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Letter

Subtropical Freshwater Cyanobacterial Blooms as Hydrogen Peroxide Hot Spots

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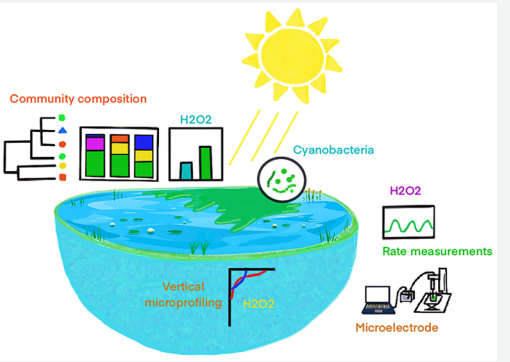
ABSTRACT: In aquatic environments, chemical and biological processes represent major sources of reactive oxygen species (ROS) such as hydrogen peroxide. Diurnal patterns of hydrogen peroxide in surface water may suggest photochemical processes affect ROS dynamics. We hypothesized that thin surface hydrogen peroxide maxima could be detected through millimeter-scale depth profiling. These maxima were previously overlooked because they cannot be detected using standard surface water sampling techniques. Combined field and laboratory experiments demonstrated that cyanobacterial blooms could create extremely high concentrations of hydrogen peroxide in a thin layer of surface water (5−60 mm). Hydrogen peroxide concentrations were higher within surface scums of *Microcystis aeruginosa* than in areas without scum. The cyanobacterial scum increased the temperature of the ambient water, and hydrogen peroxide concentrations were higher at locations exposed to sunlight that at locations in the shade. We found that scum samples directly collected from the field could release hydrogen peroxide to the surrounding water when the biomass was exposed by the light, while 20 laboratory cultures tested did not. The production of hydrogen peroxide from cyanobacteria may depend on the physiological condition of cells. Overall, we identified thin surface water layers during subtropical freshwater cyanobacterial blooms as hydrogen peroxide hot spots.



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INTRODUCTION

In aquatic environments, photochemical and biological processes represent major sources of reactive oxygen species (ROS) such as hydrogen peroxide.[1−3] Diel patterns of hydrogen peroxide in surface water have been documented, suggesting that photochemical processes affect hydrogen peroxide concentrations.[4,5] Additionally, atmospheric wet deposition serves as another high-end source of hydrogen peroxide.[6−8] The photosynthetic production of hydrogen peroxide by cyanobacteria has been reported under laboratory conditions.[9,10] However, documentation of the environmental interaction between cyanobacterial blooms and naturally occurring hydrogen peroxide is strictly limited.[8,11]

Initially, we aimed to understand the ecological significance of the production of hydrogen peroxide by *Microcystis aeruginosa* in southwest Florida, which is a subtropical zone characterized by various factors that can potentially enhance hydrogen peroxide production, such as strong sunlight, high organic matter content, warm temperatures, and heavy precipitation during the rainy season.[8] Through our pilot research, we hypothesized that thin surface hydrogen peroxide maxima could be detected through millimeter-scale hydrogen peroxide depth profiling. These maxima may have been overlooked in past research because they cannot be detected using standard surface water sampling techniques. To see if the maxima occur universally, we then took in situ measurements from a variety of water bodies. We combined field and laboratory experiments using fresh biomass of cyanobacterial blooms to examine if cyanobacterial blooms could create an extremely high concentration of hydrogen peroxide in a thin layer of surface water and if sunlight enhances the process.

MATERIALS AND METHODS

Field Sites, Water Sample Collections, and Water Analysis. We examined seven surface water samples collected from oligotrophic to hypertrophic water bodies in southwest Florida in 2017 and 2018 (Figure 1). Hydrogen peroxide concentrations were determined from the thin surface layer (5−60 mm) of four lakes. Vertical water column samples (0−1.5 m) were collected using a Van Dorn water sampler. Physiochemical parameter, chlorophyll *a*, total iron, and nutrient analyses were performed as described previously.[8]

Quantification of Hydrogen Peroxide Using a Hydrogen Peroxide Microsensor. This study utilized a fast response amperometric 250 μm diameter tip hydrogen peroxide microelectrode with a built-in reference electrode

