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Role of Suspended Sediments and Mixing in Reducing Photoinhibition in the Bloom-Forming Cyanobacterium *Microcystis*

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ABSTRACT

Toxic cyanobacterial blooms are becoming a global problem. Previous research of cyanobacterial bloom development has examined how high nutrient concentrations promote cyanobacteria dominance, and how positive buoyancy provides an ecological advantage over sinking phytoplankton. Tributaries responsible for loading nutrients into lakes often simultaneously contribute high concentrations of suspended sediments. High concentrations of suspended sediments may also influence blooms by affecting the ambient light climate, reducing photodamage, and increasing the efficiency of photosynthesis. We examined the effects of sediments and vertical mixing in potentially reducing photodamage to *Microcystis* by measuring photosynthetic parameters and pigment content of *Microcystis* in western Lake Erie during the 2008 bloom and in laboratory experiments. Photosynthetic efficiency increased with increasing sediment concentration in the lake and laboratory experiment. Content of photo-protective carotenoid pigments per dry weight decreased with increasing sediment concentrations, while the light-harvesting pigments, chl *a* and phycocyanin, increased with sediments. These results indicate that suspended sediments reduce photoinhibition for *Microcystis*. Further, photosynthetic damage was higher when *Microcystis* was concentrated on the surface compared to a mixed water column. Measurements of *Microcystis* abundance and light were also recorded, in addition to photosynthetic measurements. Greatest *Microcystis* abundances in Lake Erie were recorded during light-limiting conditions, which offer *Microcystis* both physiological and ecological benefits by reducing photoinhibition and increasing *Microcystis*' advantage in light competition via buoyancy. Efforts to reduce cyanobacterial blooms may include reducing suspended sediments loads in combination with reducing nutrient loading.

Keywords: Chlorophyll Fluorescence; Cyanobacteria; Harmful Algae Bloom; Lake Erie; *Microcystis*; Suspended Sediments

1. Introduction

High biomasses of cyanobacteria, often called "blooms", are one of the foremost problems facing the protection of water quality [1]. Cyanobacterial blooms are a concern due to their toxins that affect aquatic animals, livestock, and humans [2], and negatively impact local economies [3]. Cyanobacterial blooms have become a global problem as a result of excess inputs of anthropogenic nutriaents [4]. Research devoted to the development of cyanobacterial blooms has been focused on high nutrient concentration, especially phosphorus (P) and nitrogen (N) [5,6], low N-to-P ratios [7], water column stability [8,9], global climate change [10,11], and *Dreissena* mussel selective rejection [12]. Tributaries that are often responsible for high nutrient concentrations in the adjacent waters of lakes may simultaneously contribute high concentrations of suspended sediments [13,14]. The impacts of high suspended sediments on zooplankton, fish, and benthic invertebrates is well known [15]. However, the effect of suspended sediments on cyanobacterial bloom development, specifically *Microcystis* spp., is less understood.

Suspended sediments increase the rate at which light is attenuated with depth in aquatic ecosystems, as does high phytoplankton abundance and dissolved organic compounds [16]. Light attenuation affects photosynthesis as phytoplankton acclimate to changes in light intensity in time scales of seconds to days by altering their pigment composition and photosynthetic rates [17]. High attenuation results in less phytoplankton biomass due to light-limited conditions [18], favoring cyanobacteria that can regulate their vertical position in the water column and remain in the photic zone. For example, the highly-buoyant cyanobacterium *Microcystis* [9] can accumulate

high biomasses at the surface of a lake (often called a "surface scum") during periods of calm winds, no precipitation, and high atmospheric pressure [19]. Surface scums can be exposed to high-light intensities for prolonged lengths of time, damaging photosynthetic machinery [20]. However, buoyancy only allows *Microcystis* to form surface scums when the upward migration rate exceeds the turbulent mixing of the water column [21]. Wind speeds greater than 3 $m \cdot s^{-1}$ will break up a surface scum [19,22,23] and also circulate negatively buoyant phytoplankton species into the photic zone, thus negating the advantage of buoyancy regulation [9]. Previous research has shown that vertical mixing of the water column provides relief from high-light intensities by circulating *Microcystis* to deeper depths [24,25]. Furthermore, river-generated sediment plumes increase phytoplankton primary production [26]. However, there is currently a poor understanding of how the interaction between mixing of the water column and sediment plumes affects *Microcystis* bloom formation.

Suspended sediments and nutrient concentrations often co-vary in nearshore zones. In this manuscript we isolate the effects of suspended sediments from the effects of nutrients on the photosynthetic status of *Microcystis* blooms in western Lake Erie and in laboratory experiments. In another report, Chaffin *et al*. [27], analyzed the nutrient status of the samples collected for this manuscript and showed that all were N-replete while the majority of samples had a moderate P deficiency. Sediments are loaded into Lake Erie from the Maumee River at the rate of 800 tonnes per day [14] and the concentrations of suspended sediments decreases from nearshore to offshore [28], which makes western Lake Erie an ideal location to study the effects of suspended sediments on *Microcystis* bloom development. Furthermore, the spatial pattern of *Microcystis* blooms in western Lake Erie closely aligns with the Maumee River sediment plume [27]. We use physiological measurements (chlorophyll fluorescence and pigment content) as tools to determine *Microcystis*'s photosynthetic status in response to the difference of light intensity between sediment plume water and clear water, and between calm water and mixed water. We hypothesized that *Microcystis* surface scums will be more photo-inhibited than *Microcystis* in a mixed water column. We also hypothesized that high concentrations of suspended sediments not only give buoyant *Microcystis* an ecological advantage for light competition, but also create a more favorable light climate for photosynthesis, providing a physiological benefit.

2. Materials and Methods

2.1. Study Site

The Maumee River drains a large (16,376 km^2) agricultural (87.8%) watershed [29] that empties into the western corner of Lake Erie (**Figure 1**). The high sediment load from the river [14] results in a steep gradient of high suspended sediments and nutrient concentrations from the Maumee River mouth to offshore Western Lake Erie [28]. Further, the shallowness of Maumee Bay (<2 m) and the western basin (mean depth of 7.4 m) allows for frequent wind-induced sediment re-suspension from the lake bottom [30]. Although a persistent summer thermocline does not develop in western Lake Erie, diurnal stratification is common [31]. However on calm days diurnal thermal stratification (1˚C difference between surface to bottom water) can suppress water column mixing [32]. Longer calm periods may lead to episodic (>2˚C) thermal stratification for periods ranging from 2 to 10 days [33]. *Microcystis* has an ecological advantage during the periods of stratification [9], but also is exposed to high-light intensity that may cause photoinhibition.

