

The spatial variability of algal bloom development in shallow lakes

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Keywords: spatial heterogeneity, spatial analysis, rarefaction analysis, macrophytes, eutrophic

This manuscript has been submitted for publication in *Freshwater Biology*. Please note that, despite having undergone peer review, the manuscript has yet to be formally accepted for publication. Subsequent versions of this manuscript may have slightly different content. If accepted, the final version of this manuscript will be available via the 'Peer-reviewed Publication DOI' link on the right-hand side of this webpage. Please feel free to contact any of the authors; we welcome feedback.

Abstract

1. Algal blooms can have profound effects on the structure and function of aquatic ecosystems and have the potential to interrupt valuable ecosystem services. Despite the potential ecological and economic consequences of algal blooms, the spatial dynamics of bloom development in spatially complex ecosystems such as shallow lakes remain poorly characterized. Our goal was to evaluate the magnitude and drivers of spatial variability of algal biomass, dissolved oxygen and pH over the course of a season, in a shallow lake in order to better understand the spatial dynamics of algal blooms in these ecosystems.
2. We sampled 98 locations in a small eutrophic lake on a 65m grid for several parameters (chlorophyll *a*, phycocyanin, dissolved oxygen, pH, and temperature), weekly over 122 days. This was done to estimate the dynamics of variability and spatial autocorrelation during the course of multiple bloom events. We also compared the spatial measurements to a high frequency sensor deployed at a fix station and estimated the optimal spatial sampling resolution by performing a rarefaction analysis.
3. Spatial heterogeneity of algal pigments was high, particularly during bloom events, and this pattern and the overall severity of the bloom was not well captured with the fixed station monitoring. The pattern of algal pigments and other limnologically important variables (dissolved oxygen and pH) was largely controlled by the location of dense macrophyte patches. Finally, from the rarefaction analysis we found that minimal information was gained about the mean state of the ecosystem after ~30 locations had been sampled.
4. This study revealed how spatially heterogeneous shallow lakes are over the course of a single season, and that the magnitude of variability was highest during biologically-intensive periods such as algal blooms. As such, continued research is needed across a range of trophic conditions to better understand the structure of horizontal variability in lakes. Overall, these data demonstrate the need for spatially-explicit monitoring to better understand the dynamics and drivers of algal blooms in shallow lakes and to better manage ecosystem services.

Introduction

Lakes are highly dynamic ecosystems that can undergo rapid physical and chemical changes at an individual location, throughout their water column, and across the entire lake surface at the scale of hours, days, seasons, and years (Laas, Noges, Koiv, & Noges, 2012; Read et al., 2011; Wynne & Stumpf, 2015). Quantifying heterogeneity in aquatic ecosystem structure and function not only improves our understanding of lake ecology and the underlying mechanisms that drive spatial and temporal heterogeneity, but also provide insights that improve management of these ecosystems and the services they provide. With the development of sophisticated sensor technology, high frequency measurements of variables such as dissolved oxygen and temperature have helped limnologists grasp the scale of temporal heterogeneity in lakes (S. R. Carpenter et al., 2020; Chaffin, Kane, & Johnson, 2020; Cotterill, Hamilton, Puddick, Suren, & Wood, 2019). Detailed temporal monitoring has led to advances in understanding several lake mechanisms such as diel cycles in primary production (Solomon et al., 2013; Staehr, Christensen, Batt, & Read, 2012) temperature effects on biogeochemical processes (Medeiros et al., 2012), and early warnings of the transition to alternative stable states (S. R. Carpenter et al., 2011; Wilkinson et al., 2018). Additionally, high frequency measurements have been used to better understand heterogeneity over depth (vertical spatial heterogeneity) for important processes such as stratification (Bohrer & Schultze, 2008; Read et al., 2011). Despite these advances, less is known about the dynamics of spatial heterogeneity in the surface waters of lakes (horizontal spatial heterogeneity).

The vast majority of our understanding of lentic ecosystem structure and function comes from single station sampling, with measurements taken through time over the deepest point in the lake (Stanley et al., 2019). This location is usually selected to be representative of the

conditions in the lake; however, the representativeness of a single location is likely to vary both with time due to interacting forces such as wind, hydrology, bathymetry, and biology (Chaffin et al., 2020; Schilder et al., 2013; Wu et al., 2010; Zhou, Obenour, Scavia, Johengen, & Michalak, 2013) and based on the variable being measured. For example, ecosystem metabolism measured at dozens of locations for 10 days in two north temperate lakes varied 1-2 orders of magnitude, with more than three-quarters of the variability attributable to the measurement location within the lake (Van de Bogert et al., 2012). Transect-based studies of reservoirs have revealed directional gradients in algae pigments, pH, and nutrients with differences varying between 25%-180% within a waterbody (Moreno-Ostos, Cruz-Pizarro, Basanta, & George, 2009; Rychtecky & Znachor, 2011; Smith, 2018). Recently, satellite-based studies have demonstrated the ability to detect distinct spatial patterns at a high resolution for optical variables in large lakes (Lekki et al., 2019). Despite these advances, relatively few studies have quantified horizontal spatial variability over time in lakes (Buttita et al. 2017, Vilas et al. 2017), hampering our understanding of the magnitude of heterogeneity in variables important for managing water quality and ecosystem services.

The development of algal blooms is expected to be a spatially heterogeneous phenomenon (Buelo, Carpenter, & Pace, 2018; Buttita, Carpenter, Loken, Pace, & Stanley, 2017; Pace et al., 2017; Serizawa, Amemiya, & Itoh, 2008) due to both local heterogeneity in nutrient limitation, zooplankton grazing, and temperature (Davis, Berry, Boyer, & Gobler, 2009; Hansen, Andersen, & Jensen, 1997) and population scale heterogeneity due to wind (George & Heaney, 1978). Algal blooms can have a negative effect on ecosystem services, and therefore are often a target for ecosystem monitoring and management. Some bloom-forming taxa, particularly cyanobacteria, can produce toxins that can rise to dangerous concentrations for humans, pets, and

livestock (Codd, Morrison, & Metcalf, 2005; Corbel, Mougin, & Bouaicha, 2014). Additionally, the mineralization of settling phytoplankton leads to anoxic bottom waters, while intense periods of primary production cause large variation in dissolved oxygen and pH (in poorly buffered ecosystems) over the course of the day, which is stressful for aquatic organisms (Gilbert, 2017; Landsberg, 2002). Furthermore, the perceived recreational value of lakes declines when blooms form (Angradi, Ringold, & Hall, 2018), which in turn can negatively affect local economies (Dodds et al., 2009). Despite the risk of economic loss, loss in biodiversity, and potential human harm, the spatial dynamics of bloom development in spatially complex ecosystems such as shallow lakes remain poorly characterized.

Shallow lakes have a large interface between the sediment and water relative to deeper lakes, making them more susceptible to rapid changes in water residence time and nutrient inputs (Christensen, Sand-Jensen, & Staehr, 2013; Rennella & Quiros, 2006; Romo, Soria, Fernandez, Ouahid, & Baron-Sola, 2013). Due to the expansive littoral zones, shallow lakes can be dominated by macrophytes which modify the light climate and turbulence at the sediment-water interface (Andersen, Kragh, & Sand-Jensen, 2017; Moller & Rordam, 1985; Vilas, Marti, Adams, Oldham, & Hipsey, 2017). Many shallow lakes are also polymictic, experiencing multiple periods of stratification followed by mixing during the ice-free season. During periods of water column stability, cyanobacteria can thrive, initiating blooms (Carey, Ibelings, Hoffmann, Hamilton, & Brookes, 2012). Additionally, episodic nutrient loading from the watershed (S. Carpenter, Booth, Kucharik, & Lathrop, 2015; Kelly, Renwick, Knoll, & Vanni, 2019), spatial gradients in nutrient availability due to stream inlets and morphology (e.g. embayments), and wind-driven circulation (Schoen, Stretch, & Tirok, 2014) can all contribute to spatial heterogeneity of algal blooms over time in shallow lakes.

Spatial heterogeneity can be quantified by calculating the spatial variance (e.g., coefficient of variation; CV) or spatial autocorrelation (Moran's I, Moran, 1950). Increasing spatial variance is indicative of increasing patchiness in the ecosystem, such as areas of high-density algal biomass and areas of low-density biomass within a lake. Spatial autocorrelation accounts for the location of those patches within the ecosystem in relationship to each other. Moran's I quantifies how similar the density of algae is at one location compared to the density of surrounding neighbors. When measured over time for variables that are indices of algal biomass (e.g., the pigments chlorophyll *a* and phycocyanin), both of these metrics of spatial heterogeneity can provide insight into the dynamics of algal bloom development. In models of algal blooms, both spatial variance and autocorrelation are expected to be high during the bloom period (Buelo et al. 2018).

In order to better understand the spatial dynamics of algal blooms in shallow lakes, we performed intensive spatial sampling on Swan Lake (Iowa, USA), a spatially complex, shallow, hypereutrophic waterbody with a history of toxic cyanobacteria algal blooms. In addition to measuring algal pigments throughout the lake over the course of 122 days, we also measured temperature, dissolved oxygen, and pH. The spatial sampling captured two bloom events and coincided with high frequency monitoring of the same variables using autonomous sensors deployed at a fix station (D. Ortiz, Palmer, & Wilkinson, 2020). Using these data, we addressed the following questions: 1) how does spatial variability of algae, dissolved oxygen, and pH change over the course of a season, 2) are high frequency measurements at a fixed station an adequate characterization of surface water dynamics in a shallow lake, and 3) what is the optimal spatial sampling frequency to capture the mean state of a waterbody before, during, and after an

algal bloom? Evaluating these questions with data from a spatially complex, hypereutrophic lake will provide valuable ecological and management-relevant insights into algal bloom dynamics.