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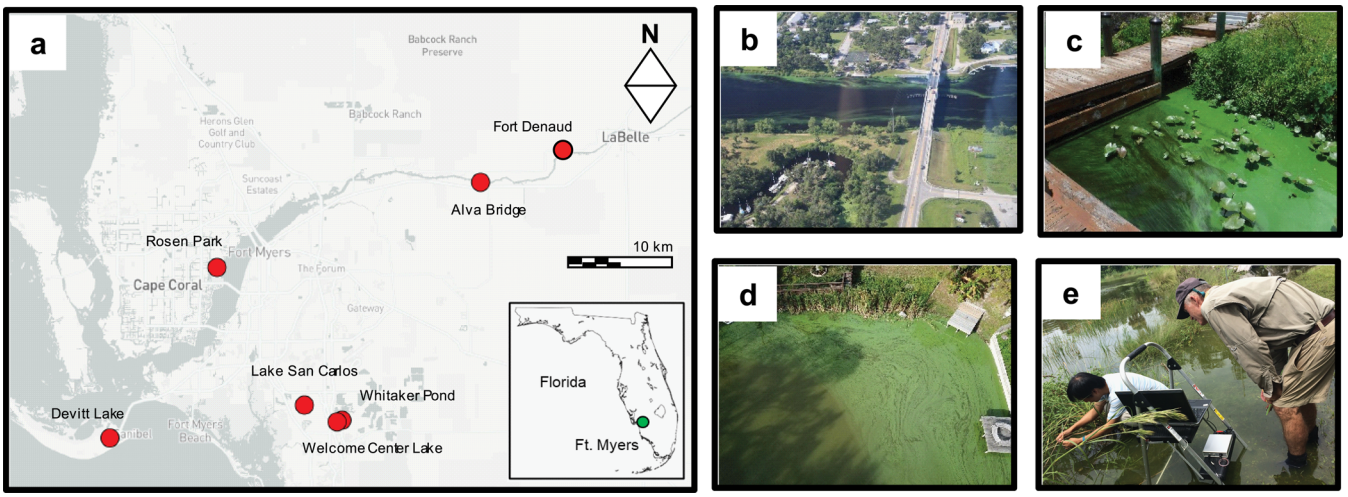

Figure 1. Field study. (a) Map of sampling events: Lake San Carlos, Fort Myers, Devitt Lake, Sanibel Island, Welcome Center Lake, Whitaker Pond at the Florida Gulf Coast University campus, and the Caloosahatchee River at Alva Bridge, Fort Denaud Bridge, and Rosen Park. (b) Aerial image of the 2018 Caloosahatchee River algal bloom (credit John Cassani). (c) Bloom at Alva Bridge. (d) Bloom in Lake San Carlos (credit Brett Bleiweiss). (e) Direct hydrogen peroxide measurement in Lake Devitt using a microelectrode. All blooms were caused by *Microcystis aeruginosa*.

(HP-250, Innovative Instruments) featuring a lower detection limit of 50 nM. The operation, background adjustment, and standard preparation were described previously.[8] At least six replicate readings were recorded and used to calculate the mean and standard deviation of each measurement. In this study, we partially used this microelectrode system on site to take in situ hydrogen peroxide measurements in a thin surface water layer (Figure 1). Hydrogen peroxide concentrations were determined from the thin surface layer (5−60 mm) of the four lakes at 5 mm intervals using a handmade stand connected with a 15 cm universal clear plastic ruler. Additionally, vertical water samples from two lakes were collected from the surface to the bottom at 50 cm intervals using a Van Dorn water sampler and a kayak at Lake San Carlos on October 31, 2017, and November 8, 2017, and Devitt Lake on August 28, 2017.

Temperature Measurements within and Adjacent to Cyanobacterial Surface Scums. When *Microcystis aeruginosa* was blooming in the tidal Caloosahatchee Estuary in July 2018, a sample was collected from the thick surface scum layer in a sterile 20 L carboy bottle. The sample was transported to an on-campus laboratory under ambient conditions (<2 h). Upon arrival, three 500 mL glass beakers were filled with bloom water, ensuring each beaker had a 20 mm thick cyanobacterial surface layer, while three other beakers were filled with deionized water as controls. All samples were placed in sunlight on a secluded fourth-floor balcony of a campus building. The air temperature and surface water temperature of both bloom and control samples were recorded between 2:00 and 6:00 p.m. for three consecutive days.

Light-Induced Production of Hydrogen Peroxide by Cyanobacteria. In the laboratory, light-induced hydrogen peroxide production patterns were examined for fresh bloom samples collected in Lake San Carlos, the Caloosahatchee River at the Alva Bridge site, and *Microcystis* sp. strain 22-6. Cyanobacterial samples were adjusted to a 15 mm thickness at the surface of a 60 mm diameter glass beaker. A Clark-type oxygen electrode microsensor (Unisense) was simultaneously used along with the hydrogen peroxide electrode. Photosynthetic active radiation (PAR) was measured using a LI-190R Quantum sensor connected to a model LI-1400 data logger (LI-COR). Microelectrode measurements were repeated several times at <10 min intervals at room temperature (24 °C) in the presence of light (160−200 μmol s^{-1} m^{-2}). The production and decay of hydrogen peroxide were estimated on the basis of the slopes of the voltage reading (picoamperes) and time (seconds) with a conversion factor from a linear regression equation of a standard curve.

To examine if hydrogen peroxide production patterns vary among cyanobacterial species, 20 additional algal cultures were used to test light-induced hydrogen peroxide production (Supporting Information).

