

LETTER

Wind and trophic status explain within and among-lake variability of algal biomass

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Scientific Significance Statement

Mean phytoplankton biomass and production in lakes are known to be strongly related to nutrients, light, weather, water column mixing, and grazing. However, much less is known about the factors that are related to variation in phytoplankton biomass and production, particularly at the scale of hours, days, and months, due in part to the labor-intensive nature of phytoplankton sampling. We used high-frequency monitoring of chlorophyll fluorescence in 18 lakes across the world to address this important knowledge gap. We found that among lakes, phytoplankton biomass variation increased as trophic status increased; whereas, within lakes, phytoplankton biomass variation increased as variation in wind speed increased. Studies focusing on predicting change in phytoplankton biomass will need to incorporate these key variables and consider the scales at which they operate.

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Author Contribution Statement: This project was initiated in a workshop at the Global Lakes Ecological Observatory Network meeting in Sunapee, New Hampshire, USA in 2011. The authors are listed in three groups: JAR-KCR; SPH-LAW; and RA-GZ. The first group is listed in order of contribution. The second group, listed alphabetically, includes authors who attended the workshop and were substantively involved in the initial framing of the project and contributed to data interpretation and writing the manuscript. The third group, listed alphabetically, contributed data and feedback on the manuscript. The lead author, JAR, coordinated the project, conducted early data analysis, and wrote the initial manuscript. AJT performed the Bayesian variance component analysis and associated statistical tests as well as generated text and figures for the primary results and contributed to writing the manuscript. JLK and KCR contributed to the initial framing of the project, and were extensively involved in data interpretation, in writing the manuscript and in project management. ER, KCR, and LAW coordinated initial data collection and data management. JAR, JLK, SPH, EJ, AL, DP, ER, DSW, LAW, RA, LA, EE, HF, MH, VI, IDJ, CGM, SRS, PAS, DS, and GZ contributed data. All authors reviewed, edited, and approved the manuscript.

Data Availability Statement: Data are available at the Environmental Data Initiative data repository at <https://portal.edirepository.org/nis/mapbrowse?packageid=edi.133.2>.

Additional Supporting Information may be found in the online version of this article.

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Abstract

Phytoplankton biomass and production regulates key aspects of freshwater ecosystems yet its variability and subsequent predictability is poorly understood. We estimated within-lake variation in biomass using high-frequency chlorophyll fluorescence data from 18 globally distributed lakes. We tested how variation in fluorescence at monthly, daily, and hourly scales was related to high-frequency variability of wind, water temperature, and radiation within lakes as well as productivity and physical attributes among lakes. Within lakes, monthly variation dominated, but combined daily and hourly variation were equivalent to that expressed monthly. Among lakes, biomass variability increased with trophic status while, within-lake biomass variation increased with increasing variability in wind speed. Our results highlight the benefits of high-frequency chlorophyll monitoring and suggest that predicted changes associated with climate, as well as ongoing cultural eutrophication, are likely to substantially increase the temporal variability of algal biomass and thus the predictability of the services it provides.

Phytoplankton (~ planktonic algae) form the base of most aquatic food webs and their abundance and dynamics regulate the services aquatic ecosystems provide (Platt et al. 2003; Qin et al. 2010). Because variation in the provisioning of ecosystem services can complicate management efforts (Carpenter et al. 2015), the ability to reliably predict changes in these services depends on understanding the environmental controls of algae and how algal variability is expressed in space and time (Cottingham et al. 2000; Fraterrigo and Rusak 2008). Algae respond to a range of habitat fluctuations including temperature, light, nutrients, water column mixing, and herbivory (Reynolds 2006). Consequently, the ongoing planetary shifts in surface-water temperature (O'Reilly et al. 2015), thermal stratification (Adrian et al. 2009), solar dimming and brightening (Wild 2012), nutrient availability (Smith 2003), wind speeds (Vautard et al. 2010), and food webs (Cross et al. 2015) and their interactions will likely have dramatic consequences for variation in the production of algal biomass as well as the services that are derived from this vital resource.

Apart from general relationships over broad spatial gradients (Dillon and Rigler 1974), predicting how algal biomass responds to changes in environmental drivers has proven exceedingly difficult (Kara et al. 2012; Winder and Sommer 2012). We can often accurately model the physical and chemical dynamics of lakes (Mooij et al. 2010), but algal communities can be variable and unpredictable from one lake to another or even within an individual lake over time (Litchman 1998; Winder and Cloern 2010), although high-frequency data has recently shown promise in predicting mean phytoplankton abundance at submonthly frequencies (Thomas et al. 2018). More fundamentally, relatively little is known of how variation in algal biomass itself is apportioned within and among systems, particularly at fine temporal scales (e.g., hours to days). This uncertainty hinders our ability to manage aquatic ecosystems, particularly in an increasingly complex world with multiple interacting stressors (Benincá et al. 2008; Jackson et al. 2016).

Attempts to quantify variability *per se* in algal biomass have revealed that most spatial and temporal variation remains difficult to characterize. For example, Cloern and Jassby (2010) quantified variability within and among coastal and estuarine systems sampled at monthly intervals using traditional spectrophotometric determinations of extracted chlorophyll *a* (Chl *a*). They partitioned variance at monthly and annual timescales and found that variation occurred somewhat equally at seasonal (monthly) and annual scales across sites. However, the largest fraction of the variation was unexplained by month or year and occurred at time periods shorter than their monthly sampling frequency. Although seasonal patterns in mean biomass are common in many lakes (Sommer et al. 2012), the variation around this seasonality is poorly characterized (Cloern and Jassby 2010; Winder and Cloern 2010). In support, Istvánovics et al. (2005) estimated the characteristic period of algal biomass in Lake Balaton to be on the order of 5–7 d which necessitates a sampling frequency of 2–3 d to adequately capture algal dynamics.