Methods

Study Site

Swan Lake (42.0396, -94.8454) has an average depth of 2 m, surface area of 40.5 hectares, watershed of 350 hectares (92% agricultural land use), and a shoreline development index value of 1.54. The estimated water residence time is approximately 1.5 years. During the ice-free period of 2018, Swan Lake had an average total phosphorus concentration of $280 \mu\text{g L}^{-1}$ and a total nitrogen concentration of 1.61 mg L^{-1} , making it hypereutrophic (Carlson, 1977). Total nitrogen was measured as the sum of total Kjeldahl nitrogen (method 351.2 v2, US EPA, 1993c) and nitrate + nitrite measured using the cadmium reduction method (method 4500-NO₃-F, US EPA, 1993a). Total phosphorus was measured using the ascorbic acid method (method 365.1 v2, US EPA, 1993b). The average total alkalinity during the same period was $139 \text{ mg CaCO}_3 \text{ L}^{-1}$ determined through end point titration (APHA, 1998). In addition to seasonal algal blooms, Swan Lake also has non-continuous beds of *Nelumbo lutea* (American Lotus) and *Stuckenia pectinata* (Sago pondweed) that peak in biomass in the latter half of the summer and then begin senescing. The main surface inlet to the lake enters on the western side and the outlet is at the southern edge of the waterbody (Figure 1).

Field Methods

The spatial sampling occurred approximately weekly from day of year (DOY) 142 to DOY 264, encompassing the late spring, summer, and early autumn. A total of 16 spatial

sampling events occurred over the course of the 122 days. Measurements of chlorophyll *a*, phycocyanin, temperature, dissolved oxygen saturation and pH were taken 0.25 m below the surface at 98 sampling stations using a YSI Pro DSS multiparameter sonde (Yellow Springs Instrument, Yellow Springs, OH). The sensors, which included the fluorometric Total Algae (chlorophyll *a* and phycocyanin), optical dissolved oxygen, and Ag/AgCl pH sensors, were calibrated weekly prior to each sampling event. The sampling stations were laid out in a 65 x 65 m grid across the lake (Figure 1) with each location measured in a consistent order (north to south) during each week. This spatial resolution was selected to allow for many sampling locations to be measured in a relatively short window of time, thereby minimizing the chance that the differences observed between sampling locations was not due to time of day.

Measurements were taken between 10:00 and 14:00, except for the first two and last three weeks when sampling lasted until 16:00. Beginning on DOY 177 when submerged macrophytes could be quantified from the boat, the presence or absence of submerged or floating leaf macrophytes was noted at each sampling station.

The fixed station high frequency monitoring of Swan Lake was performed using a YSI EXO2 (Yellow Springs Instrument, Yellow Springs, OH) multiparameter sonde equipped with the same sensors as the YSI ProDSS used for the spatial sampling. The sonde recorded measurements of chlorophyll *a*, phycocyanin, dissolved oxygen saturation, and pH every 15 minutes. The instrument was deployed on DOY 135 over the deepest point in the lake (3.8 m deep), hanging approximately 0.5m below the surface, and removed on DOY 264 after the spatial sampling event on that day. The fixed station sonde was monitored weekly for drift and calibrated according to manufacturer instructions when indicated by the quality control algorithm in the KorEXO software. Hourly precipitation, wind speed and wind direction were collected at

the Arthur N. Neu Airport in Carroll, Iowa located 4.5 km from the lake (Supplement Figures 1-4). The meteorological data were used to aid in the interpretation of spatial dynamics over the course of the summer.

Data analysis

Prior to analysis, extreme outliers in the algal pigments were removed from the spatial dataset as they were well outside the operating range of the Total Algae sensor or there was known interference with the sensor resulting in an inaccurate measurement. This resulted in five chlorophyll *a* and three phycocyanin measurements being removed out of 3,136 total pigment measurements. Spatial autocorrelation (AC) and the coefficient of variation (CV) were calculated for each variable on each sampling date in order to evaluate the dynamics of these parameters over time. The CV is the ratio of standard deviation over the mean and expressed as a percent. Spatial AC was calculated as Moran's I with a queen's distance neighbor list (92 meters) with no weight assumed on neighbors, as to not impose any assumptions on possible spatial patterns in the variables. We limited our analysis to surrounding neighbors because distances beyond this have not shown high spatial autocorrelation of algal pigments under experimental conditions (Butitta et al. 2017). Moran's I values near 1.0 reflect high spatial AC within neighbors, zero indicates a random distribution, whereas spatial AC values nearing -1.0 indicate a perfectly dispersed distribution (e.g. checkerboard pattern) in the variable being measured. The dynamics and extent of the spatial AC of temperature was compared to the dynamics of spatial AC in the other variables in order to tease apart the effect of physically versus biologically-driven spatial patterns. Additionally, in order to better visualize the spatial patterns in chlorophyll *a*,

phycocyanin, temperature, dissolved oxygen, and pH over the course of the season, the data were interpolated using inverse distance weighting across a 25m grid. (Figure 2).

In order to evaluate if high frequency measurements at a fixed station are an adequate characterization of the surface water dynamics in a shallow lake, we compared the measurements taken by the fixed station sonde during the same time period as a spatial sampling event. High frequency data from the fixed station sonde were trimmed to the period that we sampled the lake spatially, generally from 10:00 to 14:00, with exception of the first two and last three sample events which occurred between 12:00 to 16:00. A t-test with a Bonferroni correction, to account for the multiple comparisons, was performed to compare the distribution from the 98 sampling stations to the fixed station measurements from the same day for each of the four variables.

Finally, in order to evaluate the optimal spatial sampling frequency to capture the mean state of a variable at a given point throughout the season, we performed a rarefaction analysis. This was done by randomly selecting n number of spatial sampling data points ($n=2-97$) during a sampling event, calculating the mean value from that subset, and then calculating the root mean square error (RMSE) comparing the mean estimate from the subset to the mean of all sampling points during that event. This was repeated 1000 times for each value of n , and each iteration was then averaged. The averaged RMSE values for each subset of n were fit using a local polynomial regression with a smoothing factor of 0.1 and each sampling event's RMSE curve was standardized by subtracting the mean of all iterations ("global mean") from the mean at n number of stations, to aid in visual comparison. The spatial data are available through (David Ortiz & Wilkinson, 2019) and the fixed station data are available in (David Ortiz, Palmer, & Wilkinson, 2019) and further analyzed in Ortiz et al. (2020). All analyses were performed using

R 4.0.2 (R Core Team, 2020) using the *gstat* (Pebesma, 2004), *rstatix* (Kassambara, 2020), & *sf* packages (Pebesma, 2018).

Results

There were two bloom events during the summer of 2018 in Swan Lake. The first bloom occurred from DOY 156 – 184 and was dominated by the diatom *Aulacoseira spp.* based on a sample taken on DOY 177 examined under a compound microscope at 400x magnification. However, the phycocyanin concentrations on DOY 177 were the lowest during this first bloom period (Figure 2), and no cyanobacteria were identified in the sample. The second bloom, peaking on DOY 236, was dominated by the cyanobacterium *Microcystis spp.* There were also two large precipitation events during the summer, occurring after sampling on DOY 170 and lasting through DOY 171, and on DOY 232 (Supplemental Figure 4). The prevailing winds 24 hours prior to the sampling event were from the north during the first half of the summer (DOY 142 – 191), switched to being predominantly from the south from DOY 198 – 219, and returned to being from the north for the remainder of the season (DOY 226 – 264) (Supplemental Figure S2). The median wind speed for the first period when winds were out of the north was 3.6 m s^{-1} . When the winds switched to being predominantly from the south between DOY 198 – 219, the median wind speed was lower at 2.5 m s^{-1} , and when the winds returned to being from the north in fall, the median wind speed increased again to 3.3 m s^{-1} (Supplemental Figure 3).

Spatial dynamics

During the two bloom periods there was not a latitudinal or longitudinal trend in chlorophyll *a* concentrations; instead, there were patches of high chlorophyll *a* concentration on otherwise low-concentration dates (Figure 2). Unlike chlorophyll *a*, phycocyanin had a strong

latitudinal trend with higher concentrations in the northern portion (sample sites A1-G4) of the lake during the first bloom. This spatial pattern is readily observed on DOY 184 but is also noticeable for many of the sampling events during the first bloom. During sampling events with a strong latitudinal gradient in phycocyanin (DOY 166 – 184, and 236) the mean concentration in the northern portion of the lake was nearly double the concentration in the southern portion of the lake (7.29 and 3.76 $\mu\text{g L}^{-1}$, respectively). On these dates, the prevailing winds 24 hours prior to the sampling event were out of the north (Supplemental Figure S2), yet the lowest concentrations of phycocyanin were not found in the southern portion of the lake. Even when the lake was not blooming, there were patches of high concentrations of phycocyanin in the northern portion of the lake (e.g., DOY 212), located among the densest macrophyte patches (Figure 1).

The percent saturation of dissolved oxygen varied the most out of the five variables monitored, ranging from borderline hypoxic (30% saturation) to supersaturated (up to 350%) (Figure 2). While the dissolved oxygen saturation increased near the peak of the bloom, the highest average saturation was on DOY 191, after the first bloom had collapsed. There was a weak pattern over the course of the season of higher saturation in the northern portion of the lake, similar to the distribution of higher phycocyanin concentrations. However, within the northern portion of the lake, regions of low dissolved oxygen saturation formed in the surface waters, particularly later in the summer, in the areas with high macrophyte density (Figure 1). The distribution of pH also had a weak spatial pattern during the summer, with slightly elevated values in the northern portion of the lake during the first bloom (e.g. DOY 177; Figure 2). While pH became elevated at the onset of the first bloom period from DOY 149 – 170, it was highest overall on DOY 191 and 198 after the first bloom had collapsed. Unlike the other variables, temperature had a subtle south to north latitudinal gradient with warmer temperatures in the

southern portion of the lake and colder in the north during the latter half of the summer (Figure 2). On average this difference between the northern portion of the lake and the southern was 0.5°C. The warmest day of sampling was DOY 191.

Spatial variability in algal pigments during the first bloom event was low, with two exceptions. There was an increase in the CV of chlorophyll *a* on the last day of the bloom (DOY 184; Figure 3a) that continued to increase as the bloom collapsed. There was also a temporary increase in phycocyanin CV during the first bloom on DOY 177, coinciding with a temporary decline in phycocyanin concentration across the lake (Figure 3b). Conversely, the CV of pH and dissolved oxygen were elevated during the first bloom period, with pH CV declining and remaining low after the first bloom (Figure 3c) and dissolved oxygen CV only temporarily declining after the first bloom (Figure 3d). Temperature had low variability throughout the first bloom until DOY 177, when the lake began to heat up, peaking in both temperature and spatial variability on DOY 191 (Figure 3e). Between the first and second bloom, DOY 191-226, there was a decrease in spatial variability among the algal pigments and pH as the bloom collapsed, while temperature and dissolved oxygen CV remained relatively high and variable. During the second bloom period, CV was low for all variables except for chlorophyll *a*. In general, the CV, of temperature and pH, expressed as a percentage, was an order of magnitude lower than the other variables.

