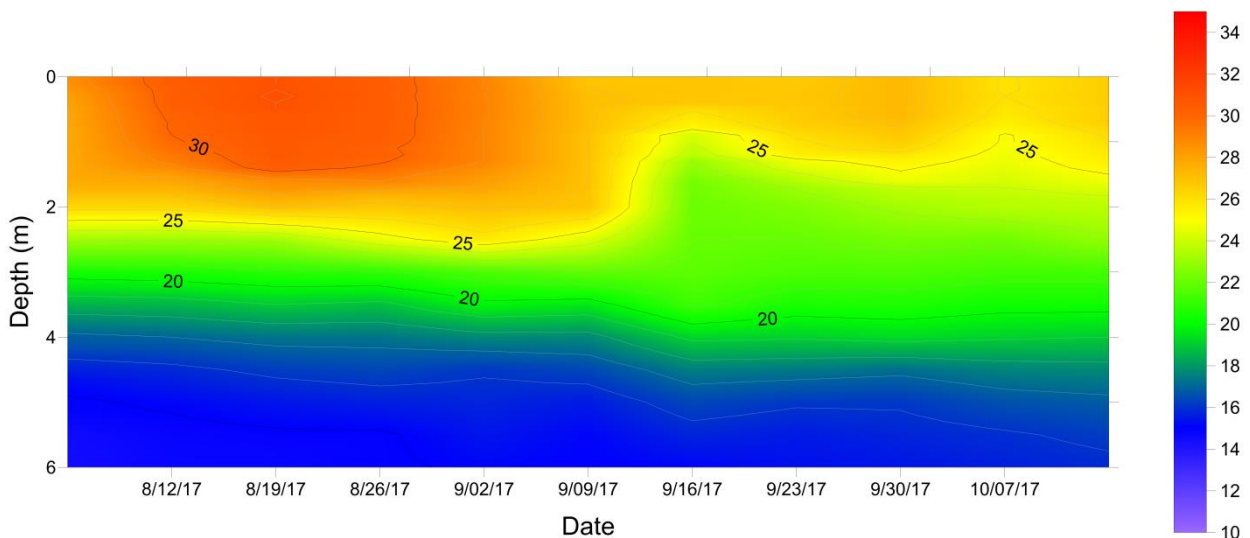


Figure 2. Temperature profiles for the period from August 5, 2017, to October 14, 2017. Temperatures are given in degrees Celsius.

