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Effects of small-scale turbulence at the air-water interface on *microcystis* surface scum formation

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ABSTRACT

Cyanobacterial surface scum (here defined as visible Cyanobacteria colonies accumulating at the lake surface) is a harmful phenomenon that negatively affects water quality, human and animal health. Colony-forming *Microcystis* is one of the most important and ubiquitous genera that can suddenly accumulate at water surfaces. Turbulent water motion, e.g., generated by wind, can vertically disperse this scum layer, which later can re-establish by upward migration of *Microcystis* colonies. However, the role of wind-generated turbulence in scum formation and development is still poorly understood. Here we present results from a laboratory mesocosm study where we analysed the processes of scum formation and its response to wind-generated turbulence at low wind speed ($\leq$3.6 m s^{-1}). *Microcystis* colony size and flow velocity at the water surface and in the bulk water were measured using a microscope camera and particle tracking velocimetry. The surface scum formed by aggregation of colonies at the water surface, where they formed loose clusters of increasing size. The presence of large colony aggregations or of a surface film determined the stability of the scum layer. For the largest applied wind speed, most of the aggregations were broken down to sizes <2 mm, which were dispersed to the bulk water. The surface scum recovered quickly from such disturbances after the wind speed decreased. We further observed reduced momentum transfer from wind to water with the growing scum layer. The presence of the scum increased the threshold wind speed for the onset of flow and reduced the flow velocities that were generated above that threshold. This effect was likely caused by the presence of a film of surface-active material at the water surface (surface microlayer), which is related to the presence of *Microcystis*. Both the small-scale turbulence and surface microlayer might play an important, yet largely unexplored role in *Microcystis* surface scum development in aquatic ecosystems. Improved understanding of the interplay of both processes will be instrumental for improving current mechanistic models for predicting surface bloom dynamics.

1. Introduction

Cyanobacterial blooms are a frequent and problematic feature of many freshwater bodies worldwide (Chorus and Bartram, 1999; Harke et al., 2016; Paerl and Otten, 2013). *Microcystis* spp. that can form colonies from a few micrometers to millimeters in size, is the most common and ubiquitous genus responsible for toxic blooms under warmer climate (Kosten et al., 2012; Lürling et al., 2017). *Microcystis* cells can aggregate to colonies and float upwards to form nuisance *Microcystis* blooms, causing depletion of dissolved oxygen in the water and disruption to the functioning of aquatic ecosystems (Carey et al., 2012; Carmichael, 1992).

Microcystis blooms can occur as dispersed cells and colonies in the epilimnion or as surface scum, i.e., the accumulation of *Microcystis* colonies at the lake surface (Li et al., 2018; Rowe et al., 2016). Bloom formation is controlled by a combination of biotic and abiotic factors, including nutrient enrichment and temperature (Klemer, 1991; Paerl and Paul, 2012; Soranno, 1997; Zhang et al., 2012), hydrodynamic conditions (Aparicio et al., 2013; Wang et al., 2017), predation (Wang et al., 2010) and buoyancy of *Microcystis* colonies (Kromkamp and Mur, 1984; Medrano et al., 2016). Formation of colonies is an adaptive strategy among phytoplankton

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that provides various advantages and plays an important role in the occurrence of *Microcystis* blooms (Li et al., 2014; Reynolds et al., 1987; Walsby and McAllister, 1987). Regulation of buoyancy allows *Microcystis* to outcompete other phytoplankton for light and nutrients and makes its spatial distribution highly heterogeneous (Li et al., 2014; Wu and Kong, 2009; Zhu et al., 2016; Zohary et al., 2017). As a complex ecological phenomenon, the formation of mucilaginous *Microcystis* colonies at the air-water interface (surface scum) is a multi-factor process, and its underlying mechanism is still under debate (Liu et al., 2019; Xiao et al., 2018; Yamamoto et al., 2011).

Wind-generated turbulent mixing is known to be a determining factor for the spatial distribution of surface blooms by vertically dispersing the surface scum layer and by affecting the size distribution of colonies in the water column (Chen et al., 2003; Li et al., 2013; Samoudi et al., 2016). Under strong wind conditions, shear forces cause disaggregation of *Microcystis* colonies (Li et al., 2018; Lin et al., 2015) and smaller colonies and cells are mixed throughout the water column, preventing the formation of a scum layer or subsurface bloom. A wind speed threshold for surface scum formation of around 3 m s^{-1} has been estimated by remote sensing at Taihu Lake (Hu et al., 2010; Huang et al., 2015; Qi et al., 2018). While field observations of *Microcystis* bloom and scum formation mostly lack detailed characterization of the turbulent flow, laboratory experiments showed that small-scale turbulence only marginally modulated algal nutrient uptake and *Microcystis* growth rate in comparison to a stagnant control (Wilkinson et al., 2016; Xiao et al., 2016). Counter-intuitively, small-scale turbulence stimulates colony formation in *Microcystis aeruginosa* during the lag growth phase but disaggregates colonies during the exponential growth phase (Li et al., 2013). Extremely strong turbulence, simulating typhoon-induced mixing, was also found to be beneficial for algal growth and favored colony-forming *Microcystis* on a longer time span (Liu et al., 2019). In all previous laboratory experiments, however, turbulence was generated by oscillating grids (Liu et al., 2019; Regel et al., 2004) or submerged impellers (Li et al., 2018). The resulting flows were characterized by large spatial heterogeneities and strong shear forces in the vicinity of the moving parts of the turbulence generator. The vertical distribution of turbulence can be expected to differ strongly from the vertical structure of turbulence in a wind-mixed water column. Hence, there is little mechanistic understanding about the role of small-scale turbulence generated at low wind speed (<3 m s^{-1}) on the aggregation dynamics of *Microcystis* colonies and surface scum formation.

