



## Climate and food web effects on the spring clear-water phase in two north-temperate eutrophic lakes

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### Abstract

Although climate change has shifted the phenological timing of plankton in lakes, few studies have explicitly addressed the relative contributions of climate change and other factors, including planktivory and nutrient availability. The spring clear-water phase is a period of marked reduction in algal biomass and increased water transparency observed in many lakes. Here, we quantified the phenological patterns in the start date, maximum date, duration, and magnitude of the clear-water phase over 38 yr in Lakes Mendota and Monona, and examined the effects of water temperature, total phosphorus, and food web structure (proportion of large-bodied *Daphnia pulicaria* and density of invasive *Bythotrephes*) and interactions between temperature and other predictors on these clear-water phase metrics. We found that climate and food web structure affected the clear-water phase, but the effects differed among the metrics. Higher water temperature led to earlier clear-water phase start dates and maximum dates in both lakes. The proportion of *D. pulicaria* affected all clear-water phase metrics in both lakes. When *D. pulicaria* proportion was higher, the clear-water phase occurred earlier, lasted longer, and the water was clearer. Moreover, high *Bythotrephes* density delayed clear-water phase start dates (both lakes), and decreased clear-water phase duration (Lake Mendota) in the following year. These results suggest that variation in food web structure changes the full phenological dynamics of the clear-water phase, while variation in climate condition affects clear-water phase timing only. Our findings highlight the importance of large-bodied grazers for managing water quality under climate change.

Evidence from long-term studies has shown that climate change is causing phenological shifts in freshwater and marine phytoplankton and zooplankton (Edwards and Richardson 2004; Thackeray et al. 2016; Winder et al. 2012). In many studies, events such as blooms have shifted earlier, but it has also been reported that phenology can respond to interannual variability in water temperature (Thackeray et al. 2008). These phenological changes and the associated trophic mismatch can influence the growth and reproduction of phytoplankton and zooplankton and ultimately alter community composition and ecosystem function (Winder and Schindler 2004a; Domis et al. 2013). However, phytoplankton and zooplankton communities are strongly affected by other pressures, including predation and nutrient availability (Carpenter et al. 2001; Hampton et al. 2006). Therefore, it is important to more fully understand how climate and other

factors drive phenological changes in plankton communities (Winder and Schindler 2004b; Thackeray et al. 2008; Boyce et al. 2017). Such understanding can inform how to better manage water quality in a changing climate (Thackeray et al. 2016).

Phenology is more than a date—rather it is a sequential and dynamic process that includes duration and magnitude (Thackeray et al. 2012, 2013). While peak timing is commonly used to measure long-term change in phenology, the patterns and drivers of phenological events may differ depending on what aspect of a dynamic phenological process is considered (Boyce et al. 2017). Boyce et al. (2017) showed that in marine phytoplankton, the timing of the seasonal chlorophyll maximum was inversely related to nitrate concentration, while the amplitude of phytoplankton biomass (maximum chlorophyll values – minimum chlorophyll values) was inversely related to surface water temperature. Similarly, Winder et al. (2012) reported that the peak timing of freshwater phytoplankton was influenced by water temperature, while the magnitude of the peaks was not affected by water temperature but instead was influenced by light intensity. Use of multiple metrics to

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

measure phenology may be effective for exploring changes in phenological events and seasonal succession in responses to climate change and other drivers.