Traditional estimates of chlorophyll concentrations are labor-intensive and typically conducted at weekly to monthly frequencies. Recent advances in high-frequency monitoring of chlorophyll fluorescence (chlF) provide a proxy for algal biomass (Baker 2008; Brentrup et al. 2016), and although subject to some methodological constraints (Serra et al. 2009), have made it possible to investigate algal variability at temporal scales that were previously inaccessible (i.e., minutes to hours). Similarly, many limnological events with the potential to influence algal biomass are temporally dynamic and are only captured by high-frequency monitoring efforts. For example, thermal stratification events with a duration of < 1 d represented 80% of all stratified periods within a polymictic lake (Wilhelm and Adrian 2008) and the range in day to night surface-water temperature has been found to vary dramatically among lakes of differing size (Woolway et al. 2016).

To better understand the patterns of variability at higher frequencies, we analyzed nearly 100,000 measurements of

chlF from 18 freshwater lakes and reservoirs around the globe to (1) quantify how variation in algal biomass is apportioned at hourly, daily, and monthly scales across our study lakes using a hierarchical Bayesian framework, and (2) identify predictors of this variation. These predictors (Table 1) fell into two major categories: (1) among-lake descriptors of lake morphology, productivity, and transparency, and (2) within-lake high-frequency data for local meteorological and limnological drivers (wind speed, solar radiation, and water temperature). Among lakes, we hypothesized a positive correlation between variability in algal biomass and productivity because nutrient enrichment has previously been shown to increase the variability of algal biomass in whole-lake experiments (Cottingham et al. 2000). Within lakes, we tested whether hourly, daily, and monthly variation in algal biomass positively covaried with variation in high-frequency measurements of wind speed (Carrick et al. 1993), surface-water temperature (Robarts and Zohary 1987), and photosynthetically active radiation (PAR) (Slegers et al. 2011). Covariation with locally measured physical variables indicates pathways by which environmental change may alter the variability of algal dynamics.

Our results demonstrated that increasing trophic status among lakes, and variation in wind speed within a lake, were significant positive correlates of variation in algal biomass. These findings suggest that increasing variability in wind, potentially driven by increases in extreme storm events (Knutson and Tuleya 2004; Meehl et al. 2005), and nutrient inputs (Carpenter et al. 2008; Schindler 2012) have the potential to increase variability in algal biomass and thereby reduce predictability in the delivery of associated aquatic ecosystem services.

Methods

Study sites

We used data from 18 lakes (Supporting Information Fig. S1) encompassing broad gradients of physical and biological characteristics including area, depth, residence time, Chl *a*, water clarity, and mixing regime (Supporting Information Table S1). A total of 3834 lake-days from 18 lakes were used; the number of days from each lake ranged from 96 to 363 with a mean \pm standard error of 213 ± 21 d. For each lake, chlF was sampled during the growing season from 1 yr during the period 2008–2013. All data were from lakes in the Global Lakes Ecological Observatory Network (GLEON; <http://gleon.org>).

Data collection and postprocessing

High-frequency hourly time series measurements (Winslow et al. 2017) of chlF (following excitation of algal cells with light of ~ 470 nm), wind speed, water temperature, and PAR were collected by automated observation platforms on each lake for a minimum of 4 months during the ice-free season.

Table 1. Median correlation coefficients between among and within-lake attributes and chlF VCs at hourly, daily, and monthly timescales (in columns 2–4). Within lakes, we calculated VCs at hourly, daily, and monthly scales for wind speed (“Wind”), water temperature (“Temp”), and PAR. We only calculated correlations between these VCs and chlF at matching (or more temporally aggregated) explanatory variable timescales, thus eliminating unrealistic relationships. Bolded values have 95% CIs that exclude zero. Latitude and longitude were included to test whether geography influenced any of the documented relationships.

Attribute	Hour VC	Day VC	Month VC
AMONG LAKES			
Latitude	−0.45	−0.35	−0.22
Longitude	0.23	0.04	−0.06
Lake area	−0.19	0.12	0.33
Max depth	0.22	−0.33	−0.17
Mean depth	0.37	−0.15	0.02
Residence time	0.11	−0.27	−0.20
Trophic Status	0.18	0.57	0.51
Water clarity	−0.38	0.10	0.19
WITHIN LAKES			
Wind hour VC	0.48	0.50	0.69
Wind day VC		0.42	0.75
Wind month VC			0.57
Temp hour VC	−0.36	0.03	−0.12
Temp day VC		0.01	−0.34
Temp month VC			0.44
PAR hour VC	−0.15	0.22	0.10
PAR day VC		0.15	0.12
PAR month VC			0.55

For some sites, short-wave radiation was measured and converted to PAR (Papaioannou et al. 1993). Fluorescence sensors were deployed at approximately 1 m depth to measure typical conditions in the surface mixed layer. For temperature, we used sensor data measured closest to a depth of 1 m. Accurate determination of mixing depths was not possible for all lakes because of differences in sensor distribution. We therefore calculated the difference between surface temperatures and the temperature at a depth of approximately one-tenth of the maximum depth in each lake as a measure of water column stability. The constant percent depth increment allowed us to standardize this measure across lakes of differing depths (Supporting Information Table S1). High-frequency data were quality checked and interpolated where possible. We interpolated these datasets to fill in short periods of missing data (no longer than one-tenth of a day) using the spline interpolation method from MATLAB (v2011a). All lakes were down-sampled to a 1 h sampling interval by averaging all samples during each previous hour to facilitate comparisons of model fits across lakes. Because we wished to examine variation in

absolute concentrations of chlF and some datasets were collected as relative fluorescence units instead of $\mu\text{g L}^{-1}$, we standardized hourly values in all lakes by multiplying hourly chlF by a lake-specific scaling factor (the ratio of extracted mean annual Chl *a* to mean of chlF values [see Supporting Information Table S1]).

Lake characteristics including lake area, latitude, longitude, mean and maximum depth, mean Chl *a*, and the diffuse attenuation coefficient (Kd) were measured or estimated from related variables during the period of high-frequency data collection (Supporting Information Table S1). We used traditional extracted mean annual Chl *a* data (measured by spectrophotometry, fluorometry, or high-performance liquid chromatography), as our proxy of lake trophic status (*sensu* Carlson 1977 who chose algal biomass, represented as Chl *a*, as the basis for his trophic state index). Kd was derived from the log-linear portion of PAR irradiance vs. depth data, or, when clarity was not measured directly, it was estimated by a model incorporating dissolved organic carbon and Chl *a* (Morris et al. 1995) or from a modeled conversion of Secchi depth (Kirk 1994). All non-normal data were natural logarithm-transformed prior to analysis.

