

Uncoupling indicators of water quality due to the invasive zooplankter, *Bythotrephes longimanus*

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Abstract

Cultural eutrophication of lakes due to excess loading of nutrients is a global problem affecting the provisioning of freshwater ecosystem services. Lake water quality is often described by trophic state indicators such as water clarity or concentrations of nutrients, chlorophyll, and cyanobacteria toxins. While these indicators are widely assumed to covary, capturing the same basic aspects of water quality, they can be uncoupled by changes in lake food webs. Outbreak of the invasive predatory zooplankton, *Bythotrephes longimanus*, in Lakes Mendota and Monona, Wisconsin (U.S.A.) in 2009 led to a decline in the herbivore, *Daphnia pulicaria*, and in turn, water clarity. We use 20-yr datasets for Lakes Mendota and Monona to evaluate interactions among nutrients, zooplankton, and phytoplankton that resulted in this trophic cascade. After invasion, diatoms increased in both lakes resulting in reduced water clarity, whereas cyanobacteria did not change in either lake. Multivariate time series analysis revealed that *D. pulicaria* grazing controlled edible diatoms in both lakes. Cyanobacteria biomass was positively associated with both *D. pulicaria* and summer nutrient concentrations. These results further clarify the limitations of top-down control in eutrophic lakes: grazing by zooplankton can control edible phytoplankton taxa, but largely inedible cyanobacteria may be more limited by nutrient concentrations. Accordingly, despite declining clarity in Lake Mendota, the number of beach closures due to cyanobacteria blooms declined following *Bythotrephes* invasion. Our study reveals how these two indicators of water quality—water clarity and cyanobacteria blooms—can become uncoupled during a food web shift.

Eutrophication is a global driver of change in lakes and is often managed through reducing water nutrient concentrations (Carpenter et al. 2011). Many indicators of water quality are used to measure the efficacy of such efforts (sensu Carlson 1977). While these indicators are often correlated with one another and with lake trophic state, they can become uncoupled and vary in counterintuitive, but informative directions (e.g., Carlson and Havens 2005; Peckham et al. 2006; Yuan and Pollard 2014). As indicators of water quality can be valued differently (Kosenius 2010; Walsh and Milon 2016), understanding how water quality indicators are coupled—or become uncoupled—is important for managing freshwater systems (Genkai-Kato and Carpenter 2005). For example, phytoplankton derive nutrients directly from the water that results in their standing biomass, bloom frequency, and species composition. Accordingly, phytoplankton are useful indicators of eutrophication and water quality in lakes (e.g., Carvalho et al. 2013; Katsiapi et al. 2016).

However, phytoplankton are comprised of diverse species of widely different cell shapes and sizes (including colonies or elongated filaments of cells), such that each water quality indicator related to phytoplankton may be driven by different ecological factors. Here, we focus on two facets of the phytoplankton that are used as indicators of water quality—water clarity and the frequency and intensity of harmful cyanobacteria blooms—to explore how indicators of water quality respond to ecological drivers.

These two dimensions of water quality represent different elements of phytoplankton community biomass and composition. Water clarity can be a measure of algal abundance in “green” freshwater ecosystems (i.e., lakes where clarity is most influenced by algal abundance rather than dissolved humic substances). While water clarity is economically valuable (Stumborg et al. 2001; Krysel et al. 2003) and a useful measure of water quality, equating water clarity with water quality can be misleading due to complexity of the phytoplankton community. Water quality also refers to the frequency and intensity of harmful cyanobacteria blooms (Carpenter et al. 2011). While cyanobacteria blooms degrade water clarity, they are most damaging through the harmful toxins that some species of cyanobacteria produce. Dense

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blooms of cyanobacteria lead to beach closures due to toxin concerns, but blooms also cause both fish kills from low oxygen levels and generally noxious scum pile-ups along shorelines. In this way, phytoplankton community composition determines whether water clarity and cyanobacteria blooms are coupled to the same ecological drivers (e.g., nutrient availability or grazing pressure). Understanding the ecological factors that drive each is critical for managing water quality, as water clarity and fewer cyanobacteria blooms have been shown to be valued differently by the public (e.g., clarity was found to be more valuable in the Gulf of Finland; Kosenius 2010).

Phytoplankton community composition and biomass in lakes are thought to be driven primarily by food web composition and nutrients (Carpenter et al. 1987), sometimes referred to as “top-down” and “bottom-up” processes, respectively (Shapiro 1975; Benndorf 1990). Food webs that support abundant populations of large grazers, like *Daphnia*, have lower phytoplankton biomass (Hansson et al. 1998; Ekvall et al. 2014). For this reason, *Daphnia* are thought to improve water quality by reducing phytoplankton biomass and increasing water clarity. However, this interaction is mediated by the availability of resources (e.g., phosphorus) to phytoplankton (Smith 2003). In highly eutrophic lakes, the ability of *Daphnia* to graze summer phytoplankton (especially cyanobacteria) is limited (Gliwicz 1990; Elser and Goldman 1991). Also, *Daphnia* are only capable of grazing a certain cell or colony size range of phytoplankton; larger cells or colonies including filamentous forms of algae are not grazed (Brooks and Dodson 1965; Hall et al. 1976; Sommer et al. 1986). Therefore, water quality is more strongly influenced by nutrients in lakes with high external nutrient loading that produces phytoplankton of a size or shape resistant to grazing. Consequently, the frequency and intensity of cyanobacteria blooms increases with external nutrient loading where smaller forms of cyanobacteria are removed by grazing.

Invasive species change the biological make-up of ecosystems (Clavero and García-Berthou 2005; Pejchar and Mooney 2009; Ehrenfeld 2010; Gallardo et al. 2015). In freshwater ecosystems, these changes can be responsible for altered and even degraded water quality (Carpenter et al. 2011). However, species invasions also provide natural experiments that generate new insights into the ecological factors governing different components of water quality, analogous to the role of other massive food web changes in understanding water quality (e.g., fish mortality; Vanni et al. 1990).

Lake Mendota, Wisconsin (U.S.A.) has been a useful study system for understanding the role of food webs in driving water quality in eutrophic lakes. Much of this understanding originated from the natural experiment provided by a massive planktivorous fish mortality in 1987 (Rudstam et al. 1993) followed by the subsequent stocking of piscivorous fishes (Kitchell 1992). These changes to the lake food web relieved predation pressure on *Daphnia pulicaria*, in turn

reducing phytoplankton biomass and increasing water clarity (Lathrop et al. 2002). The invasive predatory zooplankton, spiny water flea (*Bythotrephes longimanus*) was detected in Lake Mendota and downstream Lake Monona in 2009. Predation by *Bythotrephes* has since reversed much of the gains in *D. pulicaria* biomass and water clarity that resulted from the 1987 fish die-off and subsequent lake biomanipulation (Walsh et al. 2017), incurring large economic damages to Lake Mendota (Walsh et al. 2016a). Yet, seasonally the largest decline in clarity was observed in the spring, likely because of lower *D. pulicaria* biomass. In spring, *D. pulicaria* grazing on edible phytoplankton often produces a clear-water phase (which has become weaker and shorter since 2009; Walsh et al. 2016a), but this occurs prior to harmful cyanobacteria blooms that are more common in summer. Understanding the ecological mechanisms of these changes could help to further clarify the role of food webs—and *Daphnia* in particular—in the provisioning of water quality in temperate lakes (Gliwicz 1990; Vanni et al. 1990).

Here, we use the food web changes driven by *Bythotrephes* invasion to investigate the changes in the Lake Mendota and Lake Monona phytoplankton and zooplankton communities that drove the decline in water clarity. We evaluate the drivers of phytoplankton community composition as well as the role that phytoplankton community structure plays in water clarity and cyanobacteria blooms, two important indicators of water quality.

