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Using wavelet analyses to examine variability in phytoplankton seasonal succession and annual periodicity

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In most north temperate lakes, phytoplankton biomass oscillates on an annual scale. While phytoplankton seasonal succession within a year has been described for many lakes, much less is known about variability in seasonal succession over multiple years. Here, we describe how continuous wavelet transforms can be used to identify variation in the periodicity in phytoplankton time series at multiple timescales. To demonstrate our approach, we analyzed 16 years of biweekly phytoplankton data from eutrophic Lake Mendota, USA, that coincided with substantial variability in climate and nutrient loading. Throughout the time series, the wavelet transforms identified the annual scale as the dominant scale of variation in aggregated phytoplankton, except for a 3-year period when there was no significant dominant scale. This period coincided with drought and decreased nutrient loading. During this time, phytoplankton biomass was markedly lower, and the phytoplankton community exhibited a unimodal, not bimodal, pattern of seasonal succession. Our results highlight the utility of wavelet techniques for identifying changes in seasonal succession in long-term phytoplankton records, which are becoming more available for many lakes. As aquatic ecosystems increasingly experience exogenous forcings at multiple timescales, wavelet analyses provide a powerful tool for determining how phytoplankton communities may respond.

KEYWORDS: community dynamics; continuous wavelet transforms; cyanobacteria; Lake Mendota; PEG model; phenology

INTRODUCTION

The annual succession of phytoplankton has been well documented in many dimictic north temperate lakes (reviewed by Sommer, 1989; Reynolds, 2006). This yearly oscillation in phytoplankton biomass has been described in the Plankton Ecology Group (PEG) model, a conceptual

framework that examines the effects of both abiotic factors (e.g. light, temperature, nutrients) and biotic factors (e.g. zooplankton grazing) on phytoplankton seasonal succession (Sommer et al., 1986). Sommer *et al.*'s (Sommer et al., 1986) paper outlining the 24 successional steps of phytoplankton in the PEG model remains one of the most cited in plankton ecology, and has motivated decades of research examining phytoplankton seasonal succession within a year (e.g. Padisak et al., 2010; Sommer et al., 2012).

According to the PEG model, the phytoplankton community should exhibit predictable, cyclical dynamics on an annual scale in deep, thermally stratified temperate lakes. In eutrophic systems, it is expected that the community should exhibit two or three distinct peaks within a year (a spring bloom of diatoms, summer bloom of chlorophytes and/or cyanobacteria and potentially a fall diatom bloom), and in oligotrophic lakes, it is expected that there should be a unimodal phytoplankton maximum in the spring due to nutrient limitation (Sommer et al., 1986, 2012). Although deviations from the PEG model have been documented for several lakes (Jeppesen et al., 1997; Alvarez-Cobelas et al., 2005; Moustaka-Gouni et al., 2014), and recent advances in our understanding of the microbial loop, phytoplankton food quality and parasites are not represented in the model (De Senerpont Domis et al., 2013), the PEG template provides an important starting point for examining lake phytoplankton community dynamics (e.g. Padisak et al., 2010).

While many studies have examined phytoplankton succession within years, much less is known about community dynamics from years to decades, primarily due to the absence of data. While the PEG model predicts that the dominant annual pattern of phytoplankton succession should generally persist over time (Sommer et al., 1986), changes to the magnitude or timing of phytoplankton blooms due to altered nutrient loading or climate, for example, could weaken the annual cycle of phytoplankton periodicity (e.g. Winder and Schindler, 2004; Elliott et al., 2006; Drake et al., 2010). Inter-annual variability may be an intrinsic property of plankton communities in north temperate latitudes (Dakos et al., 2009), but there have been relatively few datasets available to examine these dynamics. Long-term phytoplankton data are now becoming more readily available, providing the opportunity to re-address assumptions about phytoplankton seasonal succession. In particular, little is known about the variability of community succession patterns from year to year, especially in response to changing environmental drivers (Jassby et al., 1990; Anneville et al., 2002; Arhonditis et al., 2004; Roelke et al., 2004).

Here, we describe the application of wavelet transforms to quantify the strength and persistence of patterns in phytoplankton biovolume through time. Wavelet transforms are useful tools for determining the dominant scales of variation in time series (Chatfield, 1989) and are increasingly used to examine periodicities in plankton communities (e.g. Keitt and Fischer, 2006; Vasseur and Gaedke, 2007; Cloern and Jassby, 2010; Winder and Cloern, 2010; Vasseur et al., 2014). Time series for many environmental variables show multiple scales of variation, and quantifying the occurrence and magnitude of those patterns provides clues to the underlying ecosystem processes controlling them.

We use the example of dissolved oxygen concentrations, an important indicator of ecosystem state and function (Odum, 1956), to illustrate how wavelet analyses can be used to examine periodicity in biologically relevant time series data. Dissolved oxygen concentrations in lakes fluctuate at multiple scales: e.g. oscillations on the minute to hour scales detected by *in situ* high-frequency sensors can indicate fluctuations in water column stratification; daily oscillations tend to be driven by the balance of primary productivity and respiration; seasonal oscillations are driven by the wax and wane of phytoplankton communities; and annual patterns are driven by temperature (Hanson et al., 2006; Langman et al., 2010). Quantifying how these scales contribute to the overall variability of the time series is the basis of spectral analysis. For our dissolved oxygen example, the hierarchy of variability contributed by the different scales is decadal > annual > daily > hourly (Hanson et al., 2006). However, the overall hierarchy does not tell us when during the time series each of the scales contributes significantly to the variance, because the importance of certain scales may vary over time. For example, the daily oscillation of dissolved oxygen, which is pronounced during summer, disappears during winter, indicating greatly reduced metabolism. Thus, we need to use continuous wavelet transforms, which decompose the time series of a response variable by estimating its spectral characteristics as a function of time (Torrence and Compo, 1998); this approach determines how the importance of different scales, or periods, varies over a time series (Daubechies, 1992).

We can use continuous wavelet transforms to examine the importance of different timescales in phytoplankton time series in much the same way as described for dissolved oxygen above. An important difference, however, is that phytoplankton time series are usually composed of biweekly to monthly resolution discrete samples, limiting the minimum scale of analysis to weeks, rather than minutes. A decadal dataset of biweekly (i.e. fortnightly) phytoplankton samples would allow us to examine a minimum scale of variation of 28 days and a maximum scale of variation roughly $\frac{1}{2}$ the total duration of the time series, following the Nyquist–Shannon sampling theorem (Nyquist, 1928; Shannon, 1949), and thus compare the relative importance of monthly, seasonal and annual scales. Monthly oscillations of phytoplankton indicate blooms; seasonal

oscillations reflect succession patterns of different phytoplankton groups and annual oscillations indicate differences in exogenous factors, such as nutrient loading or climate.

