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Eutrophication drives divergent water clarity responses to decadal variation in lake level

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Abstract

Water clarity is an important attribute of lakes, but climatic effects on clarity remain obscure, because lake physical and chemical conditions generate complex responses. Here, we examine how hydrologic variation influences water clarity (Secchi depth) over 30 yr across 24 lakes in northwest Wisconsin (U.S.A.) along a gradient in lake phosphorus (P) concentration and lake attributes (e.g., depth, area, land use, and trophic status). We took a multivariate time-series approach to explore shared temporal patterns in Secchi depth among lakes and to evaluate the relative strength of hydrological time-series (lake level, Palmer Drought Severity Index [PDSI], and antecedent precipitation) as a component of water clarity change. Decadal fluctuations in lake level best explain annual shifts in water clarity, but not precipitation or PDSI. The sign and magnitude of the response varies among lakes by trophic status. Oligotrophic lakes become clearer when lake levels decline, and more turbid when lake levels rise, presumably due to increased watershed loading of dissolved organic matter and nutrients. Dilution and stronger stratification during wet years may drive the opposite response observed in eutrophic lakes, which become clearer in wet years and more turbid during drought. Overall, the water clarity response to lake level increased with P concentration and was more positive in shallow polymictic vs. dimictic lakes. Although further study is required, we suggest that trophic status and lake mixis mediate water clarity's response to lake level fluctuations. We propose that eutrophication not only changes mean lake clarity but also the natural relationship of water clarity to hydrology.

Water clarity is a fundamental characteristic of all lakes that reflects how light is attenuated in the water column due to particles such as suspended clay, dissolved organic matter (DOM), and algae that scatter or absorb light (Wetzel 2001). Over 45 yr of research describes how nutrient loading of phosphorus (P) results in greater algal abundance and decreased water clarity (Edmondson 1970; Schindler 1974; Lathrop 1992) in lakes draining watersheds with agricultural and urban development (Vollenweider 1968; Edmondson 1970; Dillon and Kirchner 1975). Changes in the water cycle are expected, and for many regions that will include more frequent extreme precipitation events and prolonged drought periods, which may exacerbate P and lake eutrophication (Trenberth et al. 2013; Carpenter

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et al. 2015). Still, it is unknown how water clarity responds to drought and flood periods in different lakes (Mosley 2015).

In most oligotrophic lakes, the concentration of chromophoric DOM (CDOM) accounts for the majority of light attenuation (Morris et al. 1995; Fee et al. 1996; Williamson et al. 1996). In recent decades, increasing dissolved organic carbon (DOC, a measure of DOM) has darkened many streams and lakes in the northern hemisphere (Roulet and Moore 2006). This browning effect is thought to be associated with recovery from acid rain deposition (Evans et al. 2006; Monteith et al. 2007) or with changes to precipitation and runoff regimes (Eimers et al. 2008; Zhang et al. 2010; Oni et al. 2013; Jane et al. 2017; Rose et al. 2017). DOC loading from the watershed increases when precipitation is high. This is especially true in lakes with large watershed areas that are heavily forested or contain wetlands (Rose et al. 2017). Increased DOC is also associated with more watershed-derived N and P (Corman et al. 2018), which may spur algal blooms if lakes are not light limited (Carpenter et al. 1998; Robertson et al. 2009). Conversely, drought is correlated with clearer water in oligotrophic lakes due to reduced watershed loading of DOC and nutrients. Extended dry weather also exposes DOM to longer periods of

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ultraviolet bleaching and thereby produces clearer lakes (Xenopoulos et al. 2000; Williamson et al. 2016).

It is generally accepted that the effect of hydrological variation on water clarity in eutrophic lakes is similar to oligotrophic lakes. Increased precipitation will increase loading of humanderived nutrients (P) from watershed runoff, which will increase algal growth and decrease water clarity (Wetzel 2001; Lathrop 2007; Carpenter et al. 2015). Conversely, reduced runoff and nutrient loading during drought increase water clarity. However, water clarity's response to drought in eutrophic lakes can be muted (Rose et al. 2017) or even opposite to that of oligotrophic lakes. For instance, reduced inflow and longer water residence time during drought can concentrate nutrients and algae and decrease water clarity. Drought conditions can also warm surface waters and promote blue-green algal blooms (Dillon and Kirchner 1975; Mosley et al. 2012). Further, internal fluxes of P from hypolimnetic water and sediments in shallow lakes can resupply surface-oriented algae and N-fixing cyanobacteria with P during summer stratification periods (Mayer et al. 1982; Soranno et al. 1997; Søndergaard et al. 2003). Conversely, higher rates of precipitation can decrease water residence time and flush nutrients through the lake, minimizing algal blooms and increasing water clarity. In shallow polymictic lakes that mix throughout summer, higher lake levels can increase the strength and duration of stratification and reduce internal nutrient loading (Juckem and Robertson 2013; Mosley 2015).