Microcystis spp. blooms have become an annual occurrence in western Lake Erie in recent years [34]. The spatial pattern of the blooms closely coincides with the near-shore suspended sediment plume [27,28], which suggests conditions in the plume promote *Microcystis* blooms. In the sediment plumes total P can reach concentrations greater than 5 $\mu mol \cdot L^{-1}$ and secchi disk depths are less than 50 cm due to high suspended sediments [27].

The light attenuation coefficient (k_d) was used as a proxy for suspended sediments. Both suspended sediments and phytoplankton can influence the k_d measurements. In Maumee Bay and western Lake Erie, however, suspended inorganic particles are the major factor in reducing water clarity [28,30]. Past measurements of suspended sediments (as non-volatile suspended solids (NVSS)) at our sample sites indicate that suspended sediments can be predicted from k_d ($NVSS\ mg \cdot L^{-1} = (12.936 \times k_d) - 11.244$; $N = 52$, $p < 0.001$, $r^2 = 0.87$, Bridgeman unpublished data). There was no relationship between k_d and chlorophyll *a* ($p = 0.671$, $r^2 = 0.004$, Bridgeman unpublished data). Therefore, we use k_d as an index of suspended sediment concentration.

2.2. Limnological Measurements and *Microcystis* Collection

In this report, we refer to the *Microcystis* spp. community collectively as *Microcystis*. *Microcystis aeruginosa* makes up the majority of the *Microcystis* population in Lake Erie, but other species may be present [35]. Collections and measurements were made at six sites along an approximately 80 km route in western Lake Erie and in Maumee Bay (**Figure 1**) on ten dates from 7 July to 25 September 2008, approximately once every 14 days. All

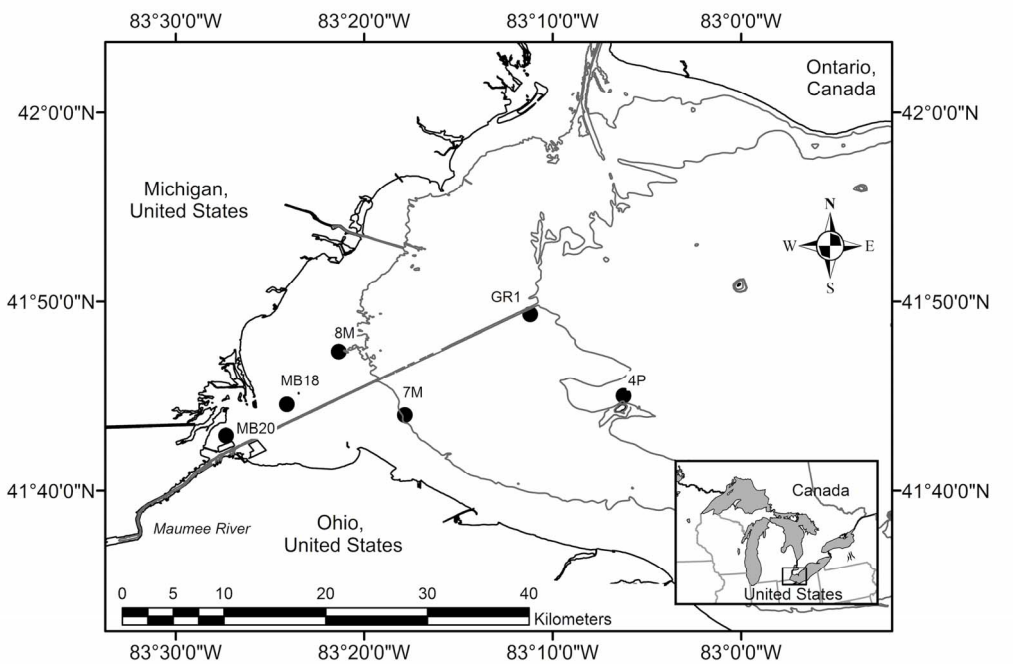

Figure 1. Sample locations in western Lake Erie. Contour lines are 5 meters and 9 meters. Site GR1 is located near the end of a dredged shipping channel.

collections and field measurements were recorded between 10:00 am to 3:00 pm on full-sun days. At each site, *Microcystis* abundance was estimated by the biovolume retained in vertical plankton tow samples using a 112 μm mesh net as a part of a long-term study of *Microcystis* abundance in western Lake Erie [27]. For photosynthetic and pigment content measurements to be made in the laboratory, *Microcystis* was collected from the lake using a 64 μm net, which captures 99% of *Microcystis* cells [27]. The *Microcystis* collected was stored in dark polyethylene bottles at ambient lake temperature during transportation back to the laboratory. Depending on sample location, two to six hours passed between collection on the lake and laboratory analysis. Upon arriving at the laboratory, *Microcystis* was separated from other plankton via buoyancy separation in Imhoff cones [27] and examined for the presence of other phytoplankton species by microscopy. These separated net samples were nearly 100% *Microcystis*, with exception of a trace amount of *Anabaena* 24 July and 6 August.

Vertical profiles of water temperature, pH, and dissolved oxygen were recorded using a YSI #6600 probe (Yellow Springs Instruments, Yellow Springs, OH, USA). Wind speed and direction were measured approximately 2 m above the surface of the water using a hand-held anemometer (Kestrel #1000, Birmingham, MI, USA) integrated over 15 seconds. Underwater photon flux density PAR (Li-Cor # LI - 188B with spherical sensor, Lincoln, NE, USA) was recorded at every half-meter from surface to 2 meters and at every one-meter from 2 meters to 5 meters, or at quarter-meter intervals in highly turbid water. Light attenuation coefficients of PAR (k_d) were calculated as the linear regression slope of the natural log of PAR vs depth [16]. The depth of the photic zone was determined as the depth where light intensity was 1% of that surface light intensity. Vertical position of phytoplankton and *Microcystis* was determined by chl *a* and phycocyanin (PC) concentration from lake water collected at surface, 1 m, 3 m, and 5 m using a Van Dorn bottle (see methods below).