Examining the hierarchy of monthly, seasonal and annual scales over the time series provides valuable information on phytoplankton seasonal succession. For example, a phytoplankton community that exhibits a consistent pattern of seasonal succession year after year, as expected by the PEG model, will exhibit a dominant annual scale of variation throughout its time series. Similarly, years when the annual scale of variation is weakened may indicate deviations in seasonal succession from the typical pattern.

Recent studies have used wavelet analyses to determine that the annual scale is generally the most dominant scale of variation in total phytoplankton biomass in temperate lakes, which provides an important baseline for identifying when seasonal succession may be disrupted (Vasseur and Gaedke, 2007; Winder and Cloern, 2010). In a meta-analysis of total phytoplankton biomass time series from marine, estuarine and freshwater ecosystems, Winder and Cloern (Winder and Cloern, 2010) observed that the dominant scale of variation of chlorophyll *a* in most, but not all, temperate lakes was at the annual scale. In a complementary analysis, Vasseur and Gaedke (Vasseur and Gaedke, 2007) found that the annual scale was also the dominant scale of variability of the aggregated phytoplankton community in north temperate Lake Constance (Germany). Both studies were primarily focused on determining the overall most important scale of variation of the time series, not how the dominant scale may change over time. Consequently, it remains untested if wavelet analyses can be used to examine the variability in phytoplankton seasonal succession over time.

Here, we used wavelet transforms to identify the dominant scales of variability of a phytoplankton community over 16 years. We used the phytoplankton record of Lake Mendota, WI, USA, a eutrophic north temperate lake that experiences considerable inter-annual variation in environmental conditions that may affect seasonal succession (Lathrop and Carpenter, 1992a). We hypothesized that the annual scale of variation in phytoplankton would be weakened during years with disrupted seasonal succession. Following the PEG paradigm, we expected that cyanobacteria and chlorophytes would exhibit a dominant annual scale that persisted through the time series, and that diatoms would exhibit a dominant bi-annual scale, consistent with a spring and fall bloom. The overarching goal of this Lake Mendota case study was to demonstrate the increasing utility and value of wavelet techniques for analyzing variability in long-term phytoplankton time series.

METHOD

Observational data

We analyzed phytoplankton dynamics in Lake Mendota, WI, USA (43°6′, 24″N; 89°25′29″W). Lake Mendota is a eutrophic north temperate lake that has been extensively studied for over a century (for an in-depth description, see Brock, 1985; Kitchell, 1992; Lathrop, 2007) and has been sampled as part of the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) site since 1995 (http://lter.limnology.wisc.edu; Carpenter et al., 2007). The lake is ice-covered typically from December or January to March or April and has a mean residence time of 4.3 years, a surface area of 40 km^2 and mean and maximum depths of 12 and 25 m, respectively.

We focused on 1995–2010 as our study period because Lake Mendota experienced substantial environmental variability during this time, as exemplified by trends in annual phosphorus (P) loads (Fig. 1) that might affect phytoplankton seasonal succession. In particular, loads were low ($\leq$4000 kg P $year^{-1}$) during a drought period with little runoff during 2002–2003; whereas loads were very high (>21 000 kg P $year^{-1}$) during 2008 and 2009 due to major runoff events in late spring and late winter in the two respective years (Fig. 1; Lathrop and Carpenter, 2014). Annual P loads to Lake Mendota are highly correlated to both inorganic and organic nitrogen (N) loads to the lake (Lathrop, 1992), so it is likely that the concentration of both nutrients in the lake exhibited substantial variability during 1995–2010. We expected that this variability in nutrients, as well as other environmental factors (see below), would result in year-to-year differences in phytoplankton succession (Lathrop and Carpenter, 1992a).

The phytoplankton community in Lake Mendota was sampled biweekly to monthly during 1995–2010 as part of the routine NTL-LTER monitoring (for detailed methodological information and data, see: http://lter.limnology.wisc.edu). In summary, phytoplankton were collected during both the open-water period and through the ice at the deepest part of the lake with an integrated 8-m tube, pooled into a composite 0–8-m sample and immediately preserved with glutaraldehyde. More than 400 natural units (i.e. cells, filaments or colonies) were identified to species per sample using an Olympus BX51 compound microscope following a stratified counting modification of the method of Utermöhl (Utermöhl, 1958), as described by St. Amand (St. Amand, 1990). Biovolume was calculated for up to 15 natural units of each species per sample by approximating cells to geometric shapes, and represented our primary phytoplankton response variable (Hillebrand et al., 1999). Importantly, all phytoplankton microscopic analyses were conducted

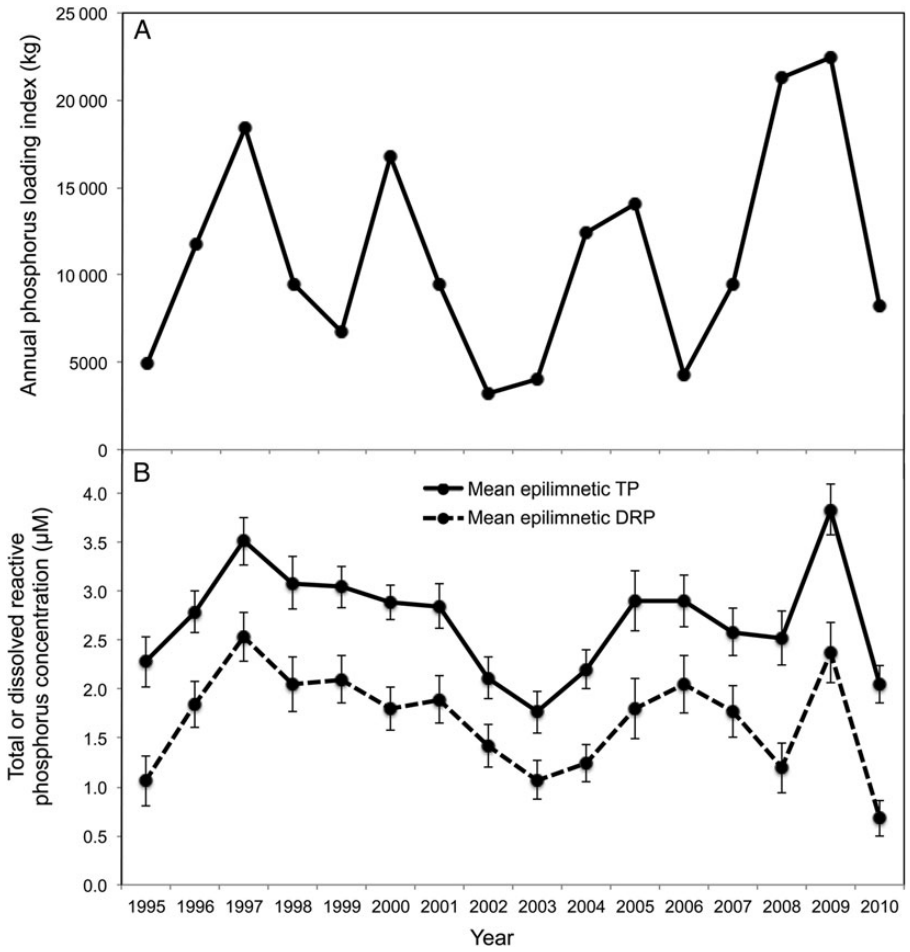


Fig. 1. (**A**) Annual phosphorus loading index, a metric of the total amount of phosphorus entering Lake Mendota as runoff each calendar year from 1995 to 2010 (for more information on this index, *see* Lathrop and Carpenter, 2014). (**B**) Mean epilimnetic total phosphorus (TP, solid line) and dissolved reactive phosphorus (DRP, dashed line) for each year of the time series.

by the same taxonomist throughout the time series (A.L.S.).