While isolated case studies suggest contrasting responses in water transparency to hydrology, less is known about lakes at regional scales where neighboring lakes might experience the same climate but respond differently because of lake-specific chemical and physical attributes. At regional scales (10^3-10^4 km^2) , we might gain further insight on how climatic effects can be mediated by lake-specific attributes. Separating lake-specific attributes that act independently from shared regional drivers will be important for meeting water quality targets under future climate regimes.

Here, we attempt to shed light on this knowledge-gap by examining water clarity fluctuations across three decades of summer Secchi depth measurements collected by citizen scientists from 24 neighboring lakes in northwest Wisconsin. Due to their proximity to one another (max distance ~ 100 km; Fig. 1a), we assumed that all lakes experienced similar climate conditions over periods of low and high water. We hypothesized that these lakes would share common fluctuations in summer water clarity but that the effect of hydrologic signatures would be mediated by lake-specific attributes such as watershed development, lake area, depth, and trophic status. We used dynamic factor analysis (DFA) to detect temporal coherence between time-series and to test the relative strength of three hydrologic covariates (antecedent precipitation, lake level fluctuations, and Palmer Drought Severity Index [PDSI]) as components of water clarity change. This approach offers a strong test of how lake-specific attributes alter water clarity responses to climate.

Methods

We gathered water clarity (Secchi depth) records from 24 lakes spanning 30 yr (1987–2016) in northwest Wisconsin, U.S.A. (45.51°N, 91.74°W; Fig. 1a). Volunteer scientists measured Secchi depths as part of the Wisconsin Citizen Lake Monitoring Network, organized by the Wisconsin Department of Natural Resources (WDNR) and UW-Extension Lakes (http://dnr.wi.gov/lakes/clmn/). We calculated annual mean summer Secchi depth (July and August) when lakes are typically stratified (Supporting Information Table S1).

We selected lakes with the longest history of monitoring and lakes that span a large gradient in clarity, P, and morphology. Lakes are collectively part of the Red Cedar River basin but most reside in isolated subdrainages or small seepages. The study lakes cover a gradient in agricultural intensity (0-52% of the watershed), morphology (3-32 m deep), and mean summer Secchi depth (0.5-6.3 m; Table 1). Resuspension of nutrients may occur in 10 polymictic lakes and 7 lakes with carp (Cyprinus carpio; Table 1). Citizen scientists also collected water samples for total phosphorus (TP, μg^{-1} L) and algal biomass (chlorophyll *a* [Chl *a*] μg^{-1} L) but not every year. Only two lakes had Secchi disk readings for all 30 yr, most lakes had 23 yr, and the shortest record was 13 yr. We summarized lake biological condition by its trophic state index (TSI) (Carlson 1977; Secchi disk formulation), which defines a lake as oligotrophic (TSI < 40), mesotrophic (40-50), or eutrophic (50-70; Table 1). Polymictic lakes were determined using the equation: (maximum depth – 0.1)/(log₁₀ lake area) ≤ 3.8 , where depth is in meters and area is in hectares (Lathrop and Lillie 1980). We were not able to directly determine contribution of nonalgal sources (DOC) to light attention, because dissolved absorbance and total suspended solids data were not available for the study lakes.

Basic watershed characteristics of each lake were calculated in ArcGIS (version 10.3) using the 24K hydro-geodatabase from WDNR (hydro_va_24K) and the 2006 national land cover database. We summarized the variation of physical lake and watershed attributes using principal component analysis (PCA) on an environmental matrix of lake maximum depth, lake area, watershed area, and percent agriculture (Fig. 1b). Phosphorus was also displayed on the ordination plot and regressed against the PCA components to examine its relationship with watershed attributes (Fig. 1b). A power function was then fitted to Secchi depth against TP and Chl *a* to illustrate how P pollution influences mean water clarity of lakes in this region (Fig. 1c).