2.3. Photosynthetic Parameters of Lake Samples

In this section, we made photosynthetic measurements aboard the research vessel and collected samples for additional photosynthetic measurements to be made in the laboratory. Photosynthetic efficiency was measured as the quantum yield of photosystem II (PSII) electron transport (Φ_{et}). PSII is often the weak link of photosynthetic electron transport, as it is most vulnerable to light-induced damage, *i.e.* photoinhibition [36]. Φ_{et} naturally decreases with increased light intensity, but decreases in Φ_{et} at a given light intensity indicate either damage to PSII or post PSII electron transport, or photoprotective down-regulation of electron transport [37]. Φ_{et} is proportional to carbon fixation at a given light level [38]. Onboard, Φ_{et} of the whole phytoplankton community was measured on phytoplankton collected at the surface and at 1 m depth for sample dates after 24 July —when *Microcystis* was present. Water was collected

using a Van Dorn bottle, transferred to dark polyethylene bottles, and immediately filtered through Whatman GF/C filters or Fisher Brand G4 filters (1.2 μm pore sizes) [39] using low vacuum pressure (<10 cm Hg). Approximately 20 to 50 mL of water was used per filter. Filtering and measuring of Φ_{et} took place in the boat's cabin to avoid direct sunlight. The Φ_{et} of phytoplankton was determined within 60 seconds from collection, using an OS1-FL Opti-Sciences modulated fluorometer (Hudson, NH, USA).

In the laboratory, light-response (PI) curves and the maximal PSII quantum yield (F_v/F_m) measurements were made with *Microcystis* collected from the lake. PI curves were generated by measuring Φ_{et} at nine light intensities from 20 to 1640 μmol photons $m^{-2} \cdot s^{-1}$ using a Walz fluorometer (model PAM 101/103, Effeltrich, Germany) and light pulse provided by a Schott flash lamp (model KL1500, Elmsford, NY, USA) [40,41]. The relative electron transport rate (rETR) was calculated from Φ_{et} and light intensity [42]: rETR = Φ_{et} × PAR × absorbance constant, PAR is the light intensity, and 0.85 was assumed to be the absorbance constant. The PI curve data were fit to the equation of Zhang *et al*. [43], and then the maximum rETR ($rETR_{max}$) was calculated. F_v/F_m was determined on separate samples that had been dark-acclimated for 30 minutes [42]. Decreases in dark F_v/F_m indicate damage to PSII. Even though the fluorometers used here were designed for plants, they have been used for cyanobacteria and have been shown to positively correlate with net photosynthesis of cyanobacteria [40]. For further description of the chlorophyll fluorescence parameters, please see Schreiber *et al*. [42], Campbell *et al*. [40], or Maxwell and Johnson [36].

2.4. Pigment Content of Lake Samples

To determine the ability of *Microcystis* to alter photosynthetic pigment content (also to assist in interrupting the photosynthetic fluorescence data, see Discussion), chl *a*, PC, and total carotenoid content were determined on *Microcystis* collected from the lake. *Microcystis* was separated in Imhoff cones (as above), concentrated, and then stored at –80˚C until analysis. Photosynthetic pigments were extracted from still-frozen *Microcystis*. Chl *a* and total carotenoid were extracted in dimethyl sulfoxide heated to 70˚C for 45 minutes, then centrifuged at 21,000 *g* for 10 minutes to remove debris. Chl *a* and total carotenoid were calculated from absorbance read using a UV - 1650 PC Shimadzu (Columbia, MD, USA) spectrophotometer [44]. Total carotenoid are presented relative to chl *a*. PC was extracted in 0.1 M sodium phosphate buffer pH 6.8 [45] with cells lysed by sonication (Bransonic #1510, Danbury, CT, USA) in an ice bath for 15 minutes. Samples were incubated at 4˚C for 60 minutes and then centrifuged for 10 minutes at 4600 g. PC fluorescence was recorded in a 10 - AU Turner Design fluorometer (Sunnyvale, CA, USA) with P/N 10 - 305 filters. PC was quantified using a standard curve of C-PC standards. Pigment content was corrected for dry weight (mg of pigment per g of dry weight tissue) determined by drying tissue until a constant weight at 70˚C. Dry weight was constant after 24 hours.

2.5. Laboratory Experiment

Suspended sediment concentration and nutrients often co-vary, and each may potentially affect photosynthesis. Water column mixing might also generate suspended sediments in shallow lakes, possibly producing another interaction effect. To isolate the effects of suspended sediments, nutrients, and mixing, a 2 × 2 × 2 × 2 factorial experiment was used to test the effects of nutrient concentration (low and high nutrients), suspended sediments (low and high), mixing (mixed or non-mixing), and sample depth (surface and at depth) on photosynthetic efficiency and pigments. All six treatment combinations (nutrient × suspended sediments × mixing) were randomized between trials and samples were collected from both depth in each trial. The experiment was replicated in three independent trials, with each treatment combination in each trial. Experimental tanks were constructed of 61 × 9 × 90 cm (36.5 L) polyethylene bins. Experiments were conducted in a greenhouse and exposed to natural sunlight (up to 1500 μmol photons $m^{-2} \cdot s^{-1}$) at ambient temperature (25˚C - 28˚C).

De-chlorinated water was used for this experiment. Mixing of the chamber was achieved using powerhead pumps (Aquatic gardens #601, San Diego CA, USA), so that the intake hose was placed at the bottom of the chamber and outflow just beneath the surface. Suspended sediments and nutrient treatments were chosen to reflect conditions in Maumee Bay (high sediments and high nutrients) and the center of the western basin (low sediments and low nutrients). Sieved (400 μm) Lake Erie top-layer (0 - 2 cm) sediments were added to bring the high sediment level to 30 NTU and low sediment level was 1 NTU. After sediments were added, sodium nitrate and sodium phosphate were added to bring the initial concentration up to 215 μmol N L^{-1} and 4.85 μmol P L^{-1} for the high nutrient and 43 μmol N L^{-1} and 0.97 μmol P L^{-1} for the low nutrient treatment, which reflect Maumee Bay and offshore western basin, respectively [27]. All other nutrients were at half concentration of the WC medium [46] and were the same among all experimental treatments. Cultures of *Microcystis* with a know chl *a* level were added so that each chamber had an initial chl *a* of 2.5 $\mu g \cdot L^{-1}$. *Microcystis* that was intended for the experiment were grown in separate liquid cultures with the nutrient concentration of the low treatment level for

two weeks before use in the experiment, to insure that internal phosphorus storage did not take place. This *Microcystis* was collected from Lake Erie during 2008 and cultured in laboratory.

