Factors affecting the timing of surface scums and epilimnetic blooms of blue-green algae in a eutrophic lake

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1 author:

P.A. Soranno
Michigan State University

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P.A. Soranno

Abstract: Blue-green algal blooms, which can occur mixed throughout the epilimnion or as scums at the lake surface, develop in response to a variety of factors. However, it is still unclear what conditions suggest that blooms are imminent or how far in advance blooms can be forecast. I assessed the predictability of surface scums and epilimnetic blooms from limnological, physical, and meteorological variables using data sampled daily during summer and fall 1993 in Lake Mendota, Wisconsin. Daily chlorophyll *a* (a measure of blue-green algal biomass) was correlated to some weather, physical, and grazing variables at lags ranging from 0 to 9 days. Conditions immediately preceding surface scums were variable, making predictions difficult. However, during surface scums, Secchi disk depth, wind velocity, atmospheric pressure, and precipitation were significantly different than when the scums were absent. Based on predictors examined in this study, I developed criteria that identify the conditions sufficient for scums to form. In Lake Mendota, conditions sufficient for surface scum formation (proper weather and water column conditions and a pre-existing algal population) occur much more often than scums are observed. This study shows the importance of weather in determining both epilimnetic blue-green algal biomass and surface scum formation.

Résumé : Les proliférations d'algues bleu-vert, qui peuvent survenir sous forme mélangée dans toute l'épaisseur de l'hypolimnion ou sous forme d'écume à la surface du lac, surviennent en réaction à divers facteurs. Toutefois, on ignore encore quelles conditions indiquent l'imminence des proliférations ou combien de temps d'avance on peut prévoir les proliférations. J'ai évalué la prévisibilité de l'écume de surface et les proliférations épilimnétiques à partir des variables limnologiques, physiques et météorologiques en utilisant les données provenant d'échantillonnages quotidiens réalisés au cours de l'été et de l'automne 1993 dans le lac Mendota, en Wisconsin. La concentration quotidienne de chlorophylle *a* (une mesure de la biomasse des algues bleu-vert) était corrélée à certaines variables météorologiques, physiques et de broutage avec des décalages variant de 0 à 9 jours. Les conditions précédant immédiatement la formation d'écume de surface étaient variables, rendant ainsi difficiles les prévisions. Toutefois, au cours des épisodes d'écume de surface, la profondeur au disque de Secchi, la vitesse du vent, la pression atmosphérique et les précipitations étaient substantiellement différentes qu'en l'absence d'écume. À partir des prédicteurs examinés au cours de la présente étude, j'ai élaboré des critères qui permettent de reconnaître les conditions qui suffisent pour la formation d'écume. Dans le lac Mendota, les conditions suffisantes pour la formation d'écume de surface (conditions appropriées du point de vue de la météorologie et de la colonne d'eau, et une population d'algues préexistante) surviennent beaucoup plus souvent que l'on observe d'écume. Cette étude montre l'importance des conditions météorologiques pour déterminer à la fois la biomasse épilimnétique des algues bleu-vert et la formation d'écume de surface.
[Traduit par la Rédaction]

Introduction

Populations of blue-green algae (cyanobacteria), common to many eutrophic lakes, are usually dispersed throughout the epilimnion but can accumulate at the lake surface and create scums. Consequently, blue-green algal blooms have been defined as "... [population maxima] in the epilimnion that envelop the photic zone and that, depending on the degree of surface layer turbulence, may or may not form surface scums." (Klemer and Konopka 1989). Both surface scums and epilimnetic blooms have been attributed to a variety of physical, chemical, and biotic factors, and although the development of both can be correlated, they respond to different environmental cues (Reynolds and Walsby 1975; Paerl 1988). Many water-quality models assume that epilimnetic blue-green algal biomass and surface scums are directly related, but few studies have directly tested this assumption. By considering both the surface and epilimnetic components of blue-green algal blooms, we may better identify key factors that regulate algal biomass. Being able to predict the likelihood of bloom formation is important for lake management, where often the expected return on costly nutrient-reduction efforts is fewer algal blooms.

The success of blue-green algae in many aquatic ecosystems are well documented (reviewed by Reynolds and Walsby 1975; Paerl 1988; and Oliver 1994). During the summer stratified season, conditions allowing blue-green algae to dominate algal assemblages include a stable water column, reduced grazing by large herbivores, low ratios of nitrogen:phosphorus (N:P), high nutrient levels, and high pH (Paerl 1988). Blue-green algal blooms can follow inputs of nutrients, especially

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P.A. Soranno.[1] Center for Limnology, University of Wisconsin, Madison, WI 53706, U.S.A.

[1] Present address: Department of Fisheries and Wildlife, Michigan State University, 10A Natural Resources Building, East Lansing, MI 48824, U.S.A.

P, supplied by storm runoff or sustained windy periods that mix nutrient-rich hypolimnetic water into the epilimnion (Stauffer and Lee 1973; Kortmann et al. 1982; Kononen et al. 1996), and blooms of *Aphanizomenon flos-aquae* can be associated with large grazers such as *Daphnia pulex* that effectively reduce other algal species (Lynch 1981; Carpenter 1989).

A major factor leading to the success of blue-green algae lies in their ability to regulate their buoyancy to take advantage of optimal nutrient and light conditions, which can lead to the formation of surface scums (Paerl 1988; Oliver 1994). Predicting when surface scums are likely to occur should depend in part on predicting the dynamics of buoyancy control. Buoyancy in blue-green algae is regulated by three major mechanisms that each respond to a variety of environmental cues (Walsby and Booker 1980; Paerl and Ustach 1982; Kromkamp et al. 1986; Oliver 1994). In fact, identifying the complex interplay of physical, chemical, and biological cues involved in buoyancy regulation of blue-green algae has been an active area of research (Oliver 1994). Factors that potentially influence the timing of surface scums include limitation by light, nutrients, weather conditions, and turbulence (Paerl and Ustach 1982; Paerl 1988; Klemer 1991). Ultimately for surface scums to form, surface layer turbulence caused by wind must be low enough for the upward velocity of migrating cells to overcome the downward forcing of wind turbulence (Reynolds and Walsby 1975). Although some have suggested that surface scums should form when there is a stratified water column, low surface layer turbulence, and a pre-existing algal population (Reynolds and Walsby 1975), these conditions have not always been found to be sufficient (Zohary and Breen 1989).

Despite this well-developed understanding of the potential mechanisms behind buoyancy regulation, it has been difficult to predict the timing and magnitude of surface scums and epilimnetic blooms in individual lakes within a given summer. Although certain weather conditions, such as low wind velocity and high solar radiation, are usually observed during surface scums (Paerl 1988), the importance of weather in scum formation has only seldom been quantified. Furthermore, the role of weather in predicting epilimnetic blooms has seldom been examined either alone (Collins 1995) or in combination with other in-lake variables and, then, only at the weekly, monthly, or seasonal scale (Zohary and Robarts 1989; Havens 1994; James and Havens 1996). Because algae respond at shorter time scales, especially to weather which can vary markedly at the daily scale, examining these relationships at finer scales is warranted.