In lakes, a spring clear-water phase is one of the most distinctive and visible events of the seasonal plankton succession (Lampert et al. 1986; Lampert and Sommer 2007). The clear-water phase is a period of marked reduction in algal biomass in late spring–early summer (in north temperate latitudes usually during May and June) caused by the grazing activity of large herbivores such as *Daphnia*, and mostly occurs in meso- and eutrophic lakes (Lampert et al. 1986; Sommer et al. 1986; Carpenter et al. 1993). Because the clear-water phase coincides with the substantial increase in water clarity, the phenology of the clear-water phase is an informative indicator of ecosystem status (Lathrop et al. 1996; Scheffer et al. 2001). The timing of the clear-water phase (the date of maximum Secchi depth) tends to be earlier as water temperature increases (Straile 2002; Winder and Schindler 2004b; Droscher et al. 2009). However, other studies have documented the importance of food web structure (i.e., trophic cascade) in shaping the magnitude and timing of this event (Luecke et al. 1990; Kitchell 1992; Rudstam et al. 1993; Lathrop and Carpenter 2014). For example, Rudstam et al. (1993) found that the clear-water phase started later and was shorter under high planktivory conditions. While these previous studies examined the impacts of either climate or food web structure on the clear-water phase, several theoretical studies suggest that both factors can influence the clear-water phase; the clear-water phase is expected to occur earlier with both increasing water temperature and decreasing zooplanktivorous fish density (Scheffer et al. 2001; Schallau et al. 2008).

Predatory invertebrates can also contribute significantly to total planktivory, in turn affecting the clear-water phase through trophic cascades (Lunte and Luecke 1990). The predatory zooplankton, spiny water flea, *Bythotrephes cederströmii* has invaded many lakes in North America (Yan and Pawson 1997). In Lake Mendota, *Bythotrephes*, first detected in 2009, ultimately caused a 60% reduction in *Daphnia* biomass and a nearly 1-m reduction in water clarity (Walsh et al. 2016). Because planktivory by *Bythotrephes* was high in fall while planktivory by fishes (e.g., perch) peaked in summer, *Bythotrephes* and fishes likely had different impacts on *Daphnia* populations and the clear-water phase (Walsh et al. 2017). Walsh et al. (2017) also suggested that the duration of the clear-water phase in Lake Mendota decreased after the 2009 *Bythotrephes* invasion and was especially short in 2014 and 2015. However, the relative importance of *Bythotrephes* vs. other factors, such as climate and nutrient availability, in influencing the clear-water phase was unknown.

We hypothesized that not only climate variability but also food web structure and nutrient availability would influence the spring clear-water phase in eutrophic lakes, and that these different drivers would affect the timing, duration, and magnitude of the clear-water phase. To test these hypotheses, we

analyzed the long-term limnological records of two north-temperate eutrophic lakes; Lakes Mendota and Monona, Wisconsin, and quantified long-term phenological patterns of the spring clear-water phase. The lakes are adjacent to each other, separated by a narrow isthmus, but differ in physical characteristics (e.g., area, mean depth, water residence time, ice breakup date) and biotic characteristics (e.g., fish fauna, *Bythotrephes* density) (Magnuson et al. 2006; Walsh et al. 2018). Using a 38-yr time series (1980–2017) of Secchi depth readings measured biweekly, we quantified the start date, maximum date (date of greatest water clarity), duration, and magnitude of the clear-water phase in each year (Supporting Information Fig. S1). We found no significant linear trends in almost all clear-water phase metrics in the two lakes. Yet climate variability (spring water temperature), nutrients (total phosphorus), food web structure (proportion of large-bodied *Daphnia pulicaria* and density of invasive *Bythotrephes*), and climate-related interactions (i.e., water temperature and other drivers) explained inter-annual variation in the four clear-water phase metrics.

## Materials and methods

### Study lakes

The Yahara chain of lakes—Mendota, Monona, Waubesa, and Kegonsa—is located near Madison in south central Wisconsin, USA. Detailed description of these sites are provided by Lathrop (2007) and Lathrop and Carpenter (2014). Lake Mendota is the largest (39.6 km<sup>2</sup>), deepest (25.3 m max depth, 12.6 m mean depth), and most upstream lake. The watershed is predominantly agricultural with some urban areas. Lake Monona (immediately downstream of Mendota) is smaller (13.2 km<sup>2</sup>) and shallower (22.6 m max depth, 8.3 m mean depth) than Mendota. While the majority of Monona's direct drainage basin is urban, it receives a large portion of its hydrologic and phosphorus inputs from Lake Mendota via the Yahara River (Lathrop and Carpenter 2014). The average water residence times of Mendota and Monona are 4.34 and 0.77 yr, respectively.