Once treatments were set up and *Microcystis* added, 96 hours were allowed for growth. Following the 96 hours, samples were collected at the surface and at a depth of 70 cm. At 70 cm, light levels in the low-sediment treatment were approximately 20% of surface light (measured just beneath water surface). In the high-sediment treatment, light levels at 70 cm were <0.5% of the surface irradiance. At the end of the incubation period, 100 mL of water containing phytoplankton was filtered onto GF/F filters and Φ_{et} was measured within 60 seconds after collection. Separate samples were dark-acclimated for 30 minutes and F_v/F_m was determined. Φ_{et} and F_v/F_m were determined on filters as above. Chl *a* and total carotenoid concentration were determined on the filters as above. Photosynthetic measurements and light levels were recorded between 12:00 pm and 2:00 pm on sunny days.

2.6. Data Analysis

Past studies of cyanobacteria surface scum formation [19] classified the presence or absence of a surface scum based on visual observations of cyanobacterial colonies at the surface. In this study, we attempt to determine if a surface scum is present or absent based on quantitative measurements of wind speed, water temperature profiles, and phytoplankton vertical position (**Table 1**). Water temperature profiles are often used to separate the epilimnion from the hypolimnion; however, western Lake Erie usually lacks thermal stratification. The concentration of photosynthetic pigments (chl *a* and PC) at the surface relative to 1 meter allows determination of how much of the phytoplankton is concentrated at the surface (hence a surface scum). PC concentration gives insights to how much of the chl *a* is due to *Microcystis*. Samples that were collected when *Microcystis* was concentrated at the surface (low wind speed, high ratio of surface:1 meter pigment concentration) were classified as a "surface scum", while samples collected when *Microcystis* was circulated down to deeper depths (high wind speeds, low ratios of surface:1 meter pigments) were classified as "mixed".

To determine the effects of suspended sediments, vertical mixing of the water column, and depth on the phytoplankton community *in situ* Φ_{et} (n = 59), ANCOVA models were used to tests for the effects of depth (0 meter, 1 meter), mixing (surface scum or mixed), and suspended sediments (k_d, range: 0.44 to 4.83 m^{-1}) on Φ_{et}. Statistics were computed using PROC REG of the statistical software SAS® (v. 9.1, Cary, NC, USA) by converting our categorical factors (depth, mixing) into indicator variables [47] and k_d was the covariate. Significance was determined with $\alpha = 0.05$ for all tests.

The effect of suspended sediments on photosynthetic parameters measured from the PI curve, F_v/F_m, and pigments (chl *a*, PC, total carotenoid:chl *a*) was analyzed using linear regressions vs k_d. Surface scums and mixed samples were analyzed separately because ANCOVA test for parallel slopes indicated that slopes were not parallel for all parameters, hence not appropriate for ANCOVA test.

For the laboratory experiment, four-way ANOVAs were performed to test for the effect of mixing (mixed or calm), sediments (high or low), nutrients (high or low), and sample depth (surface and at depth) on Φ_{et}, F_v/F_m, and total carotenoid:chl *a*. Tukey HSD test was performed for multiple comparisons. PROC GLM of SAS® was used [47].

Table 1. Classification of "surface scum" or "mixed" conditions based on wind speed, chlorophyll (chl) *a*, and phycocyanin (PC) profiles. Surface:1 meter is the ratio of chl *a* or PC measured at the surface relative to chl *a* or PC measured at 1 meter. Values greater than 1 indicate that phytoplankton is concentrated at the surface. PC:Chl *a* is the ratio of PC to Chl *a* averaged across all six sites and depths. Values are averages (±SE) across 6 sample sites.

Surface Scum	July 24	August 6	August 12	August 21	September 1	September 25
	Mixed	Present	Present	Mixed	Mixed	Present
Wind Speed ($m \cdot s^{-1}$)	3.83 ± 0.38	1.28 ± 0.30	1.62 ± 0.25	3.90 ± 0.19	3.62 ± 0.29	1.73 ± 0.43
Surface Chl *a* ($\mu g \cdot L^{-1}$)	15.42 ± 10.4	38.47 ± 18.2	28.52 ± 15.6	15.24 ± 2.9	31.80 ± 2.1	227.17 ± 176.0
Surface Chl *a*:1 m Chl *a*	1.00 ± 0.05	1.81 ± 0.61	3.02 ± 1.96	0.99 ± 0.03	1.07 ± 0.07	6.95 ± 4.99
Surface PC ($\mu g \cdot L^{-1}$)	0.38 ± 0.2	35.25 ± 18.1	46.47 ± 39.9	14.63 ± 5.4	22.67 ± 3.5	89.04 ± 66.2
Surface PC:1 m PC	1.38 ± 0.21	5.31 ± 2.63	9.70 ± 8.11	1.51 ± 0.08	1.04 ± 0.08	17.41 ± 11.35
PC:Chl *a*	0.03 ± 0.01	0.47 ± 0.17	0.97 ± 0.45	0.67 ± 0.15	0.66 ± 0.07	0.33 ± 0.09

3. Results

3.1. Lake Properties

Figure 2 displays *Microcystis* abundance, light availability, and water temperature in western Lake Erie during 2008. *Microcystis* was absent from net tows until 24 July, and during this time the photic depth to lake depth ratio was greater than 0.5, indicating a high-light environment. Between 12 August and 21 August *Microcystis* biovolume retained in nets increased nearly four-fold and remained high for the rest of the summer. On 21 August through rest of summer, the photic depth to lake depth ratio was less than 0.2. Water temperature was between 22˚C and 26˚C during the *Microcystis* bloom. Dissolved oxygen (DO) ranged from 7.6 to 10.2 ($mg \cdot L^{-1}$) and pH from 8.0 to 8.6 from measurements at 1 meter depth at all sites and dates. DO and pH did not vary with depth except on 6 August when there was a 1.1 $mg \cdot L^{-1}$ difference in DO and 0.5 in pH between surface and near sediments at stratified sites. k_d was relatively low from June to mid August at all sites except MB20– the site closest to the Maumee River (**Figure 3**). Much higher k_d was recorded following mid August. On each sample date, there was a general pattern with highest k_d measured in Maumee Bay (sites MB20 and MB18), and lower k_d further from shore (sites GR1 and 4P).