High-Throughput Amplicon Sequencing of the Cyanobacterial 23S rRNA Gene and Eukaryotic Chloroplast 23S rRNA Gene. Bloom-forming algal communities were examined using universal PCR primers amplifying a 23S rRNA gene plastid marker in eukaryotic algae and a large subunit rRNA of cyanobacteria.[12,13] To identify the dominant cyanobacterial species in Lake San Carlos and Devitt Lake blooms, 50 mL bloomed-algal biomass samples were collected from each lake. Algal samples were filtered (0.22 μm) and stored at −20 °C before being analyzed. DNA was extracted using a King Fisher system, and amplicon sequences were determined by using Illumina MiSeq (Illumina) as described previously.[14] Further data analysis and phylogenetic analysis were performed as previously described.[14] High-throughput amplicon sequence data sets were deposited in GenBank under BioProject PRJNA497120.

RESULTS AND DISCUSSION

Regular-Scale Vertical Measurements of Hydrogen Peroxide Concentrations. In three vertical depth profiles in two shallow small lakes (Table S1), gradients of hydrogen peroxide concentrations were observed with the highest hydrogen peroxide levels at the surface (1.71−3.55 μM) and a gradual decrease with depth. These gradients were in accordance with previously documented vertical profiles of hydrogen peroxide in lake water.[15] High Chl *a* concentrations were recorded throughout the water columns, and the highest concentrations were detected in the heavy November bloom at Lake San Carlos (Chl *a*, 814 μg/L). Previously documented bottom water hydrogen peroxide peaks associated with

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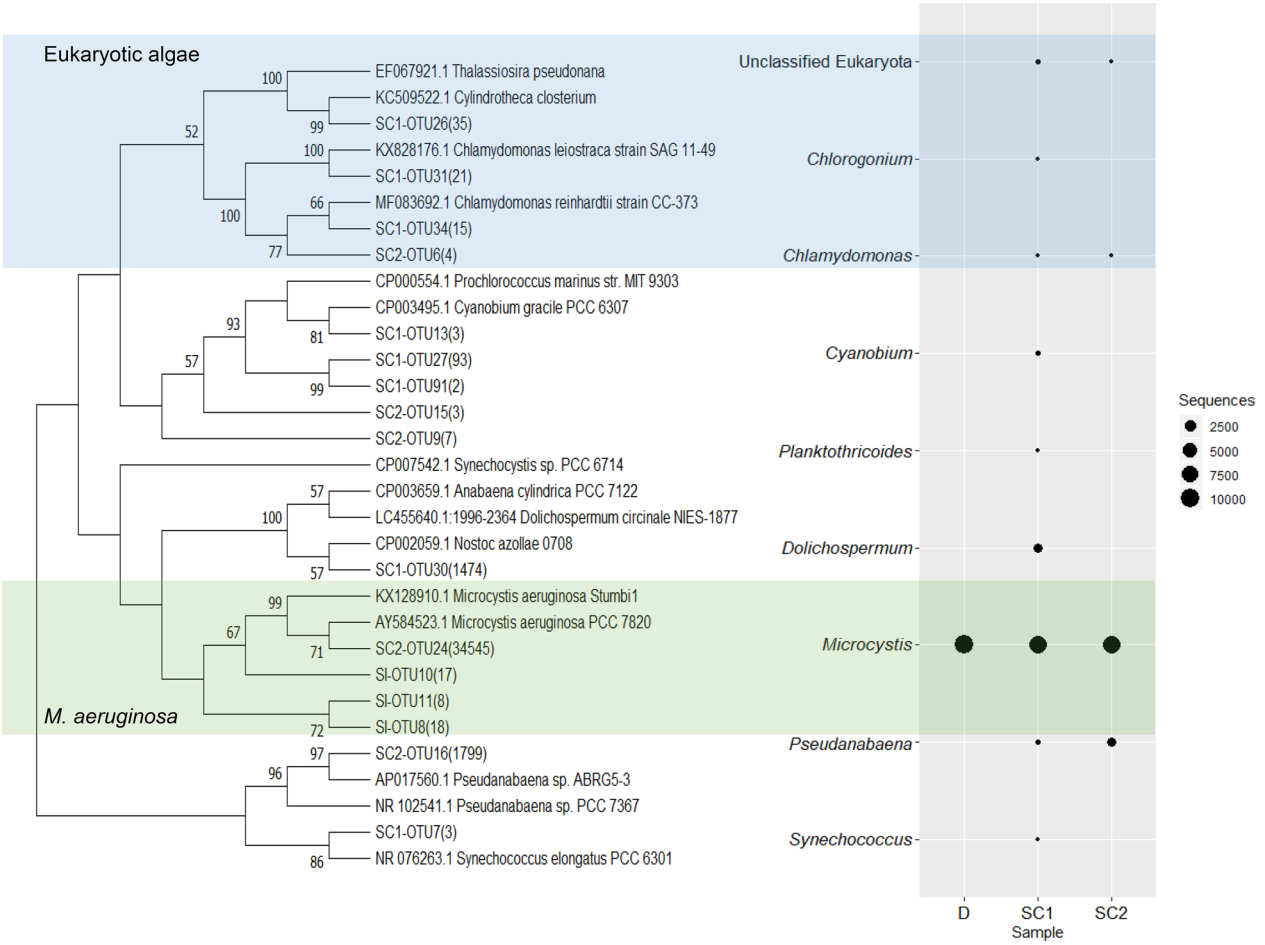