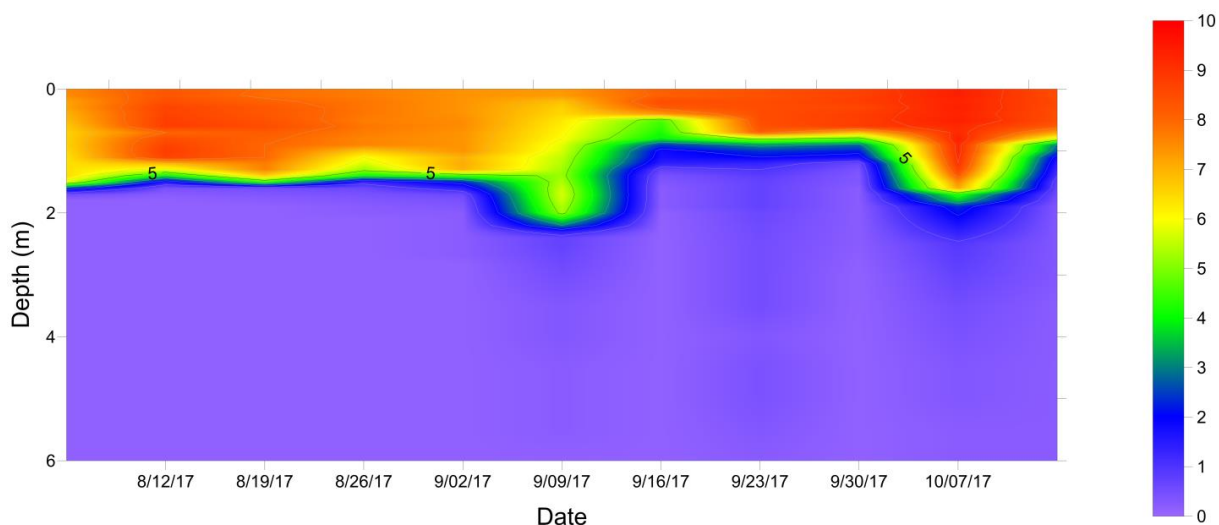


Figure 3. Oxygen profiles for the period from August 5, 2017, to October 14, 2017. Oxygen concentrations are given in milliliters per liter.

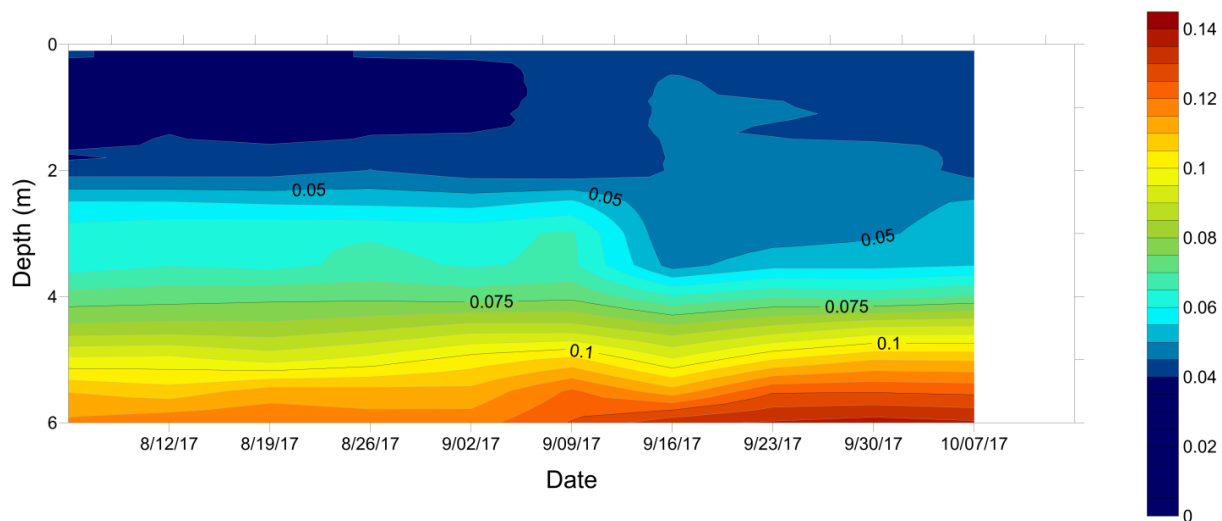


Figure 4. Conductivity profiles for the period from August 5, 2017, to October 14, 2017. Units are milliseimens per centimeter.

absent, even from the surface. None of the profiles had returned to the prehurricane conditions by the end of the season.

The changes to the physical environment are mirrored by changes in the phytoplankton association. Prior to the passage of the hurricane, chlorophyll profiles (Figure 5) indicate a robust phytoplankton association, with maximal development at a depth of about 3 m, and with chlorophyll-*b*-producing members playing a dominant role