Improved knowledge about the physical processes and environmental conditions that govern and promote *Microcystis* scum formation is critical for successful prediction and development of lake management and mitigation strategies. To study the effect of small-scale turbulence generated at the water surface at low wind speed on the formation and persistence of *Microcystis* scum, we conducted laboratory experiments in an annular flume. The wind-driven flow was simulated by controlled air circulation above the water surface and simulated a diurnal wind pattern. Colony size distributions and velocities were measured at the water surface and at multiple depths in the bulk water. The results are expected to contribute to mechanistic understanding of the effect of wind-generated turbulence on surface scum dynamics and guidance for future improvements of predictive models.

2. Materials and methods

2.1. Source of material

Microcystis colonies used in our experiment were collected on January 20, 2019 in Guanqiao fish pond (Wuhan, China). The colonies were collected from the water surface (0–30 cm depth) with silk plankton net of 63 μm mesh size. To select predominantly *Microcystis* colonies, the samples were filtered through a 200 μm sieve and then the filtrate was concentrated with a 63 μm sieve immediately after transport to the laboratory. The filtered *Microcystis* scum samples were cultured in BG11 medium at 23 °C and continuous light of 18 μmol photons s^{-1} m^{-2}. Microscopic observations showed that the sieved *Microcystis* colonies consisted of various morphospecies (mainly *Microcystis viridis*, *M. aeruginosa* and *M. wesenbergii*.) with >99% dominance of the entire phytoplankton. The *Microcystis* colony size ranged between 50 and 200 μm (Fig. S1), hereafter we will refer to colony size distribution (CSD) based on volume fraction of the *Microcystis* population. The CSD of *Microcystis* colonies were measured before sampling at 20 cm depth in the pond by using a Laser *In-Situ* Scattering and Transmissometry instrument (LISST-200x, Sequoia, USA), which reflects the "natural" size distribution in the pond. At the beginning of the experiment, CSD was additionally measured in the laboratory using LISST 100x (Sequoia, USA).

2.2. Experimental design

The dynamics of *Microcystis* colony aggregation, scum formation, breakup and re-establishment were studied in an annular flume with outer and inner diameters of 700 and 580 mm, respectively (Fig. S2). Eight circularly arranged fans (5 cm diameter, 12 V maximum supply voltage) generated wind above the water surface. The air flow was adjusted by changing the input voltage of the fans (0, 4.9, 8.0, 12.0 V). The wind speed corresponding to each voltage was measured 2.5 cm above the water surface at nine different positions between two fans using a hot-wire anemometer (Testo 425, Germany). Illumination was applied from above through a transparent plexiglas lid of the flume by two 75 W Light-Emitting Diode (LED) panels (TOPLANET, 301 × 301 × 17 mm; wave length 450–660 nm). The luminous flux at the water surface was 1086 ± 18 lux (measured by a luxmeter, PCE-174, PCE, Meschede, Germany).

The flume was initially filled with distilled water (40 L, water depth: 35 cm). 24 h after filling (January 23, 2019, 8 pm), both nutrients (40 mL of BG11 stock solution, see Table S1) and *Microcystis* colonies (3L stock solution with a concentration of 1.4×10^6 colonies L^{-1} estimated under the microscope) were added into the flume. To promote the development of a scum layer, the algae were growing in the flume under a very low wind speed (1.4 m s^{-1}) for 12 h in darkness. According to Chen et al. (2009), more colonies can float up in turbulent environments than in static water. During the following 3-day experimental period (January 24–26, 2019), we applied a diurnal light cycle (12: 12 h light: dark periods, darkness from 20:00 to 08:00 h) combined with a typical diurnal wind distribution with maximum wind speed (3.6 m s^{-1}) at noon (Fig. 1). On each day, the wind speed was stepwise increased and then decreased (0, 1.4, 2.5 and 3.6 m s^{-1}), where each wind speed was applied for 1–2 h duration. For each wind speed, we measured flow velocities and *Microcystis* colony size distributions at the water surface and at different depths in the bulk water. The measurement started at 08:00 h on January 24, 2019 (Fig. 1). During the dark cycle, wind speed was kept constant at the lowest level (1.4 m s^{-1}) in the first night, but increased to 2.5 m s^{-1} in the second night, when the surface scum did not move under the lowest wind speed. Water temperature was monitored using a four-channel thermometer (Voltcraft K204, Germany). The average temperature and standard deviation was 22.9 ± 1.3 °C and no temperature difference between the water surface and the bottom of the flume was observed.