In Lake Mendota, stocking of piscivorous fishes (walleye and northern pike) was conducted during 1987–1992 (with continued but less intense stocking in subsequent years) to improve water quality and fishing (Kitchell 1992; Lathrop et al. 2002). The biomanipulation, coupled with a massive die-off of zooplanktivorous cisco in summer 1987, allowed large-bodied *D. pulicaria* to dominate in most years after 1988 with concomitantly greater water clarity (Lathrop et al. 2002). For a decade prior to 1988, water clarity was not as great, and the dominant grazer was the small-bodied *Daphnia galeata mendotae*. In the summer of 2009, the invasive predatory zooplankton, spiny water flea (*B. cederströmii*) was detected in Lake Mendota and Lake Monona. In subsequent years, *D. pulicaria* biomass was notably lower, resulting in

reduced water clarity especially in Lake Mendota (Walsh et al. 2017, 2018).

### Long-term monitoring

Secchi depth, water temperature, nutrient (total phosphorus), and zooplankton (*D. galeata mendotae*, *D. pulicaria*, and *Bythotrephes*) data for Lake Mendota and Lake Monona between 1980 and 2017 were obtained from the North Temperate Lakes Long Term Ecological Research (NTL-LTER; <https://lter.limnology.wisc.edu>) program database (Lathrop 2000; North Temperate Lakes 2019a,b,c; Walsh and Vander Zanden 2019). The monitoring of Lake Mendota and Lake Monona was conducted by the University of Wisconsin-Madison Center for Limnology and the Wisconsin Department of Natural Resources. Both lakes were sampled at the deepest location on a biweekly schedule beginning after ice-out from spring through summer and sometimes monthly in fall, and at least once during winter when the lakes were ice-covered (Lathrop et al. 1996, 2002; Walsh et al. 2017, 2018). Although Secchi depth in some years was recorded more frequently than biweekly in Mendota, in this study we used biweekly Secchi depth data that corresponded to the sampling dates of zooplankton and nutrient monitoring data to match temporal resolution.

### Clear-water phase metrics

Using Secchi depth data (Supporting Information Figs. S2, S3), we quantified the start date, maximum date, duration, and magnitude of the clear-water phase (Supporting Information Fig. S1). In this study, we defined the clear-water phase as the time period for which Secchi depth exceeded 3.5 m, a period following spring phytoplankton blooms and generally during April–June (and occasionally extending into July in a few years). While the threshold of Secchi depth for the definition of the clear-water phase has ranged from 2.5 to 7.0 m (Straile 2000; Winder and Schindler 2004b; Wagner and Benndorf 2007), previous studies on Lake Mendota used 3.0 m and 4.0 m as the threshold (Luecke et al. 1990; Rudstam et al. 1993; Lathrop et al. 1999; Walsh et al. 2017, 2018).

For each year in each lake, the start date of the clear-water phase was defined as the day of year when Secchi depth increased to the 3.5 m threshold after the spring phytoplankton bloom. We estimated the start date of the clear-water phase by linear interpolation between the preceding Secchi reading and the first reading after the threshold was exceeded. Similarly, we estimated the end date of the clear-water phase by linear interpolation between successive Secchi readings when the second reading dropped below the clear-water phase threshold. Phase duration was determined as the number of days between the start date and end date. In a few years, Secchi depth decreased slightly below the threshold but immediately increased again. In that case, we calculated the total number of days above the threshold during spring and early summer. The date of maximum clear-water phase was