In this study, I examined what limnological, physical, or meteorological symptoms suggested that both surface scums and epilimnetic blooms were imminent and how far in advance they could be forecast. To address these issues, I sampled Lake Mendota, Wisconsin, daily during summer and fall 1993. I determined how algal variables (chlorophyll *a*, surface scum presence–absence, and Secchi disk depth) responded to the following groups of predictor variables: limnological (nutrients and zooplankton grazing), physical (water column characteristics), and meteorological (daily weather variables).

Study site

Lake Mendota (3895 ha, 12.7 m mean depth) is a well-studied eutrophic lake located in south-central Wisconsin (43°6′N, 89°24′W). As in other medium–large and relatively deep eutrophic lakes, blue-green algal biomass is characterized by high inter- and intra-annual variability (Konopka et al. 1978; Lathrop and Carpenter 1992). The species that usually dominate the blue-green algal assemblage in Lake Mendota are large colonial and filamentous species (*Aphanizomenon flos-aquae*, *Microcystis aeruginosa*, and *Oscillatoria agardhii*) capable of rapid vertical migration into and out of the photic zone (Konopka et al. 1978; Brock 1985; Lathrop and Carpenter 1992). Since the 1850s, nutrient loading to the lake has been high (Lathrop 1992), and since at least the 1880s, blooms of blue-green algae have been observed, typically between June and November (Trelease 1889; Lathrop and Carpenter 1992). Despite extensive long-term records of algal populations and nutrients (Brock 1985; Lathrop and Carpenter 1992) and intensive short-term studies in Lake Mendota (Konopka et al. 1978) and other lakes (Paerl 1988, Trimbee and Prepas 1988), it remains difficult to predict the magnitude and timing of blue-green algal biomass.

Methods

Algal response variables

I sampled Lake Mendota daily for 132 days from 11 June to 20 October 1993 at one central sampling station located at the deepest part of the lake (24 m) for three algal-related variables: chlorophyll *a*, surface scum presence–absence, and Secchi disk transparency. Surface scums were determined using a visual index based on whether cell or colonies accumulated at the surface at the time of sampling (between 09:00 and 11:00) at the central lake station. Small, nearshore scums were not included in the analysis. Because sampling variability may be affected by the presence of surface scums owing to increased spatial patchiness, I took three replicate water samples for chlorophyll *a* analysis to calculate the coefficient of variation (CV). Samples were taken using an integrated tube (5.1 cm diameter) from the surface to 8 m. This depth represents the average epilimnetic depth during the summer stratified season. Epilimnetic chlorophyll *a* concentrations were measured on both a total water sample and a sample prefiltered through a 35 μm mesh net (cells <35 μm were assumed to be edible by grazers). The difference between the two samples represents the large colonial blue-green algae (>35 μm) that bloom in Lake Mendota during summer and fall (Lathrop and Carpenter 1992). Chlorophyll samples were filtered onto Whatman GF/F filters within 2 h of sampling and frozen until further analysis. Samples were extracted for 24 h in methanol at 5°C and analyzed fluorometrically, correcting for pheopigments by acidification (Marker et al. 1980). Means and CVs of the triplicate samples were calculated and used for all analyses. Biweekly microscopic counts of phytoplankton mounted in acrylic resin (St. Amand 1990) were used to determine the contribution of blue-green algae to total phytoplankton biovolume.

Predictor variables

Limnological

I measured three limnological variables that were expected to be directly related to algal blooms: P supply from external sources (watershed inputs), P supply from internal sources (entrainment from the hypolimnion), and grazing by *Daphnia*.

External total phosphorus (TP) loading was calculated from continuous monitoring stations on two of the five major streams draining into the lake and one of the two main storm sewers connected to the lake (USGS 1994), which together constitute about 53% of the total external load entering the lake (Lathrop 1979). Phosphorus loads from the gauged streams and storm sewer were calculated by direct integration (USGS 1994). Ratios of monitored to unmonitored stream inputs were estimated from 2 years of complete loading measurements for all major streams draining into Lake Mendota (Lathrop 1979) and used to calculate total external P loading entering Lake Mendota during 1993 (Soranno 1995). In-lake TP was sampled weekly every 4 m between 1 and 20 m and also at 22 m. Concentrations of P from all inputs and in the lake were measured spectrophotometrically by forming phosphomolybdate complexes after persulfate digestion (Strickland and Parsons 1968).

I also measured daily internal P loading caused by entrainment of nutrient-rich hypolimnetic water into the epilimnion following mixing from storms. Entrainment was calculated by measuring daily temperature profiles using a thermistor chain and datalogger attached to a moored buoy at the central lake station, and weekly P profiles as described in Soranno et al. (1997). Total P mass transported into the epilimnion following thermocline deepening was calculated by multiplying the volume of water added to the epilimnion by the average P concentration in the thermocline region (Stauffer 1987; Soranno et al. 1997).

Beginning 1 July, I estimated *Daphnia* densities in the mixed layer daily by counting the number of animals collected on the filters for the total chlorophyll analysis. I compared these estimates with density estimates made from biweekly vertical net hauls (0–20 m) enumerated under the microscope. Although actual densities estimated from the filters were consistently higher than densities estimated for the entire water column, the two methods were highly correlated (r = 0.98). Since I was only interested in the timing of daphnid population peaks, the difference between the two methods did not bias my results. Missing data for Secchi disk depth, chlorophyll *a*, and *Daphnia* densities were linearly interpolated. Only 18 of the 132 dates had missing data, and no more than two consecutive days passed without sampling.

Physical

Four physical characteristics of the water column were measured daily: epilimnion depth (Z_{epi}), photic zone depth (Z_{pho}), ratio of epilimnion depth to photic zone depth (Z_{epi}/Z_{pho}), and water column stability. Except for photic depth, all variables were calculated from the daily temperature profiles. The values for Z_{epi} were obtained from visual inspection of the daily temperature profiles and were defined as the depth where the temperature change was $\geq 1°C \cdot m^{-1}$. The values of Z_{pho} were not measured directly but were estimated by multiplying Secchi disk depth by 2.7 (Margalef 1983). The ratio Z_{epi}/Z_{pho} was calculated and used as an index of light limitation (Talling 1971). Water column stability, S ($g \cdot cm^{-1}$), was calculated from the daily temperature profiles using the Schmidt stability index (Likens 1985):

$$S = A_0^{-1} \sum (z - z^*)\ (\rho_z - \rho^*)\ A_z\ \Delta z$$

where A_0 is surface area of the lake, A_z is the lake area at depth z, ρ_z is density as calculated from the temperature at depth z, ρ^* is the lake's mean density, and z^* is the depth where the mean density occurs. The summation is taken over all depths (z) at an interval Δz = 1 m.

Meteorological

Four daily weather variables (wind, precipitation, solar radiation, and atmospheric pressure) were collected from the Madison weather station at the Dane County Truax airport about 7 km northeast from the lake. Except for precipitation, daily values represent averages of hourly measurements across each day.