We compared time-series of three annual indices of hydrology (years 1987 to 2016; Supporting Information Table S2) as explanatory covariates of water clarity for: (1) previous year total precipitation by water year (October–October, www. drought.gov, northwest WI), (2) the PDSI (www.drought.gov, July northwest WI; Palmer 1965), and (3) a seepage lake-level time-series from one of the study lakes (Shell Lake, WI;



Fig. 1. (a) Study lakes in northwest Wisconsin, U.S.A. Numbers correspond to lakes identified in Table 1 and are ordered by increasing water clarity. (b) PCA of lake and watershed characteristics with each lake shaded by its mean total phosphorus concentrations (μ g L⁻¹). (c) Mean summer Secchi depth as a power function of lake total phosphorus (solid curve, filled points) or mean summer Chl *a* (μ g L⁻¹), dashed curve, open points).

www.shelllake.org). As a measure of annual runoff from spring snowmelt and summer rainfall, we anticipated that previous year precipitation would be strongly correlated with water clarity change in Wisconsin lakes (Rose et al. 2017). We verified that annual water year precipitation fluctuated coherently across the spatial and temporal extent of the study area among seven meteorological stations (Supporting Information Fig. S1). The Palmer drought index is a more complex measure of regional dryness based on variation in surface air temperature, soil moisture content, and antecedent precipitation (Alley 1984). The July index captures late spring to middle summer by integrating regional dryness over the previous several months.

Last, lake level data came from the City of Shell Lake, which monitors lake stage at a single station approximately weekly during the ice-free period. The lake lacks a dam or other annual surface regulation except in extreme circumstances. Shell Lake's surface depth was lowered by 0.6 m from November 2003 to July 2005 because of flooding to the lakeshore community. We used the corrected version of the lake level record that accounted for the hydrological manipulation (Juckem and Robertson 2013). We verified that lake levels fluctuate similarly in several other study lakes (Supporting Information Fig. S2). Compared to PDSI or antecedent precipitation, seepage lake level fluctuations reflect longer term (months to decades) changes in water balance among evaporation, surface inflows, and groundwater exchange (Watras et al. 2014).

Time-series analysis

Secchi depth time-series were analyzed using DFA (Zuur et al. 2003) to evaluate common patterns in water clarity among lakes with the MARSS package (Holmes et al. 2012) in R (R Development Core Team 2015). DFA is a dimension reduction technique specifically designed for multivariate time-series and accounts for the autocorrelated nature of time-series data. Covariate time-series require complete records, but response time-series (i.e., Secchi depth) can vary in length and contain missing values.

We used DFA to characterize shared latent trends among N = 24 time-series and estimate the strength of drought represented in three covariate time-series, shared latent trends, and error. Specifically, following Zuur et al. (2003) the DFA model is

$$\mathbf{y}_t = \mathbf{Z}\mathbf{x}_t + \mathbf{D}\mathbf{g}_t + \mathbf{v}_t \quad where \ \mathbf{v}_t \stackrel{\sim}{} MVN(0, \mathbf{R}) \tag{1}$$

$$x_t = x_{t-1} + w_t. \qquad \text{where } w_t ~ MVN(0, \mathbf{Q}) \tag{2}$$

The shared latent trend (x_t) , is modeled as a random walk through time such that the value at time t is equal to its value at time t - 1 plus some random normally distributed error (w_t) with a mean (**0**) and variance (**Q**). The shared latent trend can be thought of as an aggregate of environmental drivers not captured by a covariate time-series. The $N \times 1$ vector of data observed at time t (**y**_t) are modeled as a linear combination of latent trend(s) (x_t) , a $P \times 1$ vector of explanatory variables

Table 1. Lake and watershed characteristics ordered by increasing mean Secchi depth. Other descriptors include mean TP, mean Chl *a* concentrations, maximum lake depth (depth), percent agriculture in the watershed (% Ag), TSI from Secchi, watershed area (WSA), lake area (LA), and the ratio of lake area to watershed area LA : WSA.