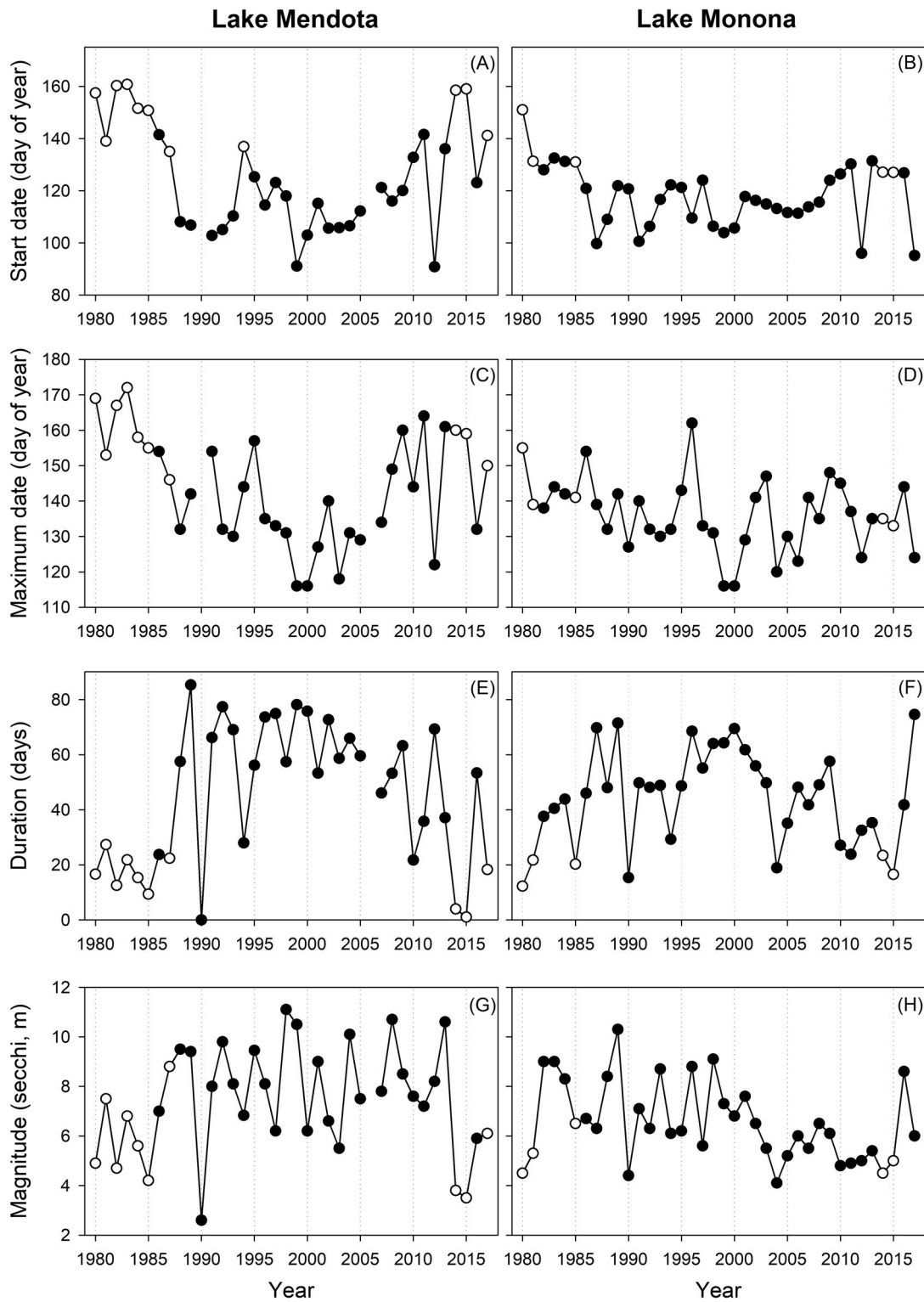
identified as the Julian day of the greatest Secchi depth, and the magnitude of the clear-water phase was defined as that maximum observed Secchi depth.