Methods

Study systems

Lake Mendota, located near Madison, Wisconsin, U.S.A., is the largest (39.6 km²) deepest (25.3 m max depth, 12.6 m mean depth) and most upstream lake in the eutrophic Yahara River chain of four lakes; its watershed is mostly agricultural with some urban areas. Lake Monona (immediately downstream of Mendota) is smaller (13.2 km²) and shallower (22.6 m max depth, 8.3 m mean depth). While the majority of Lake Monona's direct drainage area is urban, it receives a large portion of its phosphorus from Lake Mendota via the Yahara River (Lathrop and Carpenter 2014). *Bythotrephes* was detected in the Yahara lakes in 2009. However, *Bythotrephes* occurred at much lower densities in Lake Monona than Lake Mendota, and the coincident declines in *D. pulicaria* biomass and water clarity have been less pronounced in Lake Monona. Therefore, the lakes provide a useful contrast for studying the factors influencing water quality and the effects of *Bythotrephes* invasion.

Time series

Phytoplankton, zooplankton, nutrient (total phosphorus), and lake temperature time series data were obtained from the North Temperate Lakes Long Term Ecological Research (NTL-LTER; <http://lter.limnology.wisc.edu/>) program database (North Temperate Lakes Long-Term Ecological Research, NSF 2015a,b,c,d). Both lakes were sampled biweekly

beginning after ice-out from spring through summer and monthly in fall, and at least once during ice cover in winter.

Both phytoplankton and zooplankton were identified to the lowest taxonomic level possible (generally to species). All phytoplankton analyses were conducted by PhycoTech, a private lab specializing in phytoplankton analyses. Phytoplankton biomass was calculated using species counts from mounted slides and obtaining cell measurements to calculate the biovolume and biomass for geometric solids (e.g., spheres, cylinders, and cones). Here, we focus on biomass of the broad taxonomic groups containing cyanophyta and bacillariophyta (i.e., diatoms), which comprised over 80% of observed phytoplankton biomass in Lake Mendota and over 85% of observed biomass in Lake Monona. While other phytoplankton taxa were periodically abundant and important (e.g., green algae can comprise as much as 90% of total biomass during a given sampling trip but just 12% on average), we chose to limit model variates by selecting diatoms as a surrogate for edible phytoplankton (we explore including other edible taxa, green algae, and cryptomonads, in the Supporting Information). Phytoplankton natural unit (e.g., cell, colony, or filament) size was measured by the length of the greatest axial linear dimension (GALD). Because GALD is related to edibility (i.e., lower GALD phytoplankton are more edible by zooplankton), we calculated monthly mean GALD in cyanobacteria and diatoms to approximate annual changes in edibility in the two taxonomic groups. We defined edible phytoplankton as any species with a mean observed GALD less than 30 μm on a given sampling day. We calculated zooplankton biomass using zooplankton abundance, mean measured length, and published length-to-dry-weight relationships (McCauley 1984). Notably, LTER estimated zooplankton density using a 30-cm diameter net with an 83-micron mesh and *Bythotrephes* density estimates can be 4–7 times higher using a larger, 50-cm net with a coarser, 150-micron, mesh. As we do not include *Bythotrephes* in our time series modeling here, we did not adjust this difference in sampling efficiency in our analyses. For each sampling, we calculated the average of the top 5 m for surface temperatures and total phosphorus concentrations in each lake to represent epilimnetic conditions.

Observing change with *Bythotrephes* invasion

We observed changes in each time series with *Bythotrephes* invasion by fitting generalized additive models (GAM) of plankton biomass and total phosphorus (raw, uninterpolated data) fitted to day of the year using cyclic cubic regression smoothers (i.e., day of the year is cyclical) with the exception of *Bythotrephes*, which is fitted using a non-cyclical thin-plate regression smoother (“mgcv” in R; Wood 2015). Unlike other plankton and total phosphorus, *Bythotrephes* are always undetectable in the water column during winter ice cover. Therefore, a cyclical cubic regression smoother would lead to over-estimated abundance during ice cover as a result of

over-smoothing between the last sampling event in late fall and the sampling event during ice-cover. Here, we fit a GAM for both pre- and post-2009 time periods in each lake to allow for seasonal trend comparisons over both time periods for total algal biomass, Secchi depth, total phosphorus, diatom biomass, and cyanobacteria biomass.

Observing ecological interactions in plankton

To investigate the ecological interactions driving the biomass of the two dominant phytoplankton divisions, diatoms and cyanobacteria, in Lakes Mendota and Monona, we constructed multivariate autoregressive state space models (Holmes et al. 2012) using package “MARSS” in R (Holmes et al. 2013). The models take the following form:

$$\begin{bmatrix} x_s \\ x_c \end{bmatrix}_t = \begin{bmatrix} B_s & C \\ 0 & B_c \end{bmatrix} \begin{bmatrix} x_s \\ x_c \end{bmatrix}_{t-1} + u + w_t, w \sim \text{MVN} \left(0, \begin{bmatrix} Q_s & 0 \\ 0 & Q_v \end{bmatrix} \right)$$

$$\begin{bmatrix} y_s \\ y_c \end{bmatrix}_t = \begin{bmatrix} x_s \\ x_c \end{bmatrix}_t + a + v_t, v \sim \text{MVN} \left(0, \begin{bmatrix} R_s & 0 \\ 0 & R_v \end{bmatrix} \right)$$

Where a vector of variable observations, $\mathbf{y}_s$ (e.g., total phosphorus concentrations, *D. pulicaria* biomass, and phytoplankton biomasses), and covariates, $\mathbf{y}_c$ (e.g., surface-water temperature), at time $\mathbf{t}$ are described by a vector of state values, $\mathbf{x}_s$ and $\mathbf{x}_c$, respectively. State values $\mathbf{x}_s$ and $\mathbf{x}_c$ (with $\mathbf{w}$ process errors having variable and covariate covariances $\mathbf{Q}_s$ and $\mathbf{Q}_v$, respectively) represent true values of system variables and covariates with errors $\mathbf{v}$ having covariances $\mathbf{R}_s$ and $\mathbf{R}_v$, respectively. Variable and covariate observations were log-transformed (excepting surface-water temperature), transformed to z-scores, and linearly interpolated to fortnightly time steps to align time series for analysis. As all variables and covariates were z-scored, we set $\mathbf{u}$ and $\mathbf{a}$ (vectors of estimated intercepts in the state and observation equations, respectively) to zero.

$\mathbf{B}$ is a matrix of potential interactions between state processes that allows us to estimate the direction and magnitude of food web interactions (e.g., drivers of phytoplankton biomass and interactions among drivers). We did not include higher trophic levels such as planktivores (either fishes or invertebrates) or piscivores in our $\mathbf{B}$ matrix, but rather focused solely on those variables that would directly influence phytoplankton. Within the $\mathbf{B}$ matrix, we allowed top-down grazing interactions of *D. pulicaria* on diatom and cyanobacteria biomass and bottom-up nutrient availability to diatoms and cyanobacteria. We also added a term to capture effects of *D. pulicaria* on total phosphorus (TP) concentrations as they are likely to be related. We allowed $\mathbf{Q}$ to remain unconstrained off the diagonal of the variates (phytoplankton, *D. pulicaria*, and total phosphorus) and set $\mathbf{Q}$ terms to zero off the diagonal of the covariate, surface-water temperature. We allowed the model to estimate terms along the diagonal of the $\mathbf{R}$ matrix with off-diagonal values set to zero.