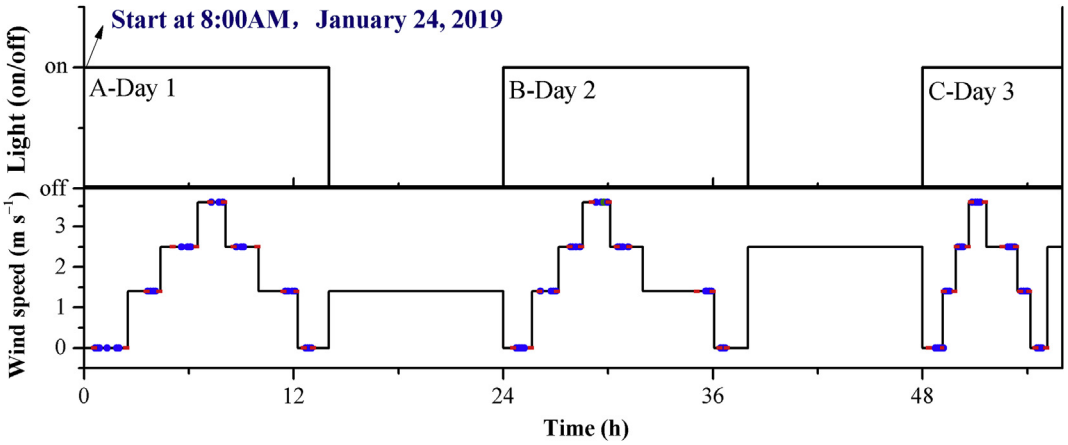

Fig. 1. Diurnal variations of light (upper panel) and wind speed (lower panel) during the 3-day experiment. The red points mark measurement times of colony size and velocity at the water surface by using a microscope camera, blue points mark corresponding measurement times of colony size and velocity in the bulk water. The reason for the prolonged duration of low wind speed on the second day was a technical problem with video recording. Shorter duration of wind periods on the third day were chosen because of more stable surface scum (no detectable motion) and an increased number of larger colonies. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.3. *Microcystis* scum dynamic at the water surface

Time-resolved observations of the surface scum formation and development were carried out for each wind speed. Color images of the water surface were recorded from above through binoculars (Stemi, 2000-C, Zeiss Germany) equipped with a digital camera (NEX-7, Sony, Japan). Bursts of images were recorded during 5–10 min (200–400 images) at the beginning and at the end of each wind speed. All pictures were combined for subsequent analysis. During recording, additional illumination of the water surface was provided by a cold-light source (KL 1500 LCD, Zeiss, Germany). The images were calibrated using a ruler and had a resolution of 2.12 μm pixel^{-1} within a field of view of 9.0 × 5.1 mm.

Individual *Microcystis* colonies were identified in each image by automated image processing (Matlab image processing toolbox, MathWorks, USA). The analysis provided distributions of colony area (and equivalent spherical diameter), as well as the surface areal coverage of *Microcystis* (calculated as the percentage of water surface that was covered by colonies). Size distributions were binned in logarithmically distributed classes from 0.05 to 9 mm. The equivalent diameter of colonies of complex shape represents a diameter of a volume-equivalent sphere.

Additional videos (resolution of 6.25 μm pixel^{-1}, frame rate of 25 Hz) were recorded starting from the second day of the experiment to measure the flow velocity of the surface scum layer. The mean flow velocity of the water surface was estimated as the product of the frame rate and the mean horizontal displacement of colonies within the field of view of the camera. The displacement was calculated as the maximum of the spatial cross-correlation function of two subsequently recorded images.

Water samples containing *Microcystis* colonies were carefully collected from a thin surface layer (a few upper millimeters from the surface, representing *Microcystis* "surface scum") using a 5 mL pipette after each change in wind speed. The water was collected into 50 mL conical sterile polypropylene tubes for biomass estimation: Optical density measurements were performed at 680 nm on a Novaspec II spectrophotometer (Amersham Pharmacia Biotech Inc, UK) and fluorimeter (LS55, PerkinElmer, USA) using a cuvette with a 1 cm light path.

2.4. *Microcystis* colony size and velocities in the water column

Microcystis colony size and velocity in the bulk water were measured for each wind speed at three different depths: near the water surface (approx. 0–2.4 cm depth), in a middle layer (20–22.4 cm depth) and close to the flume bottom (approx. 32.6–35 cm depth). At each sampling depths, a vertically oriented plane within the central region of the flume was illuminated by short (4 ns) pulses of green laser light (wavelength 532 nm, Nano L 200-15, Litron, UK) at a repetition rate of 7.4 Hz. Colonies within the approximately 3 mm thick light sheet were observed using a digital camera (1200 × 1600 pixel, 14 bit greyscale intensity resolution, HiSense 610 PCO, Germany) in a perpendicular arrangement (Fig. S2). The field of view of the camera was 18 × 24 mm with a calibrated resolution of 15 μm pixel^{-1}. Laser illumination and image acquisition were synchronized using the software Dynamic Studio (version 3.20, Dantec Dynamics, Germany).

Images were recorded for 3 min for each measurement. Individual *Microcystis* colonies were detected in each image based on intensity thresholding and object detection in Matlab. The analysis, was similar to that described above for colonies at the water surface, and provided the distributions of colony area (and equivalent spherical diameter), as well as the areal colony density of *Microcystis* (calculated as the area covered by colonies divided by the total area of the field of view in each image). Size distributions were binned in logarithmically distributed size classes from 0.05 mm to 2 mm. Taken that the results of CSD are presented as a volume distribution, the volumetric median of colony diameter (*Dv*50, μm, the colony size value when the volume percentile is 50%) was computed to compare the average colony size of *Microcystis* under different wind speed conditions at three different depth of water column.