Data analysis

Epilimnetic algal biomass

Time-series analysis was used to examine relationships between the 3 algal response variables and 10 predictor (limnological, physical, and meteorological) variables. Because photic depth is a linear function of Secchi disk depth (a response variable), I excluded photic depth from this analysis. All time series were first filtered using ARMA models to remove serial correlations (Wei 1990). The response variables were cross-correlated to all predictor variables at time lags from 0 to 15 days. Because I was interested in the ability of the potential predictor variables to forecast algal conditions, I only present and discuss correlations at positive lags.

Surface scum formation

To examine whether conditions during surface scums were significantly different from conditions when surface scums were absent, I performed univariate t tests on the means of all variables during days when scums were present (N = 10) compared with the means of all variables during nonscum days (N = 122). In addition to testing the three algal response variables, I also tested the CV of the three chlorophyll *a* replicates to examine sampling variability during surface scums. In addition, because photic depth is a linear function of Secchi disk depth, I excluded it from the analysis (the significance test would be identical to that for Secchi disk depth).

The effect of all 11 predictor variables combined was examined using multivariate discriminant function analysis (Tabachnick and Fidell 1983) to determine whether the values of the predictor variables during surface scums could be distinguished from the conditions when scums were absent. To determine the relative importance of each predictor variable, group function coefficients and correlations of variables to the canonical factor were calculated.

Using the measured daily data, I determined the conditions that were sufficient for surface scums to form. I developed models that predicted the total possible number of days where surface scums could occur during summer 1993. I developed criteria for each predictor variable that represented a threshold above (or below) which a surface scum could not occur. Each criterion was defined as the observed minimum value (or maximum, depending on the variable) of the predictor variable that occurred on observed surface bloom days. The decision of whether a maximum or minimum was used was based on the means of each predictor variable during scum and nonscum days (see Table 2). For example, if the mean wind velocity on days when surface scums were present was lower than that on the days when scums were absent, the criterion was set as the maximum wind velocity observed during the 10 scum days. In other words, surface scums could potentially occur if wind velocity on a given day was less than or equal to the maximum wind velocity measured during the 10 observed bloom days. If the average value for a predictor variable was larger during scum days compared with nonscum days, then a minimum value was used. Using all the data, the number of days when the criterion was met (e.g., when wind velocity was less than or equal to the maximum) was then counted and compared with the actual number of observed surface bloom days. Models composed of various combinations of limnological, physical, and meteorological variables were compared. Because I was interested in determining whether we could identify when surface blooms are present on the lake, I included Secchi disk depth in the analysis as a predictor variable. An outlier for wind velocity in mid-July during one of the surface scum days was removed from the analysis.

Results

Biweekly phytoplankton counts showed that blue-green algae made up 98% of the total algal biomass during summer and fall. Therefore, epilimnetic chlorophyll *a* can be used as a measure of blue-green algal biomass in Lake Mendota during 1993. The major bloom-forming species was *Aphanizomenon flos-aquae*, although *Microcystis aeruginosa* dominated on a few dates.

Fig. 1. Daily time series of algal variables during summer and fall, 1993: (A) chlorophyll *a*, (B) edible chlorophyll *a* (< 35 µm), (C) Secchi depth, and (D) coefficient of variation (CV) for chlorophyll *a* measurements of triplicate samples. The gray vertical bars are days when surface scums were present.

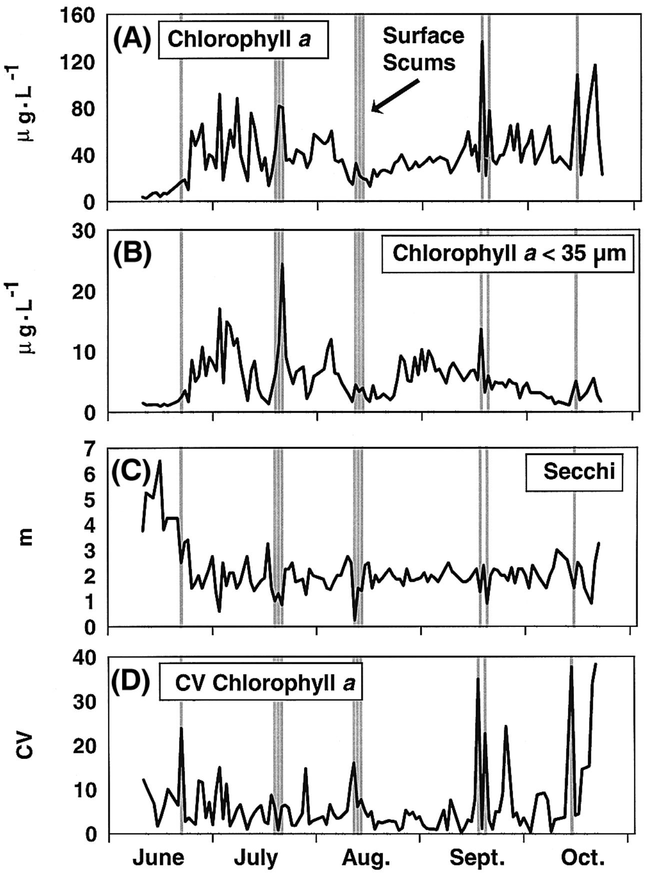
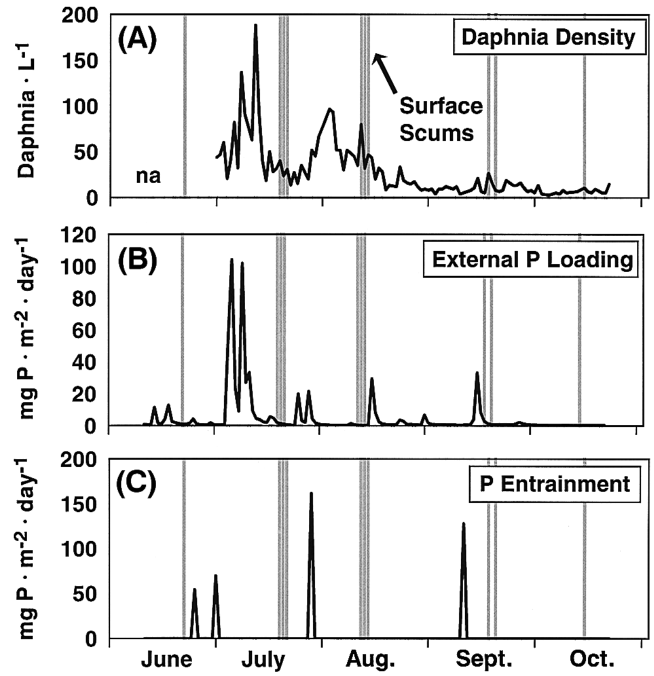


Fig. 2. Daily time series of limnological variables during summer and fall, 1993: (A) *Daphnia* density, (B) external P loading, and (C) entrainment of P into the epilimnion. The gray vertical bars are days when surface scums were present.