MARSS allows for fitting values of $\mathbf{B}$ that vary through time and we construct models with $\mathbf{B}$ estimates that vary by

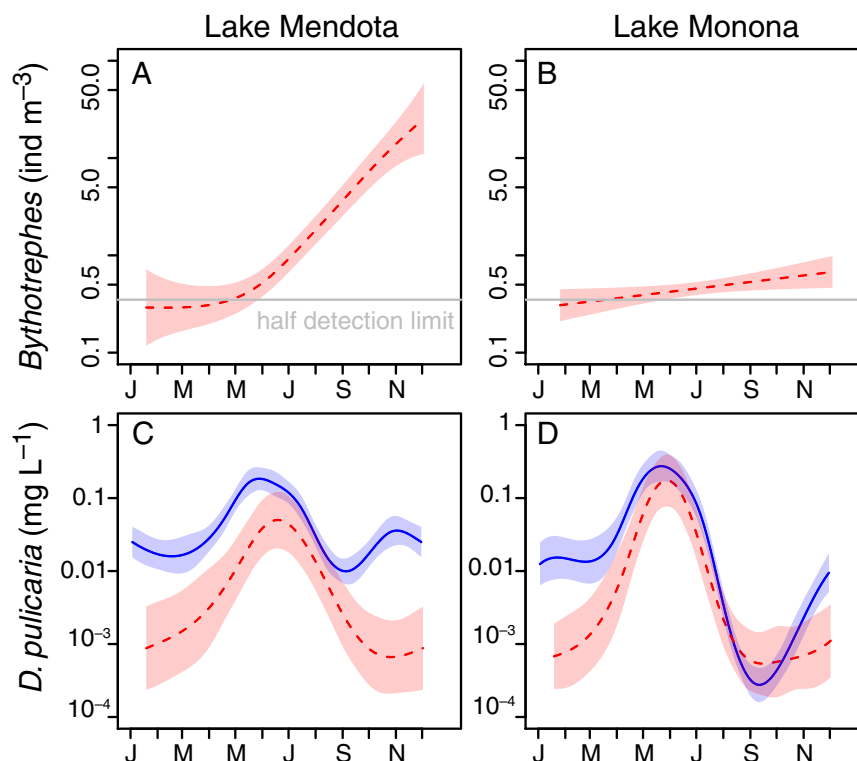


Fig. 1. GAM of *Bythotrephes* abundance (individuals m⁻³ + half detection limit; A, B) and *D. pulicaria* biomass (mg L⁻¹ + half detection limit; C, D) fitted to day of the year in Lake Mendota (A, C) and Lake Monona (B, D) before (solid blue line) and after (dashed red line) *Bythotrephes* was detected in each lake in 2009. Shaded areas represent ±95% C.I. LTER zooplankton densities are estimated using a 30-cm net, which dramatically underestimate *Bythotrephes* densities. *Bythotrephes* densities were chosen rather than biomass to facilitate comparisons to density estimates from other lakes. Note that the y-axes of each plot are log-scaled.

season in each lake. Here, we defined seasons by lake stratification and warming within a year for six lake seasons total—a period of ice cover (“ice cover”), a period for the onset of stratification (“early stratification”), a period of stratification during summer warming (“early summer”; $\geq +2^{\circ}\text{C}$ per fortnight), a period of stratification during peak summer temperatures (“late summer”; $< +2^{\circ}\text{C}$ per fortnight and $> -2^{\circ}\text{C}$ per fortnight), a period of stratification during cooling temperatures (“fall”; $\leq -2^{\circ}\text{C}$ per fortnight), and a period of the break-up of stratification (“destratification”). We allowed the model algorithm to estimate **R** terms as zero in cases where the number of parameters exceed the model’s capacity to estimate observation and process errors separately. Finally, we note that surface-water temperature is highly seasonal (“fortnight” as a factor accounts for 96% of the variation in the surface temperature time series relative to just 0.59% for “year” as a factor). As a result, temperature as a covariate is more akin to a “seasonal surrogate” in the non-seasonally varying models. A seasonally-varying **B** matrix may account for some of this seasonality, allowing for a more direct interpretation of temperatures role in the food webs of each lake.

MARSS models are fit with maximum likelihood using a combination of the Kalman filter and an Expectation-

Maximization algorithm. The best models were selected using akaike information criterion (AIC) and previously published ecological interactions among variables. We also provide conditional R^2 of the diatom and cyanobacteria model components as a measure of model fit. Here, we define conditional R^2 as the amount of variation in the change from time $t-1$ to time t in phytoplankton biomass that can be described by the model. We verified model stationarity by calculating the magnitude of the eigenvalues of the **B**-matrix, which all should be less than one in a stationary system (i.e., **B** is within the unit circle; Holmes et al. 2013). For consistency, we fit the same model structures to the time-varying MARSS models as were used in the basic models while noting during which seasons the **B** matrix would indicate a non-stationary system. All calculations and analyses were conducted in R (R Core Team 2016).

Results

Bythotrephes was on average an order of magnitude more abundant in Lake Mendota than in Lake Monona (Fig. 1A,B). Overall, *D. pulicaria* biomass declined in both lakes, but to a much larger extent in Lake Mendota (Fig. 1C,D). Total algal

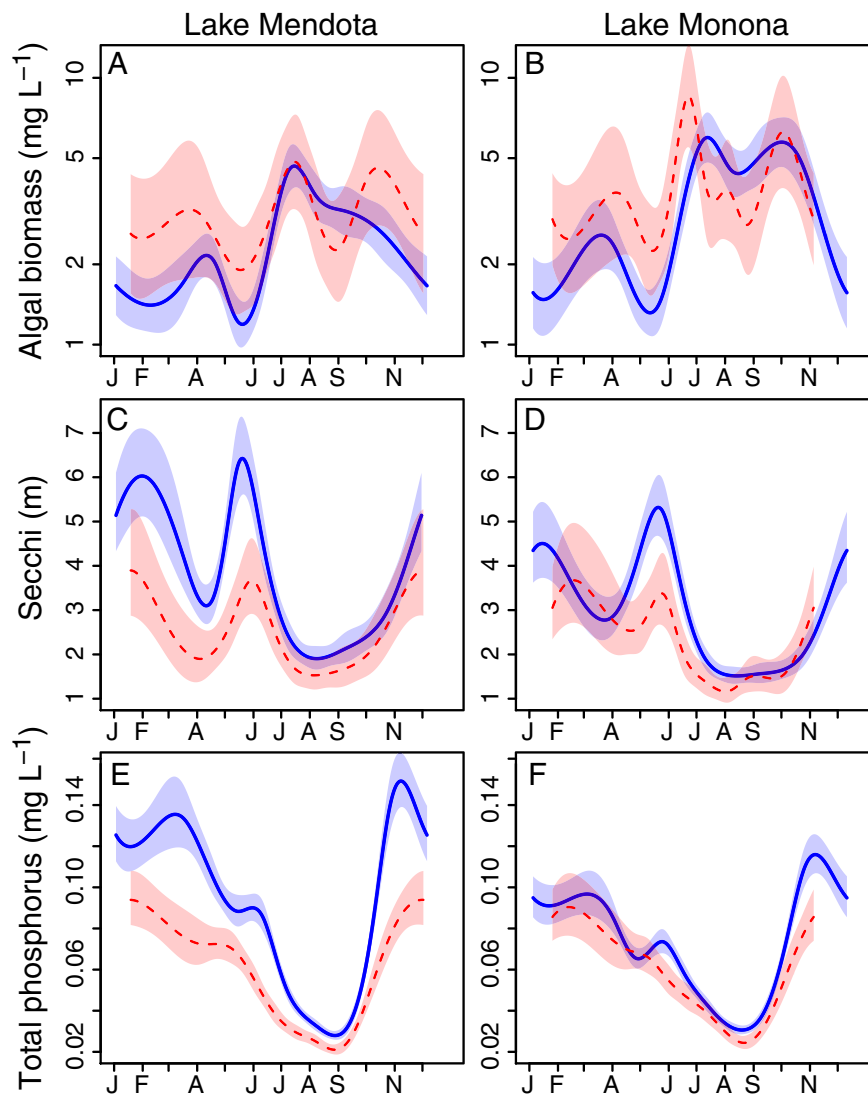


Fig. 2. GAM of algal biomass (mg L^{-1} ; **A, B**), Secchi depth (m; **C, D**), and total phosphorus (mg L^{-1} ; **E, F**) fitted to day of the year in Lake Mendota (**A, C, E**) and Lake Monona (**B, D, F**) for both before (solid blue line) and after (dashed red line) *Bythotrephes* was detected in each lake in 2009. Shaded areas represent $\pm 95\%$ C.I. Note that the y-axes of panels (**A**) and (**B**) are log-scaled.