at this depth. This is consistent with unpublished observations from prior years. Immediately after the passage of Irma, there was a sharp decrease in chlorophyll concentrations from the surface to a depth of 4 m. In fact, the chlorophyll maximum at 3 m completely disappeared, as did the chlorophyll *b* signal. There was concurrent decrease in the density of the phytoplankton association during this week as indicated by the results derived from imaging flow cytometry (Figure 6). By two weeks after the passage of the hurricane, the phytoplankton association began to increase again, but with some differences. The chlorophyll maximum and the strong chlorophyll *b* signal at a depth of 3 m were absent for the remainder of the season. Instead, the maximum chlorophyll concentrations shifted to the surface waters, with maximal development at a depth of about 1 m (Figure 5). There was a concurrent increase in chlorophyll *c* producers (data not shown), although not to the extent seen earlier with chlorophyll *b* producers. This upward shift is also seen in the population densities derived from imaging flow cytometry (Figure 6). In this case, population densities after Irma exceed 10,000 particles (cells, colonies, and filaments) per milliliter in the upper 2 m of the lake. The high concentrations of phytoplankton are coincident with the downward spike in oxygen profiles seen on October 7 (Figure 3). The changes in the composition of the phytoplankton association with immediately before and immediately after the storm, as determined by imaging flow cytometry, are shown in Figure 7 (4× objective) and Figure 8 (10× objective). In each instance, the association is dominated by filamentous cyanobacteria (*Dolichospermum* and *Aphanizomenon* in the upper 2 m, *Planktolyngbya* and a form tentatively identified as *Prochlorothrix* in deeper layers). Other important groups include colonial cyanobacteria (identified as *Woronichinia*, *Microcystis*, and tight and loose clusters) and several species of euglenoids.

In order to test whether the structure of the association changed as a result of the storm, profiles based on the reduced set for the two weeks prior to the passage and the two weeks after the passage of Irma were compared using the Friedman test. This is a nonparametric test used to compare changes in the ranks of categories over subsequent testing periods (Zar 2010, 277). When we performed the test using the population density of each category, significant differences ($p < 0.05$) were found in the associations at each depth over the four-week period. However, when we performed the same test using percent of association instead of absolute population densities, none of the changes were significant at the same level. We interpret this to mean that the significant differences were associated with changes in absolute population densities resulting from the storm, especially the decrease in densities seen at most depths immediately after the storm, followed by increases starting a week later. Changes in the relative proportions of the categories in a particular association may not have been affected as strongly. The results from flow cytometry, supplemented with light microscopy, indicate that the bloom that developed about four weeks after the passage of the hurricane was dominated by *Dolichospermum* spp., especially *D. circinalis*, and colonial cyanobacteria (*Microcystis aeruginosa* and *Woronichinia nagelii*); euglenoids were also present in significant numbers. The cyanobacterial species have also been observed to form dense populations early in the season, as the waters warm up from winter lows (unpublished observations).

By November 4, 2017, the bloom had dissipated and chlorophyll concentrations were at background levels throughout the water column. By December 9, 2017, the water column was isothermal at 15.5 °C, removing all immediate traces of the passage of Hurricane Irma.