Both lakes exhibited a distinct clear-water phase in all years except 1990 when spring and summer Secchi depths did not reach 3.5 m (Fig. 1, Supporting Information Fig. S2A); the clear-water phase duration was zero and the magnitude was 2.6 m that year, but the values were added to our dataset. In 2006, clear-water phase characteristics were not included in our analyses due to the lack of zooplankton data (Supporting Information Fig. S2B).

### Potential drivers of the clear-water phase

We investigated the influences of climate conditions, nutrient availability, and food web structure on clear-water phase processes. For climate conditions, we used the 0–5 m volume-weighted mean water temperatures on May 1st calculated by interpolating between successive sampling date recorded temperatures (Lathrop et al. 2019). We chose May 1st water temperature as an indicator of climate variability because that temperature metric represented how rapidly the lakes warmed during April, slightly more than a month following the 1980–2017 average ice-out date of 27 March and 23 March for Lakes Mendota and Monona, respectively. May 1st has also been shown to be representative of the clear-water phase timing in north temperate latitudes (Lampert and Sommer 2007). For our study, May 1st (Day 121) was also close to the 1980–2017 averages of the clear-water phase start date for Lakes Mendota and Monona (Day 125.7 and Day 118.2, respectively, see also Fig. 1). For the nutrient indicator, we used May–June mean total phosphorus (TP) concentration in surface waters. For these predictor variables that involved choosing a date or time period, we also considered whether choosing alternative dates (for water temperature, TP, and *D. pulicaria* proportion) influenced the overall findings, because the specific choice of periods can influence the prediction of phenological metrics (Straile et al. 2012). We found that using alternative dates or months did not alter any of the major conclusions of this study (Supplemental Information Appendix S1).

As indicators of food web structure, we used *D. pulicaria* proportion and the density of the invasive predatory zooplankter *Bythotrephes*. In Lakes Mendota and Monona, *D. pulicaria* and *D. galeata mendotae* are the two major *Daphnia* species. While *D. pulicaria* has a larger body mass and greater algal grazing potential than *D. galeata mendotae*, *D. pulicaria* is more vulnerable to size-selective predation by fish and invertebrate predators (Threlkeld 1979; Luecke et al. 1990; Kasprzak et al. 1999). Therefore, *D. pulicaria* proportion, defined as the *D. pulicaria* biomass divided by the total biomass of *D. pulicaria* and *D. galeata mendotae*, is a good indicator of the trophic cascade effects from planktivory (Kitchell 1992; Rudstam et al. 1993; Johnson and Kitchell 1996; Lathrop et al. 1996). We obtained areal *Daphnia* density (individuals/m<sup>2</sup>) and average length from the NTL-LTER database. We



**Fig. 1.** Temporal changes in the clear-water processes between 1980 and 2017 in Lake Mendota (A, C, E, G) and Lake Monona (B, D, F, H). Black circles are  $\geq 50\%$  *D. pulicaria* proportion, while white circles are  $< 50\%$  *D. pulicaria* proportion. There was no clear-water phase in Lake Mendota in 1990, thus no start and maximum dates were identified. The clear-water phase of 2006 in Lake Mendota was not evaluated due to the lack of zooplankton data.

computed the biomasses ( $\text{g}/\text{m}^2$ ) of *D. pulicaria* and *D. galeata mendotae* using the length-dry mass equations from the literature (Lynch et al. 1986) and calculated the mean *D. pulicaria* proportion, as the biomass of *D. pulicaria* to the total biomasses of *D. pulicaria* and *D. galeata mendotae*, during May–June.