Lake name	Lat.	Long.	Secchi (m)	TP (μ g L ⁻¹)	Chl <i>a</i> (μ g L ⁻¹)	Depth (m)	% Ag	TSI-SD	WSA (km ²)	LA (km ²)	LA : WSA
1. Mud*	45.36	-91.65	0.5	89.0	147.0	4.6 [†]	22	68.7	148.8	2.3	0.017
2. Prairie	45.36	-91.68	0.5	84.5	82.2	4.6^{\dagger}	9	68.7	60.6	5.3	0.099
Pokegama*	44.25	-90.20	0.6	88.3	165.0	5.8^{\dagger}	38	67.9	19.3	1.8	0.029
4. Tenmile	45.29	-91.61	0.6	108.0	60.0	3.0^{\dagger}	28	67.1	123.7	1.5	0.094
5. Chetek	45.24	-91.64	0.8	84.8	65.7	5.5^{\dagger}	24	63.9	231.0	3.5	0.013
6. Staples	45.50	-92.15	0.9	91.9	154.1	5.5^{\dagger}	39	61.8	46.8	1.3	0.016
7. Tainter*	44.98	-91.86	1.0	129.0	78.2	11.3	52	59.5	1512.2	5.2	0.004
8. Desair	45.33	-91.64	1.2	74.5	50.7	9.1	52	56.8	15.1	0.3	0.023
9. Granite*	45.58	-92.01	1.5	34.3	15.8	10.3	25	53.9	8.4	0.5	0.040
10. Wapogasset*	45.33	-92.43	1.7	44.0	33.1	9 .7 [†]	42	52.6	120.8	4.5	0.060
11. UpperTurtle*	45.42	-92.10	1.9	38.5	24.0	7.6^{\dagger}	35	50.8	20.8	1.7	0.078
12. Kirby [‡]	45.60	-92.07	1.9	26.2	14.2	5.8^{\dagger}	4	50.8	5.1	0.4	0.089
13. Bear	45.63	-91.82	2.1	21.6	11.0	27.4	17	49.5	94.3	5.5	0.087
14. Long	45.71	-91.67	2.1	24.1	11.5	19.8	7	49.5	173.8	14.1	0.062
15. Big dummy [‡]	45.57	-91.98	2.6	24.9	5.9	16.7	20	46.1	3.1	0.5	0.161
16. Red cedar	45.61	-91.59	2.6	24.9	13.8	18.2	10	46.1	184.9	7.2	0.042
17. Sand	45.85	-91.50	2.7	20.7	8.9	15.2	19	45.6	37.5	3.8	0.119
18. McKenzie*	45.92	-92.04	3.0	19.1	7.6	25.8	15	44.1	38.5	4.3	0.109
19. Spider	46.10	-91.22	3.2	13.4	3.2	15.2	0	43.1	41.2	4.8	0.125
20. Shell [‡]	45.73	91.90	3.6	14.2	8.2	9 .7 [†]	19	41.7	55.5	9.5	0.183
21. Whitefish	45.86	-91.45	3.9	15.4	3.3	30.4	9	40.3	28.7	3.0	0.113
22. Silver [‡]	45.58	-91.92	4.1	13.4	5.8	15.2	7	39.5	7.9	1.4	0.184
23. Beaver Dam [‡]	45.55	92.03	4.5	10.6	2.6	32.2	19	38.2	20.3	3.1	0.165
24. Stone [‡]	45.84	-91.56	6.2	9.2	1.6	13.7	9	33.6	8.4	2.1	0.271

*Lakes with known populations of carp.

[†]Polymictic lakes.

[‡]Seepage lakes (no inlet or outlet streams).

(\mathbf{g}_t , e.g., lake level, antecedent precipitation, or PDSI), and an $N \times 1$ vector of observation (sampling) errors (\mathbf{v}_t), which are distributed as a multivariate normal with mean **0** and $N \times N$ variance–covariance matrix **R**. The $N \times 1$ vector Z contains a matrix of factor loadings on the shared latent trends, and $N \times P$ matrix **D** contains regression coefficients of the covariate effect sizes.

We tested the fit of several candidate models that contained either one or up to three shared latent trends and tested the strength of covariate time-series that together best describe the variation in water transparency across all lakes. Data were standardized (Z-score) to account for the differences in the means and variance in scaling. Candidate models and error structures were compared using small-sample Akaike Information Criterion (AICc), based on the maximum likelihood of the model fit and number of parameters in each model (Holmes et al. 2012). We tested three different error structures: (1) each lake has the same variance, (2) each lake has a different variance, or (3) errors of lakes have the same variance and off-diagonal covariance. We present results using equal variance and covariance because AICc suggested little support for other error structures. Post hoc, we used ordinary least squares to examine if variation in lake-specific factor loadings on the shared latent trend (\mathbb{Z}) and covariate effect sizes (\mathbb{D}) could be explained by lake attributes (principal component [PC1] and PC2) or TP concentrations.