Statistical approach

Using a single hierarchical model, we partitioned the variation in chlF associated with hourly, daily, and monthly timescales in each lake simultaneously and tested whether these values were associated with similarly calculated variance components (VCs) for our other high-frequency measurements (surface-water temperature, wind speeds, and PAR) and lake-level attributes (latitude, longitude, area, depth, clarity, residence time, trophic status, and the means of wind speed, surface temperature, and PAR) commonly thought to influence algal biomass. Our approach was thus analogous to the variance partitioning undertaken by Cloern and Jassby (2010), but had the advantages of incorporating all levels of temporal variation in a single analysis and being able to quantify the uncertainty associated with our VCs.

Briefly, we assumed that the m -dimensional vector \mathbf{X} of VCs at each temporal scale for each of the four high-frequency responses, along with the observed values of the 12 lake-level attributes, could be described in each lake by a multivariate normal distribution $\mathbf{X} \sim N(\boldsymbol{\mu}, \boldsymbol{\Sigma})$. Because the VCs were only partially observed, they were treated as latent variables that were constrained by observed high-frequency data and sampled from a log-normal multivariate hyper-prior distribution that placed relatively uninformative priors on each hyper-parameter. $\boldsymbol{\mu}$ was a vector of mean values across lakes for each parameter and $\boldsymbol{\Sigma}$ was an estimated covariance matrix. As $\boldsymbol{\Sigma}$ could ultimately be decomposed into a product of a vector of the standard deviations of each of the m parameters and a matrix of their pairwise median correlation coefficients, we were able to test directly the associations among our focal parameters. Although all $m-1$ combinations of correlations

were estimated, we only examined those between explanatory variables and chlF where the timescales of the VCs matched or were more aggregated for chlorophyll (i.e., variability in daily wind might influence variability in daily or monthly algal biomass but is unlikely to affect hourly chlorophyll). All model fitting was performed with a Bayesian framework, so we subsequently report mean and 95% credible intervals (CIs) from the posterior distributions of VCs and correlation coefficients. We also summarized model fit by calculating a Bayesian R^2 at the level of our observed data (analogous to frequentist linear regression—Gelman and Pardoe 2006). Full model details are given in Supporting Information. R code (R Development Core Team, 2015) for the model is provided as Supporting Information.

Results

ChlF modeling results fit the data well across lakes with a mean Bayesian R^2 (95% CI) of 0.96 (0.96–0.96) (Supporting Information Fig. S2). The estimated variances for hour, day, and month in each lake covaried with each other, with mean correlations ranging between 0.54 and 0.70, all with 95% CIs that excluded zero. There were no correlations between the width of CIs for our model parameters and the length of the individual lake time series, emphasizing that variation in monitoring duration among lakes did not confound our analyses (mean correlation coefficient between duration and CI estimates for hour, day, and month: $r = 0.01, 0.03,$ and 0.24 , respectively; for all, 95% CIs overlapped zero).

Most of the variation in chlF across the dataset was explained at the monthly rather than hourly or daily timescale. Across lakes, a mean of between 22% and 64% of the total variance could be explained by month, and monthly variation significantly exceeded that of either daily or hourly scales in 14 of the 18 study lakes (Fig. 1), as measured by differences in 95% CIs among estimates that were positive and nonoverlapping zero. In the remaining four lakes, there were no differences between monthly and either hourly or daily variation, though hourly and daily variation did differ from each other in three of these lakes (Harp, Lillinonah, and Vedsted in Fig. 1).

Significant environmental correlates of among and within-lake variation in chlF were surprisingly few (Table 1). Within lakes, variation in wind speed (Supporting Information Fig. S3) was positively correlated with variation in chlF at all temporal scales (Fig. 2; Table 1). Monthly variance in PAR (Supporting Information Fig. S4) was also significantly correlated with monthly chlF VCs (Fig. 3), but no relationships between chlF VCs and water temperature (Supporting Information Fig. S5) were evident at any temporal scale examined. Among lakes, we found support for our *a priori* among-lake prediction of positive covariation in daily and monthly chlF variability and lake trophic status (Fig. 4). We also noted, both here and in Fig. 1, that monthly chlF variation increased up to a potential threshold around 10–20 $\mu\text{g L}^{-1}$ before reaching an

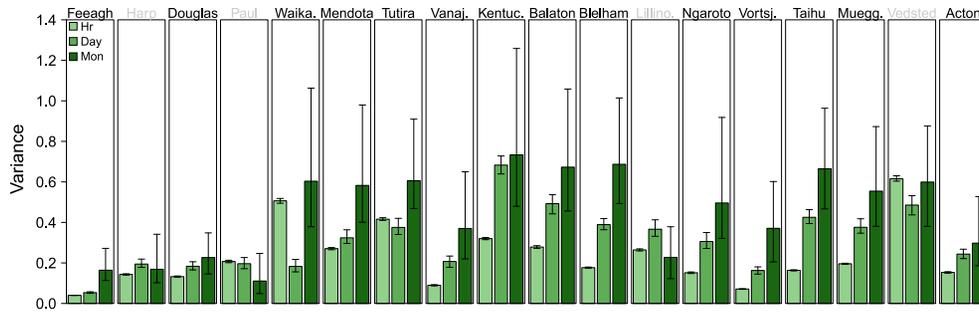


Fig. 1. Variance components on a standard deviation scale derived from fitting a Bayesian hierarchical model to the chlF data from 18 lakes (Supporting Information Fig. S1 and Table S1), accounting for hourly (light green shading), daily (intermediate green shading), and monthly (dark green shading) variation. VCs are median estimates and error bars are ± 95% CIs. Bolded sites have greater monthly variation than at either daily and/or hourly scales. Lakes are sorted in increasing trophic status from left to right and monthly VCs appear to reach maximum values in lakes with mean algal biomass values of approximately 10–20 $\mu\text{g L}^{-1}$ (also see Table 1).

asymptote and decreasing slightly. Finally, absolute latitude was negatively correlated with hourly chlF VCs (Table 1). This correlation was potentially spurious and unlikely to be indicative of any causal pattern as absolute latitude was also strongly negatively correlated with hourly wind speed VCs (mean correlation = -0.50, 95% CI = -0.76 to -0.09).