Figure 2. Phytoplankton community compositions determined by 23S rRNA gene amplicon sequencing. Relative abundance of high-throughput sequencing reads: surface scum samples from Devitt Lake (D) and Lake San Carlos in October (SC1) and November (SC2). Neighbor-joining cladogram of sequenced 23S rRNA operational taxonomic units (OTUs) from each sample and reference sequences. Bootstrap values of >50% are shown at each node. Numbers in parentheses indicate the numbers of OTUs found. Highlighted sections show clusters of *M. aeruginosa* and eukaryotic algae.

sediment microbial communities[15] were not found in this study. Conversely, the concentration of hydrogen peroxide was lowest at the greatest water depth (1.5−2 m, 0.24−0.86 μM).

Identification of Algal Communities. To identify major agents of observed blooms, molecular characterization of cyanobacteria and eukaryotic algae communities was carried out using 23S rRNA gene amplicon sequencing.[13] In Lake San Carlos, there was a dominance of cyanobacteria (99% of the total community) of the genera *Microcystis* (85%), *Dolichospermum* (14%), and *Cyanobium* (0.87%) (Figure 2). Two eukaryotes, *Chlamydomonas* (0.09%) and *Chlorogonium* (0.19%), were detected as minor fractions. In the following month of November, 86.9% of sequences were identified as *M. aeruginosa* followed by *Pseudanabaena* (13.7%), while <0.1% of sequences were identified as *Chlamydomonas*. *M. aeruginosa* exclusively dominated Devitt Lake (>99%). Neighbor-joining analysis demonstrated the affiliation of major OTUs within the cluster of *M. aeruginosa* with 99% of the bootstrap value. Altogether, we identified that the major agent of these blooms was *M. aeruginosa*.

Millimeter-Scale Vertical Measurements of Hydrogen Peroxide. Millimeter-scale on-site profiles indicated that the hydrogen peroxide level in a thin layer of surface water is extremely high and levels declined steeply with depth at the millimeter level. The concentrations of hydrogen peroxide were extremely high in the thin surface layer in the *M. aeruginosa* bloom in Lake San Carlos [15.97 ± 0.17 μM (n = 6)] and moderately high in Devitt Lake [2.44 ± 0.13 μM (n = 6)] (Figure 3). The hydrogen peroxide level was much lower in nonblooming oligotrophic waters, Whitaker Pond [0.9 ± 0.04 μM (n = 6)] and Welcome Center Lake [0.8 ± 0.03 μM (n = 6)]. It should be noted that this thin surface layer hydrogen peroxide maximum is undetectable in regular surface water grab sampling from shore or boat sampling using a bucket or Van Dorn water sampler and was not noticed in previous research. Therefore, we are the first to document the presence of a thin surface layer with a high hydrogen peroxide concentration in the water column.

Impact of Visible Surface Scums on Hydrogen Peroxide Levels in the Thin Surface Water. The impact of the presence and absence of surface scums on the production of hydrogen peroxide was examined in lakes and a river (Figure 4). At Devitt Lake, the hydrogen peroxide level was 20% higher within *M. aeruginosa* surface scums [3.83 ± 0.25 μM (n = 6)] than outside of scums [3.19 ± 0.32 μM (n = 6)] (Figure 4a). Similarly, at Rosen Park in the Caloosahatchee River, we found the hydrogen peroxide concentration was 17.3 times higher [10.9 ± 0.7 μM (n = 7)] in bloom surface scum

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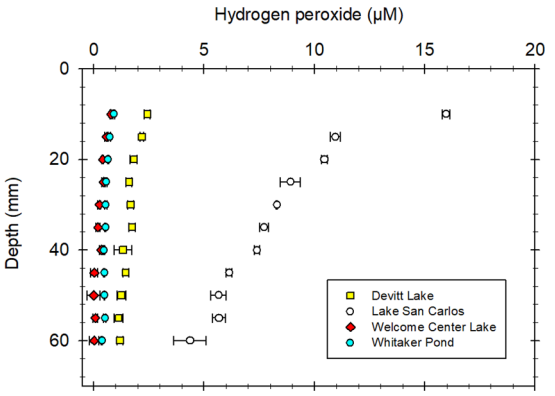

Figure 3. Depth profiles of thin surface lake water hydrogen peroxide concentrations. The profiles were obtained from Devitt Lake and Lake San Carlos under bloom conditions and Welcome Center Lake and Whitaker Pond without blooms. Data represent means and standard deviations (n = 6). Some error bars are smaller than the symbols.

than in areas without surface scum [0.63 ± 0.07 μM (n = 7)] (Figure 4b). In the next step, the impact of the presence and absence of direct sunlight on surface scums on the production of hydrogen peroxide was examined at three different waters. Hydrogen peroxide concentrations were 66% higher in Devitt Lake in direct sunlight versus in the shade (Figure 4c). Similar data were obtained from Lake San Carlos and Fort Denaud (Figure 4d,e). Our data indicated spatial hydrogen peroxide patterns may be affected by the combined dynamics of irradiation and cyanobacterial blooms.