Spatial autocorrelation (AC), quantified as Moran's I, did not fall substantially below 0 for any of the variables and peaked at 0.79 among all variables (Figure 3). The highest AC value for chlorophyll *a* and phycocyanin was during the first bloom event (Figure 3f, g); however, phycocyanin AC also increased substantially during the second bloom. During the first bloom, the AC of temperature varied similarly to both pigments' AC, particularly phycocyanin, but

became decoupled after the bloom collapsed. While the AC of temperature remained high during the inter-bloom period, the AC of the pigments was substantially lower. Conversely, the dynamics of AC of temperature, dissolved oxygen and pH remained coupled throughout the summer (Figure 3h, i). Dissolved oxygen saturation and pH both increased in AC during the first bloom and then declined throughout the rest of the season with the exception of a minor increase in AC during the second bloom event.

Fixed station versus spatial sampling

There were a greater number of days with a significant difference between the spatial and fixed station measurements than days in which the data sets were similar (Figure 4). Among all 64 comparisons (4 variables \times 16 sampling events), the spatial and fixed station data sets had a similar mean 37.5% of the time. Phycocyanin had the greatest number of events with similar values, with 7 of the 16 sampling events having non-statistically different mean values measured spatially and at the fixed station (Figure 4d). These occurrences were mainly during non-bloom periods. However, even when the mean phycocyanin values were similar between the sampling methods on a given day, the range of values captured by the fixed station was five times less than the variability captured in the spatial data. This pattern of infrequent occurrences of similar mean values between the two methods during non-bloom periods and a diminished range in the fixed station data, was shared, to a degree, among the other three variables as well. Interestingly, dissolved oxygen saturation only had 5 out of the 16 events with similar means, all of which occurred when the lake was above 100% saturation (Figure 4b).

While a majority of the comparisons between the fixed station and spatial data indicate that the algal pigments had a larger range of values in the spatial data, there were a handful of

instances where the opposite was true. During the first bloom, the fixed station sonde measured a wide range of chlorophyll *a* concentrations and had a higher mean chlorophyll *a* for all dates (Figure 4a). Similarly, we observed higher mean phycocyanin at the fixed station sonde on DOY 156, 166, 177, 191, and 219 (Figure 4c). However, this pattern did not hold true for dissolved oxygen or pH (Figure 4b, d).

Optimal Spatial Resolution

In order to evaluate the spatial sampling resolution needed to capture the mean state of the surface water on a given day, we performed a rarefaction analysis for each variable and each sampling event, calculating the RMSE of a subset of sampling locations compared to the mean value of all 98 measurements that day. The plateaus of the RMSE curves from the rarefaction analysis were used to evaluate the smallest number of spatial sampling locations needed to capture the mean across the lake during that sampling event (Figure 5). Additionally, we also evaluated the temporal pattern of the minimum number of sampling locations needed to capture the mean.

The mean value was underestimated for all variables on all sampling dates when there were less than 10 sampling stations (Figure 5). However, the severity of the underestimation differed among the variables. The rarefaction analysis for chlorophyll *a* indicated that 10 – 30 sampling locations was sufficient for capturing the mean chlorophyll *a* in Swan Lake, otherwise the mean concentration would be under estimated (Figure 5a). When an algal bloom was occurring it took more sampling locations to near the mean chlorophyll *a* concentration on that date. However, when the bloom was particularly patchy during development (DOY 226) or collapse (DOY 191), including a larger number of sampling locations led to overestimating the

mean chlorophyll *a* concentration as locations with high concentrations were over-represented in the data set. There were similar patterns in phycocyanin RMSE with most sampling dates plateauing between 20 – 30 sampling locations with a few exceptions (Figure 5c). For DOYs 156-170 (rise of the first bloom) and 212, at least 60 sampling locations were needed to capture the overall mean in phycocyanin for that sampling date. Dissolved oxygen saturation and pH were generally well characterized by approximately 10 – 15 sampling locations as both had a majority of dates in which the RMSE curves plateaued at that spatial sampling resolution (Figure 5b, d). However, at the beginning (DOY 154), peak (DOY 184), and end (DOY 205) of the first bloom, twice as many sampling locations were needed to capture the mean dissolved oxygen. Only two dates required more sampling locations for pH to capture the mean, DOY 177 and 198, which plateaued at approximately 40 sampling locations. The largest RMSE were observed during bloom conditions for all variables: DOY 177 had the largest error for phycocyanin and pH, while the largest RMSE was on DOY 184 for dissolved oxygen and on DOY 236 for chlorophyll *a* (Figure 5).

Discussion

The spatial heterogeneity of key water quality parameters was highly dynamic in Swan Lake, a shallow, hypereutrophic temperate waterbody. The dynamics over time were driven by two bloom periods, with the peak of both blooms being preceded by large precipitation events (Supplemental Figure S4). These rain events could have delivered large quantities of nutrients from the agriculturally-dominated watershed, thereby fueling the subsequent algal blooms. However, the spatial variability and pattern observed in algal pigments, dissolved oxygen saturation, pH, and water temperature at the surface of the lake are explained by the temporal

dynamics of the two algal blooms interacting with the structure and primary productivity of patchy macrophyte beds in the northern portion of the lake.

The spatial patterns that the algal blooms created were consistent with the expectations from previous modeling and experimental work (Buelo et al., 2018; Butitta et al., 2017; Serizawa et al., 2008), that spatial AC increases as algal blooms develop in lakes. This pattern was the strongest for phycocyanin, evident by the strong latitudinal gradient in concentrations during the bloom periods. However, while spatial autocorrelation was high during the blooms, contrary to our expectations, the distribution of higher concentrations of phycocyanin was opposite the prevailing wind direction. Given the consistent prevailing wind direction prior to sampling for the first portion of the summer (Supplemental Figure S2), we expected that the highest concentrations of cyanobacteria would be downwind in the southern half of the lake. This hypothesis is consistent with the pattern observed in other shallow eutrophic lakes (Wu et al. 2010). However, based on our data, it appears that the opposite pattern is true and that wind alone does not explain the spatial gradient in phycocyanin concentrations. Further underscoring the idea that the spatial variability of algae in Swan Lake was not solely driven by wind, the spatial AC of temperature, which should be reflective of physical processes in the lake (Butitta et al., 2017), was decoupled from the spatial AC dynamics of the pigments for much of the summer. Instead, we hypothesize that the macrophyte beds in the northern portion of the lake helped to control the distribution of algae over time.

Macrophytes can have a large influence on the structure of aquatic ecosystems by inducing stratification, decreasing flow, modifying the light environment, and altering dissolved oxygen availability (Green, 2006; Vilas et al., 2017). Based on the spatial patterns of phycocyanin and location of the densest macrophyte beds, we hypothesize that the macrophyte

were inducing microstratification in the water column and reducing wind-driven flow. These physical conditions are likely to favor cyanobacteria dominance, explaining the concentration of cyanobacteria in the northern portion of the lake (Carey et al., 2012). Even during sampling events where phycocyanin concentrations were low across the lake (DOY 212), there were still hotspots of phycocyanin in the still surface waters of the American Lotus bed (Figure 1) that are evident in the spatial data (Figure 2).

In addition to indirectly regulating the spatial pattern of cyanobacteria through physical processes, the macrophyte beds were also structuring the spatial and temporal dynamics of the other variables. Temperature was the only variable with a latitudinal gradient that had higher values in the southern portion of the lake. We hypothesize that the shading induced directly by the floating-leaf macrophytes and indirectly by concentrating the surface-aggregated *Microcystis* bloom helped drive the pattern of colder water in the northern portion of the lake. However, it is also possible that the inflow of stream water, fed in part by colder groundwater, contributed to the temperature gradient in the lake. At the beginning of the summer as the first algal bloom formed, the spatial patterns of dissolved oxygen and pH were similar to the algae. However, after the first bloom collapsed it was evident that the dynamics of dissolved oxygen and pH were not tied to algal biomass, as the highest values for both variables occurred immediately following the collapse. The high dissolved oxygen and pH were likely driven by high primary productivity of the macrophytes during this period. Following the period of high dissolved oxygen and pH, discrete patches of low dissolved oxygen and pH became conspicuous in the macrophyte beds. As the macrophytes began to senesce, it created hotspots of decomposition, drawing down dissolved oxygen and pH (Vilas et al., 2017).

The variables that we measured in this study are often the target of water quality monitoring as the dynamics of these variables coincide with changes in ecosystem function and services. Monitoring is often performed at a fixed station over time to capture the dynamics of the ecosystem, but this strategy could potentially result in missed information about the ecosystem's behavior. While the temporal dynamics of all the variables were synchronous between the fixed station and spatial sampling data sets in Swan Lake, our conclusions regarding the magnitude of the blooms and variability in the lake's structure would have been substantially different relying solely on the fixed station data. Among the four variables for the 16 sampling events only 37.5% of the fixed station estimates of the mean state of the lake statistically matched the estimate from the spatial sampling. The vast majority of those instances (96%) occurred during non-bloom periods, which also coincided with lower wind speed conditions and no major precipitation events. The large difference between the spatial sampling and fixed station measurements of algal pigments during blooms was likely driven, in part, by the depth of the sonde at the fixed station and the variability accumulation of cyanobacteria at the surface of the lake (Chaffin et al., 2020). However, it is clear that during periods of heightened biological activity such as blooms, fixed station monitoring is unlikely to be representative of the mean ecosystem state in shallow lakes.