To reiterate, the DFA searches for coherent temporal patterns in the multilake dataset and determines whether coherent patterns are explained by temporal variation in hydrology (annual precipitations, lake level, or PDSI). The DFA indicates how each lake's Secchi depth responds to hydrological variation. We then used each lake's physical and chemical attributes to help explain the magnitude and direction of lakespecific responses to variability in hydrology.

Results

Spatial differences in mean summer Secchi depth were correlated to land use, lake morphology, P, and Chl *a*. There were two general gradients describing physical characteristics of lakes: large lakes also have large watersheds (PC1) and shallow lakes tend to have greater percent agriculture in their watersheds (PC2; Fig. 1b). PC2 was also correlated with the gradient in lake area to watershed area (Table 1; Fig. 1b; least squares, $R^2 = 0.53$, p < 0.001, $F_{1, 22} = 24.65$). These lake and watershed attributes largely determine increasing trophic status, with greater TP and lower Secchi depth in shallow, agricultural lakes with smaller lake areas relative to their watershed areas (Fig. 1b). PC2 alone explained 81% of the variation in average summer TP across lakes (PCA regression, $R^2 = 0.81$, TP = 46.0 – 26.68 × PC2, p < 0.001) and 59% of the variation in Secchi depth (Fig. 1b; $R^2 = 0.59$, Secchi depth = $7.38 + 3.02 \times PC2$, p < 0.001). PC1 (watershed size) explained very little of the variation in TP ($R^2 = 0.007$, p = 0.69) or Secchi depth among lakes ($R^2 = 0.014$, p = 0.58). Secchi depth was negatively correlated with average summer TP and average Chl *a* concentrations (Fig. 1c, nonlinear fit, μ g L⁻¹, SD = 40.6 \times TP^{-0.89}, SD = 7.3 \times Chl *a* ^{-0.48}).

DFA indicated that a changing lake level was an important hydrological covariate in the 24 time-series of Secchi depth. The best model provided good fits to the data (Fig. 2) and contained lake level as an explanatory covariate and one shared latent trend (Supporting Information Table S3). This model was substantially better than the next best models containing two (Δ AICc = 5.1), one (Δ AICc = 5.9), or three shared latent trends (Δ AICc = 8.5) but lacked covariates. Latent-trend–only models performed better than candidate models that contained antecedent precipitation (Δ AICc = 22.3), PDSI (Δ AICc = 27.3), or combinations of these with one or two shared latent trends (Supporting Information Table S3). Thus, annual precipitation or PDSI were not informative temporal covariates. Lake level cycled between low and high water periods from 1987 to 2016. Low lake levels occurred from 1989 to 1990, lake level increased by ~ 1.9 m in 2003–2004, fell by 1.3 m in 2013, and increased again in 2014–2016 (Fig. 3a).

Lake-specific water clarity responses to lake level depended on the trophic status of the lake (Fig. 3b). When lake level was higher than average, water clarity increased in most eutrophic lakes (positive effect size). But in the three oligotrophic lakes, water clarity strongly decreased when lake level increased (negative effect size; Fig. 3b). For instance, Stone Lake Secchi depth decreased by 0.63 standard deviations for every



Fig. 2. DFA best predicted fit (line) an \pm 95% credible intervals of annual variation in summer Secchi depth (open data points) in 24 lakes from 1987 to 2016. Data are standardized with 0 as the mean and the scale set to \pm standard deviations. Inverse temporal dynamics are observed between the most turbid and top row (upper left, Mud Lake at 0.5 m mean Secchi depth) compared to the clearest study lakes, bottom row (lower right, Stone Lake at 6.2 m mean Secchi depth).

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Fig. 3. (a) Temporal dynamics in Shell Lake level. (b) Lake-level effect sizes ordered by lake TSI. (c) Association between covariate effect size and lake TP (note log₁₀ scale). (d) The shared latent trend from 1987 to 2016 of the best model. (e) Lake-specific loading scores on the shared latent trend. (f) Shared latent trend 1 loading scores associated with lake total phosphorus concentrations.

standard deviation increase in lake level (Fig. 3b). Clear water lakes such as Silver, Stone, and Beaver Dam synchronously became less transparent during floods and clearer during drought (Fig. 2). Conversely, eutrophic lakes were clearer when lake level was high and turbid when lake level was low. The Secchi depth in highly eutrophic Mud Lake increased by 0.55 standard deviations for every standard deviation increase in lake level. The responses of mesotrophic lakes were varied and lower in magnitude. Shell Lake was the only mesotrophic lake with a positive effect size greater than 0.2 (Fig. 3b). It is also the only mesotrophic lake that is polymictic (Table 1). Nine of 10 polymictic lakes had positive effect sizes (Fig. 3c). Kirby Lake was the only polymictic lake with a negative effect size, but the magnitude was near zero (Fig. 3b).