Discussion

The unprecedented collection of high-frequency data used for this study enabled us to examine unexplored temporal

patterns of variation in chlF, a widely used proxy for algal biomass. Overall, our results explained substantially more variation in chlorophyll dynamics than analyses of lower resolution traditional measures of algal biomass have provided (Cloern and Jassby 2010; Winder and Cloern 2010), suggesting that high-frequency sensor-based monitoring can greatly increase our understanding of the variability and controls of algal communities. Like these previous studies, we have identified a dominance of monthly variation in algal biomass. This finding is unsurprising given the strong seasonality inherent in phytoplankton dynamics observed in most temperate lakes

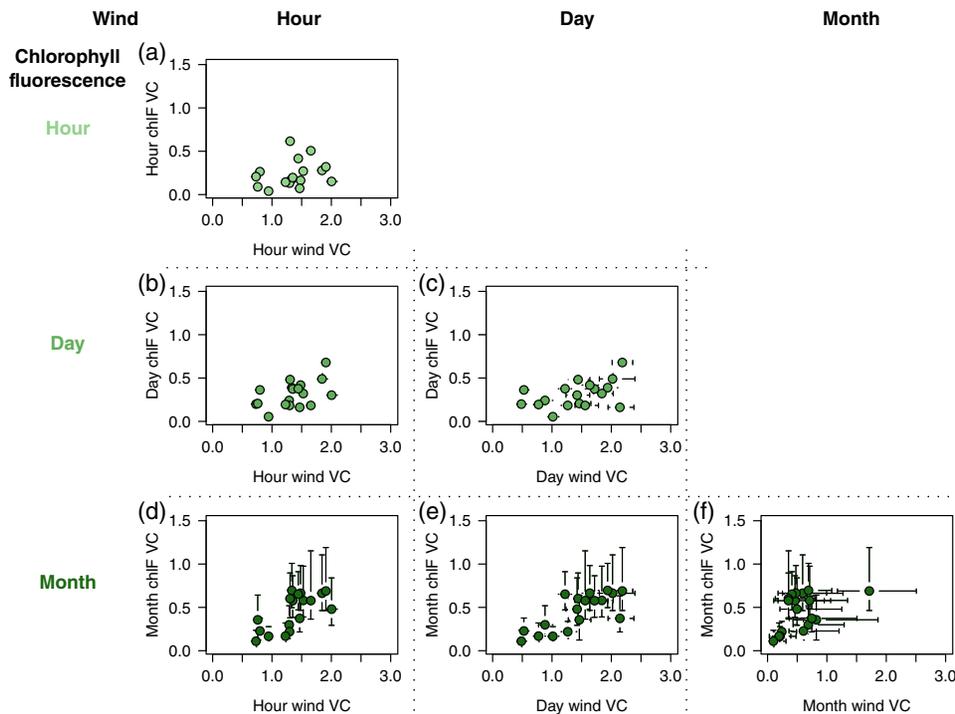


Fig. 2. Variance in chlF at hourly (top row—light green shading), daily (middle row—intermediate green shading), and monthly (bottom row—dark green shading) timescales increases with variance in wind speed (a–f) within 18 lakes. Symbols are median estimates of VCs ± 95% CIs. All relationships are statistically significant (Table 1).

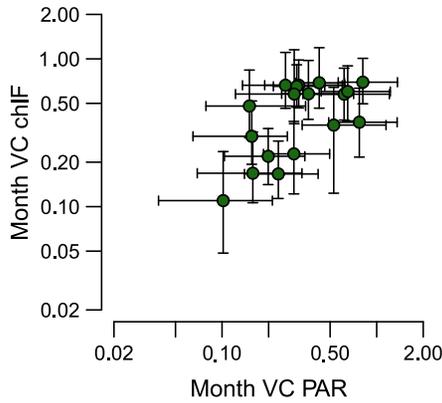


Fig. 3. Variance in chlF at monthly timescales increases with variance in PAR within 18 lakes. Symbols are median estimates of VCs \pm 95% CIs.

and is supported statistically by the correlation between monthly PAR VCs and monthly chlF variance (Fig. 3). However, because of our ability to quantify dynamics at shorter timescales with high-frequency sensors, we found monthly variation to be essentially equivalent to variation in biomass at daily and hourly scales combined (Fig. 1). Thus, on an annual time-frame, a large fraction of the total variation in algal biomass occurs at scales shorter than those typically sampled by most long-term monitoring programs used for lake management, suggesting that such monitoring programs may benefit from the incorporation of automated sensors as part of their monitoring plans.

We found variation in wind speed to be a major correlate of variability in phytoplankton abundance at all temporal scales (Fig. 2). Sustained or high winds can erode density gradients and deepen mixing, thereby altering the distribution of nutrients at longer timescales to generate variation in phytoplankton abundance (Carrick et al. 1993; Gai et al. 2012). High and variable wind speeds over the course of a day can facilitate deep and complex mixing and circulation patterns that drive three-dimensional heterogeneity in algal biomass and transport different patches, with potentially different photosynthetic capacities (Litchman 1998; Wagner et al. 2006; Lavaud et al. 2007) past measurement locations (George and Heaney 1978; Oliver et al. 2003). As wind speeds change at different temporal scales, the mixing dynamics (both horizontally and vertically) can respond based on basin size, the strength of stratification, and the relative magnitude of wind events (Spigel and Imberger 1980), but our results suggest that the latter mechanism appears to be most important to variability. In support of wind-induced mixing dynamics as a probable mechanism, the chlF VCs were also negatively correlated with a simple proxy of water column stability in our study lakes, i.e., higher variance in chlorophyll occurred under less stable conditions (Supporting Information Table S2). Convective mixing can also be an important mechanism for generating epilimnetic mixing (Fee et al. 1996), but

because its extent covaries with lake area (Read et al. 2012) and lake area was not correlated with any chlorophyll VCs, winds effects would appear to dominate in determining variance in chlF.