The enrichment ratio (ER) of *Microcystis* was calculated as the ratio of surface areal coverage and the areal colony density in the middle layer of the bulk water. Two-dimensional (vertical and longitudinal) colony velocities were estimated using particle tracking velocimetry with a backward-difference algorithm for the displacement between colonies of similar sizes in two consecutive images.

2.5. Statistical analysis

One-way analysis of variance was applied to reveal the influence of wind speeds on the median size (*Dv*50) of *Microcystis* colonies at three depth of the water column. Following ANOVA, a post hoc LSD test was conducted to determine significant groupings. The vertical

velocities of *Microcystis* colonies under different wind speed conditions during the three days of the experiments were compared using the Student's *t*-test. All statistical analysis was performed using the software package SPSS 19.0 (IBM Corp, USA). Data are presented as mean ± standard deviation (SD) and were tested for statistical significance at a significance level (p) of 0.05.

3. Results

3.1. Microcystis surface scum formation under different wind conditions

During the three-day experiment, a surface scum layer developed and the areal coverage of the water surface with *Microcystis* colonies increased from an average value of 3.3 ± 2.2% at day 1, 13.2 ± 6.5% and 17.0 ± 10.3% on day 2 and 3, respectively (Fig. 2a, sample images (micrographs) of the surface scum development are shown in Fig. S3). Meanwhile, the biomass of *Microcystis* colonies in the thin surface layer measured by both spectrophotometer and fluorimeter showed similar results and increased 3–4 fold (Fig. S4). Contrary to the increase in surface coverage, the areal colony density in the bulk water decreased, with most pronounced changes during day 1 (Fig. 2b), suggesting that the scum layer was produced by upward motion of colonies from the bulk water. Visual observations revealed that on day 2 and 3, the scum layer resembled an approximately 3 mm thick layer of loose colony assemblages directly below the water surface.

Except for day 1, the colony concentration followed the diurnal pattern of wind speed. The surface coverage by *Microcystis* decreased in response to increasing wind speed. Meanwhile the colony density in the bulk water increased (Fig. 2). This effect was most evident in the enrichment ratio (ER) of *Microcystis*. ER was below 10 on the first day, but increased to values exceeding 100 during the following two days, except for high wind speed conditions at midday (Fig. 3). This is due to the entrainment of surface scum into the water column by wind-generated vertical mixing when exposed to high wind. In response to the decreasing wind speed in the afternoon, EF fell rapidly back to their respective values at the same wind speed during the morning (increasing wind speed), suggesting a rapid recovery of the surface scum after the mixing. Moreover, on a daily basis, the EFs measured at the same wind speed during increasing and during decreasing wind speed were comparable in magnitude (Fig. 3), which suggests a dynamic equilibrium between *Microcystis* colony density at the water surface and in the bulk water.

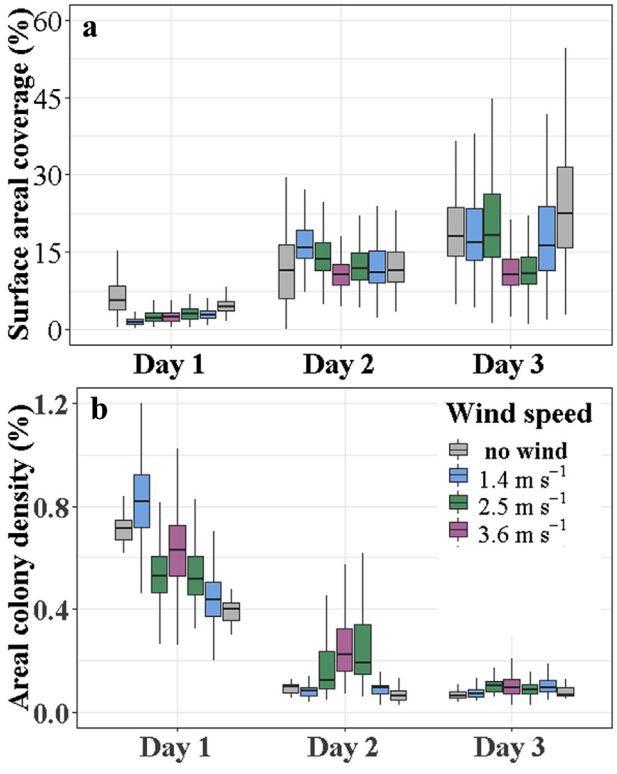

Fig. 2. (a) Relative areal coverage of *Microcystis* colonies at the water surface and (b) areal colony density in the bulk water (in the laser light sheet). Each box plot shows data obtained at different wind speed (see legend for color assignment) during the 3 days. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.2. Microcystis colony size distributions under different wind conditions

The median diameter (Dv_{50}) of *Microcystis* colonies in the bulk water at three different depth were significantly different under high wind speed (2.5 and 3.6 m s^{-1}) conditions ($p < 0.05$, one-way ANOVA). Large colonies ($Dv_{50} > 250$ μm) were only observed under high wind speed conditions (Fig. 4, Fig. 5e and Fig. 5f), and a linear decrease of Dv_{50} with increasing depth (h) was observed under the highest wind speed ($W = -0.42^{*}h + 1.64$, $R^2 = 0.99$). Under no and weak wind conditions, *Microcystis* colony size in the bulk water varied between 50 and 500 μm and was similar at each depth during the three days (Figs. 4 and Fig. 5e and f). These colonies (Dv_{50}~200 μm) were slightly larger than those measured at the beginning of the experiment and before sampling in the pond (Dv_{50}~86 μm, Fig. S1), likely due to the aggregation process during incubation in the flume under low wind conditions. At the water surface, in contrast, colony size was already larger at the time of first sampling and rapidly increased to >1 mm throughout the experimental period (Fig. 5a–c).