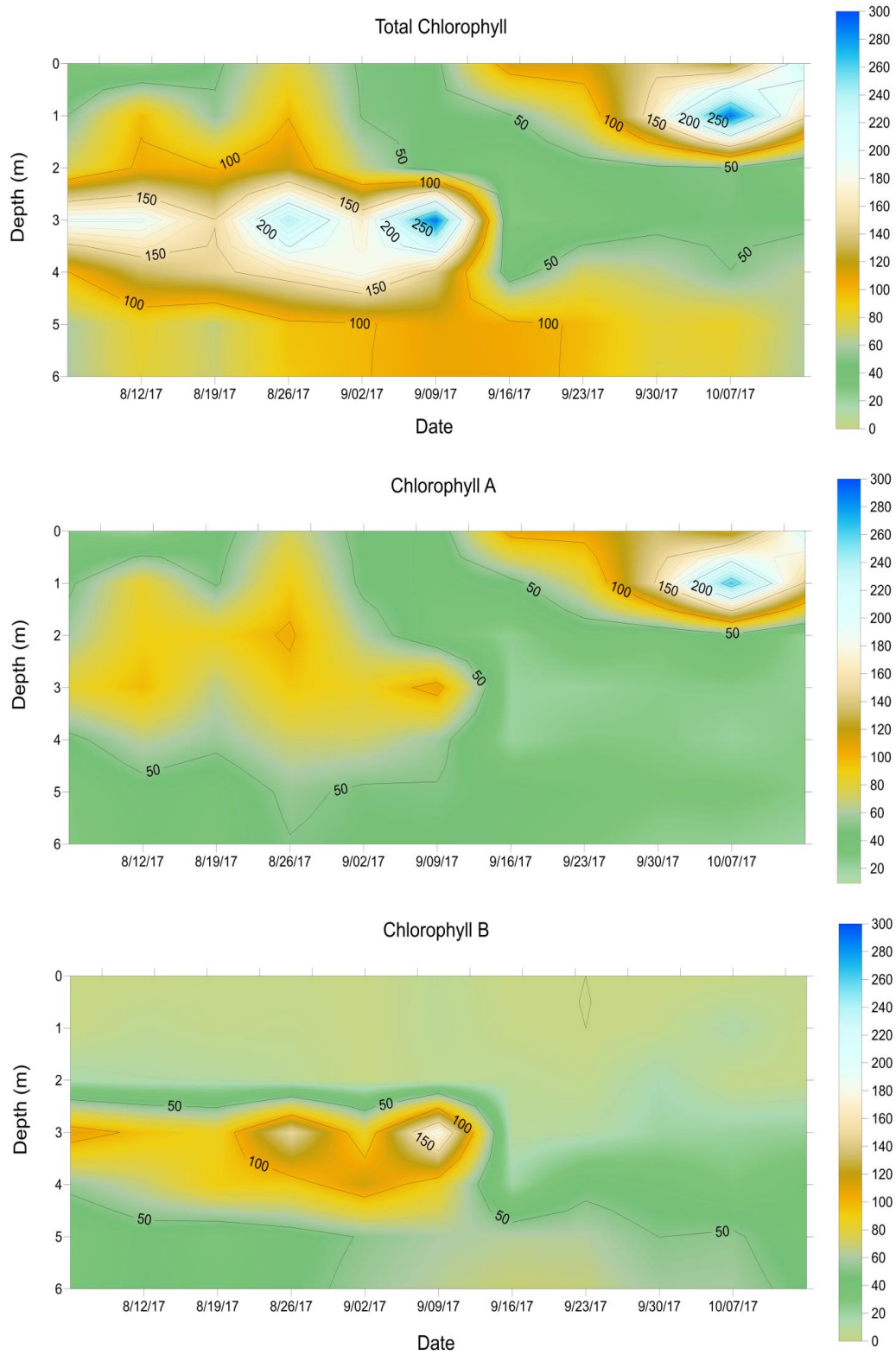


Figure 5. Total chlorophyll, chlorophyll *a*, and chlorophyll *b* profiles for the period from August 5, 2017, to October 14, 2017. Concentrations are given in micrograms per liter.