A number of physical, chemical, and biological phenomena in lakes may be responsible for some of the scatter in the relationships between chlF VCs and both wind speed VCs and trophic status. Short-term chlF measurements in surface waters are responsive to changes induced by irradiance and fluorescence emitted per unit chlorophyll in addition to changes in actual biomass (Marra 1997). Nonphotochemical quenching (NPQ) occurs when algal fluorescence is suppressed in the presence of excess light as cells shunt energy into heat rather than photochemistry or fluorescence (Marra 1997) and can complicate the estimation of algal biomass from fluorescence data (Serra et al. 2009; Huot and Babin 2010). Factors such as the rate and depth of mixing and the amount of light will control the likelihood and extent of NPQ (Serra et al. 2009). In support, only monthly PAR was significantly related to monthly chlF VCs, highlighting the absence of consistent relationships between variability in light and chlF beyond seasonal change. Other factors, such as variability in herbivory or nutrient concentration, are likely to affect variability in algal biomass (Reynolds 2006) but are rarely sampled at the high-frequency timescales necessary for our analysis. Lags between predictor and response variables as well as interactions among lake attributes may also contribute to the

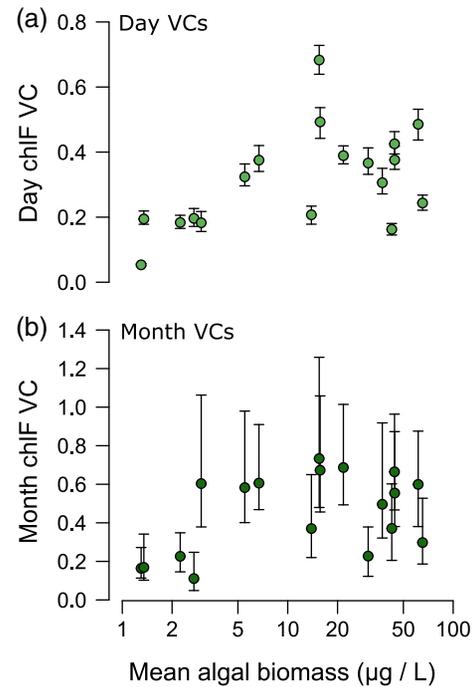


Fig. 4. Variance in chlF at daily (a—intermediate green shading) and monthly (b—dark green shading) timescales increases with the natural logarithm of mean annual Chl *a* (trophic status) among 18 lakes. Symbols for chlF are median estimates of VCs \pm 95% CIs.

scatter observed in our relationships among lakes. While such linkages have the potential to be important in generating changes in algal dynamics (e.g., Katz et al. 2015), we have restricted our initial analyses to assessing patterns of variation in algal time series at lag = 0 and note that lagged responses represent a profitable area for future research.

The consistency of the relationships between fluorescence VCs and the variance of wind speed highlights the unique nature of wind as a major driver of within-lake variation in algal biomass and chlF. Because hourly, daily, and monthly variation in wind speed may not necessarily covary with mean wind speed, we also examined the relationship between mean wind speed and chlorophyll VCs among lakes (Supporting Information Table S2). A significant positive relationship at a monthly scale was found indicating that changes in the seasonal variability of wind speed may also be related to wind speed magnitude. Globally, most lakes are located at mid-latitude (Downing et al. 2006) where there has been a particularly strong general decline in mean wind speeds (McVicar et al. 2012; Woolway et al. 2017). However, extreme wind events associated with tropical cyclones and a poleward shift in extratropical storm tracks are predicted to increase concurrent with global climate change over the 21st century (Karl 2009; IPCC 2012). Both phenomena combined (i.e., lower overall wind speeds coupled with more frequent high-wind speed storm events) have the potential to complicate predictions of variability. Lower wind speeds overall could reduce longer-term (monthly) variability of both wind and phytoplankton, but more frequent storms may increase the short-term (hourly and daily) variability of wind speed and promote the development of algal blooms (Huber et al. 2012) in this lake-rich region.

The positive relationship between variability in daily and monthly algal biomass and the overall productivity of lakes may implicate periodic algal blooms, which are more prevalent in eutrophic lakes, as one possible mechanism responsible for generating higher variability in productive systems (Paerl and Paul 2012). Cyanobacterial blooms, in particular, may be triggered during calm periods following extreme weather events which can increase nutrient availability through water column mixing, external loading, and resuspension of sediments (Reynolds et al. 1987; Wagner and Adrian 2009; Huber et al. 2012). Our wind results support this mechanism. Cloern and Jassby (2010) similarly found that eutrophic lakes exhibit high variability at the submonthly scale (the residual component in their study) and predicted that the pattern was due to algal blooms. Their study, like ours, also used methods that were robust to mean-variance scaling suggesting the observed patterns were not artifacts. Also noteworthy in a bloom context is the pronounced lack of a linear fit to the relationship between monthly chlF VCs and trophic status as the variance seems to plateau somewhere between 10 $\mu\text{g L}^{-1}$ and 20 $\mu\text{g L}^{-1}$ Chl *a*, followed by a potential slight decline (Figs. 1, 4). This pattern suggests that there

may be a lake trophic threshold that, when passed, introduces more consistent variability rather than the intermittent blooms that likely characterize lakes approaching this threshold.

Over the past century, algal blooms have increased in frequency, duration, intensity, and regional distribution and are predicted to increase further as the climate continues to warm (Carey et al. 2012; Paerl and Paul 2012; Rigosi et al. 2015; Taranu et al. 2015). Our results suggest that further increases in nutrient availability and storminess may increase the spatial and temporal variability of bloom events, which may be increasingly dominated by cyanobacteria, at subseasonal scales and reduce our ability to predict when freshwater ecosystem services are at risk (Watson et al. 2008; Brooks et al. 2016). Our finding of equivalent fractions of algal variation occurring at monthly and submonthly timescales reinforces the need for collecting higher frequency measurements similar to Thomas et al. (2018) who found an increase in predictability of mean biomass at shorter timescales (hourly to monthly). Further, these findings highlight the potential for using high-frequency time series of fluorescence as a “resilience indicator” of impending regime shifts across a wide variety of lake types (Pace et al. 2017) and quantify the magnitude of variation in algal biomass that is not currently represented in traditional monitoring programs. By capturing such data, at a temporal scale equivalent to the generation times of phytoplankton, we can better address both the causes and consequences of changes in algal biomass. Given the key role of phytoplankton in aquatic food webs and ecosystem function, these results also suggest that aquatic ecosystems may become more unpredictable in the future, thus presenting a serious challenge to management and conservation in an era of rapid environmental change.