Associated with the development of the surface scum layer, the response of the *Microcystis* colony size distributions to wind differed on the first day of the experiment from that observed during the two following diurnal wind cycles. At the first day, the size distribution in the bulk water became similar to the colony size distribution at the water surface already at the lowest applied wind speed and remained unaffected by further increase of the wind speed. The homogenization of size distributions indicates mixing of the larger colonies from the water surface into the bulk water already at the lowest wind speed (Fig. 5a and d).

After the scum layer has formed (day 2 and 3, Figs. 2 and 3), the colony size distributions became less sensitive to the applied wind speed and no, or only minor changes were observed at low (1.4 m s^{-1}) and medium (2.5 m s^{-1}) wind speed (Fig. 5e and f). Complete homogenization of the size distributions at the water surface and in the bulk water was only observed for the highest applied wind speed (3.6 m s^{-1}).

3.3. Dynamics of Microcystis colony velocity

Colony velocities in the bulk water varied between <1.5 mm s^{-1} during no wind conditions and a maximum value of 7 ± 2 mm s^{-1} in the uppermost layer at the highest wind speed on day 1 (Fig. 6a–f). The residual flow in the absence of wind forcing can be related to convective water motions caused by latent heat fluxes at the water surface or heat transfer through the flume walls. These motions caused also vertical velocity fluctuations with standard deviations of up to 0.5 mm s^{-1} and impeded direct observations of buoyancy-driven sinking or floatation of *Microcystis* colonies (mean vertical

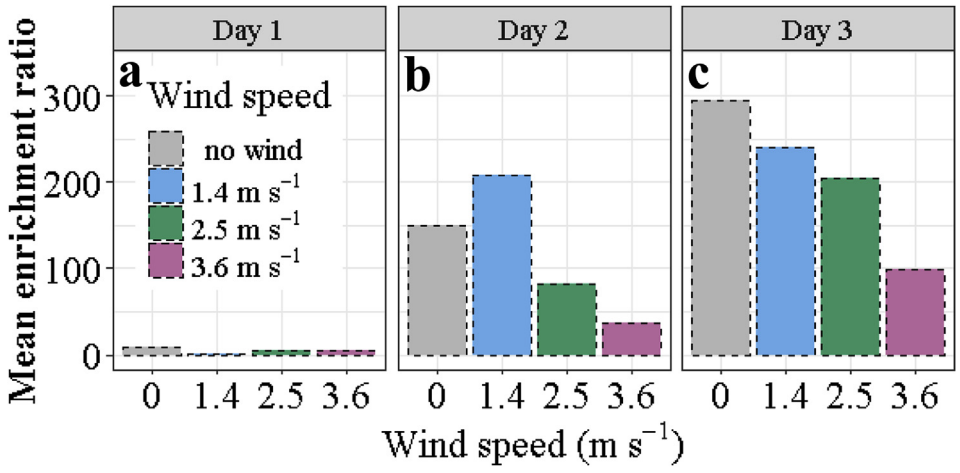

Fig. 3. Temporal dynamics (panel a, b, c) of the mean enrichment ratio (ER) of *Microcystis* colonies based on the ratio of the average surface coverage and colony density in the bulk water at each wind speed.

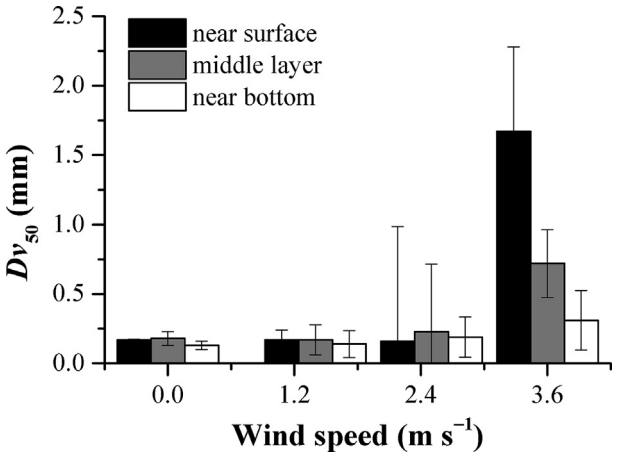

Fig. 4. The response of volume median diameter (Dv_{50}) of *Microcystis* colonies at different depths in the bulk water to the increasing wind speed no wind, 1.4, 2.5 and 3.6 m s^{-1}, respectively. Bars show mean values for all sampling times, errors bars are standard deviation.