Wavelet analyses

We used continuous wavelet transforms to determine the dominant scales of variability in the phytoplankton community over the time series. Our wavelet approach required a dataset sampled at a fixed interval throughout the time series. Because the Mendota phytoplankton were collected approximately biweekly to monthly throughout the 16-year time series, we used several approaches for converting our unevenly sampled observations into a fixed, biweekly interval dataset. To account for variation in phytoplankton identification and biovolume estimates over time, and because we were primarily interested in the succession of aggregate phytoplankton groups as described by the PEG model, we first aggregated all phytoplankton species to division. Second, we reassigned sampling days to the closest regularly spaced day on a biweekly interval throughout the time series. In the spring (after ice-off) and summer months, phytoplankton were sampled consistently on a biweekly interval (generally $\pm$ 4 days) except for the rare occasion in which sampling did not occur due to weather or equipment failure. In those few cases ($n < 10$), we linearly interpolated the missing phytoplankton data. In October to December, phytoplankton were sampled monthly, in which case we also linearly interpolated the missing biweekly values. The under-ice period had much fewer observations than the open-water period: typically only 1–2 sampling days occurred during the ~3 months of ice cover every year. We compiled a dataset of all under-ice phytoplankton observations during the 1995–2010 time series, and randomly resampled these data at a biweekly interval to create a simulated time series of under-ice observations. Because our analysis of annual succession required data at fixed intervals year-round, bootstrapping provided a practical

approach for gap-filling consecutive missing sampling days that had ice cover. These winter observations consistently exhibited an order of magnitude lower phytoplankton biovolumes than the open-water period: the median and standard deviation of the under-ice total phytoplankton biovolume was 1.96×10^5 ($\pm$ 2.89×10^5) μm^3 mL^{-1}, in comparison with 1.31×10^6 ($\pm$ 2.57×10^6) μm^3 mL^{-1} in the open-water period. Aggregated across the 16 years, the under-ice phytoplankton biovolumes were significantly lower than the open-water biovolumes (Welch one-way analysis of variance for unequal variances; $F_{1,390} = 165.40$, $P < 0.0001$). To ensure that these steps did not affect the wavelet analyses, we downsampled the final biweekly dataset to a monthly interval and found that the interpolation did not qualitatively affect our overall results.

Once the time series of phytoplankton biovolume observations for each division were finalized, we performed additional data quality control steps. We removed extreme outliers (biovolumes greater than 5 standard deviations from the mean biovolume observed for each division) and applied a standard normal transformation to all phytoplankton biovolume observations prior to analysis to enable comparison of the wavelet transforms from phytoplankton divisions that had widely varying biovolumes.

We used a continuous wavelet transform to examine cyclical fluctuations in the phytoplankton biovolumes over the entire 1995–2010 time series (Torrence and Compo, 1998; Grinsted et al., 2004). We chose the Morlet wavelet as the wavelet base function because it provides a good balance between time and frequency localization (Grinsted et al., 2004). A wavelet base function, "the wavelet," is depicted as the colored line in Fig. 2. For the analysis, only the wavelet changes by scale; however, for illustrative purposes, we have smoothed the observed Lake Mendota total phytoplankton biovolume data to 28-day, 6-month and 1-year scales to show how stretching the wavelet corresponds to different scales of variability in the observational data in Fig. 2. When applied to the time series, the length of the wavelet is often set initially to two times the sampling period (here, for a 14-day sampling period, the first wavelet is set at 28 days; Torrence and Compo, 1998). The wavelet is compared with a section at the beginning of the time series, and the correlation between the wavelet and that section of the time series is calculated as a coefficient, C (Torrence and Compo, 1998). C is calculated as an inner product of the wavelet and the time series, and is akin to a power value (i.e. square of original units), hereafter referred simply as "power." It is important to note that this usage of "power" is separate from the traditional use of the term power in a statistical sense. The wavelet is passed through the time series, and C is then calculated for successive windows within the time series.

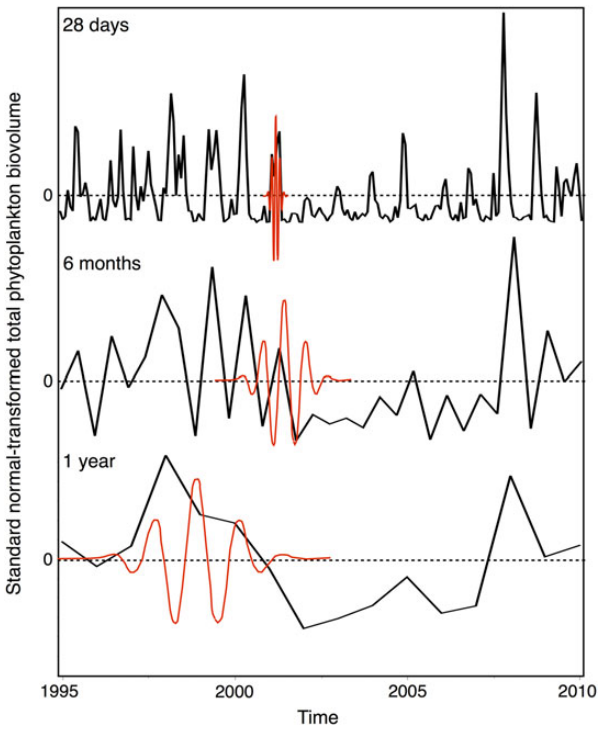


Fig. 2. An illustration of a continuous Morlet wavelet transform using total phytoplankton biovolume in Lake Mendota from 1995 to 2010, smoothed to a 28-day scale (top), 6-month scale (middle) and 1-year scale (bottom), after a standard normal transformation to center the time series on zero. The wavelet is first passed through the 28-day time series, and the correlation between the wavelets and different windows in the time series are calculated as coefficients. After the calculations for the first scale are complete, the wavelet is then "stretched" (also known as "scaled") slightly so that it represents a longer period than the previous wavelet, and C is recalculated for the new scale. This process is repeated for multiple scales, including the 6-month and 1-year scales, to create a matrix of coefficients, which are represented in heat maps (see Fig. 3).