Daily patterns

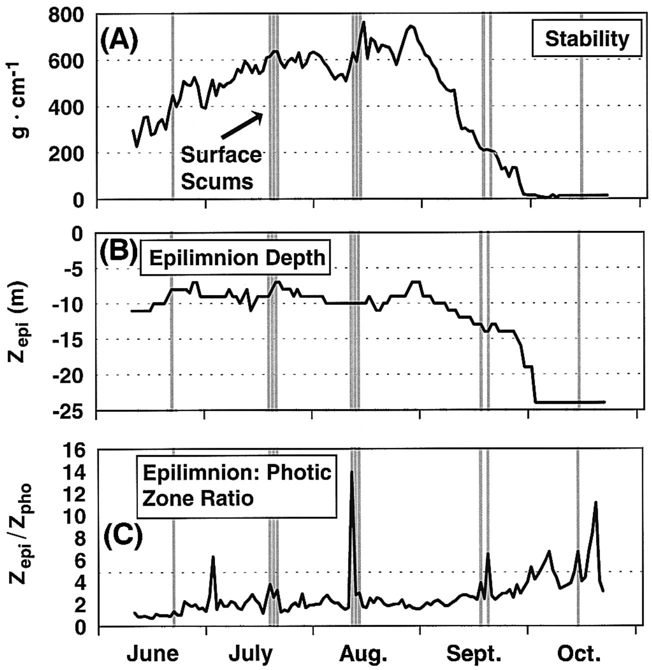
Surface scums in Lake Mendota in 1993 began in middle to late June and occurred through mid-October, well after the lake had destratified. There were five discrete surface scum "events" that lasted from 1 to 3 days with recurrence intervals ranging from 21 to 34 days. In all, there were 10 days during the summer in which surface scums were present. In remaining analyses, I either analyze all 10 days combined, or I treat these five discrete events as separate scums. Epilimnetic chlorophyll *a* levels during this same period were variable, often reaching peaks of 80–130 $\mu g \cdot L^{-1}$ (Fig. 1A). The tail end of the clear-water phase occurred in middle to late June when chlorophyll *a* concentrations were still quite low (<10 $\mu g \cdot L^{-1}$) and Secchi disk depth reached its summer maximum of 6.5 m (Fig. 1C). Afterwards, Secchi depth was consistently <2.5 m. Because chorophyll *a* was dominated by algae > 35 µm (Figs. 1A and 1B) and total chlorophyll *a* and chlorophyll *a* >35 µm were highly correlated ($r = 0.99$), all remaining analyses were done on total chlorophyll *a*, chlorophyll *a* <35 µm, and Secchi disk depth. Average CV of the triplicate samples of total chlorophyll *a* across the summer was 6.5 ± 0.6 (mean ± SE). However, the CV of the triplicates was usually greater during surface blooms (Fig. 1D).

Daphnia densities in the epilimnion peaked in early July and early August then declined to lower levels for the remainder of the summer and fall (Fig. 2A). Both external P loading and P entrainment occurred in pulses throughout summer and fall (Figs. 2B and 2C). Water column stability and epilimnion depths showed typical patterns during summer for stratified lakes (Figs. 3A and 3B). The ratio, Z_{epi}/Z_{pho} (Fig. 3C) started out quite low until early July when it increased to over 5, a value suggesting potential light limitation (Talling 1971). After July, this ratio occasionally peaked to well over 5, usually during surface blooms. Daily values for all four meteorological variables (Figs. 4A–4D) show no obvious trends through the summer except that total rainfall was higher than average during summer 1993, especially in July, when total precipitation was the third highest on record (USGS 1994).

Epilimnetic algal biomass

I hypothesized that variations in the independent variables (limnological, physical, and meteorological) would precede changes in the algal response variables (chlorophyll fractions and Secchi disk depth) at time lags ranging from 1 to 15 days. Chlorophyll variates were not significantly related to either internal or external nutrient inputs at the daily scale and were only correlated to *Daphnia* biomass at lags of 0 and 1 day (Table 1). More of the physical and weather variables were correlated to algal dynamics than were the limnological variables at time lags ranging from 0 to 9 days. For example, epilimnetic chlorophyll *a* was typically high when water column stability was high, epilimnion depth was shallow, Z_{epi}/Z_{pho} was high, wind velocity was low, and solar radiation was high.

Fig. 3. Daily time series of physical variables during summer and fall, 1993: (A) Schmidt stability, (B) epilimnion depth, and (C) the ratio of epilimnion to photic zone depth. The gray vertical bars are days when surface scums were present.



Surface scum formation

To compare conditions before, during, and after the five discrete surface scum events, variates were plotted against time axes shifted so that time 0 is when surface scums occurred (Figs. 5–7). Because these five events lasted anywhere from 1 to 3 days, I extended the "scum" period on each graph to 3 days. For three of five events, scums occurred when epilimnetic chlorophyll *a* levels were maximal (Fig. 5A). However, peaks in chlorophyll *a* did occur without scum formation, and two scum events occurred when chlorophyll *a* was as low as 20 $\mu g \cdot L^{-1}$. Except for one event, surface scums were consistently accompanied by Secchi disk depths <1.5 m (Fig. 5C).

Limnological variables showed few consistent trends across the time period before and during surface scums (Figs. 6A–6C), except that internal and external P input never occurred during the events themselves. Physical variables, on the other hand, showed some consistent patterns during scums (Figs. 7A–7C); epilimnion depth was less than, and Z_{epi}/Z_{pho} was usually greater than, the nonscum period average. On the other hand, surface scums occurred over a wide range of water column stabilities: zero (October), low (early and late stratification), and high (midsummer). But, for three of the five cases, stability increased 1–3 days before blooms to a local maximum during the event.

Meteorological variables were more strongly associated with surface scum presence than the limnological variables (Figs. 8A–D). A series of conditions were commonly observed during scums: wind velocity was low, precipitation was absent, solar radiation was higher than average (for three of the five events), and atmospheric pressure was high. Also, on the day following every surface event, wind increased, perhaps dispersing the scum, and for all scums but one, a depression

Table 1. Results of cross-correlation analyses between algal response variables (columns) and predictor variables (rows).

Group and variable	Chlorophyll *a*	Chlorophyll *a* <35 µm	Secchi disk depth
Limnological			
Daphnia biomass	+0, –1	+0, –1	–0, +1
External P	ns	ns	+5
P entrainment	ns	ns	ns
Physical			
Stability	+0	ns	–0
Epilimnion depth	–0	–0	+0
Z_{epi}/Z_{pho} [a]	+0, –1, +5, –9	+0, –1	–0, +1
Meteorological			
Wind velocity	–0	–0	+0
Precipitation	ns	+4, –8	+1, –2
Solar radiation	+0, –2, +6	ns	–0, +2
Atmospheric pressure	ns	ns	ns

Note: Values are the lag in days, and signs before numbers refer to the positive (+) or negative (–) correlation between the variable pairs. Only significant correlations at positive lags are shown (i.e., changes in predictor variables are followed in time by changes in response variables). ns, not significant.

[a] Photic depth was not included in this analysis because it is a linear function of Secchi disk depth.