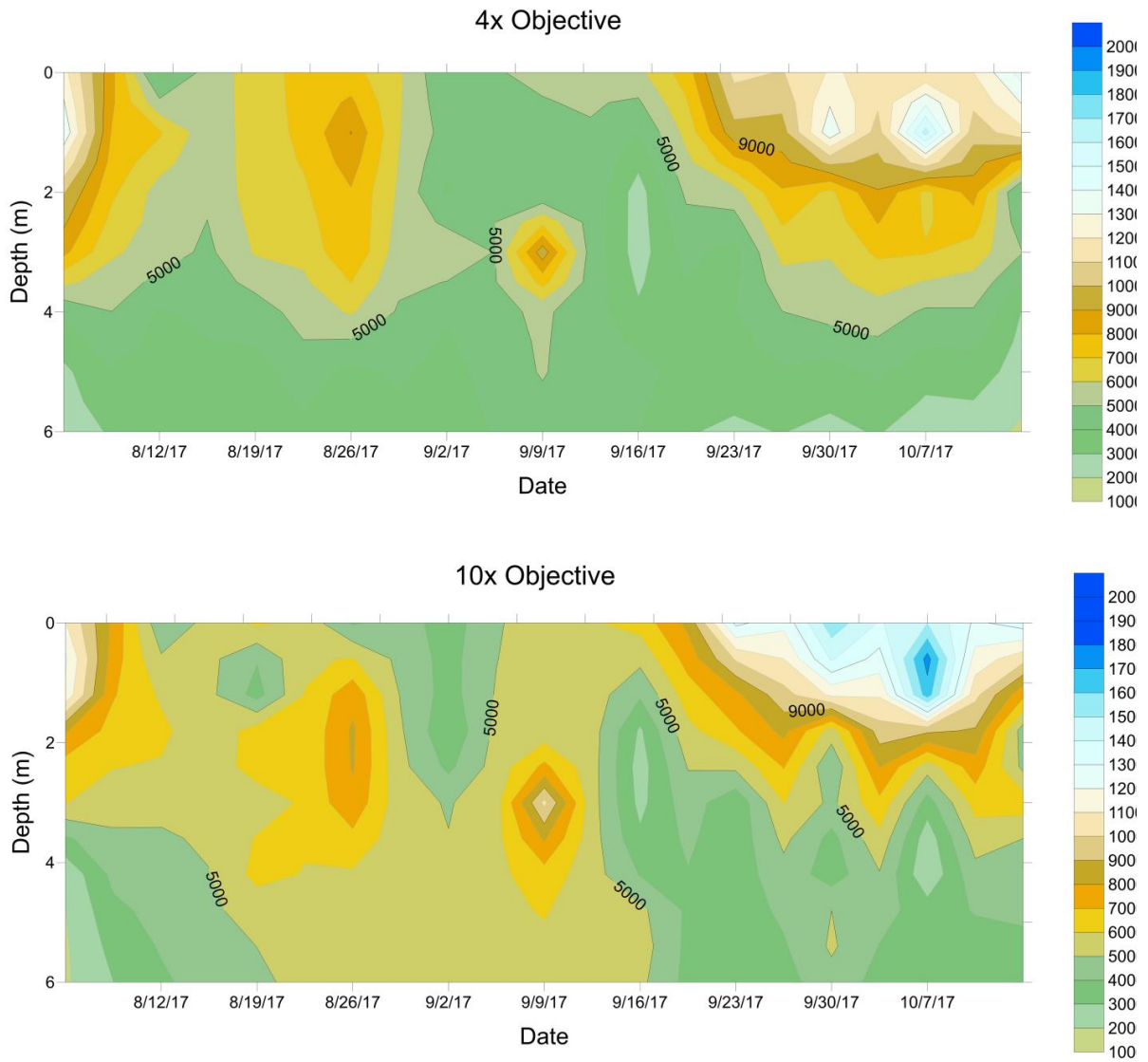


Figure 6. Population densities derived from imaging flow cytometry for the period from August 5, 2017, to October 14, 2017. Concentrations are given in particles (cells, filaments, or colonies) per milliliter.