It's important to consider the trade-offs between high frequency fixed station monitoring and higher resolution, but less frequent spatial monitoring. High frequency monitoring at a single station provides insight into ecosystem function such as metabolism (Staeher et al., 2012), early warnings of impending regime shifts (S. R. Carpenter et al., 2011; Wilkinson et al., 2018), and crucial information on diel variability in limnological conditions (Andersen et al., 2017). However, as we observed in Swan Lake, the spatial variability within a given day often exceeds

the temporal variability at a single point in a shallow lake. Without the spatial sampling snapshots, we would have underestimated the magnitude of the algal blooms, hampering our limnological understanding of the ecosystem's drivers (e.g., the role of macrophytes). From a practical stand point, the understanding gleaned from the spatial sampling could help managers design targeted algal toxin monitoring or management interventions to help control fish habitat quality in persistently hypoxic areas (Bardshaw, Allen, & Netherland, 2015). However, the time and cost investment in repeated spatial sampling at the resolution performed in this study may not be feasible for both research and management programs.

The rarefaction analysis we performed for all four of the key water quality monitoring variables revealed that minimal information was gained after ~30 locations were sampled across many conditions and variables. Often 12-20 sample locations across the 40.5 ha lake was sufficient to capture the spatial variability within the lake, with a few exceptions. These exceptions occurred during times of higher variability such as when the blooms were just starting or when the bloom began to collapse. The need for a higher spatial resolution during bloom events to fully capture their variability has also been found using remote sensing techniques in other, larger lakes (Lekki et al., 2019). As the spatial resolution of remote sensing technologies continues to improve, it may become more cost effective to capture the spatial heterogeneity of algal pigments in small lakes over time. However, one of the benefits of manual spatial sampling is being able to pair other measurements such as dissolved oxygen, pH, and nutrients (e.g., nitrate; Loken et al., 2018; Pellerin et al., 2016) with information on the distribution of algal biomass.

Our intensive spatial monitoring of a shallow, hypereutrophic lake revealed how spatially heterogeneous shallow lakes are over the course of a single season. It also allowed us to tease

apart the drivers of that spatial heterogeneity. We found that variability was greatest during biologically-intensive periods, such as during algal blooms and in areas of the lake with high macrophyte biomass, and that failure to capture this variability would have hampered our understanding of the ecosystem's functioning and overall mean state. Our data also provided an estimate of the spatial resolution needed to capture the dynamics in ecosystems similar to Swan Lake, a method which could be readily adapted to other ecosystems. While our results provide new understanding of the magnitude and temporal dynamics of spatial heterogeneity in shallow lakes, continued investigation of horizontal spatial heterogeneity in a range of aquatic ecosystems, from oligotrophic to eutrophic, is needed to better understand the structure and drivers of horizontal spatial variability in lakes.

Acknowledgments

We would like to thank Ryan Wagner, Ellen Albright, and Tyler Butts for assistance with data collection and instrument deployment and collection. We would also like to thank Rachel Fleck for assistance with nutrient analysis. Funding provided by the Center for Global and Regional Environmental Research, the Iowa State University Graduate Minority Assistantship Program, and the Iowa State University Graduate Research Assistantship Match Program.

References

- American Public Health Association (APHA), American Water Works Association (AWWA), and the Water Environmental Federation (WEF). 1998. Standard Methods for Examinations of Water and Wastewater, 20th ed. United Book Press, Inc. Baltimore, Maryland.
- Andersen, M. R., Kragh, T., & Sand-Jensen, K. (2017). Extreme diel dissolved oxygen and carbon cycles in shallow vegetated lakes. *Proceedings of the Royal Society B-Biological Sciences*, 284(1862). doi:10.1098/rspb.2017.1427

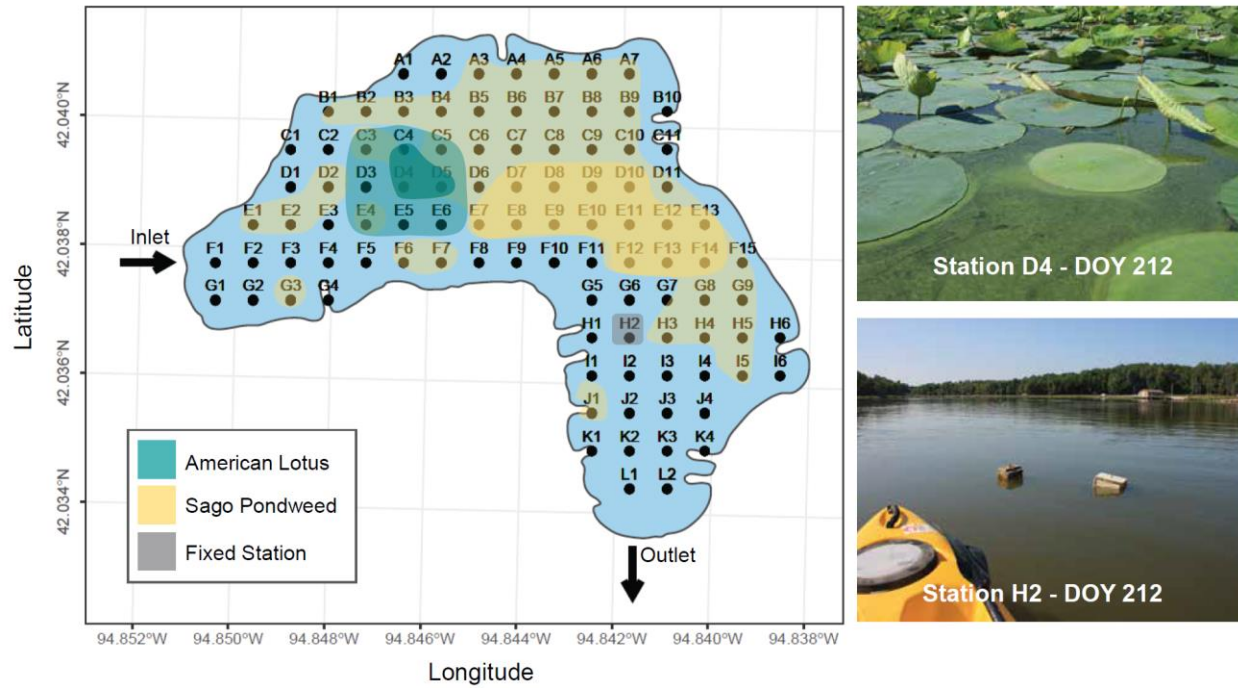
- Angradi, T. R., Ringold, P. L., & Hall, K. (2018). Water clarity measures as indicators of recreational benefits provided by US lakes: Swimming and aesthetics. *Ecological Indicators*, 93, 1005-1019. doi:10.1016/j.ecolind.2018.06.001
- Bardshaw, E. L., Allen, M. S., & Netherland, M. (2015). Spatial and temporal occurrence of hypoxia influences fish habitat quality in dense *Hydrilla verticillata*. *Journal of Freshwater Ecology*, 30(4), 491-502.
- Boehrer, B., & Schultze, M. (2008). Stratification of lakes. *Reviews of Geophysics*, 46(2). doi:10.1029/2006rg000210
- Buelo, C. D., Carpenter, S. R., & Pace, M. L. (2018). A modeling analysis of spatial statistical indicators of thresholds for algal blooms. *Limnology and Oceanography Letters*, 3(5), 384-392. doi:10.1002/lol2.10091
- Butitta, V. L., Carpenter, S. R., Loken, L. C., Pace, M. L., & Stanley, E. H. (2017). Spatial early warning signals in a lake manipulation. *Ecosphere*, 8(10). doi:10.1002/ecs2.1941
- Carey, C. C., Ibelings, B. W., Hoffmann, E. P., Hamilton, D. P., & Brookes, J. D. (2012). Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. *Water Research*, 46(5), 1394-1407. doi:10.1016/j.watres.2011.12.016
- Carlson, R. E. (1977). Trophic State Index for Lakes. *Limnology and Oceanography*, 22(2), 361-369. doi:10.4319/lo.1977.22.2.0361
- Carpenter, S., Booth, E., Kucharik, C., & Lathrop, R. (2015). Extreme daily loads: role in annual phosphorus input to a north temperate lake. *Aquatic Sciences*, 77(1), 71-79. doi:10.1007/s00027-014-0364-5
- Carpenter, S. R., Arani, B. M. S., Hanson, P. C., Scheffer, M., Stanley, E. H., & Van Nes, E. (2020). Stochastic dynamics of Cyanobacteria in long-term high-frequency observations of a eutrophic lake. *Limnology and Oceanography Letters*, 5(5), 331-336. doi:10.1002/lol2.10152
- Carpenter, S. R., Cole, J. J., Pace, M. L., Batt, R., Brock, W. A., Cline, T., . . . Weidel, B. (2011). Early Warnings of Regime Shifts: A Whole-Ecosystem Experiment. *Science*, 332(6033), 1079-1082. doi:10.1126/science.1203672
- Chaffin, J. D., Kane, D. D., & Johnson, A. (2020). Effectiveness of a fixed-depth sensor deployed from a buoy to estimate water-column cyanobacterial biomass depends on wind speed. *Journal of Environmental Sciences*, 93, 23-29. doi:10.1016/j.jes.2020.03.003
- Christensen, J. P. A., Sand-Jensen, K., & Staehr, P. A. (2013). Fluctuating water levels control water chemistry and metabolism of a charophyte-dominated pond. *Freshwater Biology*, 58(7), 1353-1365. doi:10.1111/fwb.12132
- Codd, G. A., Morrison, L. F., & Metcalf, J. S. (2005). Cyanobacterial toxins: risk management for health protection. *Toxicology and Applied Pharmacology*, 203(3), 264-272. doi:10.1016/j.taap.2004.02.016
- Corbel, S., Mougin, C., & Bouaicha, N. (2014). Cyanobacterial toxins: Modes of actions, fate in aquatic and soil ecosystems, phytotoxicity and bioaccumulation in agricultural crops. *Chemosphere*, 96, 1-15. doi:10.1016/j.chemosphere.2013.07.056
- Cotterill, V., Hamilton, D. P., Puddick, J., Suren, A., & Wood, S. A. (2019). Phycocyanin sensors as an early warning system for cyanobacteria blooms concentrations: a case study in the Rotorua lakes. *New Zealand Journal of Marine and Freshwater Research*, 53(4), 555-570. doi:10.1080/00288330.2019.1617322