Fig. 4. Daily time series of meteorological variables during summer and fall, 1993: (A) wind velocity, (B) precipitation, (C) solar radiation, and (D) atmospheric pressure. The gray vertical bars are days when surface scums were present.

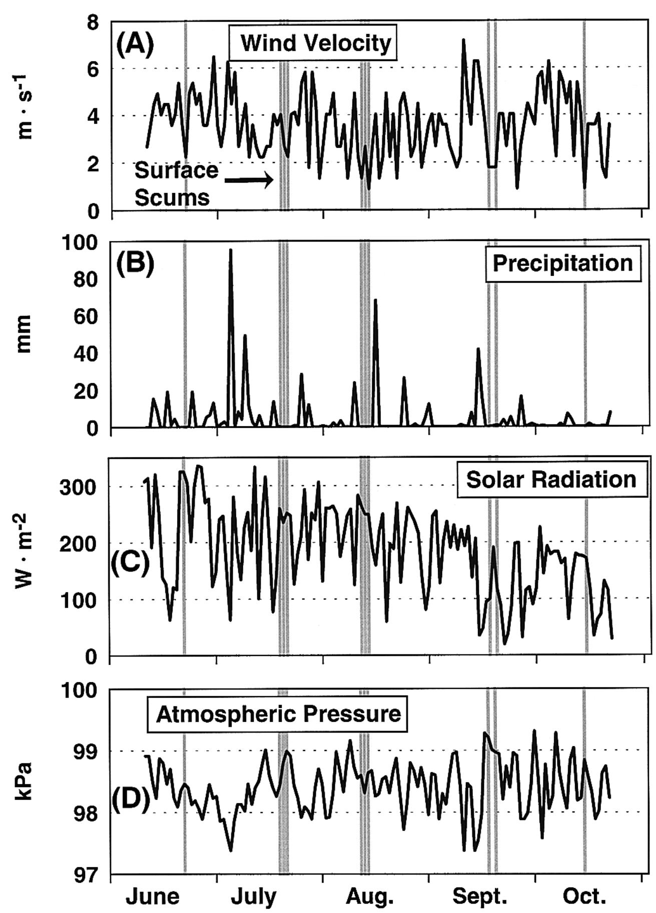
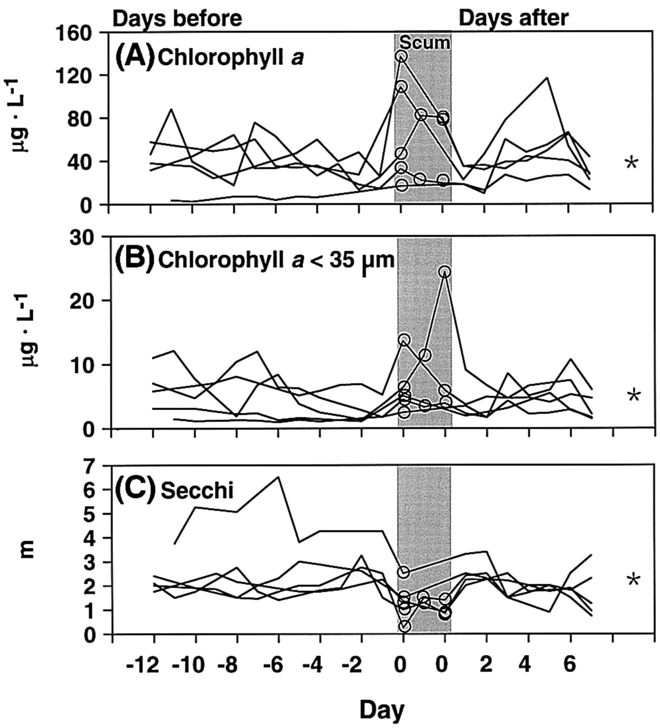


Fig. 5. Chlorophyll variables plotted on the same time scale relative to the 1–3 days that surface scums occur depending on the event (shown in gray area) for (A) chlorophyll *a*, (B) edible chlorophyll *a* (<35 μm), and (C) Secchi disk depth. Each line represents the time series for a single scum event. Open circles represent the actual days that scums are present. If an event lasts only 1 day, the line is extended to outside of the gray area. Asterisks are averages across the sampling period when surface scums are absent.



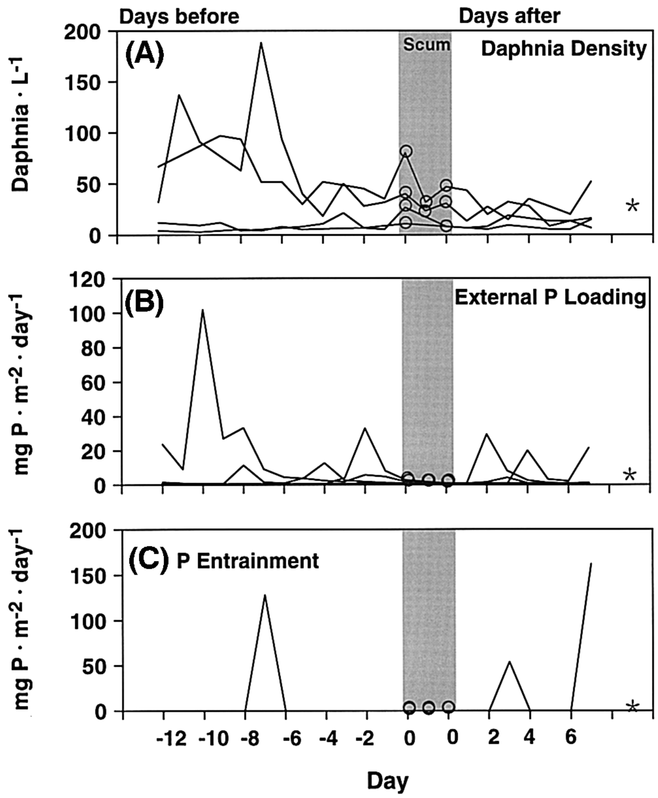
in incident solar radiation occurred 2–3 days prior to bloom formation.

The *t* tests between means on scum and nonscum days of all variables confirm the patterns observed from the above graphical analyses (Table 2). For example, means of CV of chlorophyll, Secchi disk depth, external P loading, wind, precipitation, and atmospheric pressure all differed significantly between scum and nonscum days. Thus, meteorological variates, rather than limnological or physical variates, most strongly characterized surface scum conditions.

Results from the discriminant analysis are consistent with the univariate *t* tests. Variables most important in distinguishing between surface scum and nonsurface scum days were wind velocity, atmospheric pressure, photic zone depth, and Z_{epi}/Z_{pho} (Table 3A). The overall Wilks' lambda F statistic was significant ($P < 0.001$), and 52% of the variation in the variables was explained by the canonical factor. Nevertheless, the number of days predicted to have surface scums was 50% higher than the actual number of days observed to have them (Table 3B). Based on this analysis, surface scums should have been present more often than were observed.