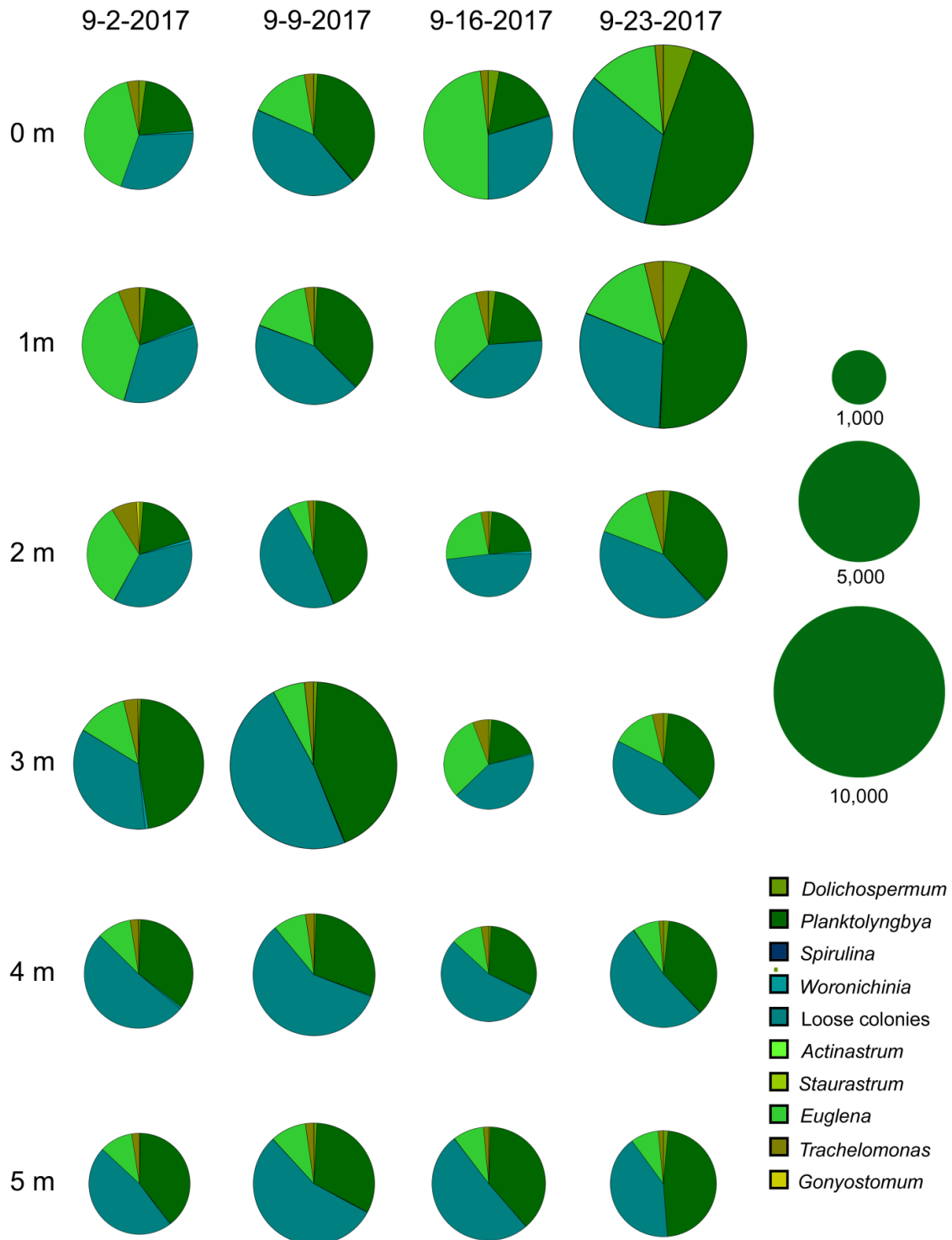


Figure 7. Association composition as determined using imaging flow cytometry with a 4× objective. The size of the circle indicates the concentration in particles (cells, filaments, or colonies) per milliliter. The wedges of the pies represent the proportion of the association composed of the indicated types.