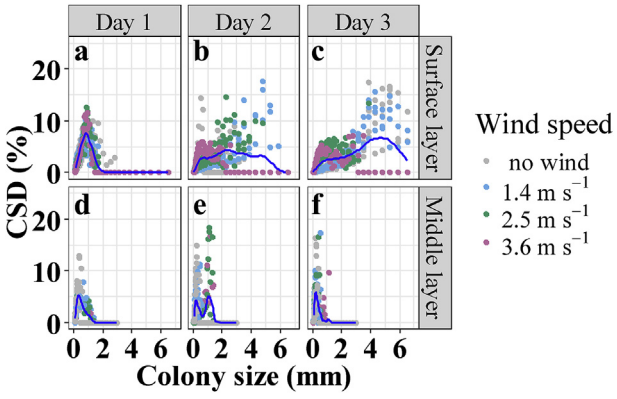

Fig. 5. The colony size distribution (CSD) of *Microcystis* calculated by biovolume at the water surface (upper panel a, b, c) and in the middle layer of the water column (lower panel d, e, f) during the three days of the experiments and at different wind speed (different color represent no wind, 1.4, 2.5 and 3.6 m s^{-1}, respectively). The blue continuous line represents the mean CSD for all wind speeds at each day in the surface and middle layer (using a non-parametric smoothers generalized additive models). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

velocities were not significantly different from zero in the absence of wind forcing using the Student's *t*-test). Because we did not observe a consistent size-dependence of colony velocities (Fig. S5), we consider the observed velocities as proxies for flow velocity.

The mean longitudinal flow velocity and fluctuations of both velocity components (longitudinal and vertical) generally increased for increasing wind speed and decreased with increasing depth (Fig. 6). The mean flow velocities observed at particular wind speeds, however decreased consistently from day 1 to day 3. The slopes of linear regressions between flow speed and wind speed decreased by more than a factor of six during the course of the experiment (Fig. 7a). Flow velocities at the water surface (microscopic camera observations) were up to a factor of five higher than in the bulk water and, in accordance with the bulk observations, surface velocities at each wind speed decreased with increasing scum development (Fig. 7b). Although the slopes were significantly different from zero at all three days, the dependence became increasingly non-linear with an obvious suppression of momentum transfer from wind to water at low and medium wind speed. There was almost no flow after day 1 under low (1.4 m s^{-1}) and after day 2 also under medium (2.5 m s^{-1}) wind speed.

4. Discussion

4.1. Effect of wind-generated turbulence on Microcystis scum

As observed in many eutrophic aquatic systems at low wind speed, *Microcystis* colonies formed a surface scum layer in our experiments. The layer was formed by aggregation of submerged *Microcystis* colonies below the water surface. The size of the aggregations continuously increased and exceeded the size of colonies in the bulk water by more than one order of magnitude. The majority of the biomass was in the surface scum starting from day 2 of the experiment. Coalescence of smaller colonies into larger aggregates in the surface layer was apparently an important mechanism during the scum formation. Recent experiments have demonstrated that this aggregation is facilitated by increased amounts of extracellular polymeric substances in colony aggregations (Xiao et al., 2018; Xu et al., 2014).

Wind stress applied to the water surface reduced the size of the aggregations at the water surface to colonies <2 mm, which were partly entrained into the bulk water. The maximum wind speed of 3.6 m s^{-1} in our experiment was sufficient to homogenize the colony size distributions at the water surface and in the bulk water, but