References

- Adrian, R., and others. 2009. Lakes as sentinels of climate change. *Limnol. Oceanogr.* **54**: 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283.
- Baker, N. R. 2008. Chlorophyll fluorescence: A probe of photosynthesis in vivo. *Annu. Rev. Plant Biol.* **59**: 89–113. <https://doi.org/10.1146/annurev.arplant.59.032607.092759>.
- Benincá, E., J. Huisman, R. Heerkloss, K. D. Johnk, P. Branco, E. H. Van Nes, M. Scheffer, and S. P. Ellner. 2008. Chaos in a long-term experiment with a plankton community. *Nature* **451**: 822–825. <https://doi.org/10.1038/nature06512>.
- Brentrup, J. A., and others. 2016. The potential of high-frequency profiling to assess vertical and seasonal patterns of phytoplankton dynamics in lakes: An extension of the Plankton Ecology Group (PEG) model. *Inland Waters* **6**: 565–580. <https://doi.org/10.5268/IW-6.4.890>.

- Brooks, B. W., and others. 2016. Are harmful algal blooms becoming the greatest inland water quality threat to public health and aquatic ecosystems? *Environ. Toxicol. Chem* **35**: 6–13. <https://doi.org/10.1002/etc.3220>.
- Carey, C. C., B. W. Ibelings, E. P. Hoffmann, D. P. Hamilton, and J. D. Brookes. 2012. Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. *Water Res.* **46**: 1394–1407. <https://doi.org/10.1016/j.watres.2011.12.016>.
- Carlson, R. E. 1977. A trophic state index for lakes. *Limnol. Oceanogr.* **22**: 361–369. <https://doi.org/10.4319/lo.1977.22.2.0361>.
- Carpenter, S. R., W. A. Brock, J. J. Cole, J. F. Kitchell, and M. L. Pace. 2008. Leading indicators of trophic cascades. *Ecol. Lett.* **11**: 128–138. <https://doi.org/10.1111/j.1461-0248.2007.01131.x>.
- Carpenter, S. R., W. A. Brock, C. Folke, E. H. van Nes, and M. Scheffer. 2015. Allowing variance may enlarge the safe operating space for exploited ecosystems. *Proc. Natl. Acad. Sci. USA* **112**: 14384–14389. <https://doi.org/10.1073/pnas.1511804112>.
- Carrick, H. J., F. J. Aldridge, and C. L. Schelske. 1993. Wind influences phytoplankton biomass and composition in a shallow, productive lake. *Limnol. Oceanogr.* **38**: 1179–1192. <https://doi.org/10.4319/lo.1993.38.6.1179>.
- Cloern, J. E., and A. D. Jassby. 2010. Patterns and scales of phytoplankton variability in estuarine–coastal ecosystems. *Estuaries Coast.* **33**: 230–241. <https://doi.org/10.1007/s12237-009-9195-3>.
- Cottingham, K. L., J. A. Rusak, and P. R. Leavitt. 2000. Increased ecosystem variability and reduced predictability following fertilisation: Evidence from palaeolimnology. *Ecol. Lett.* **3**: 340–348. <https://doi.org/10.1046/j.1461-0248.2000.00158.x>.
- Cross, W. F., J. M. Hood, J. P. Benstead, A. D. Huryn, and D. Nelson. 2015. Interactions between temperature and nutrients across levels of ecological organization. *Glob. Chang. Biol.* **21**: 1025–1040. <https://doi.org/10.1111/gcb.12809>.
- Dillon, P. J., and F. H. Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. *Limnol. Oceanogr.* **19**: 767–773. <https://doi.org/10.4319/lo.1974.19.5.0767>.
- Downing, J. A., and others. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol. Oceanogr.* **51**: 2388–2397. <https://doi.org/10.4319/lo.2006.51.5.2388>.
- Fee, E. J., R. E. Hecky, S. E. M. Kasian, and D. R. Cruikshank. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. *Limnol. Oceanogr.* **41**: 912–920. <https://doi.org/10.4319/lo.1996.41.5.0912>.
- Fraterrigo, J. M., and J. A. Rusak. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. *Ecol. Lett.* **11**: 756–770. <https://doi.org/10.1111/j.1461-0248.2008.01191.x>.
- Gai, S., H. Wang, G. Liu, L. Huang, and X. Song. 2012. Chlorophyll a increase induced by surface winds in the northern South China Sea. *Acta Oceanol. Sin.* **31**: 76–88. <https://doi.org/10.1007/s13131-012-0222-z>.
- Gelman, A., and I. Pardoe. 2006. Bayesian measures of explained variance and pooling in multilevel (hierarchical) models. *Technometrics* **48**: 241–251. <https://doi.org/10.1198/004017005000000517>.
- George, D. G., and S. I. Heaney. 1978. Factors influencing the spatial distribution of phytoplankton in a small productive lake. *J. Ecol.* **66**: 133–155. <https://doi.org/10.2307/2259185>.
- Huber, V., C. Wagner, D. Gerten, and R. Adrian. 2012. To bloom or not to bloom: Contrasting responses of cyanobacteria to recent heat waves explained by critical thresholds of abiotic drivers. *Oecologia* **169**: 245–256. <https://doi.org/10.1007/s00442-011-2186-7>.
- Huot, Y., and M. Babin. 2010. Overview of fluorescence protocols: Theory, basic concepts, and practice, p. 31–74. In D. J. Suggett, O. Prášil, and M. A. Borowitzka [eds], *Chlorophyll a fluorescence in aquatic sciences: Methods and applications*. Springer.
- IPCC. 2012. *Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of working groups I and II of the Intergovernmental Panel on Climate Change*, p. 582. Cambridge Univ. Press.
- Istvánovics, V., M. Honti, A. Osztóics, H. M. Shafik, J. Padisak, Y. Yacobi, and W. Eckert. 2005. Continuous monitoring of phytoplankton dynamics in Lake Balaton (Hungary) using on-line delayed fluorescence excitation spectroscopy. *Freshw. Biol.* **50**: 1950–1970. <https://doi.org/10.1111/j.1365-2427.2005.01442.x>.
- Jackson, M. C., C. J. G. Loewen, R. D. Vinebrooke, and C. T. Chimimba. 2016. Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. *Glob. Chang. Biol.* **22**: 180–189. <https://doi.org/10.1111/gcb.13028>.
- Kara, E. L., and others. 2012. Time-scale dependence in numerical simulations: Assessment of physical, chemical, and biological predictions in a stratified lake at temporal scales of hours to months. *Environ. Model. Softw.* **35**: 104–121. <https://doi.org/10.1016/j.envsoft.2012.02.014>.
- Karl, T. R. 2009. *Global climate change impacts in the United States*. Cambridge Univ. Press.
- Katz, S.L., L.R. Izmet'eva, S.E. Hampton, T. Ozersky, K. Shchapov, M.V. Moore, S.V. Shimaraeva, and E.A. Silov. 2015. The “Melosira years” of Lake Baikal: Winter environmental conditions at ice onset predict under-ice algal blooms in spring. *Limnol. Oceanogr.* **60**: 1950–1964. <https://doi.org/10.1002/lno.10143>.
- Kirk, J.T.O. 1994. *Light and photosynthesis in aquatic ecosystems*. Cambridge University Press.
- Knutson, T. R., and R. E. Tuleya. 2004. Impact of CO₂-induced warming on simulated hurricane intensity and precipitation:

- Sensitivity to the choice of climate model and convective parameterization. *J. Clim.* **17**: 3477–3495. [https://doi.org/10.1175/1520-0442\(2004\)017<3477:IOCWOS>2.0.CO;2](https://doi.org/10.1175/1520-0442(2004)017<3477:IOCWOS>2.0.CO;2).
- Lavaud, J., R. F. Strzepek, and P. G. Kroth. 2007. Photoprotection capacity differs among diatoms: Possible consequences on the spatial distribution of diatoms related to fluctuations in the underwater light climate. *Limnol. Oceanogr.* **52**: 1188–1194. <https://doi.org/10.4319/lo.2007.52.3.1188>.
- Litchman, E. 1998. Population and community responses of phytoplankton to fluctuating light. *Oecologia* **117**: 247–257. <https://doi.org/10.1007/s004420050655>.
- Marra, J. 1997. Analysis of diel variability in chlorophyll fluorescence. *J. Mar. Res.* **55**: 767–784. <https://doi.org/10.1357/0022240973224274>.
- McVicar, T. R., and others. 2012. Global review and synthesis of trends in observed terrestrial near-surface wind speeds: Implications for evaporation. *J. Hydrol.* **416–417**: 182–205. <https://doi.org/10.1016/j.jhydrol.2011.10.024>.
- Meehl, G. A., J. M. Arblaster, and C. Tebaldi. 2005. Understanding future patterns of increased precipitation intensity in climate model simulations. *Geophys. Res. Lett.* **32**, L18719. <https://doi.org/10.1029/2005GL023680>.
- Mooij, W., and others. 2010. Challenges and opportunities for integrating lake ecosystem modelling approaches. *Aquat. Ecol.* **44**: 633–667. <https://doi.org/10.1007/s10452-010-9339-3>.
- Morris, D.P., H. Zagarese, C.E. Williamson, E.G. Balseiro, B. R. Hargreaves, B. Modenutti, R. Moeller, and C. Queimalinos. 1995. The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnology and Oceanography*. **40**: 1381–1391. <https://doi.org/10.4319/lo.1995.40.8.1381>.
- O'Reilly, C. M., and others. 2015. Rapid and highly variable warming of lake surface waters around the globe. *Geophys. Res. Lett.* **42**: 10773–10781. <https://doi.org/10.1002/2015GL066235>.
- Oliver, R. L., J. Whittington, Z. Lorenz, and I. T. Webster. 2003. The influence of vertical mixing on the photoinhibition of variable chlorophyll a fluorescence and its inclusion in a model of phytoplankton photosynthesis. *J. Plankton Res.* **25**: 1107–1129. <https://doi.org/10.1093/plankt/25.9.1107>.
- Pace, M. L., R. D. Batt, C. D. Buelo, S. R. Carpenter, J. J. Cole, J. T. Kurtzweil, and G. M. Wilkinson. 2017. Reversal of a cyanobacterial bloom in response to early warnings. *Proc. Natl. Acad. Sci. USA* **114**: 352–357. <https://doi.org/10.1073/pnas.1612424114>.
- Paerl, H. W., and V. J. Paul. 2012. Climate change: Links to global expansion of harmful cyanobacteria. *Water Res.* **46**: 1349–1363. <https://doi.org/10.1016/j.watres.2011.08.002>.
- Papaioannou, G., N. Papanikolaou, and D. Retalis. 1993. Relationships of photosynthetically active radiation and short-wave irradiance. *Theor. Appl. Climatol.* **48**: 23–27. <https://doi.org/10.1007/BF00864910>.
- Platt, T., C. Fuentes-Yaco, and K. T. Frank. 2003. Spring algal bloom and larval fish survival. *Nature* **423**: 398–399. <https://doi.org/10.1038/423398b>.
- Qin, B., G. Zhu, G. Gao, Y. Zhang, W. Li, H. W. Paerl, and W. W. Carmichael. 2010. A drinking water crisis in Lake Taihu, China: Linkage to climatic variability and lake management. *Environ. Manag.* **45**: 105–112. <https://doi.org/10.1007/s00267-009-9393-6>.
- R Development Core Team. 2015. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Read, J. S., and others. 2012. Lake-size dependency of wind shear and convection as controls on gas exchange. *Geophys. Res. Lett.* **39**: L09405. <https://doi.org/10.1029/2012GL051886>.
- Reynolds, C. S. 2006. *The ecology of freshwater phytoplankton*. Cambridge Univ. Press.
- Reynolds, C. S., R. L. Oliver, and A. E. Walsby. 1987. Cyanobacterial dominance: The role of buoyancy regulation in dynamic lake environments. *N. Z. J. Mar. Freshw. Res.* **21**: 379–390. <https://doi.org/10.1080/00288330.1987.9516234>.
- Rigosi, A., and others. 2015. Determining the probability of cyanobacterial blooms: The application of Bayesian networks in multiple lake systems. *Ecol. Appl.* **25**: 186–199. <https://doi.org/10.1890/13-1677.1>.
- Roberts, R. D., and T. Zohary. 1987. Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. *N. Z. J. Mar. Freshw. Res.* **21**: 391–399. <https://doi.org/10.1080/00288330.1987.9516235>.
- Schindler, D. W. 2012. The dilemma of controlling cultural eutrophication of lakes. *Proc. R. Soc. B Biol. Sci.* **279**: 4322–4333. <https://doi.org/10.1098/rspb.2012.1032>.
- Serra, T., C. Borrego, X. Quintana, L. Calderer, R. López, and J. Colomer. 2009. Quantification of the effect of nonphotochemical quenching on the determination of in vivo chl a from phytoplankton along the water column of a freshwater reservoir. *Photochem. Photobiol.* **85**: 321–331. <https://doi.org/10.1111/j.1751-1097.2008.00441.x>.
- Slegers, P. M., R. H. Wijffels, G. van Straten, and A. J. B. van Boxtel. 2011. Design scenarios for flat panel photobioreactors. *Appl. Energy* **88**: 3342–3353. <https://doi.org/10.1016/j.apenergy.2010.12.037>.
- Smith, V. H. 2003. Eutrophication of freshwater and coastal marine ecosystems a global problem. *Environ. Sci. Pollut. Res.* **10**: 126–139. <https://doi.org/10.1065/espr2002.12.142>.
- Sommer, U., and others. 2012. Beyond the plankton ecology group (PEG) model: Mechanisms driving plankton succession. *Annu. Rev. Ecol. Evol. Syst.* **43**: 429–448. <https://doi.org/10.1146/annurev-ecolsys-110411-160251>.
- Spigel, R. H., and J. J. Imberger. 1980. The classification of mixed-layer dynamics of lakes of small to medium size. *J. Phys. Oceanogr.* **10**: 1104–1121. [https://doi.org/10.1175/1520-0485\(1980\)010<1104:TCOMLD>2.0.CO;2](https://doi.org/10.1175/1520-0485(1980)010<1104:TCOMLD>2.0.CO;2).
- Taranu, Z. E., and others. 2015. Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the