biomass in Lake Mendota was highly variable but increased marginally in the spring and fall following *Bythotrephes* invasion and *D. pulicaria* decline (Fig. 2A) which likely drove declines in water clarity both over the entire year (Fig. 2C) and during summer months (June–August median Secchi declined from 3.3 m to 2.0 m; Mann–Whitney test $W = 1,208$, $p = 0.009$). The decline in clarity over the entire year was driven by increases in diatom biomass (Fig. 3A), which we used as an indicator of edible algae, and no clear change in cyanobacteria biomass (Fig. 3C). Further, total phosphorus concentrations declined in Lake Mendota (Fig. 2E). While this study focuses on these two dominant phytoplankton taxa, we do note that edible green algae have been more abundant since 2009 with no apparent changes in

cryptomonads (increased biomass of 210% and 4.8%, respectively; North Temperate Lakes Long-Term Ecological Research, NSF 2015c). These changes were similar in direction, but not as large in Lake Monona (Figs. 2B,D,F, 3B,D).

The **B** matrix of the best-fit MARSS model for Lake Mendota reveals that these changes in the phytoplankton community may be due to three ecological interactions (Fig. 4). First, only diatom biomass appears to be associated with “top-down” influence from grazing with a strong negative association between *D. pulicaria* and diatom biomass in both Lake Mendota (-0.14 , $\text{SE} = 0.03$) and Lake Monona (-0.18 , $\text{SE} = 0.03$). Second, only cyanobacteria biomass appears to be associated with “bottom-up” influence from resource availability with a positive association between total phosphorus and

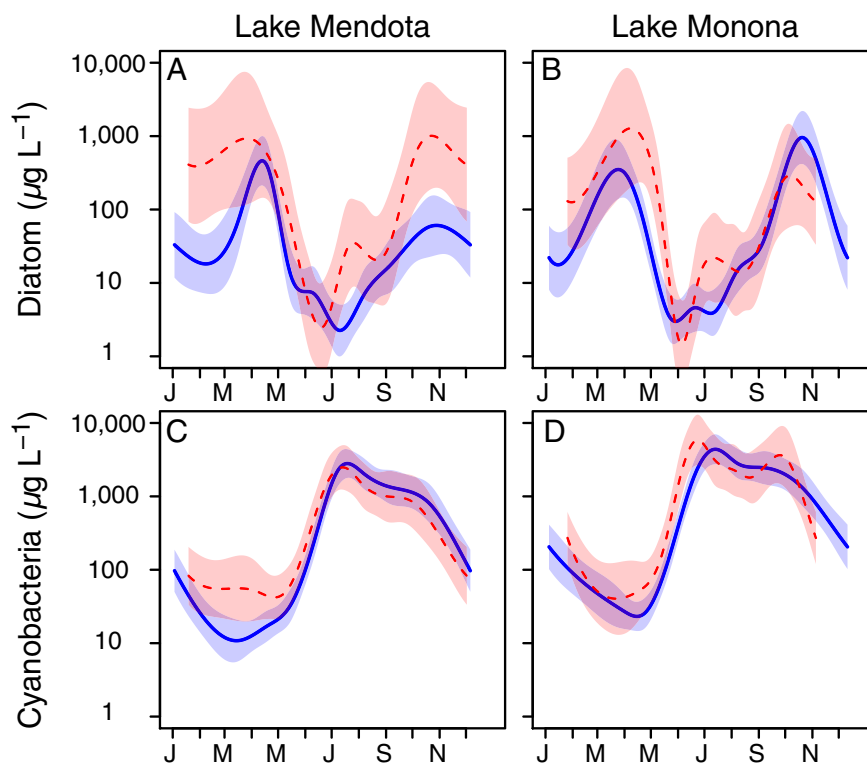


Fig. 3. GAM of diatom (**A, B**) and cyanobacteria (**C, D**) biomass ($\mu\text{g L}^{-1}$) fitted to day of the year in Lake Mendota (**A, C**) and Lake Monona (**B, D**) for both before (solid blue line) and after (dashed red line) *Bythotrephes* was detected in each lake in 2009. Shaded areas represent $\pm 95\%$ C.I. Note that the y-axes of each plot are log-scaled.

cyanobacteria biomass in Lake Mendota (0.07, SE = 0.02). Finally, *D. pulicaria* was negatively associated with total phosphorus (-0.08 , SE = 0.02 in Lake Mendota; -0.16 , SE = 0.02 in Lake Monona) and positively associated with cyanobacteria biomass in both lakes (0.06, SE = 0.01 in Lake Mendota; 0.09, SE = 0.02 in Lake Monona). In Lake Monona, neither diatoms nor cyanobacteria were significantly influenced by total phosphorus concentrations. The **B** matrices of models from both Lake Mendota and Lake Monona were found to be stationary (all eigenvalues less than 1).

Fitting a time-varying **B** matrix to account for seasonality in lake stratification and surface warming improved model fits (Table 1). While allowing **B** to vary by invasion (pre- and post-2009) modestly improved the non-time-varying model fit in Lake Mendota (AIC = 3036.1), it did not improve model fit in Lake Monona (AIC = 3128.7) nor did it improve the model fit in either time-varying model (AIC = 2778.5 in Lake Mendota; AIC = 2873.3 in Lake Monona). The **B** matrices indicated a stationary system for all seasons in Lake Mendota except during ice cover ($\lambda_1 = 1.01$) and fall ($\lambda_1 = 1.03$) and all seasons in Lake Monona except early summer ($\lambda_1 = 1.05$).

Seasonally varying parameter estimates in the **B** matrix were largely consistent with the non-varying estimates with

some key differences (Fig. 4). The negative effect of *D. pulicaria* on diatom biomass was highest in spring and summer but lowest in fall in both Lake Mendota and Lake Monona. In Lake Mendota, the direction of the effects of *D. pulicaria* on total phosphorus vary within a year from negative in summer and destratification time periods to positive in fall and possibly early stratification time periods. In Lake Monona, *D. pulicaria* was negatively associated with total phosphorus during all seasons except early stratification. Also, the positive effect of *D. pulicaria* on cyanobacteria was only significant in late summer in Lake Mendota and early stratification and early summer in Lake Monona. Finally, there was considerable variation in the estimates of the effects of total phosphorus on phytoplankton in both lakes for both the time-varying and non-varying models, particularly in diatoms. However, the time-varying models reveal that positive effect of total phosphorus on cyanobacteria was significant in early and late summer in Lake Mendota and early summer in Lake Monona. Total phosphorus was negatively associated with cyanobacteria in the destratification period of both lakes.