In the presence of sunlight, cyanobacterial blooms may locally increase surface water temperatures[16] due to light energy absorption via an array of photosynthetic and photoprotective pigments.[17−19] Our field data measured in Devitt Lake suggest that the blooming site had surface water temperatures [29.5 ± 0.71 °C, mean ± SD (n = 3)] higher than that of a nonblooming site [28.3 ± 0.56 °C (n = 3)]. To confirm this observation, we set up microcosms and found a significant difference (p < 0.001; t test) between the mean temperature of bloom scum samples [39.8 ± 2.2 °C (n = 3)] and the control water samples [35.3 ± 1.6 °C (n = 3)] under full mid-day sunlight. We attributed the significant temperature increase (4.5 °C) to cyanobacteria absorbing infrared radiation. The scum could also create some sort of inner filter effect that attenuates natural light penetration. This change in temperature may be ecologically significant because cyanobacteria can grow better in higher temperatures than other phytoplankton species, which will help them outcompete eukaryotic counterparts.[18,20,21]

Light-Induced Production of Hydrogen Peroxide by Cyanobacteria. To confirm the conducted field studies demonstrating *M. aeruginosa* plays a key role in the formation of extremely high hydrogen peroxide concentrations in surface lake water, we examined hydrogen peroxide production and decay from light-exposed cyanobacterial scums and cultures under laboratory conditions. Light-induced hydrogen peroxide production was observed in freshly collected cyanobacterial scums (Figure 5). Hydrogen peroxide production and decay rates showed a large difference between the two samples. The production and decay rates of the Lake San Carlos sample were 1.12 ± 0.96 μmol/s (n = 8) and 1.49 ± 0.89 μmol/s (n = 4), respectively (Figure 5a). The production and decay rates of the Alva Bridge sample were 4.1 ± 5.2 nmol/s (n = 3) and 4.0 ± 0.55 nmol/s (n = 4), respectively (Figure 5b). These values were smaller than that of the previously reported Mehler reaction in which 10 μM hydrogen peroxide was produced within 0.5 s.[7,22,23] The reaction synchronized with oxygen production [0.15 ± 0.05 μmol/s (n = 5)], suggesting that hydrogen peroxide production occurs (5.6 nmol/s) in the photosynthetic reaction as previously reported[10,24] (Figure 5c). However, light-induced hydrogen peroxide production was not observed from laboratory-cultured *Microcystis* sp. strain 22-6 (Figure 5d). To confirm this result, 20 additional algal cultures (19 cyanobacteria and one eukaryotic alga) were also tested to examine their light-induced hydrogen peroxide production; however, none showed evidence of light-induced immediate hydrogen peroxide release (Table S2). Three tested media showed different hydrogen peroxide concentrations, and the MA medium had the highest average concentration of 64.8 μM. The difference in culture media influenced hydrogen peroxide production more than algal species. It should be noted that although the production of ROS from culture media could directly influence the culturability of various microorganisms,[25] the report of hydrogen peroxide levels in culture media is limited.

The differential hydrogen peroxide responses induced by light are enigmatic and partially understood by the difference in the growth phase of marine algae[25] and taxonomic differences.[23] Hydrogen peroxide production has been

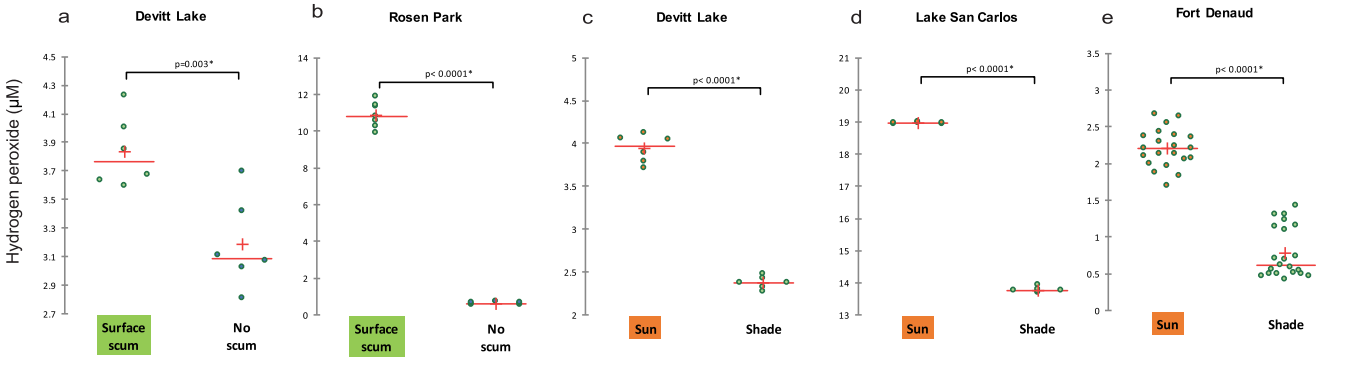

Figure 4. Effect of the presence and absence of cyanobacterial surface scums and direct sunlight on cyanobacterial blooms for thin surface hydrogen peroxide concentrations: (a) Devitt Lake, (b) Rosen Park (Caloosahatchee River), (c) Devitt Lake, (d) Lake San Carlos, and (e) Fort Denaud (Caloosahatchee River). All algal communities were dominated by *M. aeruginosa*. Data are shown as scattergrams. Crosses show the average. Bars show the median. Each dot shows measurement replication. Data show one of these reproducible field measurements.