- Davis, T. W., Berry, D. L., Boyer, G. L., & Gobler, C. J. (2009). The effects of temperature and nutrients on the growth and dynamics of toxic and non-toxic strains of *Microcystis* during cyanobacteria blooms. *Harmful Algae*, 8(5), 715-725. doi:10.1016/j.hal.2009.02.004
- Dodds, W. K., Bouska, W. W., Eitzmann, J. L., Pilger, T. J., Pitts, K. L., Riley, A. J., . . . Thornbrugh, D. J. (2009). Eutrophication of US Freshwaters: Analysis of Potential Economic Damages. *Environmental Science & Technology*, 43(1), 12-19. doi:10.1021/es801217q
- George, D. G., & Heaney, S. I. (1978). Factors influencing spatial-distribution of phytoplankton in a small productive lake. *Journal of Ecology*, 66(1), 133-155. doi:10.2307/2259185
- Gilbert, P. M. (2017). Eutrophication, harmful algae and biodiversity - Challenging paradigms in a world of complex nutrient changes. *Marine Pollution Bulletin*, 124(2), 591-606. doi:10.1016/j.marpolbul.2017.04.027
- Green, J. C. (2006). Effect of macrophyte spatial variability on channel resistance. *Advances in Water Resources*, 29(3), 426-438. doi:10.1016/j.advwatres.2005.05.010
- Hansen, A. M., Andersen, F. O., & Jensen, H. S. (1997). Seasonal pattern in nutrient limitation and grazing control of the phytoplankton community in a non-stratified lake. *Freshwater Biology*, 37(3), 523-534. doi:10.1046/j.1365-2427.1997.00182.x
- Kassambara, A. (2020). rstatix: Pipe-Friendly Framework for Basic Statistical Tests. R package version 0.6.0. Retrieved from <https://cran.r-project.org/package=rstatix>
- Kelly, P. T., Renwick, W. H., Knoll, L., & Vanni, M. J. (2019). Stream Nitrogen and Phosphorus Loads Are Differentially Affected by Storm Events and the Difference May Be Exacerbated by Conservation Tillage. *Environmental Science & Technology*, 53(10), 5613-5621. doi:10.1021/acs.est.8b05152
- Laas, A., Noges, P., Koiv, T., & Noges, T. (2012). High-frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. *Hydrobiologia*, 694(1), 57-74. doi:10.1007/s10750-012-1131-z
- Landsberg, J. H. (2002). The effects of harmful algal blooms on aquatic organisms. *Reviews in Fisheries Science*, 10(2), 113-390. doi:10.1080/20026491051695
- Lekki, J., Deutsch, E., Sayers, M., Bosse, K., Anderson, R., Tokars, R., & Sawtell, R. (2019). Determining remote sensing spatial resolution requirements for the monitoring of harmful algal blooms in the Great Lakes. *Journal of Great Lakes Research*, 45(3), 434-443. doi:10.1016/j.jglr.2019.03.014
- Loken, L. C., Crawford, J. T., Dornblaser, M. M., Striegl, R. G., Houser, J. N., Turner, P. A., & Stanley, E. H. (2018). Limited nitrate retention capacity in the Upper Mississippi River. *Environmental Research Letters*, 13(7). doi:10.1088/1748-9326/aacd51
- Medeiros, A. S., Biastoch, R. G., Luszczek, C. E., Wang, X. A., Muir, D. C. G., & Quinlan, R. (2012). Patterns in the limnology of lakes and ponds across multiple local and regional environmental gradients in the eastern Canadian Arctic. *Inland Waters*, 2(2), 59-76. doi:10.5268/iw-2.2.427
- Moller, T. R., & Rordam, C. P. (1985). Species numbers of vascular plants in relation to area, isolation and age of ponds in Denmark. *Oikos*, 45(1), 8-16. doi:10.2307/3565216
- Moran, P. A. P. (1950). Notes on Continuous Stochastic Phenomena. *Biometrika*, 37(1-2), 17-23. doi:10.2307/2332142
- Moreno-Ostos, E., Cruz-Pizarro, L., Basanta, A., & George, D. G. (2009). Spatial Heterogeneity of Cyanobacteria and Diatoms in a Thermally Stratified Canyon-Shaped Reservoir. *International Review of Hydrobiology*, 94(3), 245-257. doi:10.1002/iroh.200811123

- Ortiz, D., Palmer, J., & Wilkinson, G. (2019). Hypereutrophic lake sensor data during summer algae blooms in Iowa, USA, 2014 - 2018 ver 1. *Environmental Data Initiative*. doi:10.6073/pasta/30070d41fbcdf36387f33d9108f570f8
- Ortiz, D., Palmer, J., & Wilkinson, G. (2020). Detecting changes in statistical indicators of resilience prior to algal blooms in shallow eutrophic lakes. *Ecosphere*, *11*(10). doi:10.1002/ecs2.3200
- Ortiz, D., & Wilkinson, G. (2019). Hypereutrophic lake spatial sensor data during summer bloom, Swan Lake, Iowa, USA 2018 ver 1. *Environmental Data Initiative*. doi:10.6073/pasta/2c0ca177438a3d422925811514e86cd8
- Pace, M. L., Batt, R. D., Buelo, C. D., Carpenter, S. R., Cole, J. J., Kurtzweil, J. T., & Wilkinson, G. M. (2017). Reversal of a cyanobacterial bloom in response to early warnings. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(2), 352-357. doi:10.1073/pnas.1612424114
- Pebesma, E. J. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *R Journal*, *10*(1), 439-446.
- Pebesma, E. J. (2004). Multivariable geostatistics in S: the gstat package. *Computers & Geosciences*, *30*(7), 683-691. doi:10.1016/j.cageo.2004.03.012
- Pellerin, B. A., Stauffer, B. A., Young, D. A., Sullivan, D. J., Bricker, S. B., Walbridge, M. R., . . . Shaw, D. M. (2016). Emerging tools for continuous nutrient monitoring networks: sensors advancing science and water resources protection. *Journal of the American Water Resources Association*, *52*(4), 993-1008. doi:10.1111/1752-1688.12386
- R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.R-project.org/>
- Read, J. S., Hamilton, D. P., Jones, I. D., Muraoka, K., Winslow, L. A., Kroiss, R., . . . Gaiser, E. (2011). Derivation of lake mixing and stratification indices from high-resolution lake buoy data. *Environmental Modelling & Software*, *26*(11), 1325-1336. doi:10.1016/j.envsoft.2011.05.006
- Rennella, A. M., & Quiros, R. (2006). The effects of hydrology on plankton biomass in shallow lakes of the Pampa Plain. *Hydrobiologia*, *556*, 181-191. doi:10.1007/s10750-005-0318-y
- Romo, S., Soria, J., Fernandez, F., Ouahid, Y., & Baron-Sola, A. (2013). Water residence time and the dynamics of toxic cyanobacteria. *Freshwater Biology*, *58*(3), 513-522. doi:10.1111/j.1365-2427.2012.02734.x
- Rychtecky, P., & Znachor, P. (2011). Spatial heterogeneity and seasonal succession of phytoplankton along the longitudinal gradient in a eutrophic reservoir. *Hydrobiologia*, *663*(1), 175-186. doi:10.1007/s10750-010-0571-6
- Schilder, J., Bastviken, D., van Hardenbroek, M., Kankaala, P., Rinta, P., Stotter, T., & Heiri, O. (2013). Spatial heterogeneity and lake morphology affect diffusive greenhouse gas emission estimates of lakes. *Geophysical Research Letters*, *40*(21), 5752-5756. doi:10.1002/2013gl057669
- Schoen, J. H., Stretch, D. D., & Tirok, K. (2014). Wind-driven circulation patterns in a shallow estuarine lake: St Lucia, South Africa. *Estuarine Coastal and Shelf Science*, *146*, 49-59. doi:10.1016/j.ecss.2014.05.007
- Serizawa, H., Amemiya, T., & Itoh, K. (2008). Patchiness in a minimal nutrient - phytoplankton model. *Journal of Biosciences*, *33*(3), 391-403. doi:10.1007/s12038-008-0059-y