- Anthropocene. *Ecol. Lett.* **18**: 375–384. <https://doi.org/10.1111/ele.12420>.
- Thomas, M. K., S. Fontana, M. Reyes, M. Kehoe, and F. Pomati. 2018. The predictability of a lake phytoplankton community, over time-scales of hours to years. *Ecol. Lett.* **21**: 619–628. <https://doi.org/10.1111/ele.12927>.
- Vautard, R., J. Cattiaux, P. Yiou, J.-N. Thépaut, and P. Ciais. 2010. Northern Hemisphere atmospheric stilling partly attributed to an increase in surface roughness. *Nat. Geosci.* **3**: 756–761. <https://doi.org/10.1038/ngeo979>.
- Wagner, C., and R. Adrian. 2009. Cyanobacteria dominance: Quantifying the effects of climate change. *Limnol. Oceanogr.* **54**: 2460–2468. https://doi.org/10.4319/lo.2009.54.6_part_2.2460.
- Wagner, H., T. Jakob, and C. Wilhelm. 2006. Balancing the energy flow from captured light to biomass under fluctuating light conditions. *New Phytol.* **169**: 95–108. <https://doi.org/10.1111/j.1469-8137.2005.01550.x>.
- Watson, S. B., J. Ridal, and G. L. Boyer. 2008. Taste and odour and cyanobacterial toxins: Impairment, prediction, and management in the Great Lakes. *Can. J. Fish. Aquat. Sci.* **65**: 1779–1796. <https://doi.org/10.1139/F08-084>.
- Wild, M. 2012. Enlightening global dimming and brightening. *Bull. Am. Meteorol. Soc.* **93**: 27–37. <https://doi.org/10.1175/BAMS-D-11-00074.1>.
- Wilhelm, S., and R. Adrian. 2008. Impact of summer warming on the thermal characteristics of a polymictic lake and consequences for oxygen, nutrients and phytoplankton. *Freshw. Biol.* **53**: 226–237. <https://doi.org/10.1111/j.1365-2427.2007.01887.x>.
- Winder, M., and J. E. Cloern. 2010. The annual cycles of phytoplankton biomass. *Philos. Trans. R. Soc. B.* **365**: 3215–3226. <https://doi.org/10.1098/rstb.2010.0125>.
- Winder, M., and U. Sommer. 2012. Phytoplankton response to a changing climate. *Hydrobiologia* **698**: 5–16. <https://doi.org/10.1007/s10750-012-1149-2>.
- Winslow L., and others. 2017. High-frequency water temperature, chlorophyll fluorescence, wind speed, and photosynthetically active radiation data for 18 globally-distributed lakes 2008–2013. Environment Data Initiative.. <https://doi.org/10.6073/pasta/7d2bd7e6aea263cf0a812f0d52bb751b>.
- Woolway, R. I., and others. 2016. Diel surface temperature range scales with lake size. *PLoS One* **11**: e0152466. <https://doi.org/10.1371/journal.pone.0152466>.
- Woolway, R. I., P. Meinson, P. Nöges, I. D. Jones, and A. Laas. 2017. Atmospheric stilling leads to prolonged thermal stratification in a large shallow polymictic lake. *Clim. Change* **141**: 759–773. <https://doi.org/10.1007/s10584-017-1909-0>.

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