After the calculations for the first scale are complete, the wavelet is then "stretched" (also known as "scaled") slightly so that it represents a longer period than the previous wavelet, and C is recalculated for the new scale. This process is repeated until the length of the wavelet approaches $\frac{1}{2}$ of the length of the entire time series. The result is a matrix of C, which typically is depicted in three dimensions, with time as the x-axis, scale as the y-axis and power as the z-axis (usually visualized as a colored heat map). The coefficients are then evaluated for significance by comparing with coefficients from a red-noise power spectrum (Torrence and Compo, 1998), and regions of significance within the space-time dimensions are outlined on the heat map. A red-noise spectrum is chosen because many environmental variables have higher power at longer periods (Torrence and Compo, 1998).

Calculating every scale can be compute-intensive. For efficiency, the algorithm for stretching the wavelet between scales follows a pattern of octaves, with the maximum scale identified by the following equation:

$$\mathcal{J} = \delta j^{-1} \log_2(N\delta_t/s_0) \quad (1)$$

in which $\mathcal{J}$ is the maximum scale; δj is spacing between the scales, or the number of sub-octaves; N is the number of sampling periods within the time series; δ_t is the length of the sampling period; and s_0 is the smallest resolvable scale, usually defined at $2\delta_t$ (Torrence and Compo, 1998). For our Lake Mendota study, we specified the first scale of variation to be examined as 28 days, twice as long as the sampling interval, and set the spacing between scales at 1/12 (12 sub-octaves per octave), following Winder and Cloern (Winder and Cloern, 2010). Thus, we were able to examine the importance of 92 scales in total that ranged between 28 and 2785 days for our 16-year time series. All wavelet transforms were calculated in the R statistical environment using v. 3.1.1 (R Development Core Team 2014), using package dplR (Bunn, 2008, 2010), as described by Bruesewitz *et al.* (Bruesewitz et al., 2015).

To determine which scales were most important throughout the entire time series, we calculated the global wavelet power spectrum, or time-averaged wavelet spectrum, for each phytoplankton division (Torrence and Compo, 1998), using the R package WaveletCo (Tian and Cazelles, 2013). This is similar to a power spectrum, in which the coefficients for one scale are averaged over the length of the entire time series (Percival and Walden, 2000). This R package also calculated significance tests for each of the scales analyzed in the global wavelet power spectrum. The value of our combined continuous wavelet transform and global wavelet power spectrum approach is that we can both: (i) identify the overall most important scale of variation averaged throughout a time series via the global wavelet power spectrum, and (ii) determine how the strength of specific scales of variation (e.g. the annual scale) change throughout the time series via the continuous wavelet spectrum.

Dominant scales of variation and seasonal succession

We first constructed the global wavelet spectrum for the total phytoplankton community (i.e. all phytoplankton taxa aggregated together) to determine the overall dominant scale averaged throughout the time series. The global wavelet spectrum defined the baseline pattern of phytoplankton succession over the 16 years. Second, we analyzed the continuous wavelet transform for the biovolume of the total phytoplankton community to identify the dominant scales of variation at each 14-day sampling interval, and then compared the dominant scale over time with the global wavelet spectrum to identify when deviations in seasonal succession may have occurred. We repeated this analysis for the biovolume of each of the dominant aggregated phytoplankton divisions.

We then examined if year-to-year variability in the annual periodicity of total phytoplankton biovolume was related to seasonal succession. As an index of the annual peak magnitude of total phytoplankton biovolume, we identified the coefficient C at the annual (365-day) scale with the observed maximum power within each year. Thus, 16 values were identified from the 1995–2010 time series, each representing maximum power for a year. Hereafter, we refer to the value of this coefficient as annual peak power. The higher the annual peak power within a calendar year, the more significant the annual scale for the total phytoplankton biovolume during that particular year; conversely, the lower the annual peak power, the less likely the annual scale was an important scale of variation for the total phytoplankton biovolume in that year. Annual succession can be conceptualized as a feature of the phytoplankton time series; with the annual peak power as a metric of the strength of succession from year to year, assuming a default annual pattern.

Using the NTL-LTER monitoring data, we assembled a dataset of environmental variables that we hypothesized may have influenced phytoplankton succession and periodicity from 1995 to 2010. This analysis was conducted to determine if changes in phytoplankton succession were associated with changes in lake environmental conditions. In total, this dataset included physical drivers (Schmidt stability, or a metric of the strength of thermal stratification (Idso, 1973), water temperature), chemical drivers [total P (TP), total N (TN), TN:TP, ammonium (NH_4), nitrate–nitrite (NO_3-NO_2), dissolved reactive P (DRP), dissolved reactive silica (DRSi)] and biological drivers (*Daphnia* and cladoceran biomass, total phytoplankton biovolume). All variables were sampled consistently throughout the time series, following standardized protocols (for detailed methods, see: http://lter.limnology.wisc.edu). Nutrient concentrations were measured at multiple depths on a sampling day, so we included both surface and mean (integrated) water column values in the dataset. Schmidt stability was calculated from water column temperature profiles using LakeAnalyzer, a MATLAB (R2014a, Mathworks, Natick, MA, USA) program that derives physical limnology metrics (Read et al., 2011). The zooplankton community in Lake Mendota is dominated by *Daphnia*, primarily *D. galeata mendotae* and *D. pulicaria*, which are the primary grazers of phytoplankton in the lake (reviewed by Lathrop and

Carpenter, 1992b). Consequently, we focused on *Daphnia* and cladoceran biomass as the primary zooplankton variables affecting phytoplankton succession. Zooplankton were sampled with an 80-μm mesh net in 20-m vertical tows at the deep hole. All zooplankton abundances were corrected for net efficiency, converted to biomass using established length–weight regressions for each species, aggregated to genus and reported as g m^{-2} (following Lathrop and Carpenter, 1992b). In this study, zooplankton were reported in biomass units and phytoplankton were reported in biovolume units to be consistent with previous analyses of Mendota plankton (e.g. Brock, 1985; Kitchell, 1992; Carpenter and Kitchell, 1993).

Because these environmental variables were not measured on the same temporal frequency as the phytoplankton community and because we focused on inter-annual variability, we aggregated all environmental observations by calendar year to match the annual peak power for total phytoplankton biovolume, and calculated three summary statistics (mean, minimum and maximum) for each environmental variable by year.

We compared the annual peak power of total phytoplankton and dominant division biovolume to the full suite of environmental variables using scatterplots and Spearman rank correlations to account for potential non-linearity in associations. Because all variables were aggregated to calendar year, the maximum sample size in any correlation was 16 years (1995–2010). We conducted visual inspection of scatterplots of relationships for which $\rho > 0.5$, disregarded associations that were driven by influential outliers and adjusted α to account for multiple comparisons.