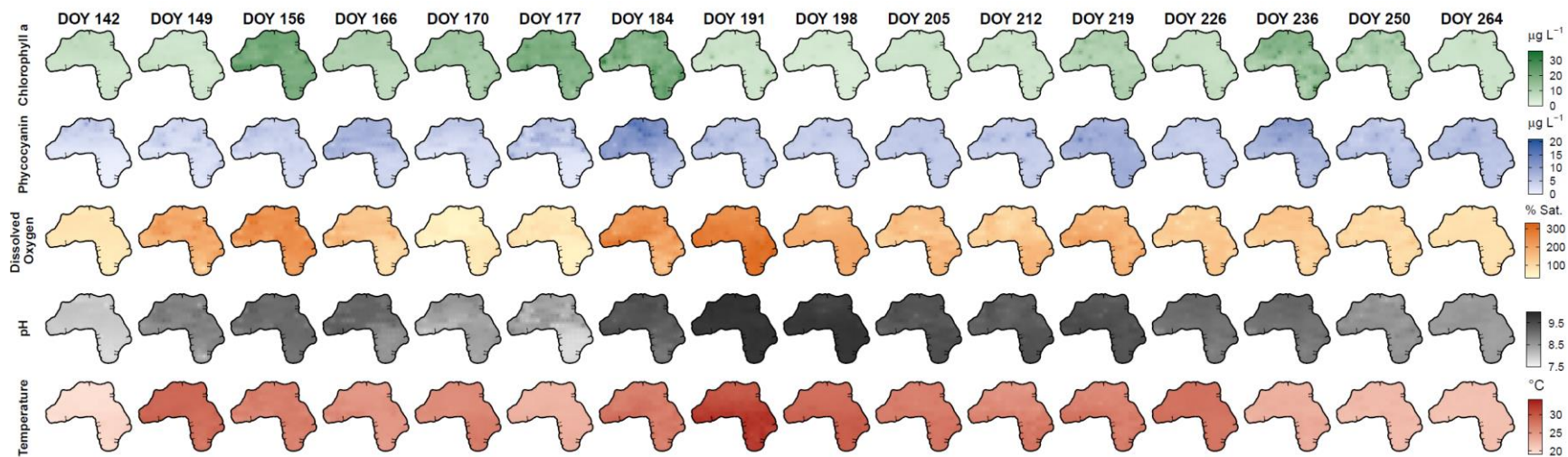
- Smith, C., D. (2018). *Temporal and Spatial Monitoring of Cyanobacterial Blooms at Willow Creek Reservoir, North-Central Oregon*. Retrieved from U.S. Geological Survey Scientific Investigations Report:
- Solomon, C. T., Bruesewitz, D. A., Richardson, D. C., Rose, K. C., Van de Bogert, M. C., Hanson, P. C., . . . Zhu, G. W. (2013). Ecosystem respiration: Drivers of daily variability and background respiration in lakes around the globe. *Limnology and Oceanography*, 58(3), 849-866. doi:10.4319/lo.2013.58.3.0849
- Staehr, P. A., Christensen, J. P. A., Batt, R. D., & Read, J. S. (2012). Ecosystem metabolism in a stratified lake. *Limnology and Oceanography*, 57(5), 1317-1330. doi:10.4319/lo.2012.57.5.1317
- Stanley, E. H., Collins, S. M., Lottig, N. R., Oliver, S. K., Webster, K. E., Cheruvilil, K. S., & Soranno, P. A. (2019). Biases in lake water quality sampling and implications for macroscale research. *Limnology and Oceanography*, 64(4), 1572-1585. doi:10.1002/lno.11136
- United States Environmental Protection Agency. (1993a). *Determination of Nitrate-Nitrite by Automated Colorimetry. Method 353.2 Revision 2.0*.
- United States Environmental Protection Agency. (1993b). *Determination of Phosphorus by Semi-Automated Colorimetry. Method 365.1 Revision 2.0*.
- United States Environmental Protection Agency. (1993c). *Determination of Total Kjeldahl Nitrogen by Semi-Automated Colorimetry Method 351.2, Revision 2.0*.
- Van de Bogert, M. C., Bade, D. L., Carpenter, S. R., Cole, J. J., Pace, M. L., Hanson, P. C., & Langman, O. C. (2012). Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. *Limnology and Oceanography*, 57(6), 1689-1700. doi:10.4319/lo.2012.57.6.1689
- Vilas, M. P., Marti, C. L., Adams, M. P., Oldham, C. E., & Hipsey, M. R. (2017). Invasive Macrophytes Control the Spatial and Temporal Patterns of Temperature and Dissolved Oxygen in a Shallow Lake: A Proposed Feedback Mechanism of Macrophyte Loss. *Frontiers in Plant Science*, 8. doi:10.3389/fpls.2017.02097
- Wilkinson, G. M., Carpenter, S. R., Cole, J. J., Pace, M. L., Batt, R. D., Buelo, C. D., & Kurtzweil, J. T. (2018). Early warning signals precede cyanobacterial blooms in multiple whole-lake experiments. *Ecological Monographs*, 88(2), 188-203. doi:10.1002/ecm.1286
- Wu, X. D., Kong, F. X., Chen, Y. W., Qian, X., Zhang, L. J., Yu, Y., . . . Xing, P. (2010). Horizontal distribution and transport processes of bloom-forming *Microcystis* in a large shallow lake (Taihu, China). *Limnologica*, 40(1), 8-15. doi:10.1016/j.limno.2009.02.001
- Wynne, T. T., & Stumpf, R. P. (2015). Spatial and Temporal Patterns in the Seasonal Distribution of Toxic Cyanobacteria in Western Lake Erie from 2002-2014. *Toxins*, 7(5), 1649-1663. doi:10.3390/toxins7051649
- Zhou, Y. T., Obenour, D. R., Scavia, D., Johengen, T. H., & Michalak, A. M. (2013). Spatial and Temporal Trends in Lake Erie Hypoxia, 1987-2007. *Environmental Science & Technology*, 47(2), 899-905. doi:10.1021/es303401b

Figures



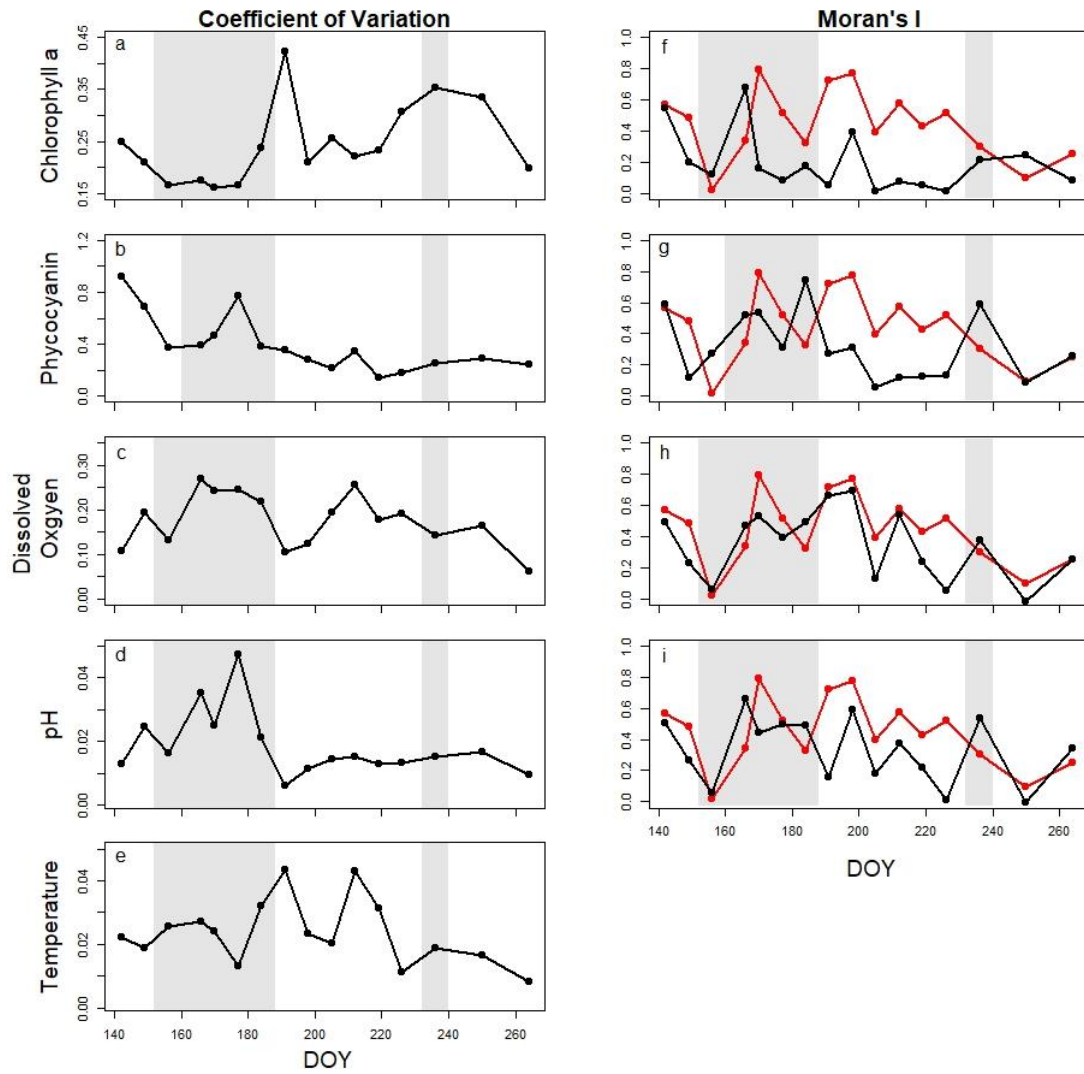
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3 **Figure 1.** Sampling locations on a 65 m square grid with the main inlet to the lake and only
 4 outlet indicated with arrows. The location of the macrophyte beds of the two dominant species
 5 within the lake are shown on the map, with darker shading indicating the regions with the
 6 densest vegetation and the location of the high frequency sensor. The photos to the right
 7 illustrate conditions in the American Lotus patch (station D4) and at the fixed station sonde
 8 (station H2) on DOY 212 during sampling.



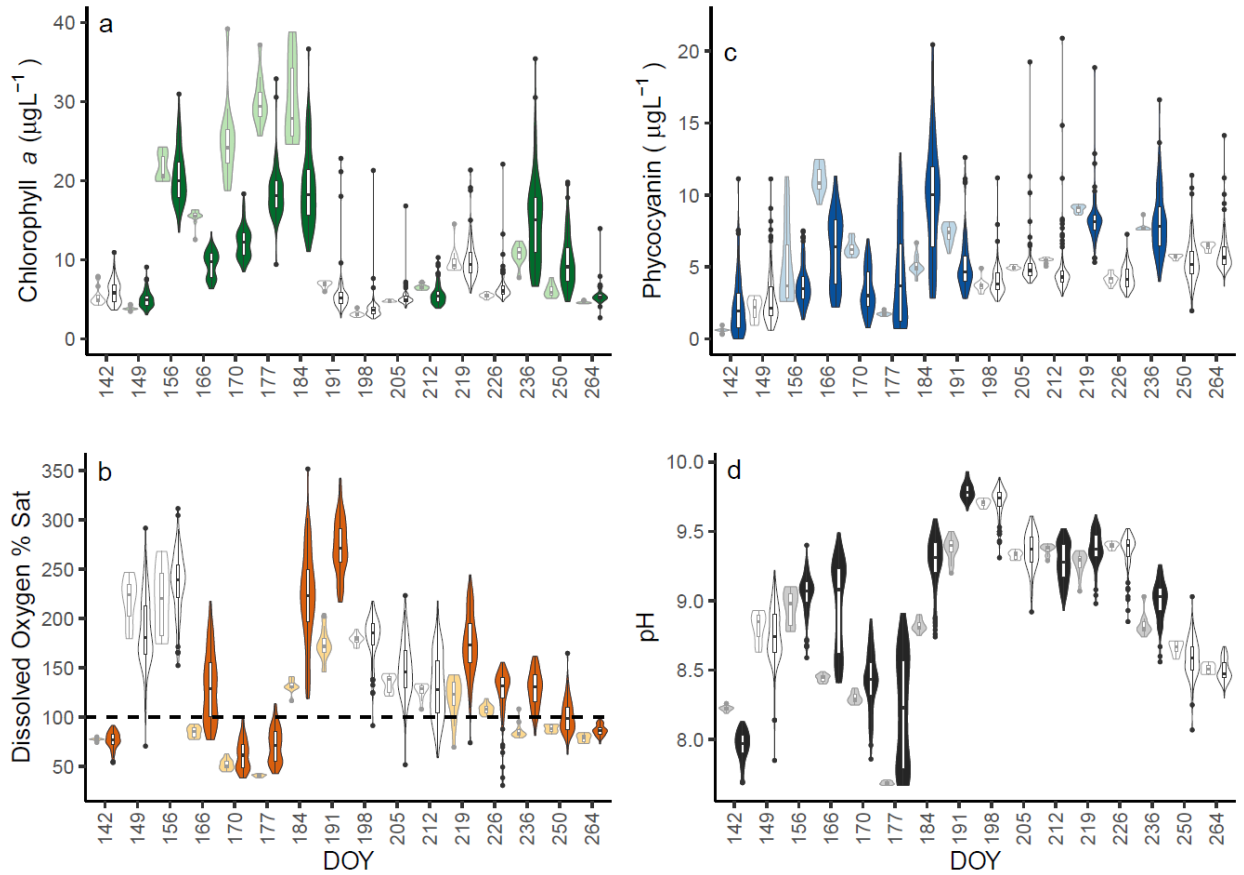
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10 **Figure 2.** The spatial pattern of each of the variables for each sampling event. The 98 sampling locations (Figure 1) were interpolated
 11 across a 25m grid using spatial inverse distance interpolation. The color ramps for each variable are scaled from the lowest to the
 12 highest value observed over the course of the season across all sampling locations.