In the non-time-varying models, surface-water temperatures were positively associated with cyanobacteria biomass (0.32, SE = 0.03 in Lake Mendota; 0.25, SE = 0.08 in Lake

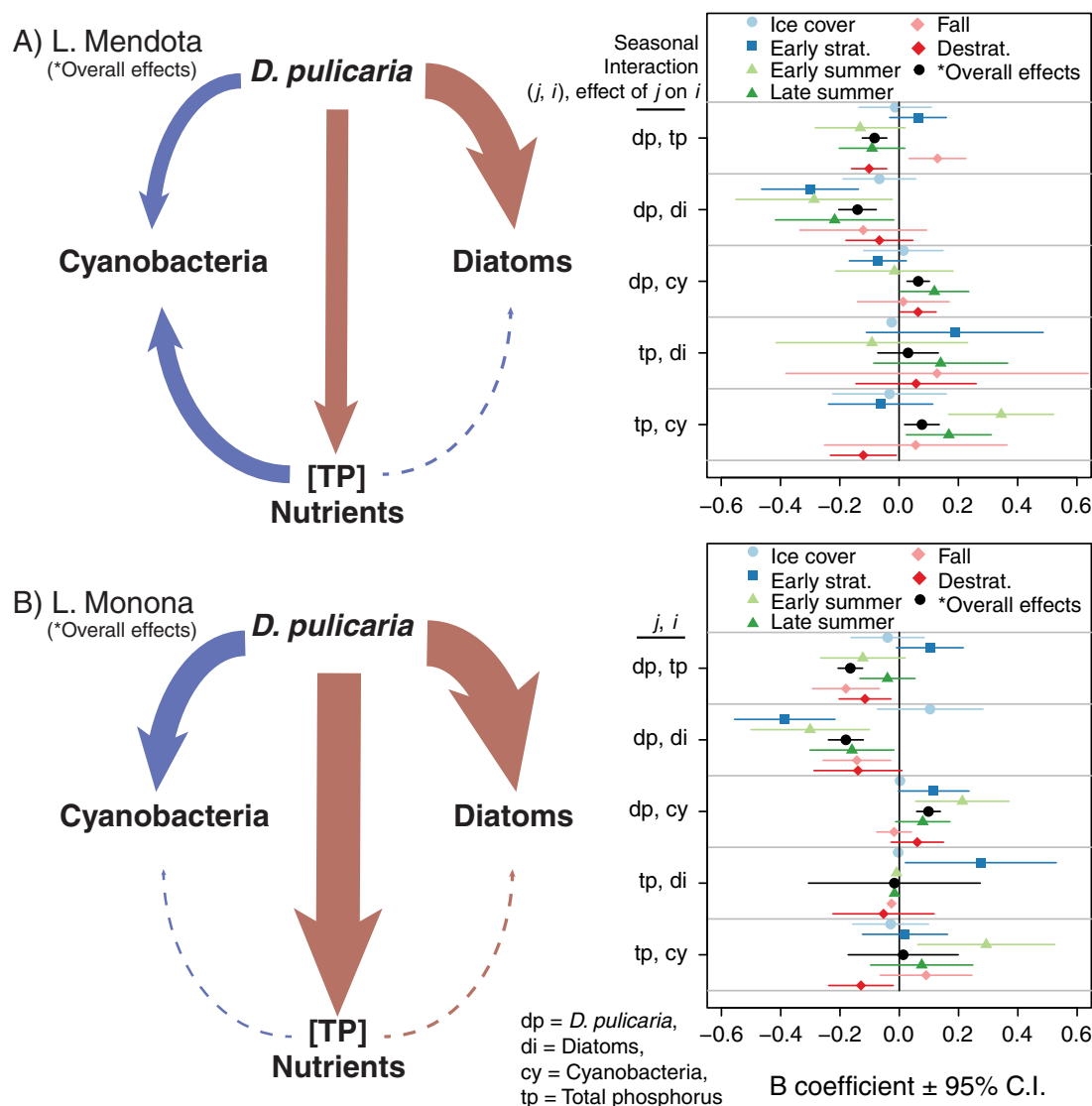


Fig. 4. B-matrix model output from the MARSS models for (A) Lake Mendota and (B) Lake Monona. Parameter estimates are scaled by the magnitude of the **B** estimate and color coded by the direction of the correlation (negatively correlated interactions in red and positively correlated interactions in blue) with nonsignificant interactions (95% C.I. spans zero) indicated by a dashed line. To the right of each diagram is the seasonal model fits where **B** is allowed to vary by lake season (* Overall effects are used for the arrows in the left diagrams).

Monona) and negatively associated with *D. pulicaria* biomass (-0.09 , $SE=0.01$ in Lake Mendota; -0.18 , $SE=0.01$ in Lake Monona) and total phosphorus (-0.05 , $SE=0.03$ or marginally significant in Lake Mendota; -0.10 , $SE=0.03$ in Lake Monona). These results were largely similar in the seasonally time-varying models, with the exceptions of positive associations between total phosphorus and temperature in the fall and destratification periods of both lakes. While surface-water temperatures were slightly higher from 2009 to 2015 than 1995 to 2008 ($+1.6^{\circ}\text{C}$), the effect of changing temperatures on model variates was negligible in both lakes in either model format (non-varying **B** and time-varying **B**).

Increasing the number of phytoplankton taxa in the non-varying and time-varying models revealed similar nutrient and grazing limitations on edible green algae and cryptomonads as edible diatoms for both lakes (Supporting Information Figs. S1, S2). This similarity suggests that diatoms—as the more dominant taxa—were generally a good surrogate for edible algae in spring. One exception to this is the effect of *D. pulicaria* on green algae in the summer in Lake Mendota, where *D. pulicaria* have a significant positive effect on green algae (we discuss this further in the Supporting Information).

We report long-term changes in epilimnetic phosphorus (e.g., particulate and dissolved; Fig. 2E; geometric mean total

Table 1. Model fit parameters for the final non-time-varying **B** and time-varying **B** models selected using AIC in Lakes Mendota and Monona (presented in Fig. 4). Conditional R^2 is presented for the focal taxa, cyanobacteria, and diatoms. Conditional R^2 describes the amount variation in the change from **t-1** to **t** that can be explained by the model.

	AIC	Cyanobacteria conditional R^2	Diatom conditional R^2
Non-varying B			
Lake Mendota	3039.8	0.51	0.63
Lake Monona	3119.5	0.54	0.61
Time-varying B			
Lake Mendota	2739.3	0.48	0.61
Lake Monona	2804.8	0.49	0.59

phosphorus pre-2009 = 0.08 mg L⁻¹ and geometric mean total phosphorus post-2009 = 0.06 mg L⁻¹) and inorganic nitrogen concentrations in the Supporting Information. Overall, the decline in TP was driven by declining soluble reactive phosphorus (Supporting Information Fig. S3) and little overall change in particulate phosphorus or dissolved inorganic nitrogen (Supporting Information Fig. S4). These changes suggest that the lakes are more often limited by phosphorus and using TP as a measure of nutrient availability is largely appropriate here. Also, there was little long-term change in external phosphorus loading (as reported in Walsh et al. 2016a) but a decline in the concentration of phosphorus in the surface waters of Lake Mendota. While it should be noted that we were most interested in modeling the effect of total phosphorus on algal biomass, the MARSS model was unable to capture declining TP, even when top-down interactions between phytoplankton and total phosphorus (e.g., resource depletion) or competition between phytoplankton taxa were allowed (i.e., all additional **B** matrix interaction coefficients were insignificant). In fact, with declining *D. pulicaria*, total phosphorus would have been expected to increase according to both time-varying and non-varying models in each lake. In other words, the limited number of drivers we supplied here (e.g., autocorrelation, surface-water temperature, phytoplankton biomass, and *D. pulicaria* biomass) did not capture the observed decline in total phosphorus.