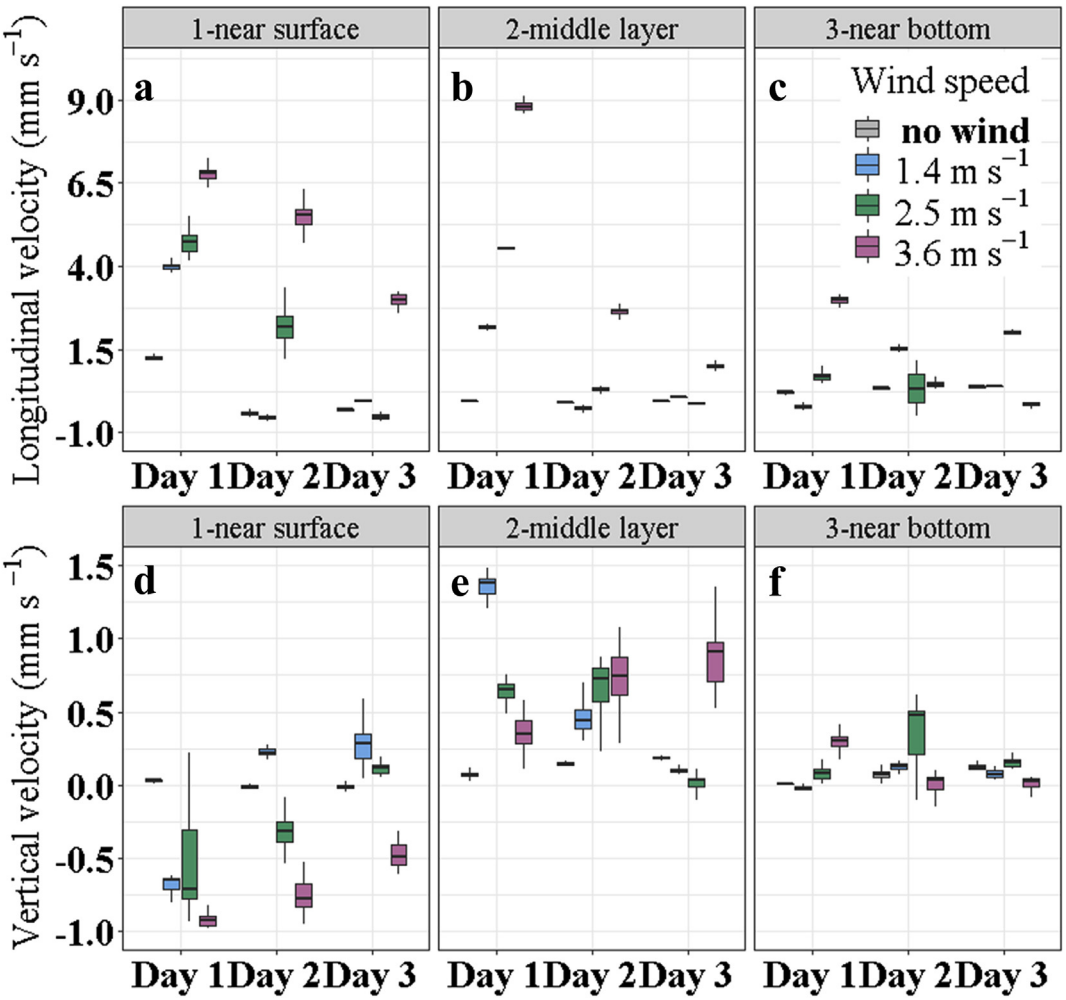

Fig. 6. Boxplots of longitudinal (upper panels a, b, c) and vertical (lower panels d, e, f) velocities of *Microcystis* colonies at different wind speed and at three different depths in the bulk water.

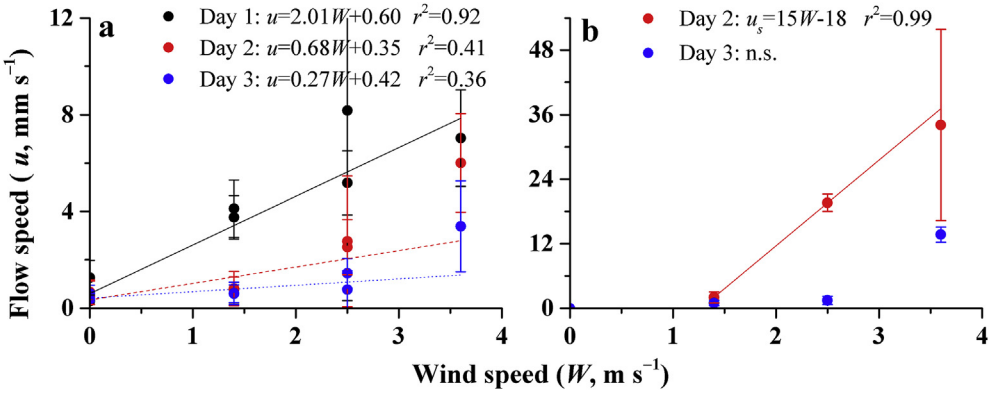

Fig. 7. Relationship between wind speed and flow velocity: (a) at approx. 0–2.4 cm depth in the bulk water (near-surface layer) and (b) at the water surface. Symbols show mean values (and error bars in b the standard deviations) for each measurement. Different symbol refers to experimental day (see legend). The lines show linear regressions according to the equation (and r^2 values) provided in the legend. All slopes are significantly different from zero ($p < 0.05$).

did not result in a complete mixing of the *Microcystis* biomass. This result is consistent with field and remote sensing observations from lakes and reservoirs, where local surface concentrations of cyanobacteria only appeared at wind speeds below 3–4 m s^{-1} (Cao et al., 2006; George and Edwards, 1976; Qi et al., 2018).

The vertical distribution of wind shear near the water surface is characterized by a viscous sublayer at the air-water interface, where turbulent motions are suppressed, and a turbulent boundary layer below (Lorke and Peeters, 2006). The thickness of the viscous sublayer is reciprocally related to wind speed (Webster and

Hutchinson, 1994) and for a wind speed of 3.6 m s^{-1}, its thickness is approximately 2 mm, which is comparable to the thickness of the observed scum layer in our experiments (~3 mm). Consistent with the maximum colony sizes observed at high wind speeds in our experiments, floating *Microcystis* colonies or colony aggregation smaller than 2 mm were immersed in the surface viscous boundary layer. Webster and Hutchinson (1994) proposed a trapping mechanism of colonies in the viscous sublayer, where colonies in the bulk water are transported upward by turbulent eddies and stick to the viscous sublayer at the air-water interface. Although we did not observe the initial development of the surface scum layer during the night between day 1 and 2, we speculate that the weak steady wind (1.4 m s^{-1}) ultimately promoted the rapid initial *Microcystis* scum formation in our experiments (Fig. 2).