RESULTS

We observed substantial variability in the biovolume of the phytoplankton community in Lake Mendota throughout 1995–2010. Total phytoplankton biovolume ranged by four orders of magnitude from 9.4×10^3 μm^3 mL^{-1} in 2002 to 2.9×10^7 μm^3 mL^{-1} in 2008 (Fig. 3A). Aggregated over the 16 years, the Cyanobacteria and Bacillariophyta contributed the largest proportion of phytoplankton biovolume (70% and 21%, respectively), whereas the other phytoplankton divisions (Chlorophyta, Cryptophyta, Pyrrophyta and Xanthophyta) each composed 5% or less of total observed biovolume (Fig. 3B). However, Bacillariophyta biovolume was markedly lower during the middle part of the time series, from 2002 to 2007.

Phytoplankton seasonal succession

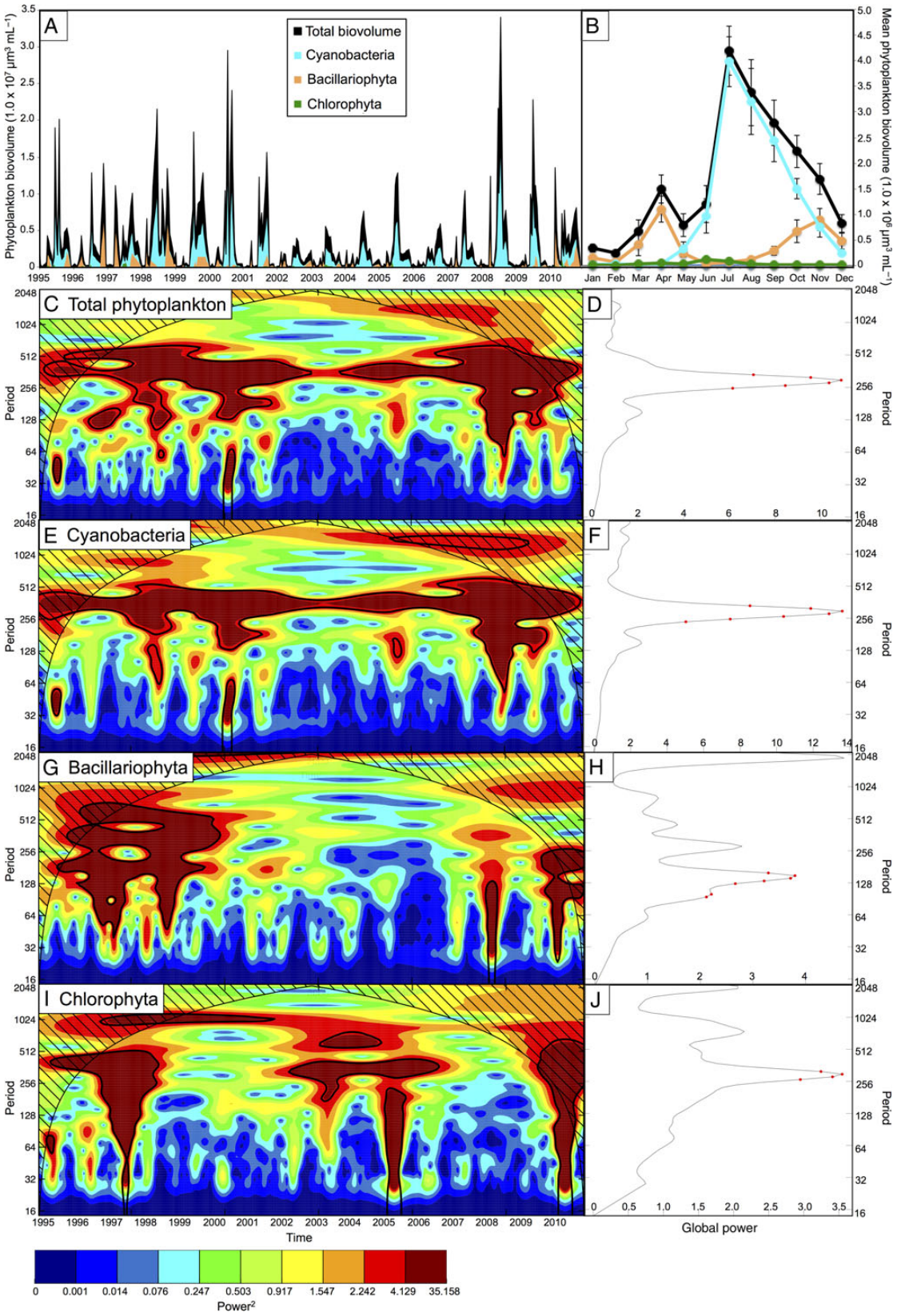
When averaged across the 16 years, the phytoplankton community exhibited a classic pattern of seasonal succession, as predicted by the PEG model for a eutrophic lake (Fig. 3B). In general, a spring bloom of Bacillariophyta occurred in April after ice-off, which crashed by the end of May and was followed by a small increase in Chlorophyta biovolume in June. The Cyanobacteria exhibited a large increase in biovolume from June to October before a late autumn diatom bloom in October and November preceded ice-on. Throughout the time series, the three major phytoplankton groups exhibited relatively similar taxonomic compositions. For example, the Bacillariophyta were dominated by centric taxa, especially *Stephanodiscus*, which contributed 70% of the observed diatom biovolume during the monitoring period; the Chlorophyta were dominated by *Sphaerocystis*, *Chlamydomonas* and *Spirogyra*, which together contributed 53% of the green algal biovolume; and the Cyanobacteria were dominated by bloom-forming filamentous taxa, especially *Aphanizomenon* and *Anabaena*, which together contributed 59% of the cyanobacterial biovolume.

As we expected, the annual pattern of phytoplankton seasonal succession was generally consistent over the 16-year monitoring period in Lake Mendota, with a notable exception in 2003–2004 (Figs 3A and 4). In 2003–2004, the typical seasonal succession pattern was disrupted: peak phytoplankton biovolume was much lower than in other years and, notably, there was not a large spring or autumn diatom bloom. As shown for 2003 in Fig. 4, the highest Cyanobacteria biovolume was observed in July in both years, a month earlier than observed in the time series' average, and the Chlorophyta composed a larger proportion of the yearly total biovolume during a longer unimodal bloom in May to August. In contrast to 2003, both the timing and magnitude of the peaks of phytoplankton biovolume were substantially different in 2008, a year that exemplified the "typical" annual pattern. In 2008, maximum phytoplankton biovolume was more than four times greater than average, with a large spring diatom bloom in April. The highest Cyanobacteria biovolume in that year was observed in August, and Chlorophyta contributed much lower biovolume throughout the summer (Fig. 4).