Thermal stratification was only observed on 6 August, with 2˚C difference between the surface and bottom waters. Wind speed, chl *a*, and PC concentration were used to classify each sample date as surface scum or mixed

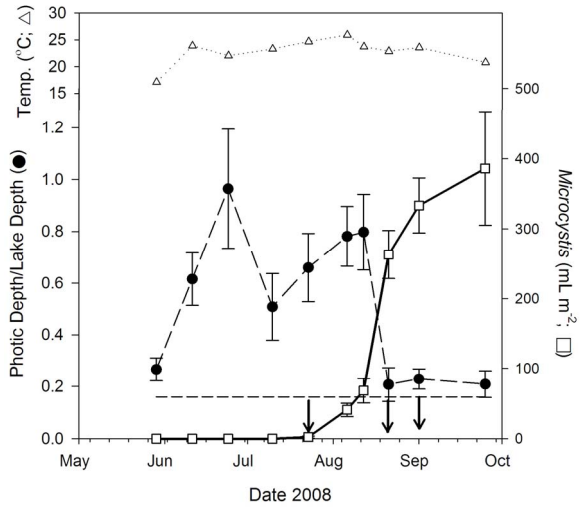

Figure 2. Light availability as photic depth/lake depth (dashed line; filled circles), temperature (dotted line; open triangles) and *Microcystis* biovolume (bold line; open squares) in western Lake Erie during 2008. Arrows represent sample dates with mixed conditions. The horizontal dashed line with no symbols corresponds to 0.16, the value that indicates light limitation of phytoplankton biomass [18]. Values are the mean (±SE) of six sites.

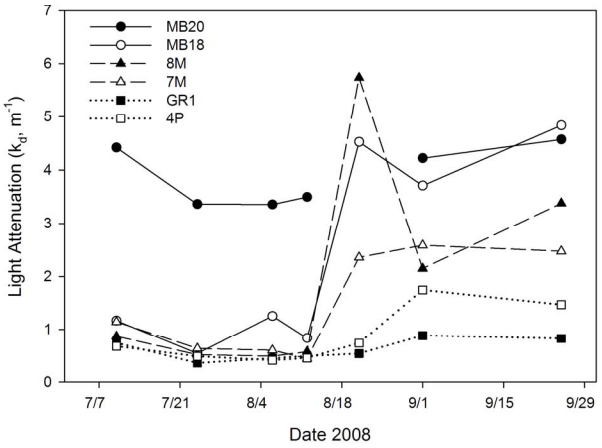

Figure 3. Light attenuation coefficients (k_d) recorded in western Lake Erie at 6 locations during summer 2008. Site MB20 was not sampled on 21 August.

(**Table 1**). *Microcystis* was concentrated as a surface scum on 6 August, 12 August, and 25 September. On these dates, wind speeds were less than 1.73 $m \cdot s^{-1}$, which allowed *Microcystis* to float and become concentrated on the surface as indicated by high surface chl *a* - 1 meter chl *a* ratios. Therefore, 6 August, 12 August, and 25 September were classified as "surface scum" dates. Wind speeds greater then 3.62 $m \cdot s^{-1}$ on 24 July, 21 August, and 1 September resulted in the *Microcystis* mixing down to deeper depths preventing a surface scum. Surface chl *a* and PC concentrations were nearly identical to chl *a* and PC concentrations measured at 1 meter and half-water-column-depth. 24 July, 21 August, and 1 September were classified at "mixed" dates because *Microcystis* was not concentrated at the surface. The low PC:Chl *a* ratio on 24 July would indicate that *Microcystis* was not the dominant phytoplankton on this date, however, large *Microcystis* colonies were visible and abundant enough on 24 July to collect with plankton net for measurements to be made in the laboratory.

3.2. Photosynthetic Parameters of Lake Samples

Φ_{et} increased linearly with increasing k_d ($p < 0.0001$) for samples collected from both the surface and 1 meter (**Figure 4**). Φ_{et} was greater at 1 meter than surface, due to lower light intensity at 1 meter. Mixing did not have a significant effect on Φ_{et} ($p = 0.345$), however, mixing increased Φ_{et} at higher k_d values compared to scum samples. Interactions were not significant ($p = 0.551$).

F_v/F_m of *Microcystis* was higher when collected when the lake was vertically mixed compared to surface scum (**Figure 5(a)**). k_d did not affect F_v/F_m for either mixed ($p = 0.11$; $r^2 = 0.196$) or surface scum ($p = 0.55$; $r^2 = 0.028$) samples. $rETR_{max}$ significantly ($p = 0.0076$; $r^2 = 0.460$) increased with k_d when collected during mixing, but was unaffected during surface scum ($p = 0.40$; $r^2 = 0.060$)

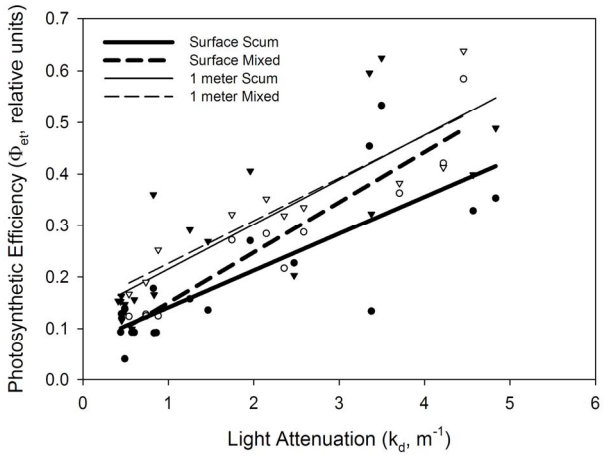

Figure 4. Photosynthetic efficiency (Φ_{et}) measured in western Lake Erie at the surface (thick lines, circles) and at 1 meter depth (thin lines, triangles), and either when surface scum was present (solid lines, filled symbols) or mixed (dashed lines, open symbols) as a function of light attenuation.