Although we measured the vertical velocity component of individual *Microcystis* colonies, buoyancy-controlled floatation or sinking velocities could not be resolved. We attribute this to the water motion, which in the absence of wind forcing was driven by convection. The residual flow velocity fluctuations in the absence of wind forcing of a few mm s^{-1} are exceeding expected floatation velocities of *Microcystis* colonies (Nakamura et al., 1993; Rowe et al., 2016) by about one order of magnitude. The existence of large-scale convective flow structures and secondary circulation at low wind can result in persistent local up- and downwelling flows within the field of view of the camera, which probably impede estimation of size dependent colony floatation velocities also from longer-term averaging and prolonged measurements. Laboratory measurements of buoyancy-controlled colony motion have typically been done in narrow settling columns, where water motion is suppressed by the small size of the chamber and better thermal insulation. Although the lack of completely stagnant conditions can be considered as a shortcoming of our experimental approach, it can be expected that such slow water motion are ubiquitously present in most environmental systems. A combination of annular flumes with separate estimates of buoyant colony velocities in settling chambers can potentially provide insight into the relative role of colony buoyancy and surface trapping in the viscous sublayer at low wind speed. Further research into this direction appears important, as current approaches for modeling and predicting *Microcystis* bloom and scum formation consider buoyancy and turbulent mixing as the major regulating processes (Aparicio et al., 2013; Wang et al., 2017; Yang and Kong, 2013).

4.2. Effect of Microcystis on turbulence generation by wind

Another important finding from our experiment was the unexpectedly strong reduction of momentum transfer from wind to water by the presence of the *Microcystis* scum layer. The threshold in wind speed for the onset of water motion increased and the flow velocity generated by each applied wind speed decreased with increasing scum development. These observations reveal a stabilizing feedback mechanism between the scum layer and its physical environment by counteracting wind-generated mixing and dispersion at low wind speeds. Two possible mechanisms can cause the reduction in momentum transfer from wind to water by the submerged scum layer: The presence of a film of surface-active material (i.e. a surface microlayer) or a change of viscosity of the water due to the presence of the scum layer.

By examining the bulk fluid properties of dense *Microcystis* aggregations, Dervaux et al. (2015) observed yield stress, i.e. more solid, behavior of the bacterial suspension at low shear rates, where viscosity increased by three orders of magnitude. If a critical shear rate was exceeded, the suspension showed Newtonian behavior with viscosity very close to that of water. The authors ascribed these observations to the stabilizing effect of extracellular polymeric substances, which provide the observed yield strength at low shear rates. The critical shear rate (10 s^{-1}) and corresponding viscosity (1.1 mPa s) reported by Dervaux et al. (2015) suggest a critical shear stress of 10^{-2} Pa, which corresponds to a wind speed of about 2.9 m s^{-1}. At lower wind speed, the increased viscosity of the scum layer can therefore suppress turbulent motions in a vertically extended viscous sublayer. Consistent with our observations, the large extent of the viscous sublayer in dense *Microcystis* aggregations provides a potential mechanism for the increased threshold for wind-generated mixing at low and medium wind speed. The change in viscosity, however, would mainly result in a changing vertical distribution of wind-generated flow velocity, while the shear stress at the air-water interface, and thereby the total momentum transfer from air to water, would remain unaffected.

The momentum transfer from wind to water is controlled by water surface roughness, which at low wind speed is predominantly affected by water surface tension (wind ripples and capillary waves). The *Microcystis* scum layer in our experiments was fully submerged, and presence of the scum layer could not have affected the surface properties directly. However, films of surface-active substances can form due to secretion of plankton (Lancelot and Mathot, 1987). Although water surface tension was not included in our measurements, we tested this hypothesis by performing additional measurements after the main experiment. This preliminary test indicated a pronounced reduction of water surface tension (up to 20%) in the presence of *Microcystis* colonies (Fig. S6).

Although surface films have not yet been linked to surface scum formation in lakes and other inland waters, biogenic surface microlayers (surface slicks or films) have been receiving increased scientific interests because of their potential importance for gas exchange, biogeochemical cycling, accumulation of pollutants and, last but not least, as a unique habitat for specialized organisms (i.e., floating plankton) (Cunliffe et al., 2013; Södergren, 1987). Similar to oil films, these layers damp capillary waves (Alpers and Hühnerfuss, 1989; Tempel and Riet, 1965) and therewith reduce the water surface roughness at low wind speed. The reduced roughness causes a reduction in momentum transfer from wind to water (Wüest and Lorke, 2003). The reduction of water surface tension by a surfactant film, excreted as or along with other extracellular polymeric substances by *Microcystis* colonies, may constitute an important process by which the scum-forming bacteria affect their physical environment towards more favorable conditions.

5. Conclusions

For the first time, we analysed the formation and persistence of a *Microcystis* scum layer under wind-generated turbulence in controlled laboratory experiments. Our experiments revealed two important physical processes occurring at the water surface at low wind speed, that may have been overlooked in former laboratory studies as well as in field assessments. The strong velocity gradient within the viscous sublayer at the air-water interface potentially promotes the growth of the scum layer by the trapping of colonies from the wind-stirred bulk water below. At high wind speed, reduction of viscous sublayer thickness lead to erosion of the scum layer and entrainment of large colonies into the bulk water.

We further found experimental evidence for a strong suppression of momentum transfer from wind to water by the presence of the surface scum layer, or by surface active material excreted by the *Microcystis* cells. The developing scum layer caused an increasing reduction of wind-generated flow and turbulence and thus provided a stabilizing feedback mechanism of the surface bloom with its physical environment. Small-scale turbulence and the

microlayer at the water surface potentially play an important, yet largely unexplored role in *Microcystis* surface scum development in water bodies. Future studies should analyze the interactions of *Microcystis* blooms with the water surface at greater detail, particularly by including observations of the surface microlayer, water surface tension and viscosity.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.watres.2019.115091.

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