Nutrient and watershed characteristics covaried with lakespecific responses to changes in hydrology. In shallow, high TP, agricultural lakes with large watershed and surface areas, water clarity increased when lake level increased (positive effect size; Fig. 3c). Conversely, water clarity decreased when lake level increased in small, deep, low TP lakes that drained nonagricultural watersheds (negative effect size; Fig. 3c). Lakespecific effect sizes to a changing lake level (D matrix) were positively correlated with \log_{10} TP ($D = -0.90 + 0.62 \times \log_{10}$ [TP], precipitat $df_{2,22} = 17.12$, $R^2 = 0.44$, p < 0.001; Fig. 3c). A better model included \log_{10} TP and an effect of lake mixing tendency (either polymictic or dimictic) as a binary factor (Fig. 3c; lowest AICc score, Δ AICc = 3). Lake mixing types shared a common regression slope as \log_{10} TP increased, but the intercept of polymictic lakes was less negative than dimictic lakes (analysis of covariance [ANCOVA]: $Z = -0.47 \pm 0.43 \times \log_{10}$ TP polymictic.

covariance [ANCOVA]; $Z = -0.47 + 0.43 \times \log_{10}$ TP polymictic; $Z = -0.72 + 0.43 \times \log_{10}$ TP dimictic lakes; $R^2 = 0.54$, p < 0.001). The difference in intercepts suggests that across all ranges in lake TP concentration, the effect size is 0.25 greater in polymictic lakes compared to dimictic lakes. In other words, the effect that lake level had on Secchi depth is increasingly positive with lake phosphorus concentration, but the effect lake level has on Secchi depth is mostly negative in dimictic lakes and positive in polymictic lakes.

Shared latent trend loading scores (*Z*) were much lower in magnitude than the effect sizes of the lake level covariate (Fig. 3e). The latent trend appears to cycle similar to lake level but shifted to an earlier period. After the 1988 drought, the shared latent trend showed increasing water clarity readings with a growing positive index from 1989 to 1998 and reduced water clarity from 2003 to 2014 (Fig. 3d). Most eutrophic lakes had positive loading scores, and most oligotrophic and mesotrophic lakes had negative loading scores on the shared latent trend. Loading scores (*Z* matrix) were best explained by a positive correlation with \log_{10} TP and lake mixing (polymictic vs. dimictic) as a binary factor (ANCOVA; *Z* = $-0.27 + 0.26 \times \log_{10}$ TP polymictic; *Z* = $-0.43 + 0.26 \times \log_{10}$ TP dimictic lakes; $R^2 = 0.61$, *p* < 0.001; Fig. 3f). Again, the intercept of polymictic lakes was less negative.

Discussion

From a modest sample of 24 neighboring lakes, we found a synchronous decadal signature of hydrologic variability on water clarity. Consistent with conventional theory, oligotrophic lakes became clearer during periods of drought and more turbid during high water. However, we found that most eutrophic and some mesotrophic lakes respond oppositely to variability in hydrology: water transparencies declined during drought conditions. Anthropogenic phosphorus loading and lake attributes mediated the response of water clarity to decadal-scale variation in hydrology. Like other cross-scale interactions (Heffernan et al. 2014), we demonstrated that lake-specific features, such as mixing regime and trophic status, influence how water clarity responds to variation in hydrology.

Among the three regionally linked hydrologic drivers, water level fluctuations best captured the variation in water clarity across our study region. Compared to similar predictors, PDSI and antecedent precipitation, lake level fluctuations are a more direct measure of hydrologic change in lakes. Lake level fluctuations integrate long-term changes in evaporation,

precipitation, and groundwater exchange (Watras et al. 2014). Given the high degree of synchrony between inland lakes in northeast Wisconsin (Watras et al. 2014), we presume that Shell Lake levels reflect water level changes experienced in other study lakes with more extreme fluctuations in seepage lakes (Robertson and Rose 2011). Despite incomplete lake level records from other study lakes, we verified that water levels in the study area fluctuated coherently over this time period (Robertson et al. 2009; Supporting Information Fig. S2). Four lakes ~ 175 km east of the study area with complete lake level records also fluctuated coherently with Shell Lake (Supporting Information Fig. S3; North Temperate Lakes LTER). As such, seepage lake levels play an important role in time-series studies that examine how complex environmental changes influence lakes (White et al. 2008). Similar to other studies that underscore varied trends in water clarity over much broader spatial scales (Lottig et al. 2014; Canfield et al. 2016; Rose et al. 2017), our study showed that local lake characteristics are important for understanding responses to shifts in hydrology across lakes that are no more than 100 km apart. Integration of fine-scaled responses with broad-scale patterns may improve our understanding of diverse environmental change and better inform policy at the scale of regions.