(**Figure 5(b)**). $rETR_{max}$ was greatest at light intensities less than 1044 µmol photons $m^{-2}\cdot s^{-1}$, thus high light caused photoinhibition, especially at low k_d. On average, $rETR_{max}$ for scum samples occurred at 348 µmol photons $m^{-2}\cdot s^{-1}$, while at 618 µmol photons $m^{-2}\cdot s^{-1}$ for mixed samples. The ability to maintain photosynthesis under high-light intensity is presented as rETR measured at 1044 µmol photons $m^{-2}\cdot s^{-1}$ (**Figure 5(c)**). Mixed samples had rETR at 1044 µmol photons $m^{-2}\cdot s^{-1}$ that significantly (p = 0.0009; r^2 = 0.676) increased with increasing k_d, while surface scum *Microcystis* were not affected (p = 0.77; r^2 = 0.007) by k_d.

3.3. Pigment Content of Lake Samples

ANCOVA analysis revealed that sample location did not significantly affect chl *a* (p = 0.81), PC (p = 0.12), and total carotenoid:chl *a* (p = 0.28). Regressions analysis revealed that the chl *a* linearly increased with increasing k_d (p = 0.0004, r^2 = 0.513), and PC increased linearly six-fold with increasing k_d (p = 0.0003, r^2 = 0.526) (**Figures 6(a)** and **(b)**). Total carotenoid:chl *a* decreased with increasing k_d (p = 0.0012, r^2 = 0.450) (**Figure 6(c)**). Total carotenoid content ranged from 2.11 $mg\cdot g^{-1}$ to 3.38 $mg\cdot g^{-1}$.

3.4. Labotory Experiment

The laboratory photosynthetic efficiency experiment produced results similar to and consistent with the lake study. Suspended sediments significantly (p < 0.0001) increased Φ_{et} for each treatment combination of mixing and depth (**Figure 7(a)**). Φ_{et} was significantly affected by the depth*mixing interaction (p < 0.0001). Nutrients

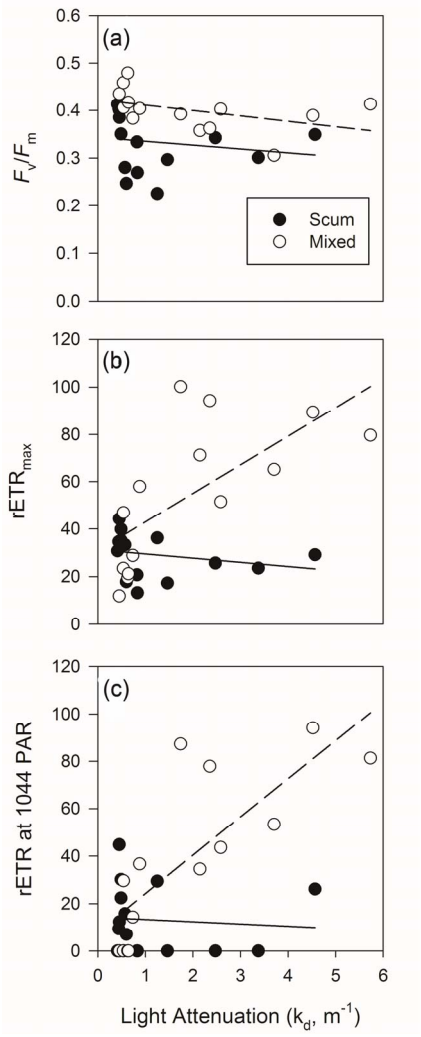

Figure 5. F_v/F_m (a), maximum relative electron transport rate ($rETR_{max}$; (b)), rETR at light intensity 1044 µmol photons $m^{-2}\cdot s^{-1}$ (c) from light response curves generated in the laboratory from *Microcystis* collected in western Lake Erie, as a function of in-lake light attenuation.

(high P and N vs low P and N) did not have a significant effect on Φ_{et}, and no other interactions were present (p > 0.5). Tukey test showed that Φ_{et} was statistically greater (p < 0.05) at depth than at the surface for the calm treatment among both suspended sediments levels.

F_v/F_m was significantly affected only by suspended sediments (p = 0.0004). F_v/F_m was greatest in the high-sediment treatment (**Figure 7(b)**). Depth, mixing, nutriaents, or their interactions did not significantly affect F_v/F_m (p > 0.1).

The total carotenoid:chl *a* ratio was only significantly affected by suspended sediments (p = 0.0007). Total carotenoid:chl was 0.412 ± 0.018 in the low-sediment treatment, and 0.318 ± 0.013 in the high-sediment treatment. Total carotenoid:chl *a* was not affected by any other factors or their interactions (p > 0.4).

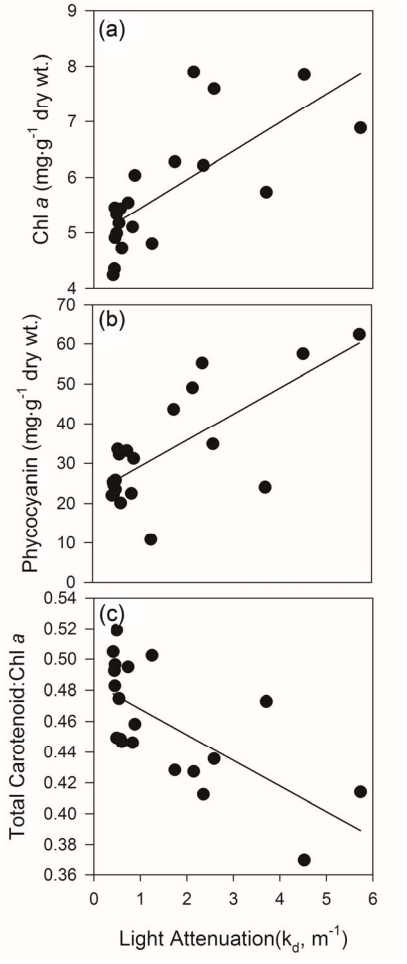

Figure 6. Chl *a* (a) and phycocyanin (b) content and the ratio of total carotenoid to chl *a* (c) of *Microcystis* collected in western Lake Erie as a function of light attenuation.