To examine when surface scums had the potential to form, I developed models to predict potential surface scum days based on minima or maxima of the predictor variables (Table 4). For example, the highest daily average wind velocity observed during a surface bloom was 2.68 $m \cdot s^{-1}$. The

Fig. 6. Limnological variables plotted on the same time scale relative to the 1–3 days that surface scums occur, depending on the event (shown in gray area) for (A) *Daphnia* density, (B) external P loading, and (C) entrainment of P into the epilimnion. Each line represents the time series for a single scum event. If an event lasts only 1 day, the line is extended to outside of the gray area. Asterisks are means across the sampling period when surface scums are absent. Note that only four events are plotted in panel A because sampling did not begin until mid-July; only three events are visible in panel B because the other two events have values of zero over the time period plotted; and only two events are visible in panel C because the other events have values of zero over the time period plotted.



number of days in which wind velocity exceeded 2.68 $m \cdot s^{-1}$ was 48 of a total of 132 days (model A). However, because surface blooms were present on only 21% of the possible 48 days, other factors were operating. Only models with the most explanatory power are presented. Models containing only weather variables (wind velocity, atmospheric pressure, and precipitation) explained the largest number of potential scum days (26%, model C). Adding factors such as Secchi disk depth or Z_{epi}/Z_{pho} explained little additional variance (models D and E).

Because surface scums that form when the lake is strongly stratified may respond to different factors than those scums that form when the lake is either weakly stratified or unstratified, I reanalyzed the models using only data during the period of thermal stratification (1 July to 4 September). The model based on weather alone (C′) still explained the same percentage of surface scum days. However, weather criteria combined with either Secchi depth (model D′) or Z_{epi}/Z_{pho} (model E′) explained 86% of the potential surface bloom days.

Fig. 7. Physical variables plotted on the same time scale relative to the 1–3 days that surface scums occur, depending on the event (shown in gray area), for (A) Schmidt stability, (B) epilimnion depth, and (C) the ratio of epilimnion to photic zone depth. Each line represents the time series for a single scum event. If an event lasts only 1 day, the line is extended to outside of the gray area. Asterisks are averages across the sampling period when surface scums are absent. Note that only four events are visible in panels A and B because the scum event in October occurred when stability was practically zero, and there was no established epilimnion during the time period plotted.

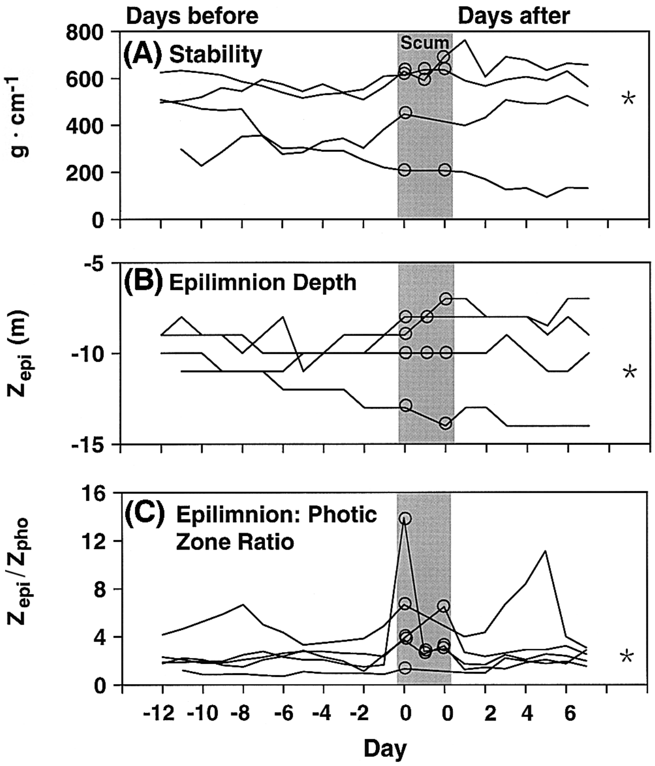
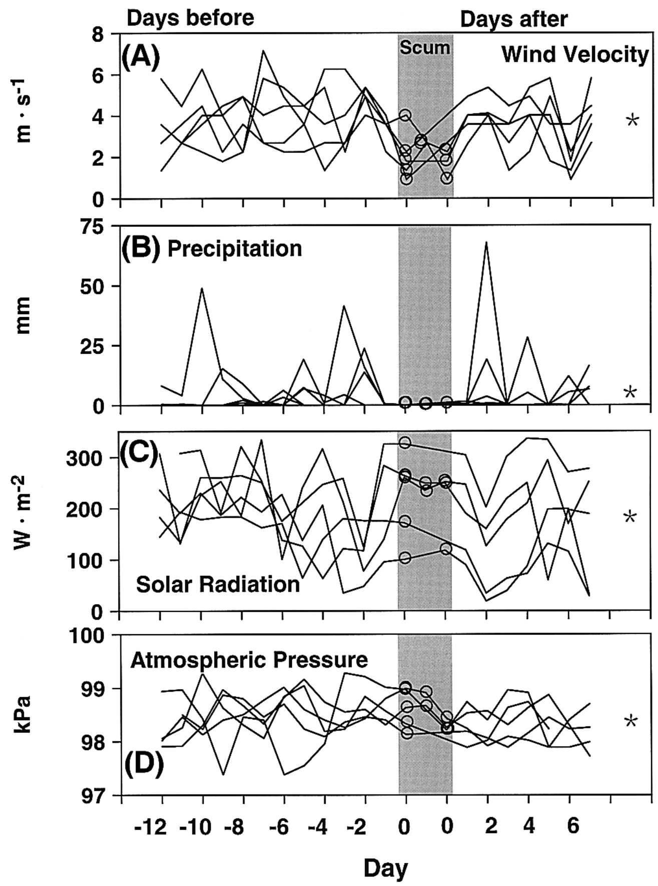


Fig. 8. Meteorological variables plotted on the same time scale relative to the 1–3 days that surface scums occur, depending on the event (shown in gray area), for (A) wind velocity, (B) precipitation, (C) solar radiation, and (D) atmospheric pressure. Each line represents the time series for a single scum event. If an event lasts only 1 day, the line is extended to outside of the gray area. Asterisks are averages across the sampling period when surface scums are absent.



Discussion

Blooms of blue-green algae in large eutrophic lakes such as Lake Mendota, Wisconsin, are often characterized by high inter- and intra-annual variability during the summer stratified season (Konopka et al. 1978; Lathrop and Carpenter 1992). The purpose of this study was to quantify variability of both epilimnetic blooms and surface scums at the daily scale and to identify the factors correlated with them during the summer and fall. At the daily scale in Lake Mendota, nutrient supply and grazing by *Daphnia* failed to explain many of the daily epilimnetic chlorophyll dynamics but physical and weather variables were correlated to some algal variates. In addition, surface scums were difficult to forecast at the daily scale, and no single variable or combination of variables appeared to strongly suggest surface scums were imminent. However, when scums were present, weather variables showed some common patterns that were significantly different than when scums were absent. At the daily scale, it is weather that fluctuates and strongly determines the physical environment of the water column, which in turn strongly influences algal dynamics. Thus, at least in eutrophic lakes such as Lake Mendota, weather and physical variables may account for a large part of observed natural variability in phytoplankton dynamics (Sephton and Harris 1984; Harris 1987), especially in the absence of nutrient limitation (Harris and Piccinin 1980).