The introduction of *Bythotrephes* could also affect the clear-water phase processes because *Bythotrephes* can influence *Daphnia* species directly and indirectly. The *Bythotrephes* population has been monitored at the deepest point of each lake using two methods: (1) surveys conducted from 2009 to 2016 in Lakes Mendota and Monona using a 30-cm zooplankton net (80  $\mu\text{m}$  mesh) designed for monitoring the whole zooplankton community and (2) surveys conducted from 2009–2014 and 2016–2018 in Lake Mendota and 2011–2014 and 2016–2018 in Lake Monona using a 50-cm zooplankton net (150  $\mu\text{m}$  mesh) designed to target large zooplankton like spiny water flea that tend to avoid smaller nets. We used the 50-cm net data to quantify *Bythotrephes* density but filled in gap years (2015 in both lakes and 2009–2010 in Lake Monona) by deriving a relationship from densities estimated in side-by-side tows of the 30- and 50-cm nets from 2016 to 2018. Since the *Bythotrephes* populations of each lake are below detection until mid-summer, we needed to account for this seasonality and variable sampling times among years to estimate *Bythotrephes* density in each lake. We used a hierarchical generalized additive model framework where *Bythotrephes* count was dependent on lake-specific seasonal ( $\sim s[\text{day of the year}]$ ) and long-term ( $\sim s[\text{year}]$ ) factor-smoothed trends that were penalized against general seasonal and long-term smoothed trends that were shared between the neighboring, connected lakes (Pedersen et al. 2019). The model was fit with Poisson-distributed error and natural log-transformed tow volume ( $\ln[\pi \times \text{net radius}^2 \times \text{tow depth}]$ ) as an offset (package “mgcv” in Wood 2015). We used the model to estimate average annual *Bythotrephes* density. Considering that *Bythotrephes* reaches maximum abundances in autumn in the study lakes and persists at high densities until the lake freezes (Walsh et al. 2017), one could imagine that the *Bythotrephes* density of the previous year (*Bythotrephes* density<sub>*t*-1</sub>) affects the spring *Daphnia* populations and clear-water phase metrics of that year by influencing *Daphnia* overwintering success. Therefore, we used *Bythotrephes* density<sub>*t*-1</sub> in the subsequent statistical analyses.

### Statistical analyses

First, we tested for temporal linear trends in the four clear-water phase metrics and the potential drivers (May 1st water temperature, TP, *D. pulicaria* proportion, and *Bythotrephes* density<sub>*t*-1</sub>) between 1980 and 2017 using a generalized least squares (GLS) model. To determine whether the residuals of each model were temporally autocorrelated, we calculated autocorrelation functions (ACF) and partial autocorrelation functions (PACF). The ACF and PACF suggested that some clear-water phase processes have a lag of 1 yr with PACF cutoff