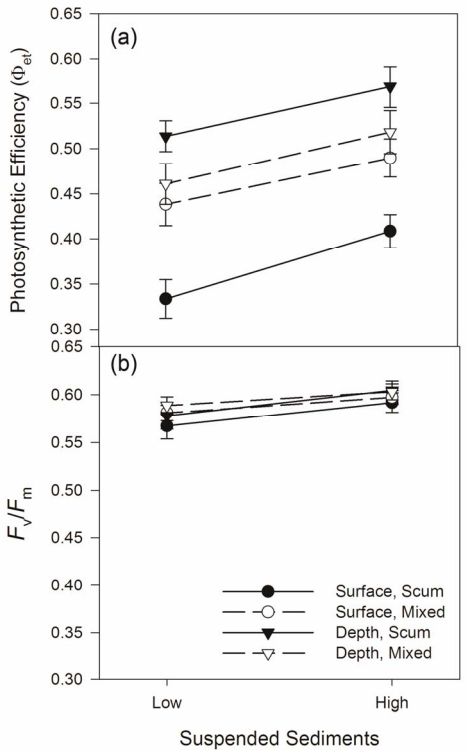

Figure 7. *In situ* quantum yield of photosystem II electron transport (Φ_{et}) of light-adapted samples (a), and F_v/F_m of dark-adapted samples (b) of Lake Erie *Microcystis* grown in laboratory conditions under natural sunlight intensities, high or low suspended sediments, and mixing or calm water.

4. Discussion

4.1. Sediment Plumes and Moderate Mixing Favor *Microcystis*

Our study conducted in western Lake Erie, which receives a heavy suspended sediment load from the Maumee River [14] and lake bottom resuspension [30], demonstrated how sediment plumes increase *Microcystis* photosynthetic status relative to clear water. Tributaries [13] and resuspension [48] also increase P concentration of lakes, but here we isolate the effects of suspended sediments and nutrients. Φ_{et} measured at the lake surface increased with increasing suspended sediments in both the lake study and laboratory experiment (**Figures 4** and **7(a)**), which indicates increased protection from high-light intensities with increasing suspended sediment concentration. The greater Φ_{et} measured at 1 meter is a factor of light attenuation with depth, hence greater Φ_{et}. The lake Φ_{et} samples were community measures, while only *Microcystis* was used to the laboratory experiment, yet they yielded similar results, because *Microcystis* dominated the lake samples. Therefore, *Microcystis* (as well as other phytoplankton) at the surface of a lake high in suspended sediments will have greater photosynthetic efficiency than *Microcystis* at the surface of a clear lake.

Microcystis is able to remain at or near the surface of the lake, which provides a competitive advantage in light-limiting conditions over negatively buoyant phytoplankton [9]. However, this advantage comes at a physiological price. Surface *Microcystis* scums become damaged, as indicated by the depressed F_v/F_m values compared to mixed water column samples (**Figure 5(a)**). Data generated from PI curves further support the hypothesis of photosynthetic damage to surface scums because $rETR_{max}$ (**Figure 5(b)**) and the ability to handle high-light intensity (**Figure 5(c)**) were not affected by k_d measured during sample collection. In contrast, the non-damaged samples collected during mixing responded with increasing $rETR_{max}$ and increasing rETR at high-light intensity with increasing k_d. However, suspended sediments increased Φ_{et} in the surface scum samples in the lake study and laboratory experiment (**Figures 4, 7(a)**). Thus, the depressed surface Φ_{et} values recorded in clear water during the lake study with low k_d must be a

result of photo-protective down-regulation, as opposed to further damage, because F_v/F_m did not change with k_d (**Figure 5(a)**). In the lake and laboratory study, among surface samples, Φ_{et} was greater in mixed-water conditions when compared to calm waters with a surface scum (**Figures 4** and **7(a)**). Surface scums in the calm water would have a high average light exposure, while average light exposure would be less in a mixed water column. Mixing would transport surface *Microcystis* and other phytoplankton downward, providing relief from high-intensities of light, while upward-mixing exposes phytoplankton that were adapted to low-light levels at depth to high-light intensities near the surface.

Vertical mixing, on the other hand, circulates *Microcystis* throughout the water column, which decreases exposure to high-light intensities preventing photosynthetic damage. However *Microcystis* growth stops in strongly-mixed waters [49,50], and the competitive edge is shifted towards negatively buoyant phytoplankton [9]. *Microcystis* would benefit from moderate winds that break up the surface scum, yet allow it to maintain a relatively higher position in the upper water column than competing species. *Microcystis* biovolume rapidly increased between 12 August and 21 August (**Figure 2**). During this time, the median mid-day wind speed measured at Toledo, Ohio was 2.23 $m \cdot s^{-1}$ (National Oceanic and Atmospheric Administration, Data Station THRO1 9063085, Toledo, OH, www.ndbc.noaa.gov/station_page.php?station=THRO1). This wind speed would provide the ideal mixing condition for *Microcystis*, allowing the buoyant *Microcystis* to maintain position in the upper portion of the water column, but also prevent long-term exposure to direct sunlight.

Reduced F_v/F_m indicates that photo-damage was observed in *Microcystis* collected from the lake; however, very little damage was seen in the laboratory experiment (**Figure 7(b)**). This difference could be due to our inability to replicate full-sunlight intensity in the laboratory. In the lake, *Microcystis* was exposed to full sunlight that exceeded 2000 μmol photons $m^{-2} \cdot s^{-1}$ PAR at the surface, while the maximum light intensity of the laboratory experiment was around 1400 μmol photons $m^{-2} \cdot s^{-1}$ PAR for shorter periods of time. This suggests that *Microcystis* may become light damaged at intensities between 1400 and 2000 μmol photons $m^{-2} \cdot s^{-1}$ PAR. UV radiation would also result in damage [39], and greenhouse glass blocks most UV radiation, thus we would have had a reduced UV effect in our experiment.

4.2. *Microcystis* Alters Pigment Content

Care needs to be taken when analyzing cyanobacteria fluorescence data [40], because, unlike higher photosynthetic organisms wherein fluorescence originates only from chlorophyll, PC also provides fluorescence in cyanobacteria. Steady-state fluorescence of light-acclimated and minimum fluorescence of dark-acclimated samples increases with PC content, therefore lowering Φ_{et} and F_v/F_m values even if PSII function is not inhibited [40]. We recorded higher PC content in turbid waters. If PSII function was similar between clear water and turbid water, we would expect decreased Φ_{et} and F_v/F_m in turbid water due to higher PC content. This was not the case, because Φ_{et} and F_v/F_m were greater in turbid water; thus, our pigment data further support our fluorescence data.