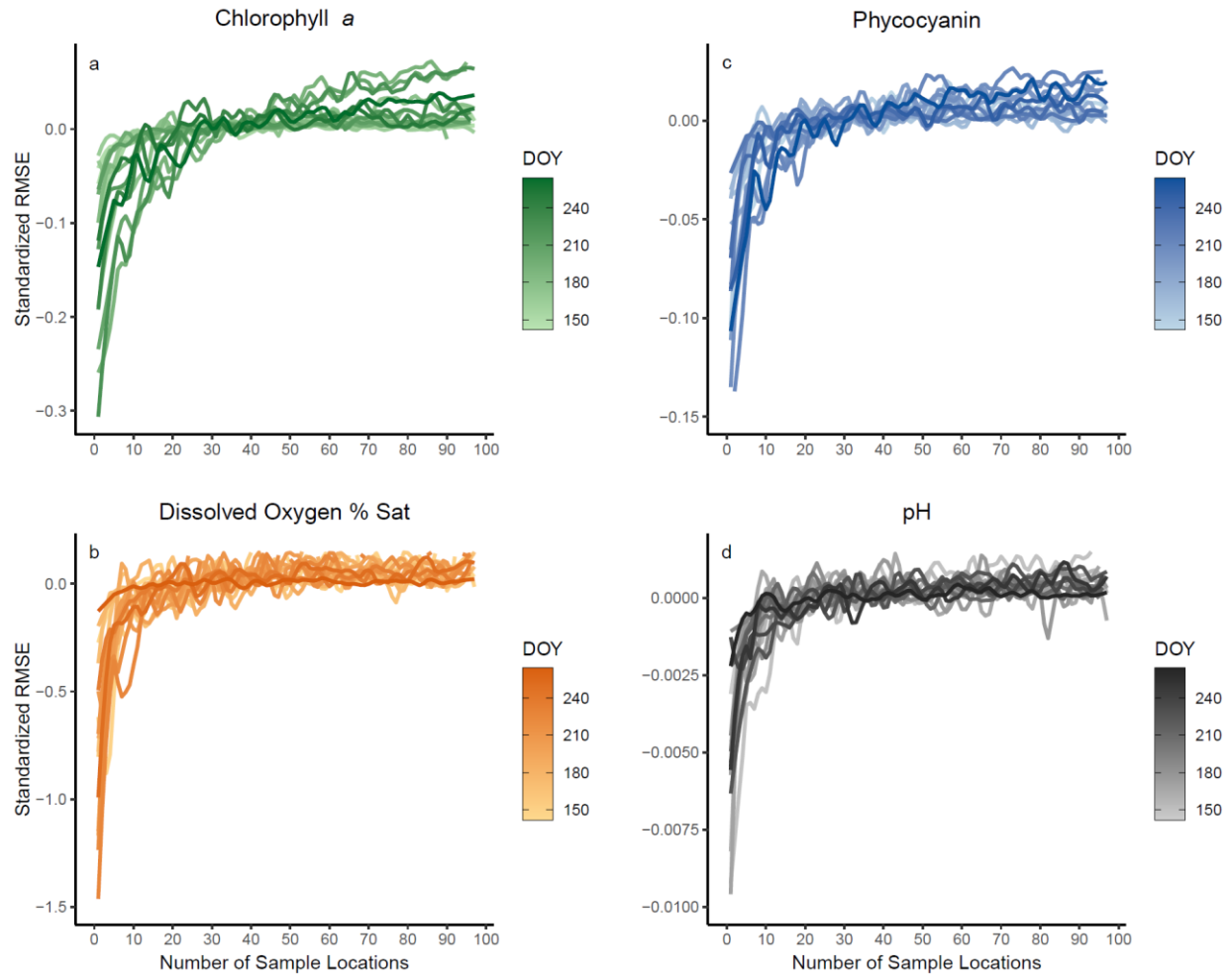
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14 **Figure 3.** Time series of the spatial coefficient of variation (CV) and spatial autocorrelation (AC;
 15 Moran's I) in Swan Lake. The gray polygons indicate periods of algal bloom. The red time
 16 series of Moran's I is for temperature.



17

18 **Figure 4.** Violin plots of the fixed station (gray outline, lighter shading) and spatial (black
 19 outline, darker shading) data, paired for every sampling event. Pairs of violin plots for a
 20 sampling date that are shaded with color indicate a statistically significant ($\alpha < 0.05$) difference
 21 in the mean of the fixed station and spatial sampling distributions during that event. The fixed
 22 station data were trimmed to the period that spatial sampling occurred.



23

24 **Figure 5.** Standardized Root Mean Squared Errors (RMSE) of rarefaction analysis. Fit lines
 25 represent each sampling dates standardized RMSE (16 in total) and the gradient from light to
 26 dark indicates first sampling event to last.

27

Supplementary material for

28 **Title:** The evolution of spatial variability during an algal bloom event in shallow lakes

29 **Authors:** Ortiz and Wilkinson

30

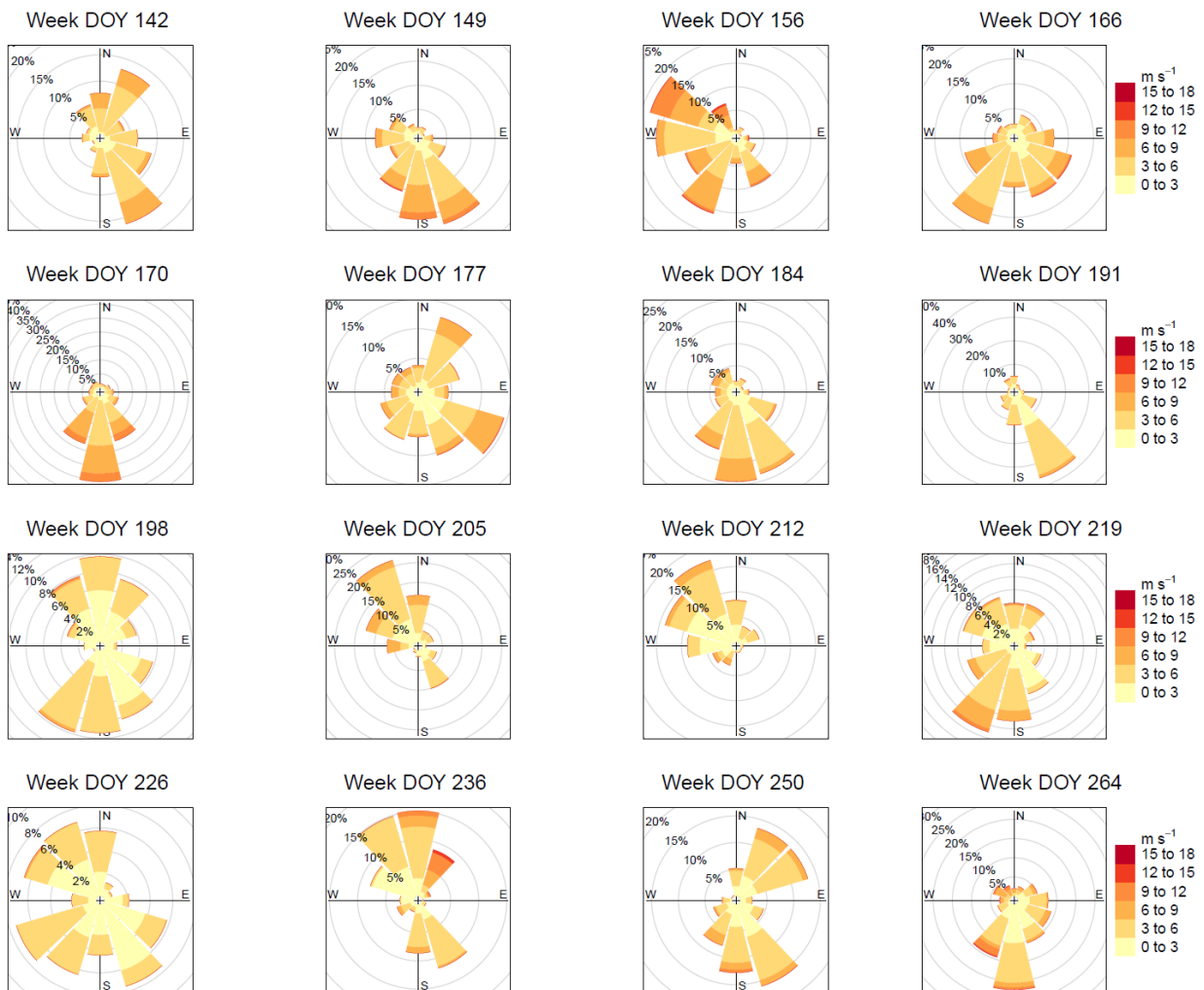
31

Hourly Weather Data

32 Hourly wind and precipitation data were downloaded from the Iowa State University Iowa
33 Environmental Mesonet (<https://mesonet.agron.iastate.edu/>) for Arthur N. Neu Airport Carroll,
34 Iowa, USA less than 5km from the lake.