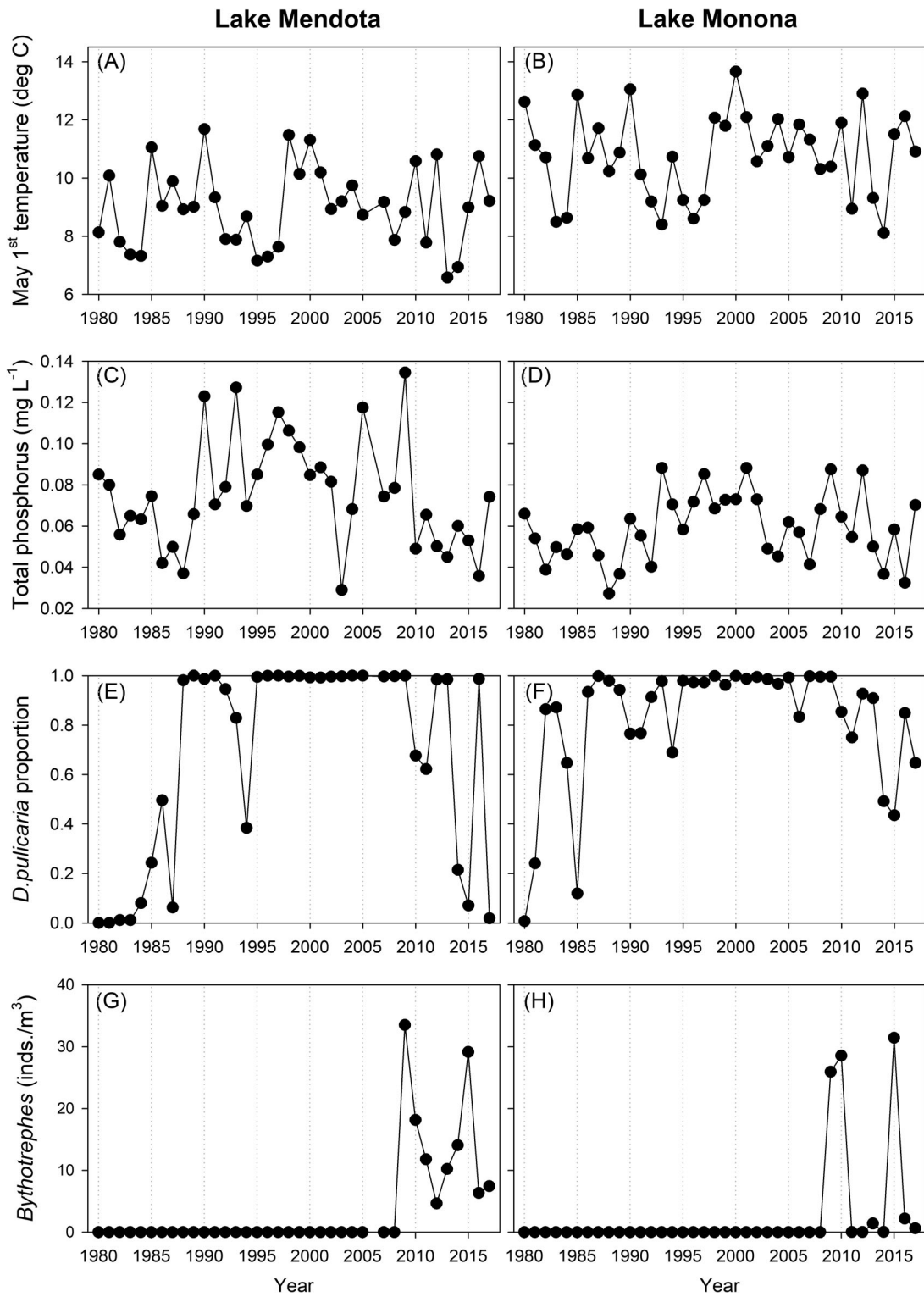
after lag 1 (Supporting Information Figs. S5, S6), allowing the process to be represented by an autoregressive model with lag 1 yr (AR1). For the clear-water phase processes with no evidence of temporal autocorrelation, we did not include any autoregressive component in the model. GLS models were analyzed in R using the *nlme* package (Pinheiro et al. 2014). The model parameters were estimated by a maximum likelihood method. We also investigated the temporal coherence of the clear-water phase metrics between Lakes Mendota and Monona using Spearman rank correlation.

Second, we explored how four drivers (May 1st water temperature, TP, *D. pulicaria* proportion, and *Bythotrephes* density<sub>*t*-1</sub>) and the interactions between May 1st water temperature and other drivers influenced the four clear-water phase metrics in each lake using GLS models. Prior to building models, we standardized all explanatory variables to have a mean of zero and variance of one. In a similar manner to the trend analysis, we assessed whether temporal autocorrelation was present in the residuals of the full model. The ACF and PACF revealed no evidence of temporal autocorrelation in all the clear-water phase process of the two lakes (Supporting Information Figs. S7, S8). Therefore, the GLS model without an autoregressive component was appropriate for our factor analyses. We also assessed multicollinearity among predictor variables by calculating variance inflation factors (VIFs) using the *olsrr* package (Hebbali 2017). The VIFs for all predictors ranged from 1.03 to 1.50 and did not indicate multicollinearity among variables. We used an information-theoretic approach for model selection and inference (Burnham and Anderson 2003). Using the *MuMIn* package (Barton 2013), we generated a candidate set of models with all possible parameter subsets and ranked the models based on the Akaike Information Criterion corrected for small sample size (AICc). For each model, we also calculated  $\Delta\text{AICc}$ , the difference in AICc between each model and the best model with the lowest AICc, and the Akaike weight ( $W_i$ ), which is the probability that model *i* would be selected as the best-fitting model if the data were collected again under identical circumstances. Models with  $\Delta\text{AICc} < 2$  were considered to have substantial support as candidate models (Burnham and Anderson 2003). We present both unstandardized and standardized coefficients. Unstandardized coefficients represent the slope of the relationship, whereas standardized coefficients allow comparison among different variables. All statistical analyses were conducted in R.3.5.3.