Numerous laboratory studies have shown that cyanobacteria grown under different light intensities photoacclimate by altering the amount of the light-harvesting pigments and photo-protective pigments [17,51]. Photoacclimation among phytoplankton in deep stratified lakes has also been shown [16,52]. The photosynthetic pigment data presented here indicates that *Microcystis* alters its pigment content in response to changes in water clarity on spatial and temporal scales in Lake Erie (**Figure 6**). These results have implications for using pigment concentration as a proxy for phytoplankton biomass, because chl *a* and PC content vary with water clarity. Therefore pigment concentration may be an inaccurate proxy for algal biomass, especially when comparing turbid-nearshore to less-turbid-offshore waters of large lakes. For example, based on an analysis of PC content alone, the *Microcystis* biomass in turbid Maumee Bay would likely be overestimated by a factor of six relative to the clearer open waters of the lake. Moreover, PC fluorescence is a new tool to monitor lakes for potential toxin-producing cyanobacteria blooms [53,54]. Chl *a* is less variable than PC with water clarity, but could still result in an overestimation of algal biomass by a factor of two over the range of water clarity conditions observed in our study. On the other hand, researchers utilizing PC fluorescence may overlook potential harmful blooms during the early low-biomass stage of bloom development in clear lakes.

Carotenoids have several functions, acting as light-harvesting pigments and also as photo-protective molecules [52]. Paerl *et al*. [55] observed a steady increase in total carotenoid:chl *a* of *Microcystis* over a summer in the Neuse River (North Carolina, USA) and attributed the high carotenoid content to its survival near the surface of lakes in high intensity sunlight. In contrast, we measured a decrease in *Microcystis*' carotenoid:chl *a* ratio throughout the summer of 2008. Our results differ from Paerl *et al*. [55] because the 2008 Lake Erie *Microcystis* bloom first appeared during relatively clear water conditions and needed more photo-protective carotenoid pigments. After the water clarity decreased in mid-August, the need for photo-protective pigments decreased and the need for light-harvesting pigments would have increased.

4.3. Effect of Nutrients

In order for phytoplankton to acclimate to different light intensities, nutrients, especially N, needs to be available [56,57], mostly due to the N demand in the chl *a* and PC molecules. In a parallel study, Chaffin *et al*. [27] assessed *Microcystis* nutrient status via cellular N and P content and ratios to carbon (C) and showed that all samples were N-replete and many of samples were moderately deficient in P, but 30% of the *Microcystis* had no nutrient deficiency. The content of chl *a* and PC explained 70% of the variation in the N content [27]. Thus, *Microcystis* had sufficient N to meet the N demand required to produce chl *a* and PC in waters with high concentrations of suspended sediments.

Low nutrient concentrations can exacerbate the effect that high-light has on photoinhibition [58]. *Microcystis* cultured in low P concentrations will have decreased rETR values of the PI curve [59]. Furthermore, low nutrient concentrations have been documented to decrease phytoplankton Φ_{et} [60] and F_v/F_m [61] including Lake Erie [62]. On the contrary, Harrison [63] showed the nutrient status of phytoplankton did not affect the F_v/F_m. In our laboratory experiment nutrients did not affect F_v/F_m or Φ_{et} , and furthermore, linear regression between F_v/F_m and the N and P quota reported in Chaffin *et al*. [27] resulted in non-significant relationships ($p > 0.1$). Our finding that nutrients did not affect F_v/F_m differs with Rattan *et al*. [62] who concluded nutrient deficiency would decrease F_v/F_m. Rattan *et al*. [62] collected data in Lake Erie during 2005 and reported that many of their samples had C:N ratios that would indicate a moderate N deficiency. We conducted our study during 2008 and *Microcystis* did not have a N deficiency. Because nutriaent concentration did not affect Φ_{et} or F_v/F_m in both the laboratory experiment and the 2008 lake samples, the photoinhibition observed in clear water was not due to lower nutrient concentration, but from lack of protective suspended sediments.

4.4. *Microcystis* Abundance

The increase of suspended sediments during mid August resulted in a light limited water column (**Figure 2**). Lakes with higher concentrations of suspended sediments often have lower total phytoplankton abundance due to light limitation [4,64]. *Microcystis* would be less affected by light limitation because of buoyancy regulation [65], which was seen in our study because *Microcystis* obtained high abundances during light limitation (**Figure 2**). The data presented here suggest suspended sediments favor *Microcystis* blooms, although other factors could have contributed to the increase of *Microcystis* abundance. Sediments and nutrients co-vary in our study site, and the increase of sediments was accompanied by total P concentrations that increased from 1.61 $\mu mol \cdot L^{-1}$ to 2.91 $\mu mol \cdot L^{-1}$ from July to September [27]. Stratification is important to the success of *Microcystis* [9]. Low wind speeds during the time *Microcystis* abundance rapidly increased would have suppressed vertical mixing [32]. Seasonal succession patterns are not evident because water temperature during 2008 was between 22˚C and 26˚C (**Figure 2**), and because the annual bloom can peak at different times of the summer [27]. Non-quantified factors such as grazers removing *Microcystis*' competetors [12,66] could also have influenced *Microcystis* abundance patterns.

5. Conclusion

The negative impacts of suspended sediments on fish and benthic macroinvertebrates are well known [15]. In this report we show suspended sediments negatively affect eutrophication by providing *Microcystis* a more favorable light climate for photosynthesis. Western Lake Erie is usually turbid due to high suspended sediment loading from the Maumee River [14,28]. Also, resuspension of lake sediments [30], dredging of the shipping canal, and open water disposal of those dredged sediments increase turbidity. Although resuspension does not affect long-term lake recovery following nutrient reductions [67], resuspension or dredging during a *Microcystis* blooms will acerbate that bloom. Thus, the effects of suspended sediments should not be ignored when planning lake restoration. Because suspended sediments can be an important factor in promoting buoyant cyanobacteria such as *Microcystis*, future efforts to reduce blooms may include components aimed at reducing suspended sediments combined with reducing nutrient loading.

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