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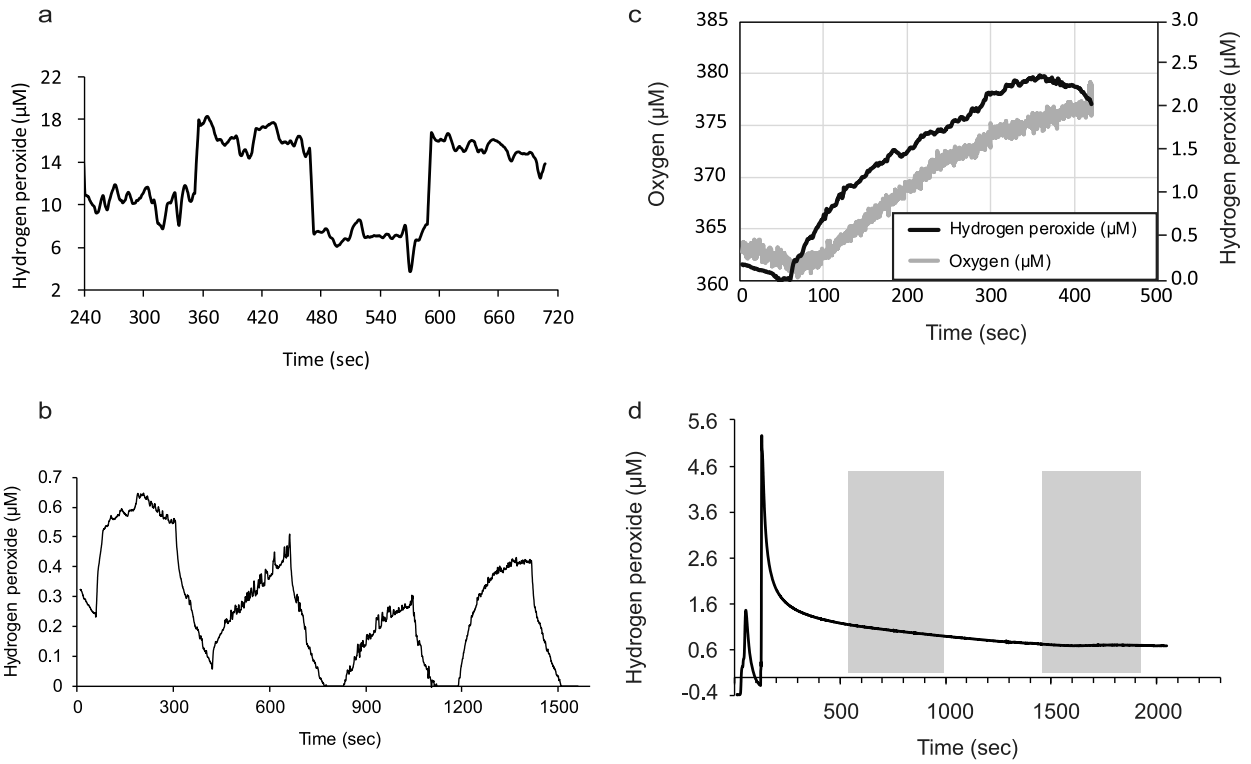

Figure 5. Light-induced production of hydrogen peroxide from the surface scum sample and cultured sample of *Microcystis*. (a) Samples were collected from Lake San Carlos. Light and dark conditions were made with 2 min intervals. (b) Samples were collected from the Caloosahatchee River at the Alva Bridge. Light and dark conditions were made with 6 min intervals. (c) Surface scum sample of *M. aeruginosa* from the Alva Bridge. The culture was exposed to light illumination for 6 min. An oxygen profile was simultaneously collected. (d) *Microcystis* sp. strain 22-6. The concentration of hydrogen peroxide from the *Microcystis* culture was assessed within 8 min intervals for two time series, in the presence and absence of light irradiation. The sensor response indicated by a high spike occurred when the sensor was dipped into the culture. The gray color indicates the time without light. Data show one of these reproducible measurements.