Across the time series, regardless of the variability in phytoplankton succession, the annual peak of *Daphnia* biomass occurred during May (Fig. 4). In general, the magnitude of *Daphnia* biomass mirrored total phytoplankton biovolume: for example, biomass was much lower in 2003 than in 2008 (Fig. 4).

Wavelet analyses

We examined if the continuous wavelet transforms were able to successfully identify variability in the annual



periodicity and seasonal succession of the phytoplankton community, as shown by the disrupted seasonal succession pattern in 2003–2004. Throughout the time series, the annual scale was the most dominant scale of variation in the total phytoplankton biovolume (Fig. 3C). All of the significant scales in the global wavelet power spectrum were clustered around 365 days (Fig. 3D), and for most of the time series, the annual scale was highly significant in comparison with a null red-noise power spectrum. However, the power of the annual scale was much lower during 2002–2004 and became non-significant during 2003–2004, the same period that exhibited altered seasonal succession. In contrast, the years with the highest annual peak power exhibited the classic eutrophic seasonal succession pattern (as exemplified by 2008, the year that exhibited the maximum annual peak power observed during the time series; Fig. 4). Some sub-annual scales were significant for short durations, especially during 2008, but none of them emerged as significant in the global wavelet power spectrum. No multi-year dominant scales of variation emerged as significant for total phytoplankton biovolume.

The biovolume of the major phytoplankton divisions exhibited different patterns in their continuous wavelet transforms. For Cyanobacteria, the annual scale of variation was consistently significant throughout the time series, even in 2002–2004 (Fig. 3E). No other scales of variation were significant in the Cyanobacteria global wavelet power spectrum (Fig. 3F). In contrast, the Bacillariophyta exhibited no significant dominant scales of variation between 2000 and 2008, and sub-annual scales from 164 to 195 days (~5.5–6.5 months) were the most significant across the time series (Fig. 3G and H). For the diatoms, the annual scale of variation was only significant from 1995 to 1999. Finally, the Chlorophyta exhibited a significant annual scale of variation during the 2002–2006 interval when the annual scale of total phytoplankton biovolume was weakest (Fig. 3I). The Chlorophyta's annual scale was non-significant when the total phytoplankton's annual signal was strongest in 1998–2002 and 2006–2009; no other scales emerged as being significant in the global wavelet power spectrum (Fig. 3J).

Drivers of variability in annual periodicity

We observed that the annual peak power for total phytoplankton biovolume and Cyanobacteria were both positively associated with N and P concentrations (Table I and Fig. 5). Aggregated by year, the annual peak power of total phytoplankton biovolume was more positively correlated with minimum surface TP than any other driver variable ($\rho = 0.78$, $P = 0.0004$). The correlations between annual peak power and N and P were robust to the summary statistic examined (maximum surface and integrated NH_4, mean integrated TN and minimum surface TP all exhibited positive relationships with annual peak power). The annual peak power of total phytoplankton biovolume was also strongly correlated to mean phytoplankton biovolume, which was expected because the wavelet coefficients were a function of the biovolume ($P = 0.004$). Cyanobacteria annual peak power was also significantly positively correlated to all of the same N, P and phytoplankton biovolume variables (all $P \leq 0.003$). No other environmental variables, including Schmidt stability or cladoceran zooplankton biomass, emerged as significant correlates of the annual peak power of total phytoplankton biovolume or Cyanobacteria, whereas the annual peak power of Bacillariophyta was only significantly correlated to maximum integrated and surface DRSi, both negatively. The annual peak power of Chlorophyta did not exhibit any significant correlations with environmental variables.

DISCUSSION

Our analyses demonstrate that continuous wavelet transforms were able to successfully detect variation in the pattern of annual phytoplankton seasonal succession over time. Throughout the time series, the annual periodicity represented the dominant scale of variation for the aggregated phytoplankton community in Lake Mendota. This result follows predictions from the eutrophic PEG model, which adequately represented phytoplankton dynamics in Lake Mendota for almost all years. In marine systems, the annual cycle of phytoplankton dynamics, embodied by the classical spring bloom, has been

Fig. 3. (**A**) Time series of the biovolume of the total aggregated phytoplankton community and Bacillariophyta, Chlorophyta and Cyanobacteria divisions from 1995 to 2010. (**B**) Mean (± 1 standard error, SE) biovolume of total phytoplankton; mean Bacillariophyta, Chlorophyta and Cyanobacteria biovolume, averaged for each month across the 1995–2010 time series. In both A and B, the difference between the total biovolume and the sum of the Bacillariophyta, Chlorophyta and Cyanobacteria biovolume is due to the biovolume of other phytoplankton groups not shown in the figure. (**C**, **E**, **G** and **I**) Continuous wavelet power spectra showing the periodicity of total phytoplankton biovolume, Cyanobacteria biovolume, Bacillariophyta biovolume and Chlorophyta biovolume, respectively. The thick black contour designates the 5% significance level against red noise, and diagonal lines denote the cone of influence (COI), where edge effects may distort the interpretation of that region of time and frequency. The continuous wavelet spectrum illustrates how the strength of the periodicities changed over time; colors reflect the strength of intensity, or power (dark red indicates high power; dark blue indicates low power; the color scale represents power squared). (**D**, **F**, **H** and **J**) Time-averaged (global) wavelet power spectra for total phytoplankton biovolume, Cyanobacteria biovolume, Bacillariophyta biovolume and Chlorophyta biovolume, respectively. The colored points denote significant ($P < 0.05$) periods.

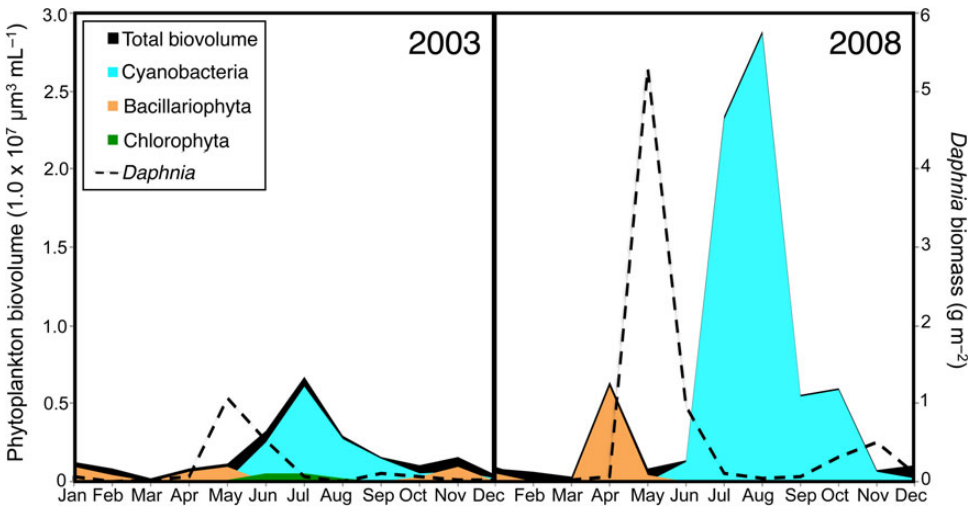


Fig. 4. The seasonal succession of the biovolume of the phytoplankton community and *Daphnia* biomass in 2003 and 2008. In 2003, the annual scale of variation for the biovolume of the total phytoplankton community was not significant. In comparison, in 2008, the annual peak power of the total phytoplankton biovolume was at its strongest during the 1995–2010 time series.