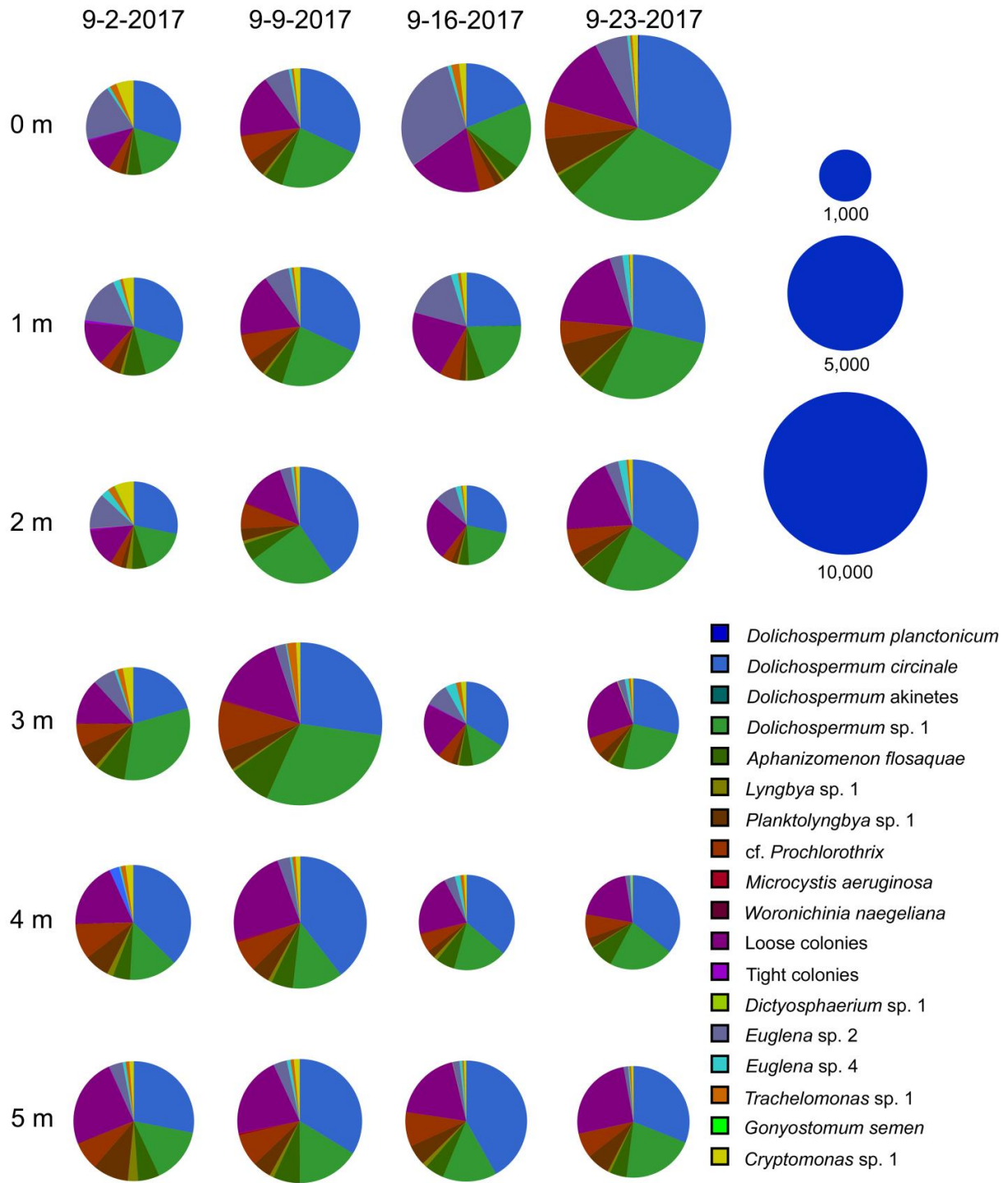


Figure 8. Association composition as determined using imaging flow cytometry with a 10× objective. The size of the circle indicates the concentration in particles (cells, filaments, or colonies) per milliliter. The wedges of the pies represent the proportion of the association composed of the indicated types.

DISCUSSION

The immediate impact of the passage of Hurricane Irma was the mixing of the water column to a depth of about 3 m. The fact the mixing was restricted to the upper layers is somewhat surprising given the degree of mixing observed in Lake Okeechobee (James et al. 2008), several lakes in New York after the passage of Hurricane Irene (Klug et al. 2012), and what would be expected in bay systems (Hagy et al. 2006). However, several factors unique to Lake Louise and Hurricane Irma may have combined to mitigate the effects (compare to Jennings et al. 2012). First, by the time Irma reached Lake Louise, it had been down-graded to a tropical storm with maximum wind gusts on the order of 25 m/s (National Weather Service 2019). Second, the trees surrounding the lake may have reduced the wind speed at the lake's surface. This, coupled with the small surface area and short fetch of the lake, would tend to reduce turbulence and vertical mixing. Third, the steep sides and relatively deep bottom of the lake would serve to shield bottom waters from mixing. These factors are all in contrast with Lake Okeechobee, a large, shallow (<3 m) lake more directly exposed to hurricane force winds (James et al. 2008).