Epilimnetic algal biomass

For phytoplankton to respond to either internal or external pulses of nutrients, growth must be limited by the nutrients that are supplied (Stauffer and Lee 1973; Kononen et al. 1996). In Lake Mendota during summer and fall 1993, algal variables were not stimulated by P inputs from either hypolimnetic entrainment or external loading (Table 1). During summer 1993, an unusually large P pool occurred in Lake Mendota owing to high spring and summer runoff. The average dissolved reactive P (DRP) concentration during the summer (62 μg P·L^{-1}) was the highest on record from the past 17 years (average summer DRP 12 ± 18 μg·L^{-1} (mean ± SD); Lathrop 1992; R.C. Lathrop, unpublished data). Thus, it is likely that nutrients were not limiting, so the importance of hypolimnetic P entrainment during average or low external loading conditions could not be tested.

Table 2. Group means and *t* tests between means on nonscum ($N = 122$) versus scum ($N = 10$) days for all variables.

Group and variable	Nonscum mean	Scum mean	*t*	*P*
Algal				
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	37.3	62.1	–1.88	0.091
CV Chlorophyll *a*	5.8	16.2	2.50	0.033
Chlorophyll *a* <35 µm ($\mu g \cdot L^{-1}$)	5.0	8.1	–1.43	0.185
Secchi disk depth (m)	2.3	1.3	5.11	<0.001
Limnological				
Daphnia ($animals \cdot L^{-1}$)[a]	27.5	33.2	–0.73	0.478
External P ($mg\ P \cdot m^{-2} \cdot day^{-1}$)	5.2	1.0	3.10	0.003
P entrainment ($mg\ P \cdot m^{-2} \cdot day^{-1}$)	3.4	0.0	—[b]	
Physical				
Stability ($g \cdot cm^{-1}$)	392.3	467.1	–0.95	0.362
Epilimnion depth (m)	12.4	11.3	0.64	0.538
Z_{epi}/Z_{pho}[c]	2.5	4.8	–1.93	0.085
Meteorological				
Wind velocity ($m \cdot s^{-1}$)	3.8	2.1	5.26	<0.001
Precipitation (mm)	4.8	0.08	4.09	<0.001
Solar radiation ($W \cdot m^{-2}$)	184.2	222.2	–1.63	0.132
Atmospheric pressure (kPa)	98.38	98.72	–3.48	0.004

[a] $N = 103$ for nonscum days and $N = 9$ for scum days
[b] Insufficient data for the test.
[c] Because photic depth is a linear function of Secchi disk depth, it was not included in this analysis.

Table 3. Results from discriminant analysis of limnological, physical, and meteorological variables that best distinguish between scum and nonscum days.

(A) Correlations of predictor variables with canonical factor and group classification function coefficients.

Group and variable	Factor	Nonscum group	Scum group
Limnological			
Daphnia biomass	–0.07	1.82	1.81
External P	0.13	0.58	0.58
P entrainment	0.08	1.89	1.89
Physical			
Stability	–0.14	0.27	0.26
Epilimnion depth	0.09	0.26	–0.18
Photic depth	0.49	–36.23	–36.36
Z_{epi}/Z_{pho}	–0.56	13.19	14.49
Meteorological			
Wind velocity	0.58	174.06	173.45
Precipitation	0.17	6.42	6.43
Solar radiation	–0.22	–0.51	–0.51
Atmospheric pressure	–0.37	1053.31	1054.90
Constants		–52 112	–52 265

(B) Predicted number of surface scum and nonscum days from the discriminant function analysis and the actual observed number of scum days.

	Predicted		
Actual	Present	Absent	Total
Present	8	2	10
Absent	7	115	122
Total	15	117	132

Even though epilimnetic blooms of *Aphanizomenon flos-aquae* have often been associated with the large herbivore, *Daphnia pulicaria* (Lynch and Shapiro 1981; Carpenter 1989), grazing by *Daphnia* explained few of the algal dynamics observed in this study. *Daphnia* densities were significantly correlated to all algal variables but only at lags of 0 and 1, so when chlorophyll was high, *Daphnia* biomass was also high. Grazing pressure may not have been significant, since there was no subsequent decline in total or edible chlorophyll at longer time lags.

Surface scums

Surface scums have been commonly perceived to represent senescing populations that are unable to regulate buoyancy when at the surface (Paerl 1988). This is usually not the case, and several studies have shown that surface scum formation represents an ecological strategy to make use of conditions at the air–water interface: access to photosynthetically active radiation, and to atmospheric carbon (C) and N (Paerl and Kellar 1979; Lewis 1983; Paerl and Ustach 1982). My results support these findings by showing that scums usually co-occur with peaks in epilimnetic chlorophyll and that these increases consequently create low light conditions. Except for one day in early July, Z_{epi}/Z_{pho} was maximum during surface scums and usually >5, the value that indicates light limitation (Talling 1971). Because surface scums can markedly change the light, nutrient, and physical environment of the water column, they can be viewed as a disturbance to the rest of the algal community (Paerl 1988; Klemer and Konopka 1989). Occurring every 20–30 days, scums can be defined as "low-frequency" disturbances (Reynolds 1988; 1993), which could potentially influence algal community succession.

So far, some useful patterns have emerged from asking when surface scums do form. However, can anything be learned from asking when they do not form? The univariate and multivariate analyses performed on these data have identified the average conditions that identify surface scums. During scum events, average wind velocity, precipitation, atmospheric pressure, and Secchi disk depth are significantly different than when they are absent (Table 2). However, rather than be defined by average conditions, surface scum formation may be better defined by threshold conditions. In other words, the average wind velocity observed during surface scums may not be as informative as the maximum wind velocity that a scum can withstand without being destroyed by surface layer turbulence. If all that is necessary for surface blooms to form is a stable water column, proper weather conditions, and a pre-existing blue-green algal population (Reynolds and Walsby 1975), then surface blooms should have occurred on 23 days when the lake was stratified (1 July to 4 September) instead of on only 6 days during summer in 1993 (model C′; Table 4), and they should not have occurred on the days in early summer and fall when the lake was either weakly or unstratified (Fig. 3). Zohary and Breen (1989) also found that a stable water column, proper weather conditions, and a pre-existing water algal population were not sufficient to predict the formation of hyperscums in a hypertrophic lake.

Nevertheless, predictions improved when the data that was analyzed was restricted to the time of thermal stratification. During stratification, a surface bloom is very likely (86%) to be present if meteorological conditions are favorable, and Secchi disk depth is ≤1.5 m or Z_{epi}/Z_{pho} ≥2.56 (Table 4, models D′ and E′). Surprisingly, Secchi disk depth alone fails to be a strong indicator of surface scums (35%). These types of models may be useful for identifying "potential scum days" from historical data using daily meteorological data, which is frequently available, and weekly or biweekly Secchi disk depth, chlorophyll, and physical data that is often available for long-term studies of single lakes. This approach seems most useful for retrospective data and only has the potential for forecasting in so far as it is possible to forecast the weather.