Table I: Environmental driver variables correlated to the annual peak power, or the maximum power of the annual scale of variation observed within a year throughout 1995–2010, for total aggregated phytoplankton and three dominant phytoplankton divisions

Phytoplankton variable	Environmental variable	Spearman's ρ coefficient	*P*-value
Total aggregated phytoplankton	Minimum surface TP	0.78	0.0004
	Maximum surface NH_4	0.76	0.0006
	Maximum integrated NH_4	0.76	0.0006
	Mean total biovolume	0.68	0.004
	Mean integrated TN	0.67	0.005
Cyanobacteria	Maximum surface NH_4	0.80	0.0002
	Maximum integrated NH_4	0.80	0.0002
	Minimum surface TP	0.78	0.0004
	Mean integrated TN	0.72	0.002
	Mean total biovolume	0.70	0.003
Bacillariophyta	Maximum integrated DRSi	−0.71	0.002
	Maximum surface DRSi	−0.68	0.004

All environmental observations were aggregated each calendar year to maximum, mean and minimum summary statistics, which were used for the Spearman correlations ($n = 16$ years for each correlation). We adjusted α to 0.005 to account for multiple comparisons. There were no significant correlations observed for Chlorophyta.

documented for decades (Sverdrup, 1953; Cushing, 1959). In freshwater lakes, the phenology of phytoplankton can be more variable (e.g. Winder and Cloern, 2010), but our data emphasize the importance of the annual cycle for total phytoplankton in eutrophic, dimictic, deep north temperate lakes such as Mendota. Earlier studies on Lake Mendota in the 1970s and 1980s also found that the phytoplankton generally exhibited a very consistent annual cycle in aggregated phytoplankton, at a similar level of biovolume (Brock, 1985; Lathrop and Carpenter, 1992a). While we focused on the division level of phytoplankton here as an example test case, wavelet analyses may also be a valuable tool for testing if individual taxa and functional groups of plankton differentially fluctuate in synchrony over time, as observed by Rocha *et al.* (Rocha et al., 2011, 2012).

The annual peak power provided a metric for quantifying the change in magnitude of the annual scale through time (Fig. 3), which was related to variability in phytoplankton seasonal succession. As noted above, annual succession can be conceptualized as a feature of the phytoplankton time series, and the wavelet transform has quantified the magnitude and change in that feature over time. While the original phytoplankton time series provided a means for quantifying change in total biovolume over time, the wavelet transforms provided a means

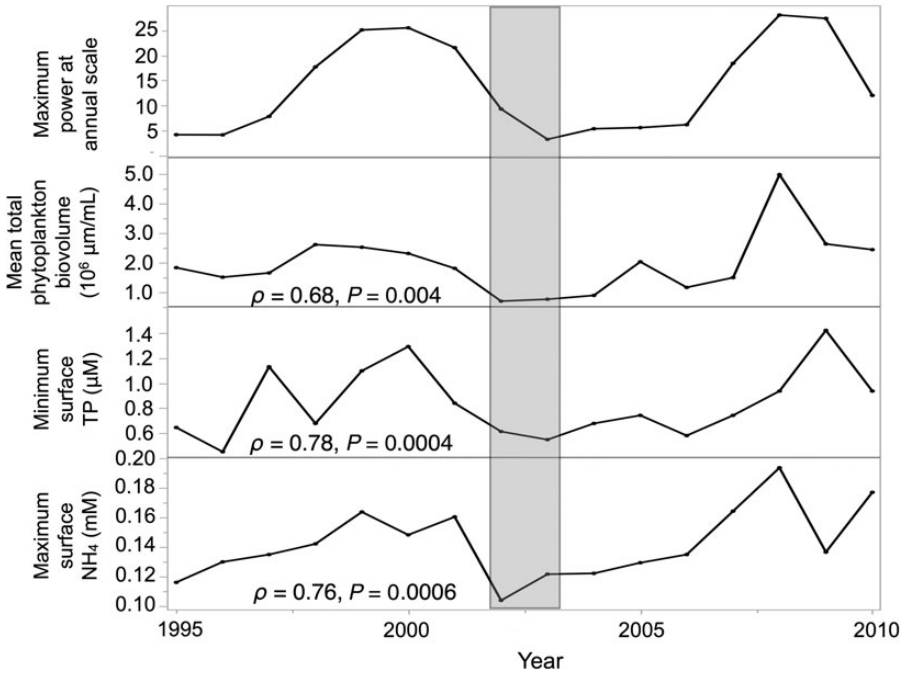


Fig. 5. Environmental drivers of total phytoplankton periodicity, aggregated to the yearly scale: annual peak power, or the maximum power of the annual scale of variation observed within a year for total phytoplankton biovolume; mean total phytoplankton biovolume (10^6 µm^3 mL^{-1}); minimum surface TP (µM); and maximum surface NH_4 (mM) during 1995–2010. The shaded area highlights the period of the time series when the annual scale of total phytoplankton was weakened and non-significant. All Spearman's ρ coefficients and *P*-values denote the relationship between the driver variable and annual peak power of total phytoplankton biovolume.

for quantifying the change in the dominant scales of variation. Consequently, the consistency of phytoplankton succession observed in many marine and freshwater systems over decadal time series indicates that our method of using continuous wavelet transforms to identify deviations from a "typical" successional pattern may be applicable for aquatic ecosystems beyond Lake Mendota.

The continuous wavelet transforms identified a temporary decrease in the strength of the annual periodicity of total phytoplankton biovolume that coincided with disrupted phytoplankton succession (Figs 3 and 4); i.e., the phytoplankton succession for that period did not fit the baseline pattern of the eutrophic PEG model. While the annual periodicity was the most important scale of variation for the phytoplankton community during 1995–2010, it was greatly weakened in 2002–2004, when it became no longer statistically significant. We hypothesize that the weakened annual signal was likely related to lower nutrient concentrations in 2002–2004 (Fig. 1). Interestingly, both N and P exhibited positive relationships with the strength of the annual scale, which is likely due to their strong correlation (Table I). Not surprisingly, lower nutrient concentrations in the water column during 2002–2004 coincided with lower total phytoplankton biovolume, primarily driven by the Cyanobacteria, during those years. In the absence of large blooms of Cyanobacteria in the open-water period, the continuous wavelet transform did not detect a strong annual scale during this period. While other factors in addition to nutrients are likely also responsible for the weakened annual signal, it is notable that one of the most important environmental drivers was the minimum annual concentration of TP at the water's surface (Table I), indicating that there may be a threshold concentration of P needed to observe a significant annual scale of total phytoplankton biovolume and Cyanobacteria.