In northern forested regions of Wisconsin, the water clarity of naturally stained oligotrophic lakes decreases during wet years likely due to greater inputs of nonalgal DOC or CDOM (Jane et al. 2017; Rose et al. 2017). Dissolved absorbance and total suspended solids data are not available for our study lakes, so we cannot directly determine nonalgal contribution to light attenuation (K_d , m⁻¹). We can get a rough sense of the relative contribution of K_{d-DOC} vs. $K_{d-algae}$ from 0.07 × Chl a concentration (mg m³; Morris et al. 1995) and K_{d-PAR} from $1.7 \times$ inverse Secchi depth (Poole and Atkins 1929). Under this calculation (Supporting Information Table S4), algal biomass might account for 41–49% of K_{d-PAR} in the two clearest oligotrophic lakes with the remainder of light attenuation coming from water and nonalgal CDOM or DOC (Supporting Information Table S4). Other formulations to determine nonalgal contribution to light attenuation would indicate that DOC is even more important (Morel and Prieur 1977; Gallegos et al. 1990). We suspect that humic sources leaching from surrounding bogs and forests likely reduces water clarity during wetter years (e.g., Stone Lake, a bog, and forested seepage lake with very low Chl *a* concentrations).

Nutrients and algae can still drive water clarity reductions in clear oligotrophic lakes. When water levels increased by 1–3 m in Silver Lake, tributary inputs and nearshore erosion tripled the dissolved P concentration, increased epilimnion Chl *a* concentrations by 6X, and decreased Secchi depth by 2.5X (Supporting Information Fig. S1; Robertson et al. 2009). Although Robertson et al. (2009) did not evaluate the effect of CDOM on water clarity, our calculations indicate that algae contributed to 99% of light attenuation in this oligotrophic lake (Supporting Information Table S4). Annual color data in Silver Lake were available for much of the record except during peak water level years. Variation in color (5 to 25 SU on the Platinum-Cobalt Scale) was large enough to influence water clarity, but the peak in water color occurred prior to the peak in water level (Supporting Information Fig. S4) despite the fact that Silver Lake water levels fluctuated in synchrony with Shell Lake (Supporting Information Fig. S2; Robertson et al. 2009).

In contrast to oligotrophic lakes, eutrophic lakes were clearer during high water periods and more turbid during drought. Lack of detailed data from all lakes prohibits strong inferences about mechanisms driving positive responses to hydrology. A complete data set that includes time-series of lake levels, Secchi depth, temperature and dissolved oxygen profiles, TP, chlorophyll, and some measure of CDOM would provide the necessary evidence to support our hypotheses, which are outlined as a conceptual model in Fig. 4.



Fig. 4. Conceptual model showing the hypothesized mechanisms responsible for the contrasting effects of hydrologic variation on water clarity in eutrophic, polymictic vs. oligotrophic, and dimictic lakes. Wider arrows correspond to strong positive (solid arrow) or negative (dashed arrow) effects and thin arrows indicate weak effects. In oligotrophic lakes, high lake levels are associated with more runoff, which increases DOC and nutrient loading to lakes. DOC directly reduces water clarity and nutrients reduce clarity by fueling algal growth. Increased DOC could shade and reduce the abundance of phytoplankton, but this indirect effect on water clarity is likely less impactful. Reduced runoff in low water years would lead to greater water clarity through the same pathways. In eutrophic lakes, water clarity declines when lake levels are low. Smaller lake volumes combined with increased water residence times concentrate nutrients and algae and favor cyanobacterial blooms, which have a more negative effect on water clarity due to their propensity to form surface scums. Low lake levels may also induce more frequent mixing events, increasing internal nutrient loads and in turn, algal blooms. DOC might decrease during low water years due to photobleaching and improve water clarity, but the magnitude of this effect is likely minimal compared to that of algae. The reverse processes increase water clarity during high water years: Flushing reduces the concentration of nutrients and prevents formation of cyanobacterial blooms.