The passage of the storm did have immediate impacts on the phytoplankton association. First, the density of the association in the upper 4 m was reduced. Much of the decrease can be attributed to washout; Irma brought significant amounts of rain to the region, more than 8.5 cm of rain just during the 24-hour period surrounding its passage, with additional rain falling before and after (National Weather Service 2019). However, while this can account for the decrease in numbers, it does not account for the loss of the chlorophyll maximum and the strong chlorophyll *b* signal at a depth of 3 m. Here, we must invoke the mixing of waters from the hypolimnion with waters from the epilimnion. This had an impact on oxygen concentration, specific conductivity, and temperature; presumably, a number of nutrients and ions were also impacted. This mixing clearly had a large negative impact on the association at this depth, an impact the association did not recover from for the rest of the year. Unfortunately, the composition of the association has not yet been completely determined, so it is not clear which aspects of the mixing caused the negative impacts. Results from imaging flow cytometry and light microscopy suggest that the association is dominated by several species of nonheterocystous filamentous cyanobacteria, all with a width of less than 3 μm . Precise identification of these forms without the aid of cultures is difficult. The large chlorophyll *b* signal associated with this depth suggests that one of the filamentous forms may be a member of the genus *Prochlorothrix*; we are currently investigating this possibility using molecular techniques.

Given the magnitude of the change it is somewhat surprising that the shift in the composition of the association at 3 m did not appear in the statistical analyses. The explanation for this failure may lie in our reliance on imaging flow cytometry. While the system is quick and versatile, it does have some limitations. The magnifications used are relatively low, making it difficult to distinguish between small species of similar size and shape. The situation can be made worse by a reliance on the optical filters to sort the images—the algorithms used by the instrument sometimes place images into the wrong category. It is possible that some of the filamentous forms that dominate the association at 3 m were improperly classified and the relative proportions in these samples are incorrect. This is a consistent problem throughout the project. It is also possible that we are simply missing the important forms. Because of the limitations of the optics, particles with dimensions less than 4 μm are not included in the counts. The source of the

chlorophyll *b* signal may be included in this group instead of one of the filamentous forms. We are investigating this possibility as well. It should be noted that the deep chlorophyll layer and chlorophyll *b* signal had returned by May 30, 2018 (data not shown).

The development of the new association in the upper 2 m beginning about two weeks after the passage of Irma may be in response to mixing caused by the hurricane. The mixing would have brought nutrient enriched waters from the hypolimnion into the epilimnion, mimicking a turnover event; similar effects were seen by Gierach et al. (2009) in a study of the passage of Hurricane Katrina over the Gulf of Mexico. Note that only the upper 3–3.5 m were involved in the mixing, and that the lake as a whole did not turn over until early December, about the time Lake Louise usually turns over. The lower water temperatures accompanying the beginning of fall may have played a role in determining the nature of the phytoplankton bloom. The composition of the association is similar to the composition of early season blooms, when nutrient levels are high, water temperatures are low, and thermal stratification has not fully developed. Additional information on the temperature and nutrient responses of the species involved is necessary to disentangle the two effects.

CONCLUSIONS

The passage of Hurricane Irma over Lake Louise directly changed the character of the phytoplankton in the lake through the combined processes of washout resulting from increased rainfall and turbulent mixing resulting from sustained strong winds. The effects of turbulent mixing were ameliorated to some degree by the small size and the depth of the lake. However, mixing did result in the premature loss of the deep chlorophyll layer and the development of a strong fall bloom. The impacts of the hurricane remained evident until the onset of cooler temperatures and isothermal conditions in early December.

ACKNOWLEDGEMENTS

This work was funded, in part, by Marine Microalgae Research Associates LLC, Valdosta Georgia, and by grants from the Major Equipment Scientific Equipment Funding Pool at Valdosta State University.

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