The ultimate driver of the decreased nutrient concentrations during 2002–2004 may be related to drought. During 2002–2003, the watershed experienced much lower precipitation, resulting in much lower P loads entering the lake (Fig. 1; Lathrop and Carpenter, 2014). This hypothesis is supported by the opposite scenario in 2008, the second wettest year on record from 1890 to the present (Madison Water Year Dataset; Wisconsin State Climatology Office), when there were very large floods and extremely high nutrient loads entering the lake (Lathrop and Carpenter, 2014). The high nutrient loads and water column nutrient concentrations in 2008 were correlated with the peak total phytoplankton biovolume observed in that year (Fig. 3A), which also coincided with the strongest observed annual peak power during the 1995–2010 time series.

The decreased nutrient concentrations in 2003 did not merely alter the magnitude of total phytoplankton biovolume, but it also affected the pattern and timing of seasonal succession (Fig. 4), which in turn altered the annual periodicity of the phytoplankton community. The largest nutrient loads entering Mendota typically occur during the late winter and spring months (Lathrop, 2007; Lathrop and Carpenter, 2014), fueling large spring diatom blooms and summer cyanobacterial blooms. In high biovolume years, such as 2008, diatoms exhibited a large bloom in April, followed by a clear-water phase in May and June before a very large cyanobacterial bloom peaked in August. This succession follows the pattern that would be predicted by the PEG model for a eutrophic, deep north temperate lake (Sommer et al., 1986). In contrast, in 2003, which was marked by much lower total phytoplankton biovolume, there was no distinct diatom bloom, and the peak cyanobacterial biovolume occurred in July before decreasing in August (Fig. 4). Consequently, the lack of a significant annual periodicity in 2002–2004 in comparison with other years in the time series may be due to the altered timing of peak biovolume, in addition to lower overall biovolume.

Interestingly, in 2003, the phytoplankton succession in Lake Mendota resembled the unimodal pattern predicted by the PEG model for an oligotrophic, north temperate lake (Sommer et al., 2012). Similarly, Lathrop and Carpenter (Lathrop and Carpenter, 2014) observed that the normally eutrophic Mendota exhibited mesotrophic conditions during 2003, according to trophic state criteria for TP concentration and Secchi depth. Consequently, our results suggest that wavelet transforms may be able to identify years in phytoplankton time series when a lake transitions between different trophic states.

Our data suggest that cladoceran zooplankton may not have been as important as nutrients in driving the inter-annual variability in total phytoplankton biovolume and succession. *Daphnia* biomass was substantially lower in 2003 than in 2008, but importantly, the timing of the clear-water phase throughout the time series did not change, and no cladoceran zooplankton variable was correlated to the strength of the annual periodicity, either for the aggregated phytoplankton community or for the individual phytoplankton divisions. It is possible that the difference in *Daphnia* biomass among years was due to limitation of phytoplankton food for zooplankton grazers, especially in 2003, when phytoplankton biovolume was at its lowest. In Vanni and Temte's (Vanni and Temte, 1990) analysis of the seasonal pattern of phytoplankton in Lake Mendota in 1987, they found that the relative importance of top-down and bottom-up control on phytoplankton varied throughout the open-water period. Among years, however, it is possible that nutrients may be the more important variable determining the magnitude of phytoplankton biovolume and the pattern of succession.

The three major phytoplankton divisions in Lake Mendota, the Cyanobacteria, Bacillariophyta and Chlorophyta, exhibited markedly different continuous wavelet transforms, indicating that each division is responding differently to environmental conditions over time. In contrast to the total phytoplankton biovolume, the annual scale of the Cyanobacteria was highly significant throughout the time series, including the 2002–2004 interval. Interestingly, the annual scale of the Chlorophyta was strongest during the drought period, when no significant dominant scales, annual or sub-annual, of the Bacillariophyta were observed. The Chlorophyta was the only major phytoplankton division that did not exhibit any significant correlations between annual peak power and the environmental variables (Table I). The highest Chlorophyta biovolume observed during the time series, driven by blooms of *Spirogyra*, was observed during the period when the Bacillariophyta and Cyanobacteria biovolumes were at their lowest, indicating that trade-offs occurring among the different phytoplankton groups may be mediated by environmental conditions. Some species of *Spirogyra* prefer mesotrophic (~1 μM TP) conditions (Hainz et al., 2009), so it is possible that the taxon was favored when nutrient loads were lower during the drought period.

The Bacillariophyta was the only division that exhibited a sub-annual (184-day, or ~6-month) dominant scale in its global wavelet power spectrum. The 6-month period roughly corresponds to a spring and autumn bloom in April and October/November, as observed in the mean succession pattern of the phytoplankton during the time series (Fig. 3B) and following the PEG model. Over the monitoring period, the lack of any significant dominant scale from 2000 to 2008 may be related to both lower diatom biovolume and altered timing of the peak diatom biovolume every year. The biovolume of all diatom taxa was extremely low during this time, with very small or completely absent spring and autumn blooms. This prolonged lack of diatoms had not been observed in previous years of monitoring: in 1985 and 1989, spring diatom blooms were absent in Lake Mendota, but those events were primarily linked to the depletion of DRSi from early, large diatom blooms the preceding year (Lathrop and Carpenter, 1992a). There were no major changes in water temperature or thermal stratification during this period and DRSi concentrations actually increased, most likely due to lower uptake, as suggested by the negative correlation between annual peak diatom power and DRSi, so other factors were likely responsible. It is possible that drought and low runoff may

have altered nutrient availability for the diatoms. The dominant diatom genus in the lake, *Stephanodiscus*, has a high cellular P requirement (Lynn et al., 2000), so its growth may have been P-limited. Alternatively, an algal parasite or virus may have been responsible for the decreased diatoms during this time period (Ibelings et al., 2011; Gsell et al., 2013), but we do not have data to test that hypothesis.

CONCLUSION

Wavelet analyses can yield insights into phytoplankton dynamics that are not immediately evident from raw abundance or biovolume data. In our Lake Mendota example, year-to-year variability in the annual cycle of the phytoplankton due to changing environmental conditions had substantial effects on the timing and pattern of phytoplankton succession. In turn, because changes in phytoplankton succession can have substantial effects on zooplankton and higher trophic levels (e.g. Winder and Schindler, 2004), determining how phytoplankton respond to environmental forcing over longer timescales is critical. Our application of wavelet analyses to phytoplankton seasonal succession at the decadal scale demonstrates that this approach can be a powerful tool for identifying altered phytoplankton dynamics.

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