reported,[10] and the study found that >50% of the 38 cyanobacterial cultures tested produced excess hydrogen peroxide when exposed to white light. Aged cyanobacterial scums (2 weeks after sampling) also did not show instant light-induced hydrogen peroxide production, although cells were still viable and seemingly healthy. We anticipate that some unidentified factors may exist and that a lack of awareness of these factors greatly predisposed the conclusions of past studies.[5] An unidentified agent could exist in natural freshwater under the cyanobacterial bloom conditions, which was missing in culture conditions, accounting for the different results. Alternatively, cyanobacterial scums that are exposed to high irradiance in direct sunlight in subtropical freshwater lakes may damage cellular ROS scavenging systems, and a portion of the produced hydrogen peroxide might be released extracellularly.[23,26] This leakage may help to reduce ROS levels within the cell, and a loose cell membrane system could explain why cyanobacteria are more sensitive to artificial hydrogen peroxide treatment when compared to other eukaryotic algal species.[23] Certain cyanobacterial bloom taxa such as *Microcystis* produce microcystins that have a protein-modulating role and hence inactivate hydrogen peroxide under high-light and -oxidative stress conditions,[21,27] thereby providing intracellular protection from this potent ROS. The ecological significance of the high observed level of hydrogen peroxide production has not yet been fully elucidated; however, it may interact with successful bloom formations,[28] cyanotoxin dynamics,[21,27] the selection of phycosphere bacteria,[29] and competition and signaling with other bacteria, viruses, and eukaryotes.[30]

In conclusion, our study focused on the production of hydrogen peroxide from cyanobacterial scum at a millimeter-scale resolution. Combined field and laboratory experiments using fresh biomass of cyanobacterial blooms demonstrated that cyanobacterial blooms could create an extremely high level of hydrogen peroxide in a thin layer of surface water and that the sunlight enhances the process. The scum of cyanobacteria also absorbed the heat energy of the sun and increased the temperature of the ambient water. We found that some *Microcystis* scum samples directly collected from the field released hydrogen peroxide to the surrounding water while laboratory cultures did not. The production of hydrogen peroxide from cyanobacteria may depend on the functional conditions of cells and environmental factors. Further studies are required to identify the main causes of variability found in this research.

■ ASSOCIATED CONTENT

Supporting Information

The Supporting Information is available free of charge at https://pubs.acs.org/doi/10.1021/acs.estlett.1c00577.

Tables S1 and S2 and Materials and Methods (PDF)

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Notes

The authors declare no competing financial interest.

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■ REFERENCES

(1) Cooper, W. J.; Zika, R. G.; Petasne, R. G.; Plane, J. M. Photochemical formation of hydrogen peroxide in natural waters exposed to sunlight. *Environ. Sci. Technol.* **1988**, *22* (10), 1156−1160.

(2) Petasne, R. G.; Zika, R. G. Hydrogen peroxide lifetimes in south Florida coastal and offshore waters. *Mar. Chem.* **1997**, *56* (3−4), 215−225.

(3) Scully, N.; McQueen, D.; Lean, D. Hydrogen peroxide formation: the interaction of ultraviolet radiation and dissolved organic carbon in lake waters along a 43−75 N gradient. *Limnol. Oceanogr.* **1996**, *41* (3), 540−548.

(4) Mostofa, K. M.; Liu, C.-Q.; Sakugawa, H.; Vione, D.; Minakata, D.; Wu, F. Photoinduced and microbial generation of hydrogen peroxide and organic peroxides in natural waters. In *Photobiogeochemistry of Organic Matter*; Allan, R., Förstner, U., Salomonas, W., Eds.; Springer: Berlin, 2013; pp 139−207.

(5) Roach, T.; Miller, R.; Aigner, S.; Kranner, I. Diurnal changes in the xanthophyll cycle pigments of freshwater algae correlate with the environmental hydrogen peroxide concentration rather than non-photochemical quenching. *Ann. Bot.* **2015**, *116* (4), 519−527.

(6) Cooper, W. J.; Saltzman, E. S.; Zika, R. G. The contribution of rainwater to variability in surface ocean hydrogen peroxide. *J. Geophys. Res.* **1987**, *92* (C3), 2970−2980.

(7) Kang, C.-M.; Han, J.-S.; Sunwoo, Y. Hydrogen peroxide concentrations in the ambient air of Seoul, Korea. *Atmos. Environ.* **2002**, *36* (35), 5509−5516.

(8) Ndungu, L. K.; Steele, J. H.; Hancock, T. L.; Bartleson, R. D.; Milbrandt, E. C.; Parsons, M. L.; Urakawa, H. Hydrogen peroxide measurements in subtropical aquatic systems and their implications for cyanobacterial blooms. *Ecological Engineering* **2019**, *138*, 444−453.

(9) Roncel, M.; Navarro, J. A.; De la Rosa, M. A. Coupling of solar energy to hydrogen peroxide production in the cyanobacterium *Anacystis nidulans*. *Appl. Environ. Microbiol.* **1989**, *55* (2), 483−487.

(10) Stevens, S., Jr; Patterson, C. P.; Myers, J. The production of hydrogen peroxide by blue-green algae: a survey 1. *J. Phycol.* **1973**, *9* (4), 427−430.