Simulation using the time-varying Lake Mendota model under different scenarios and ecological conditions reveals the strong top-down effects associated with *Bythotrephes* invasion (Fig. 5). The model captures the large increases in diatom biomass (Fig. 5B) and no change in cyanobacteria biomass observed with the invasion (Fig. 5A). Further, the model predictions reveal the strong top-down effects of *D. pulicaria* which are largely responsible for the observed change in modeled pre- and post-2009 conditions (gray lines

in Fig. 5). While the effect of changing total phosphorus concentrations was small in the model, phosphorus decline did mitigate some of the positive effects of *D. pulicaria* decline on modeled diatom biomass (Fig. 5B). Overall, we note that diatoms were largely top-down limited by *D. pulicaria*, particularly in early seasons, and cyanobacteria were largely bottom-up limited by total phosphorus, particularly in summer (Fig. 6A). The *D. pulicaria* effect on diatoms in both lakes was weakest in fall, a time when the majority of diatom biomass was comprised of large, likely inedible cells (> 30 μ m GALD; Fig. 6B).

Increases in diatom biomass were associated with declining water clarity in Lake Mendota but cyanobacteria biomass did not change substantially with the *Bythotrephes* invasion (Figs. 2, 3). These differential changes in the phytoplankton community were associated with a diverging response in two aspects of water quality. While water clarity declined with the invasion—indicative of declining water quality in Lake Mendota—the number of lake beach closures due to potentially harmful cyanobacteria blooms declined (Wilcoxon rank sum test, $W = 1$, $p = 0.008$, estimate = -46 beach days lost, a 62% decline over the pre-2009 mean, with 95% C.I. = -75 to -17 beach days lost; data from Public Health Madison and Dane County). This decline in closures occurred alongside declining total phosphorus concentrations with invasion and each of these changes would be indicative of improving water quality in Lake Mendota (Fig. 7). Beach closures also declined in Lake Monona ($W = 3.5$, $p = 0.04$, estimate = -18 beach days lost, a 35% decline over the pre-2009 mean, with 95% C.I. = -69 to -0.00005 beach days lost). Here, we include 2009 as a pre-*Bythotrephes* (pre = 2005–2009 and post = 2010–2015) year because, though it was present in net tows as early as July, *Bythotrephes* did not become abundant until September of that year and the latest beach closure occurred on 13 August.

Discussion

In this study, we show that two indicators of lake water quality are influenced by different ecological interactions in Lakes Mendota and Monona. An enormous increase in predation pressure on *D. pulicaria* (Walsh et al. 2017) produced cascading change in the phytoplankton communities of Lake Mendota and Lake Monona toward a higher biomass of small diatoms in spring, in turn dampening and shortening the length of the clear water phases of each lake (here defined as Secchi depth > 4 m; Fig. 2C,D). Our ecological results for the two lakes are largely consistent with hypotheses regarding the “eutrophic PEG-model” whereby seasonal succession of phytoplankton is driven by the seasonal timing of nutrient availability and size dependent predation by zooplankton (Sommer et al. 1986), and consistent with previous research in Lake Mendota (Lathrop et al. 1996; Carey et al. 2016). Notably, we found that the majority of diatoms in

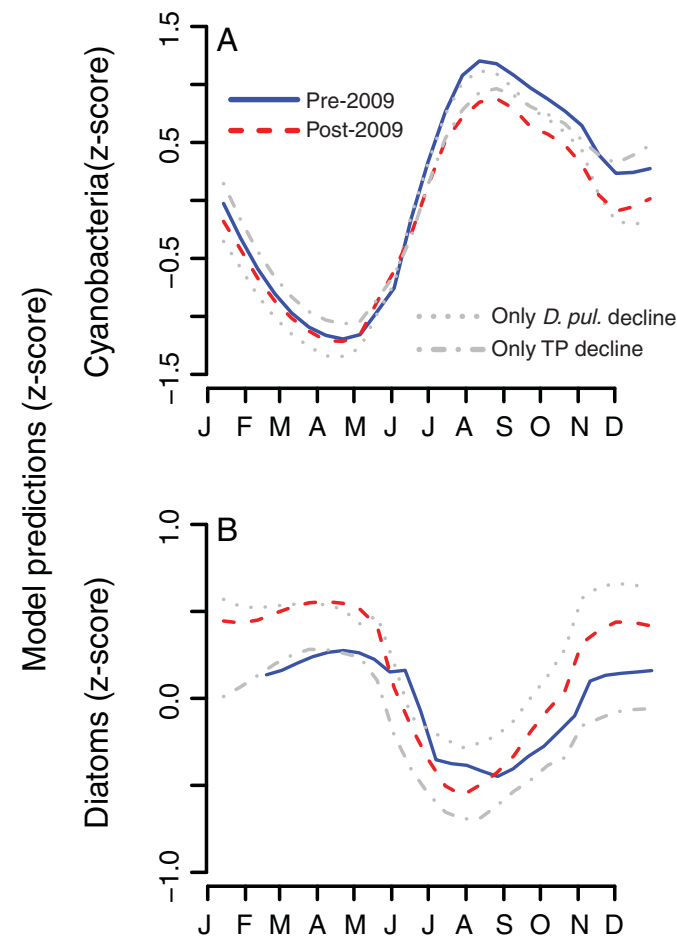


Fig. 5. Model predictions of cyanobacteria (A) and diatom (B) z-scored $\log_{10}$ biomass under different ecological conditions in Lake Mendota: pre-2009 conditions in blue solid lines, post-2009 conditions in red dashed lines, conditions under only declining *D. pulicaria* biomass (pre-2009 TP) in gray dotted lines, and conditions under only declining total phosphorus concentrations (pre-2009 *D. pulicaria*) in gray dotted and dashed lines.

fall were too large to be effectively grazed by *D. pulicaria*. Accordingly, late fall diatom biomass increased only slightly after 2009 (Fig. 3A) and water clarity only decreased slightly in fall (Fig. 2C). Our results suggest that, in both lakes, *D. pulicaria* play a relatively small role in controlling diatom biomass in fall. Additional research will be required to determine the possible causes of the fall increase in diatom biomass in Lake Mendota, as well as why this increase was less pronounced in Lake Monona.

We also report divergent responses within the phytoplankton community to the *Bythotrephes* outbreak and declining nutrient concentrations in Lake Mendota. Therefore, distinguishing between factors influencing water clarity (total algal biomass) and beach-closing cyanobacteria blooms was important for Lake Mendota. We found that diatoms are primarily limited in spring by zooplankton grazing,