Nonetheless, we suspect a couple of different mechanisms are likely. First, P dilution in wet years vs. P concentration in dry years could drive water clarity changes in eutrophic lakes (Fig. 4). In wet years, shallow drainage lakes with large riverine watersheds, such as Tainter Lake, may see clearer water due to a decrease in water residence time that flushes or dilutes P concentration (Mosley 2015). We estimated that Tainter Lake's water residence could change by a factor of 3 from 16 d during drought to 5 d during flood years (Supporting Information -Table S5). In our study, most eutrophic drainage lakes with positive effect sizes of lake level also had small lake areas relative to their watersheds and relatively short (11-160 d) water residence times (Supporting Information Table S4). Drought-induced decreases in surface flows would increase water residence time in these lakes (e.g., Supporting Information Table S5). Elsewhere, prolonged water residence times often lead to large cyanobacterial blooms (Bakker and Hilt 2016). In a Texas reservoir, this was especially true when water residence times exceeded 2 weeks and water temperatures increased (Bellinger et al. 2018). Because cyanobacteria can float to the surface and form scums (Paerl and Huisman 2008), a shift in the phytoplankton community toward buoyant cyanobacteria can reduce water clarity even more dramatically (Fig. 4).

The second probable mechanism for reduced clarity in eutrophic lakes is that internal P recycling, which promotes algal growth, is heightened in drought years. This is particularly likely in polymictic lakes that experience even more wind-driven remixing events when lake levels are low (Søndergaard et al. 2003; Mosley 2015). Nearly all eutrophic lakes in the study have anoxic hypolimnions when stratified $(< 0.5 \text{ mg O}_2 \text{ L}^{-1})$ and buildup of P in the hypolimnion through ferrous cycling (Campbell and Torgersen 1980). In Shell Lake and another shallow lake in northwest Wisconsin, stratification stabilized when water levels were high, reducing internal loading and increasing water clarity (Juckem and Robertson 2013; Robertson et al. 2018). Perhaps high-water years represent a combination of P dilution and ferrous scavenging of P, while lower water years see concentrated P, warmer overall temperatures, greater internal P loading, and more surface algae (Fig. 4).

These contrasting results suggest that P pollution has not only changed mean clarity among lakes to a eutrophic state in this region (Fig. 1b,c) but also the natural relationship of water clarity to climate-driven variation in hydrology (Fig. 3b,c). A legacy of excess agricultural P has impaired lake water clarity for many lakes in the Midwest and most are unlikely to recover for centuries without sustainable management of P on landscapes (Carpenter 2005). The regional hydrological signature appears to be muted (also see Rose et al. 2017) or even opposite in lakes with greater P pollution relative to pristine lakes with lower P concentrations.

Secchi depths fluctuated 1 to 2.5 m in this study's mesotrophic and oligotrophic lakes (Supporting Information Table S1), a noticeable difference for lake residents and ecosystems alike. Because water clarity influences so many aspects of lake ecosystems, fluctuating lake levels could have far-reaching effects. In nutrient-poor lakes, light limits primary production and higher order production of benthic invertebrates and fish (Karlsson et al. 2009). In moderately deep and clear lakes, water clarity fluctuations can amplify whole-lake warming when a lake becomes clearer or buffer warming when water clarity declines (Rose et al. 2016). The maximum depth of colonization and species composition of aquatic plants also depends on light availability (Mikulyuk et al. 2011). Optimum light conditions for walleye (Sander vitreus) are near Secchi depth of 2 m (Lester et al. 2004). Thus, changing water clarity could influence the productivity of this important recreational and commercial fishery. The recreational and economic value of lakes is also affected, with visitors willing to travel 56 min farther for a 1 m gain in clarity (Keeler et al. 2015).

Future climate change may further challenge water quality improvements, waterfront property values, ecosystem health, and recreational use of these lakes (Carpenter et al. 2015). Changes in lake water levels show that climate drives a neardecadal oscillation in lake and aquifer levels across the upper Great Lakes (White et al. 2008; Watras et al. 2014). We infer from the results that continued periodic increases in extreme precipitation will reduce water clarity of oligotrophic lakes and increase water clarity of shallow, eutrophic lakes. Simply assuming that wet years reduce water clarity is erroneous for some lakes, particularly eutrophic, polymictic lakes. Together, phosphorus, land use, and mixing tendency might provide the key for evaluating how lake clarity will respond to changes in hydrology.

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Conflict of Interest

None declared

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