(11) Cory, R. M.; Davis, T. W.; Dick, G. J.; Johengen, T.; Denef, V. J.; Berry, M. A.; Page, S. E.; Watson, S. B.; Yuhas, K.; Kling, G. W. Seasonal dynamics in dissolved organic matter, hydrogen peroxide, and cyanobacterial blooms in Lake Erie. *Front. Mar. Sci.* **2016**, *3*, 54.

(12) Sherwood, A. R.; Presting, G. G. Universal primers amplify a 23S rDNA plastid marker in eukaryotic algae and cyanobacteria. *J. Phycol.* **2007**, *43* (3), 605−608.

(13) Steven, B.; McCann, S.; Ward, N. L. Pyrosequencing of plastid 23S rRNA genes reveals diverse and dynamic cyanobacterial and algal populations in two eutrophic lakes. *FEMS Microbiol. Ecol.* **2012**, *82* (3), 607−615.

(14) Hancock, T. L.; Blonder, S. L.; Bury, A. A.; Smolinski, R. A.; Parsons, M. L.; Robertson, A.; Urakawa, H. Succession pattern and phylotype analysis of microphytobenthic communities in a simulated oil spill seagrass mesocosm experiment. *Sci. Total Environ.* **2021**, *784*, 147053.

(15) Häkkinen, P. J.; Anesio, A. M.; Granéli, W. Hydrogen peroxide distribution, production, and decay in boreal lakes. *Can. J. Fish. Aquat. Sci.* **2004**, *61* (8), 1520−1527.

(16) Kahru, M.; Leppanen, J.-M.; Rud, O. Cyanobacterial blooms cause heating of the sea surface. *Mar. Ecol.: Prog. Ser.* **1993**, *101*, 1−7.

(17) Paerl, H. W.; Bland, P. T.; Bowles, N. D.; Haibach, M. E. Adaptation to high-intensity, low-wavelength light among surface blooms of the cyanobacterium *Microcystis aeruginosa*. *Appl. Environ. Microbiol.* **1985**, *49* (5), 1046−1052.

(18) Paerl, H. W.; Huisman, J. Blooms like it hot. *Science* **2008**, *320* (5872), 57−58.

(19) Paerl, H. W.; Tucker, J.; Bland, P. T. Carotenoid enhancement and its role in maintaining blue-green algal (*Microcystis aeruginosa*) surface blooms. *Limnol. Oceanogr.* **1983**, *28* (5), 847−857.

(20) Paerl, H. W.; Huisman, J. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Environ. Microbiol. Rep.* **2009**, *1* (1), 27−37.

(21) Paerl, H. W.; Otten, T. G. Blooms bite the hand that feeds them. *Science* **2013**, *342* (6157), 433−434.

(22) Asada, K. Production and action of active oxygen species in photosynthetic tissues. In *Causes of photooxidative stress and amelioration of defense systems in plants*; CRC Press: Boca Raton, FL, 1994; pp 77−104.

(23) Drábková, M.; Admiraal, W.; Maršálek, B. Combined exposure to hydrogen peroxide and light selective effects on cyanobacteria, green algae, and diatoms. *Environ. Sci. Technol.* **2007**, *41* (1), 309−314.

(24) Collén, J.; Del Rio, M. J.; García-Reina, G.; Pedersén, M. Photosynthetic production of hydrogen peroxide by *Ulva rigida* C. Ag. (Chlorophyta). *Planta* **1995**, *196* (2), 225−230.

(25) Morris, J. J.; Johnson, Z. I.; Szul, M. J.; Keller, M.; Zinser, E. R. Dependence of the cyanobacterium *Prochlorococcus* on hydrogen peroxide scavenging microbes for growth at the ocean's surface. *PLoS One* **2011**, *6* (2), No. e16805.
(26) Zámocký, M.; Gasselhuber, B.; Furtmüller, P. G.; Obinger, C. Molecular evolution of hydrogen peroxide degrading enzymes. *Arch. Biochem. Biophys.* **2012**, *525* (2), 131−144.
(27) Zilliges, Y.; Kehr, J.-C.; Meissner, S.; Ishida, K.; Mikkat, S.; Hagemann, M.; Kaplan, A.; Boerner, T.; Dittmann, E. The cyanobacterial hepatotoxin microcystin binds to proteins and increases the fitness of Microcystis under oxidative stress conditions. *PLoS One* **2011**, *6* (3), No. e17615.
(28) Eloff, J.; Steinitz, Y.; Shilo, M. Photooxidation of cyanobacteria in natural conditions. *Appl. Environ. Microbiol.* **1976**, *31* (1), 119−126.
(29) Kim, M.; Shin, B.; Lee, J.; Park, H. Y.; Park, W. Culture-independent and culture-dependent analyses of the bacterial community in the phycosphere of cyanobloom-forming *Microcystis aeruginosa*. *Sci. Rep.* **2019**, *9* (1), 20416.
(30) Van Wichelen, J.; Vanormelingen, P.; Codd, G. A.; Vyverman, W. The common bloom-forming cyanobacterium *Microcystis* is prone to a wide array of microbial antagonists. *Harmful Algae* **2016**, *55*, 97−111.

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