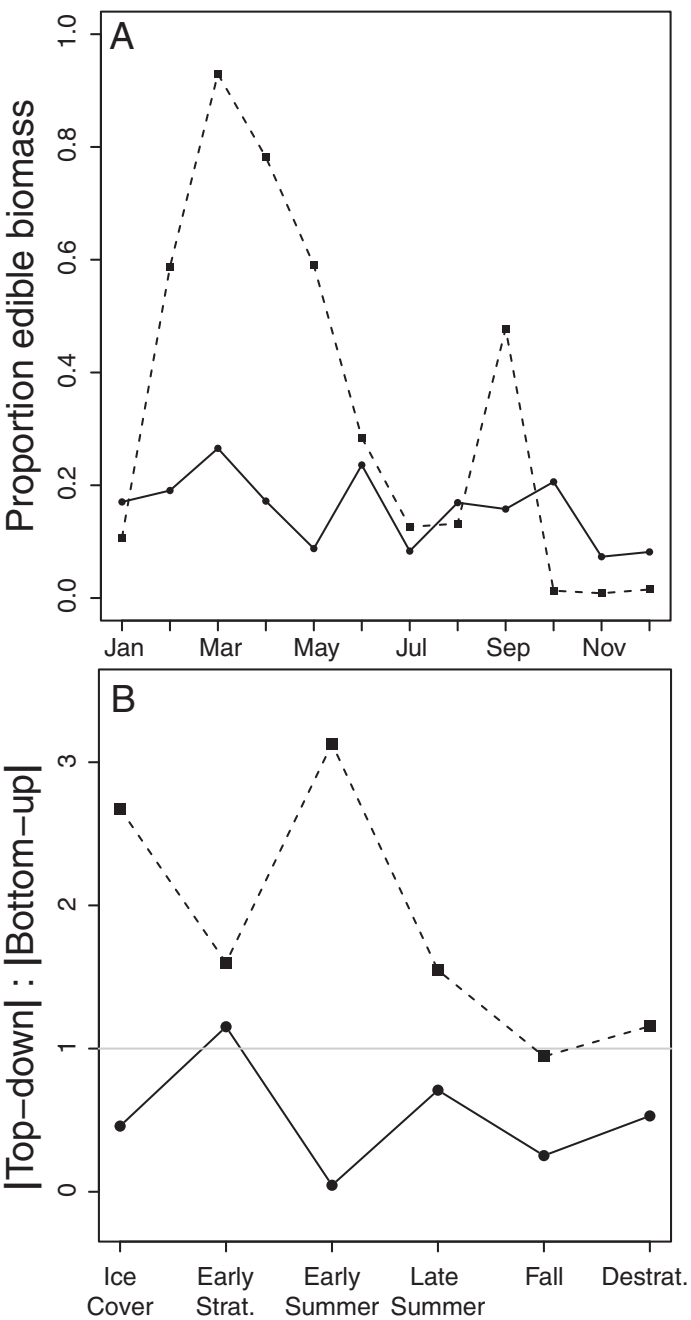


Fig. 6. (A) Proportion of edible diatom (squares and dashed line) and cyanobacteria (circles and solid line) biomass in Lake Mendota. Edibility is defined as natural units (e.g., cells, colonies, or filaments) with a GALD less than $30 \mu\text{m}$. (B) The ratio of the absolute values of the top-down (*D. pulicaria* effect on each phytoplankton) and bottom-up (total phosphorus effect on each phytoplankton) effects from the MAR B-matrix output for diatoms (squares and dashed line) and cyanobacteria (circles and solid line) across seasons (strat., stratification) in Lake Mendota. The direction (positive or negative) and significance of effects can be found in Fig. 1.

demonstrating that spring water clarity is unlikely to return unless *D. pulicaria* dominance is restored. However, this spring loss in water clarity was not accompanied by an

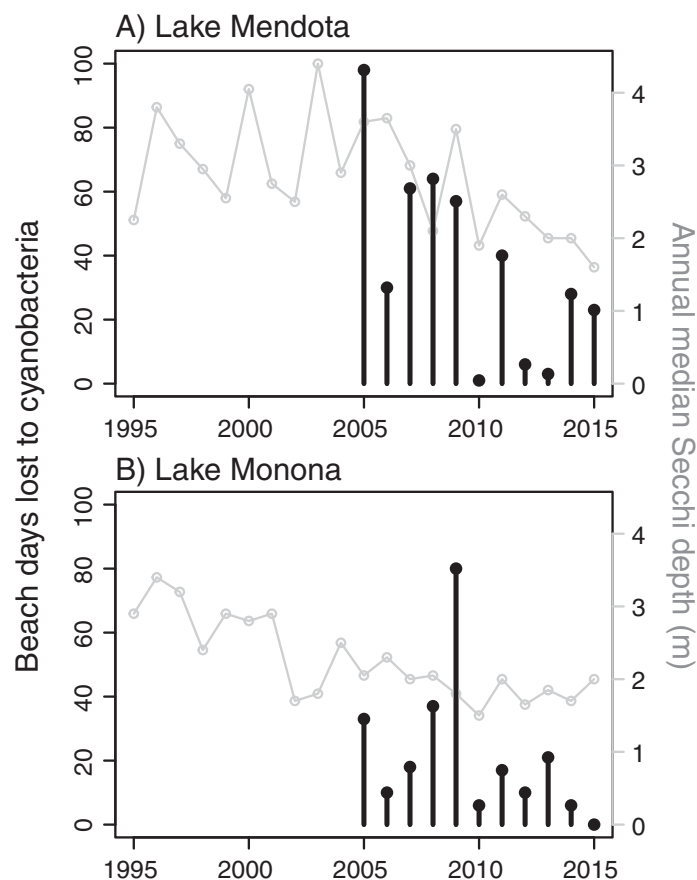


Fig. 7. Long-term changes in two indicators related to water quality in (A) Lake Mendota and (B) Lake Monona. Annual median water clarity (Secchi depth in m) is plotted in with a gray line and open circles and beach days lost to cyanobacteria blooms each year are plotted with black points and vertical lines.

increase in harmful cyanobacteria blooms. Cyanobacteria blooms are most often associated with warm surface-water temperatures (e.g., Robarts and Zohary 1987; Elliot et al. 2006; our models also point to a positive association between temperature and cyanobacteria), leading to a seasonal mismatch between the spring clear water phase and summer cyanobacteria blooms. Also, our model results suggest that cyanobacteria biomass is more likely to be controlled from the bottom-up by nutrient availability, particularly in summer. These results may clarify reports of strong top-down control of *Daphnia* (Vanni et al. 1990) that are limited to edible spring diatoms (or green algae and cryptomonads, which are edible at all times of year) rather than largely inedible summer cyanobacteria blooms (e.g., as suggested in Gliwicz 1990).

We note a decline in total phosphorus concentrations in Lake Mendota and a lesser decline in Lake Monona, but no change in summer cyanobacteria biomass. This could suggest that our model estimates do not fully capture the factors influencing summer cyanobacteria biomass. Summer

cyanobacteria biomass is likely driven by multiple factors not covered by the relatively coarse analysis here (e.g., nutrient stoichiometry). Also, it is likely that biweekly measures of cyanobacteria biomass at a lake's deepest point may not capture short-lived, scum-forming cyanobacteria blooms that accumulate at down-wind shorelines, leading to beach closures. If cyanobacteria biomass is indeed more limited by nutrient availability—as evidenced by previous research (Sommer et al. 1986; Lathrop et al. 1999; Carey et al. 2016), our time series modeling, and fewer beach closures—then these diverging responses in water quality may influence how water quality in Lake Mendota is managed depending on how each indicator is valued by the public (sensu Kosenius 2010). For example, cyanobacteria biomass could be reduced by lower in-lake phosphorus concentrations. Our results from Lake Mendota would suggest that such reductions should improve summer water quality conditions that are related to cyanobacteria biomass (both clarity and beach closing blooms) despite a limited improvement in spring clarity which is related to diatom biomass and, in turn, *Daphnia* grazing. Indeed, it is unlikely that the public would value spring clarity as highly as summer clarity and cyanobacteria conditions as the lake is used most heavily in summer months (Dane County Department of Public Works, NTL-LTER “Boat Traffic Through Yahara Locks 1976 – current”). While summer clarity did decline with *Bythotrephes* invasion and *D. pulicaria* decline (median June through August Secchi declined from 3.3 m to 2.0 m), this was not accompanied by increased cyanobacteria biomass (Figs. 2, 3, 7).

Nutrient limitation of cyanobacteria and grazer limitation of small diatoms and other edible-size phytoplankton (e.g., cryptomonads) varied seasonally, and including seasonality in our time series models improved their fit. However, seasonal changes in the modeled food web interactions were complex, often changing signs (e.g., positive to negative) by season. In some cases, this was consistent with current understanding of lake food web ecology, such as the role of phytoplankton GALD in resisting *D. pulicaria* predation in fall in each lake (Fig. 6) or thermal stratification (i.e., with warm summer temperatures) in limiting internal phosphorus loading into the epilimnion (Lathrop et al. 1999). In other cases, the differences could suggest more complex ecological interactions. For example, the effect of total phosphorus on cyanobacteria biomass was only significant and positive during summer in Lake Mendota and early summer in Lake Monona—times when epilimnetic phosphorus is scarce—which is supported by previous research on nutrient limitation of summer cyanobacteria populations (Lathrop et al. 1998, 1999). However, in both lakes, this effect became significant and negative during destratification which could be indicative of a more complex ecological interaction. Diatoms often become abundant again after lake mixing transfers remineralized hypolimnetic phosphorus and silica to the

surface, allowing diatoms and other algal taxa to outcompete cyanobacteria for nutrients (Sommer 1989).