Surface scums in Lake Mendota during summer and fall 1993 were relatively infrequent, extreme events that lasted from 1 to 3 days and occurred roughly every 20–30 days. To estimate how well traditional sampling schedules (weekly and biweekly) would have detected these scums, I resampled the daily data set at both weekly and biweekly intervals using all possible starting dates (7 for the weekly schedule, and 14 for the biweekly schedule). On average, about 1 of the 10 measured surface scum days were detected for both weekly (range 0–3 days) and biweekly (range 0–2 days) sampling schedules. Such detection rates would provide, at best, only anecdotal evidence to explain conditions that occur during and preceding surface scums. While means for chlorophyll *a* and Secchi disk depth can be accurately assessed at the weekly or biweekly scale, rare events such as blue-green algal scums cannot. However, because measuring at the daily scale is rarely feasible or affordable, innovative sampling regimes or analyses will be necessary to examine extreme events such as these (Walker 1985; Gaines and Denny 1993).

Table 4. Models predicting potential surface scum days during summer and fall 1993 and the percentage of the days that had the potential to form surface scum that actually did form scums.

(A) Data analyzed for entire sampling period (132 days analyzed).

Model	Criteria	No. of days scums possible	No. of observed scums	%
A	Wind ≤2.68	48	10	21
B	Wind ≤2.68	44	10	23
	Atm ≥98.3			
C	Wind ≤2.68	38	10	26
	Atm ≥98.3			
	Prec ≤0.76			
D	Wind ≤2.68	36	10	28
	Atm ≥98.3			
	Prec ≤0.76			
	Sec ≤2.5			
E	Wind ≤2.68	37	10	27
	Atm ≥98.3			
	Prec ≤0.76			
	Z_{epi}/Z_{pho} ≥1.3			

(B) Data analyzed during period of stratification from 1 July to 4 September 1993 only (72 days analyzed).

Model	Criteria	No. of days scums possible	No. of observed scums	%
A′	Wind ≤2.68	31	6	19
B′	Wind ≤2.68	29	6	21
	Atm ≥98.3			
C′	Wind ≤2.68	23	6	26
	Atm ≥98.3			
	Prec ≤0.76			
D′	Wind ≤2.68	7	6	86
	Atm ≥98.3			
	Prec ≤0.76			
	Sec ≤1.5			
E′	Wind ≤2.68	7	6	86
	Atm ≥98.3			
	Prec ≤0.76			
	Z_{epi}/Z_{pho} ≥2.56			

Note: Criteria were defined as the minimum or maximum value observed during the actual surface scum days (see text). Wind, wind velocity ($m \cdot s^{-1}$); Atm, atmospheric pressure (kPa); Prec, precipitation (mm); Epi, epilimnetic depth (m); Sec, Secchi disk depth (m); Z_{epi}/Z_{pho}, ratio of epilimnetic depth to photic zone depth (dimensionless).

Implications

Some have suggested that "mean" chlorophyll levels may be poor descriptors of water quality because it is extreme levels, or blooms (defined as epilimnetic blooms), that influence how the public perceives the actual lake condition (Reckhow 1988; Walker 1985). However, estimates of "true" maximum values are sensitive to the sampling regimes used. To overcome this bias, models have been fit to monitoring data and used to predict chlorophyll frequency distributions from mean epilimnetic chlorophyll concentrations (Walker 1985; Havens 1994). From these models, it is possible to predict extreme chlorophyll values from mean chlorophyll levels for a given lake. These models operate under the assumption that epilimnetic chlorophyll "blooms" are a good determinant of surface scums. However, my study shows that surface scums cannot be predicted from vertically integrated epilimnetic chlorophyll concentrations alone and, in fact, respond to a variety of factors, especially weather. In addition, surface scums lead to higher sampling variability (CV of epilimnetic chlorophyll), which could increase error in these models. It may be reasonable to assume that the probability of surface scum formation increases as algal biomass increases, but this assumption has rarely been explicitly examined and my results suggest that it certainly is not a straightforward relationship. Peaks in epilimnetic chlorophyll *a* did occur for three of five surface scums, but peaks also occurred when surface scums were absent, and scums were observed when chlorophyll *a* concentrations were quite low. Including some measure of surface scums should be considered for both modeling studies and lake-management strategies.

The important role that weather plays in both algal biomass and surface scum formation has important management implications. First, by contributing to overall algal variability, weather should negatively impact our ability to predict algal dynamics. Second, we may improve some water-quality models by incorporating weather variables explicitly (James and Havens 1996). Third, although we cannot manage the weather, we can manage nutrient inputs and, as others have shown, decreasing nutrient levels will decrease blue-green algal biomass and bloom probabilities (Stow et al. 1997; Havens 1994; James and Havens 1996). However, the recognition that, at any nutrient level, weather may decrease our ability to predict should be recognized and warrants further research.

Conclusions

This study demonstrates and extends the scale dependency of the predictability of blue-green algal biomass and blooms (Paerl 1988; Carpenter 1989). Among lakes, blue-green dominance and average summer biomass can be predicted at the seasonal scale from nutrient data (Smith 1986; Trimbee and Prepas 1987). Within a given lake, year-to-year variability in mean or monthly summer biomass or algal bloom frequency can also be predicted from various measures of nutrients, grazers, physical variables, or weather variables (Schindler 1977; McQueen and Lean 1987; Zohary and Breen 1989; Lathrop and Carpenter 1992; James and Havens 1996; Stow et al. 1997). For example, multiyear time-series analyses for Lake Mendota have shown that winters with high TP concentrations are followed by summers with unusually high blue-green algal biomass (Lathrop and Carpenter 1992), and in whole-lake experiments, blue-green algae appear and disappear depending on N:P ratios in the nutrient supply (Schindler 1977). Also, studies on hypereutrophic Haartbeesport Dam in South Africa (Zohary and Breen 1989) and the large eutrophic Lake Okeechobee in Florida (James and Havens 1996) have shown a strong relationship between wind and the formation of epilimnetic blooms at the biweekly or seasonal scale. At much finer time scales (<1 day), laboratory studies have shown the importance of limitation by light, C, and N on buoyancy control (Kromkamp et al.1986; Paerl 1988; Spencer and King 1989; Oliver 1994). This study shows that, between these two scales at the daily scale, (*i*) epilimnetic blue-green algal biomass was correlated to meteorological conditions and physical characteristics of the water column; and (*ii*) surface scum presence was strongly determined by weather, although weather alone was not sufficient to predict when scums formed. It is likely that a hierarchical framework best explains both epilimnetic blue-green algal biomass dynamics and surface scum formation (Carpenter 1989): populations respond to physical conditions that are strongly driven by weather and blue-green algal cells become positively buoyant from a variety of factors that include decreased CO_2, increased inorganic N (in the presence of low C), and decreased light availability (Oliver 1994); however, surface scums will form when additional criteria are met, such as when wind speed is below a threshold velocity, there is no precipitation, and atmospheric pressure is high.

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