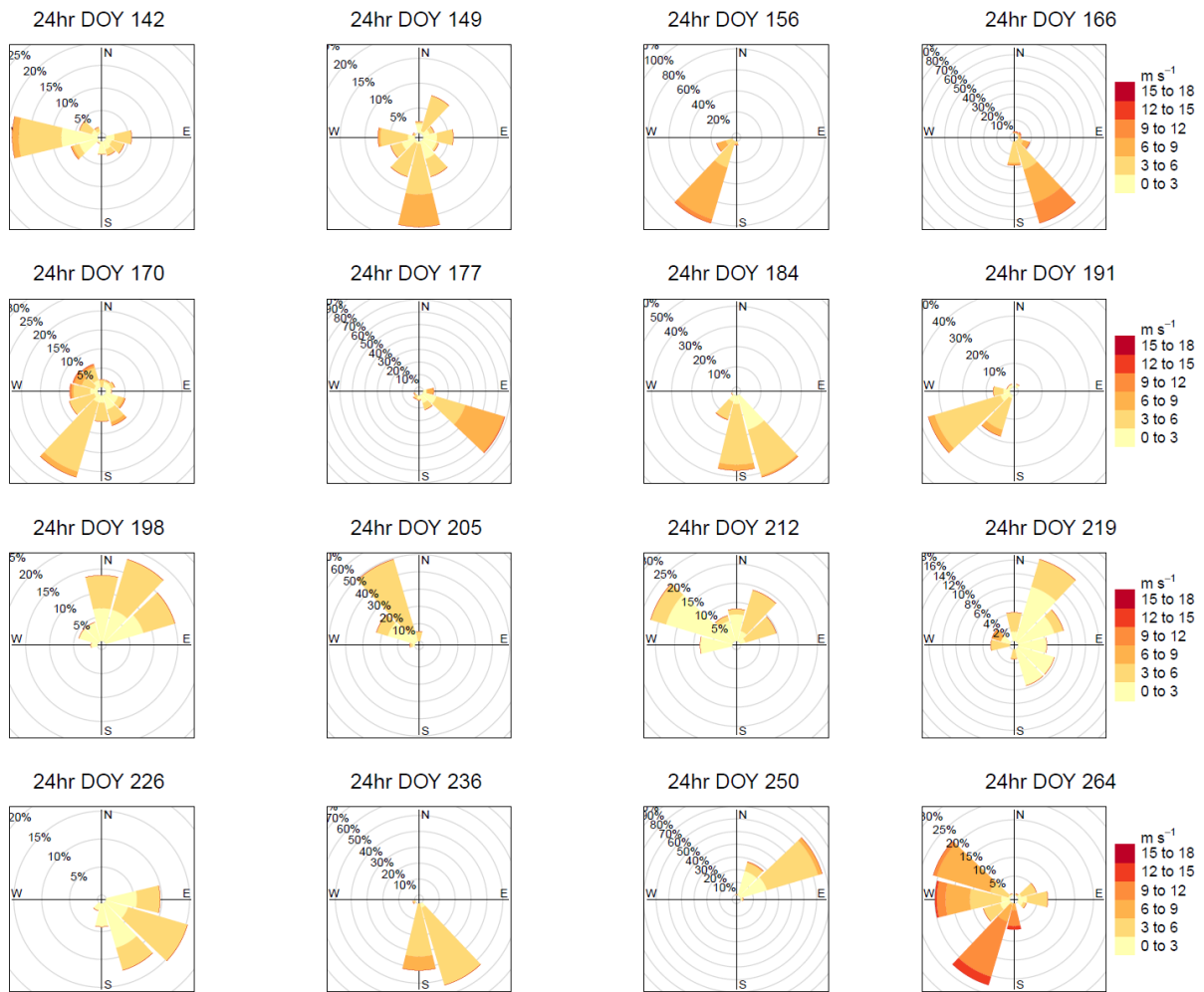
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36 Figures



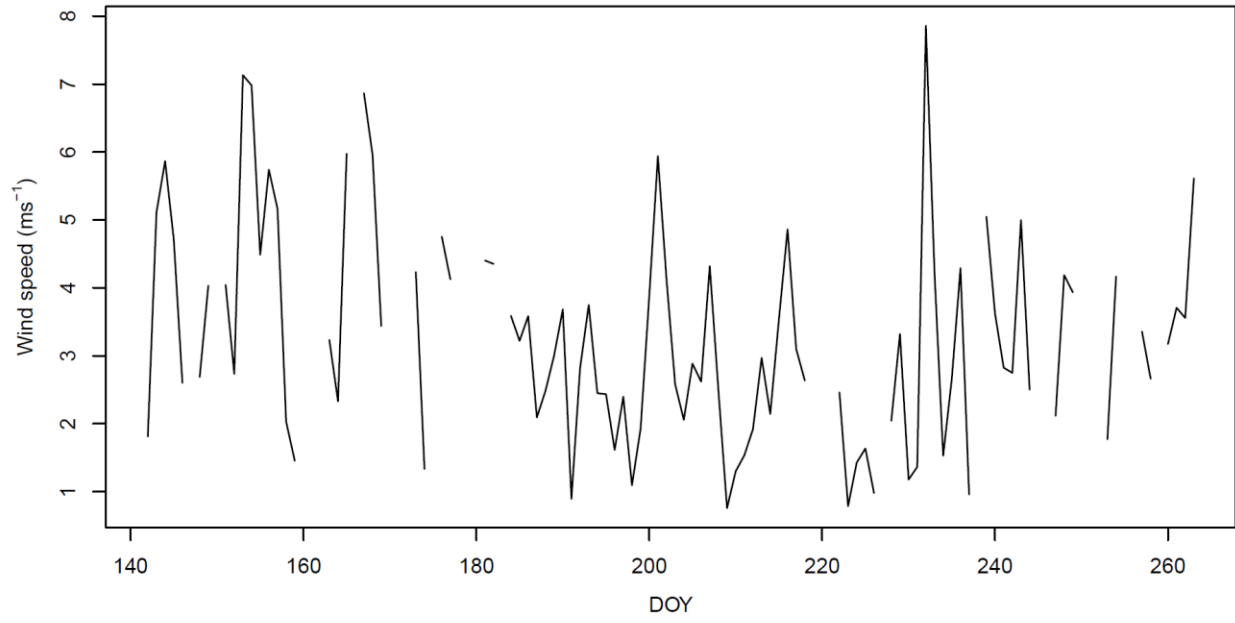
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38 **Supplement Figure 1.** Wind speed and direction one week prior to sampling date.



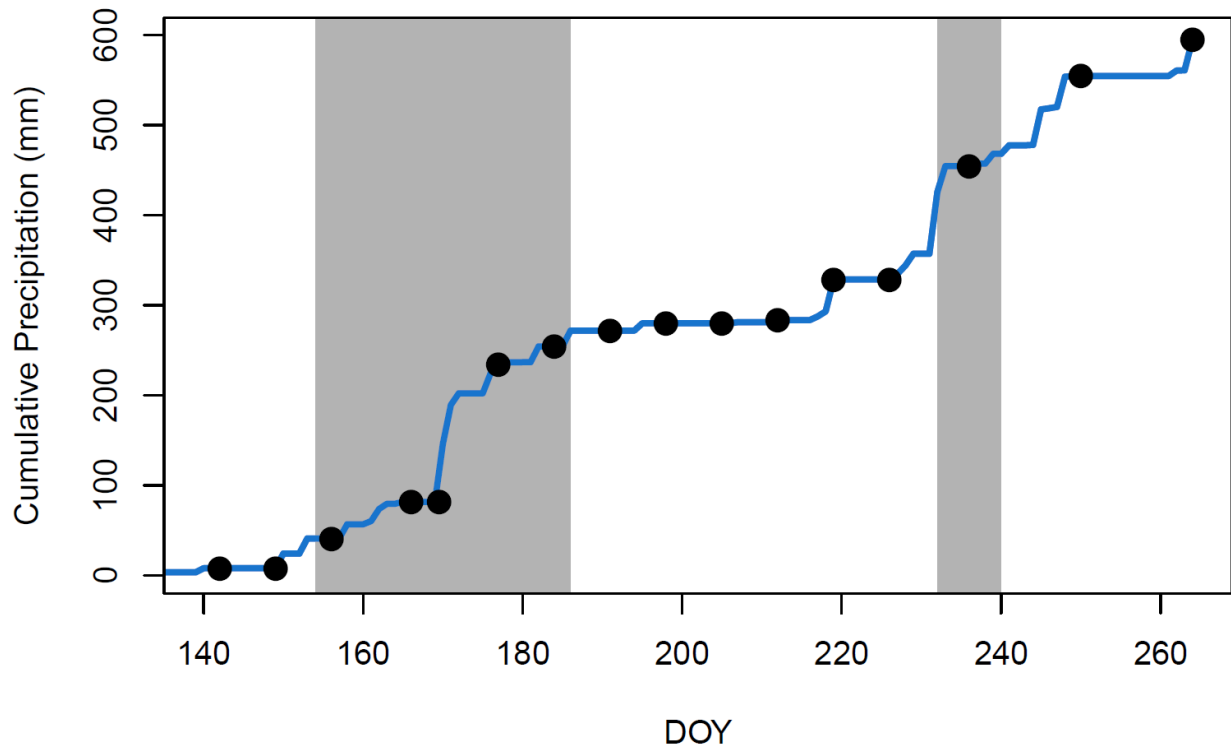
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40 **Supplement Figure 2.** Wind speed and direction 24 hours before sampling event.



41

42 **Supplement Figure 3.** Daily mean of wind speed for duration of study.



43

44 **Supplement Figure 4.** Cumulative precipitation beginning on day of year (DOY) 134 (blue line)
45 with the spatial sampling dates (black circles) plotted on top. The gray polygons are the two
46 bloom periods.