Modeling here may help to identify new hypotheses for drivers of phytoplankton biomass and water quality that can be tested with additional methods of inference. For example, changes in phytoplankton biomass were likely affected by a change in phosphorus dynamics in Lake Mendota, possibly due to *Bythotrephes* invasion. Changes in phosphorus cycling are evidenced by historically low total phosphorus concentrations in the lake's surface waters after *Bythotrephes* outbreak, despite relatively normal external phosphorus loading (Walsh et al. 2016a). We were unable to capture this decline in our modeling through either resource depletion (i.e., including a coefficient for phytoplankton effect on total phosphorus) or competition between phytoplankton (i.e., including interaction coefficients in phytoplankton). In fact, our model would have predicted increasing total phosphorus concentrations with *D. pulicaria* decline. This discrepancy could suggest that the decline in total phosphorus is not a result of linear relationships between phosphorus and either plankton or temperature in Lake Mendota. One example of a nonlinear, abrupt change in lakes that could drive epilimnetic phosphorus decline is calcite whittings, which can be caused by increasing pH due to high rates of primary production (Sarnelle 1992; Hodell et al. 1998). Phosphorus can be co-precipitated in calcite whittings, then sedimented and stored in the lake bottom (Murphy et al. 1983), acting as a significant sink of phosphorus and negative feedback on eutrophication (Hamilton et al. 2009). We have observed evidence of recent whitening events in Lake Mendota that could account for a significant sink of phosphorus from the water column (see Fig. 7 in Walsh et al. 2016b).

Daphnia are important in open-water P cycling and can act as both sources (through algal grazing and excretion; e.g., Schindler et al. 1993) and sinks (through incorporation of P into body tissue and chitin; e.g., Andersen and Hessen 1991) of epilimnetic P (Sterner and Hessen 1994). While we found a negative effect of *D. pulicaria* on TP (which is not consistent with TP decline with *D. pulicaria* decline), we did find a positive association between *D. pulicaria* biomass and cyanobacteria biomass in both lakes. This finding is consistent with the hypothesis that *D. pulicaria* can have potentially adverse effects on summer water quality through the recycling of epilimnetic P (Lynch 1980; Lathrop and Carpenter 1992). If recycled P is quickly taken up by phytoplankton, it is unlikely that we could capture this dynamic in a time series model fitted from bi-weekly measurements. However, it should be noted that *Daphnia* could promote cyanobacteria growth through both P recycling and grazing of smaller phytoplankton that are more competitive for nutrients (Lathrop and Carpenter 1992). Also, *Bythotrephes* consumption of *D. pulicaria* could redirect epilimnetic P through highly inefficient "shredding" of *Daphnia* during predation (as much as 40% of *Daphnia* tissue is lost as debris

during *Bythotrephes* consumption; Burkhardt and Lehman 1994), which would act as a P sink and could explain declining epilimnetic TP. Further investigation is required here to better understand the Lake Mendota phosphorus cycle.

Long-term changes in lake nutrient stoichiometry will remain a key research area in understanding and managing water quality in eutrophic lakes (Supporting Information Figs. S3, S4). For example, some species of cyanobacteria are capable of fixing atmospheric nitrogen, offsetting the role of N-limitation in lakes and, in turn, favoring cyanobacteria dominance in the summer phytoplankton community (Vitousek et al. 2002). However, *Microcystis*, which does not fix N, often produces water quality problems in eutrophic lakes as certain strains produce toxins. While we present a broad view into the provisioning of clear and toxin-free water in this study, these changes in cyanobacteria reveal additional complexity in managing lake water quality. Further research into interactions within the cyanobacteria community will be critical to understanding toxin production in eutrophic lakes (sensu Beversdorf et al. 2013).

The effects observed in Lake Mendota were larger than those in Lake Monona. Lake Mendota has been managed as a piscivore or "sportfish" lake supporting its walleye and northern pike fishery that in turn control yellow perch and other planktivorous fish that prey on both *D. pulicaria* and *Bythotrephes* (Lathrop et al. 2002). This may describe why *Bythotrephes* is less abundant in Lake Monona and, in turn, why Lake Monona's food web did not change to the same degree as Lake Mendota (e.g., *D. pulicaria* would severely decline in fall in Lake Monona prior to 2009). In both lakes, the dominant planktivorous fishes are known to consume *Bythotrephes* (Walsh unpubl. data), likely limiting its abundance in Lake Monona where these fishes are more abundant and there is a higher proportion of littoral area for zooplanktivorous fishes. In fact, in recent years (2014–2015), both *D. pulicaria* and water clarity have been slightly higher in Lake Monona than Lake Mendota (NTL-LTER)—a phenomenon which has not occurred since before the Lake Mendota bio-manipulation in 1988. Further investigation is required to determine the viability of manipulating Lake Mendota's fishery to control *Bythotrephes* and improve water clarity while mitigating the risk of further harm to the lake's *D. pulicaria* population.

Broadly, *Bythotrephes* has had large, negative effects on lake zooplankton communities in North America (Yan et al. 2011), with implications for both water quality (as presented here) and higher-level consumers (Staples et al. 2017). While Lake Mendota was the first report of a strong cascading effect of *Bythotrephes* predation on water clarity (Walsh et al. 2016a,b), an understanding of the relative role of nutrient limitation and grazing intensity may help to understand which lakes are most vulnerable to adverse impacts by *Bythotrephes*. For example, most studies of the effect of *Bythotrephes* on lake food webs are conducted in oligotrophic lakes

where algal biomass is possibly more limited by nutrients than grazing (Lehman and Cáceres 1993; Strecker and Arnett 2008; Strecker et al. 2011) or in the Great Lakes where water clarity is driven primarily by invasive dreissenid mussels (excluding Lake Superior, which remains nutrient-limited; Yousef et al. 2017). There are several exceptions to this where *Bythotrephes* has invaded more productive systems such as Lake Simcoe (Ontario, Canada; Kelly et al. 2017) or Kabetogama Lake (Minnesota, U.S.A.; Kerfoot et al. 2016; Staples et al. 2017) and our approach could help better describe *Bythotrephes* impact on water quality in lakes with adequate time series data. Generally, multivariate autoregressive models have been an important tool for teasing apart the effects of invasive species (Beisner et al. 2003), and similar work could improve our understanding of the effects of other aquatic invasive species.

Understanding the factors that drive water clarity and the frequency of potentially harmful cyanobacteria blooms will be important to managing water quality in light of environmental change and especially species invasions. For example, citizens were found to value water clarity in the Gulf of Finland more than fewer cyanobacteria blooms (Kosenius 2010). If there is similar differentiation in the value of the two components of water quality in Lake Mendota and the ecological pathways providing each component are different, then resources might be allocated more efficiently to manage for a particular water quality outcome (e.g., spring clarity may be less important than the frequency or intensity of cyanobacteria blooms in summer). Similarly, the costs of managing agricultural run-off or directly managing the lake's food web (e.g., through the fishery) to ameliorate top-down pressure on *Daphnia* may differ. The ecological information here and the socio-economic information from a survey sensu Kosenius (2010) would help inform water quality management in the future.

Author Contribution Statement

JRW and MJVZ designed research; JRW performed research; JRW, RCL, and MJVZ analyzed data; and JRW, RCL, and MJVZ wrote the paper.

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Conflict of Interest

None declared.

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