## Results

### Long-term trends in clear-water phase metrics

The four clear-water phase metrics and their potential drivers showed substantial year-to-year variation in the two study lakes (Figs. 1, 2 Table 1). Compared to Lake Monona, Lake Mendota had a later clear water phase start date, a later maximum date, a higher clear water phase magnitude, and a similar clear water phase duration. The averages of the start



**Fig. 2.** Temporal changes in water temperature (A, B), total phosphorus (C, D), *D. pulicaria* biomass proportion (E, F), and estimates of average annual *Bythotrephes* density (G, H) between 1980 and 2017 in Lake Mendota (left panels) and Lake Monona (right panels).

**Table 1.** Temporal linear trends in the four drivers used in our study and the clear-water phase metrics of Lakes Mendota and Monona (1980–2017). Significant linear trends ( $p < 0.05$ ) are in bold.

Lake	Variables	Estimate	SE	P
Drivers				
Mendota	Water temperature on May 1st	0.0053	0.0208	0.802
	Total phosphorus	-0.0002	0.0004	0.586
	<i>Daphnia pulicaria</i> proportion	0.0098	0.0109	0.376
	<i>Bythotrephes</i> density	<b>0.41</b>	<b>0.13</b>	<b>0.003</b>
Monona	Water temperature on May 1st	0.0065	0.0219	0.767
	Total phosphorus	0.0002	0.0002	0.344
	<i>Daphnia pulicaria</i> proportion	0.0073	0.0062	0.247
	<i>Bythotrephes</i> density	<b>0.26</b>	<b>0.11</b>	<b>0.023</b>
Clear-water phase metrics				
Mendota	Start date	-0.37	0.55	0.509
	Maximum date	-0.33	0.35	0.357
	Duration	0.26	0.54	0.631
	Magnitude	0.01	0.03	0.652
Monona	Start date	-0.26	0.17	0.145
	Maximum date	-0.27	0.15	0.079
	Duration	0.18	0.38	0.635
	Magnitude	<b>-0.05</b>	<b>0.02</b>	<b>0.019</b>

date, maximum date, duration, and magnitude of the clear-water phase of Lake Mendota and Monona between 1980 and 2017 were  $125.7 (\pm 3.4 \text{ SE})$  and  $118.2 (\pm 1.9 \text{ SE})$ ,  $144.5 (\pm 2.7 \text{ SE})$  and  $136.3 (\pm 1.7 \text{ SE})$ ,  $44.9 (\pm 4.2 \text{ SE})$  days and  $43.8 (\pm 2.8 \text{ SE})$  days, and  $7.4 (\pm 0.4 \text{ SE})$  m and  $6.5 (\pm 0.3 \text{ SE})$  m, respectively (Fig. 1). For predictors, the averages of May 1st water temperature, TP, *D. pulicaria* proportion, and *Bythotrephes* density of Lake Mendota and Monona during the study period were  $9.0 (\pm 0.2 \text{ SE})$  °C and  $10.8 (\pm 0.2 \text{ SE})$ °C,  $0.075 (\pm 0.004 \text{ SE})$  mg L<sup>-1</sup> and  $0.059 (\pm 0.003 \text{ SE})$  mg L<sup>-1</sup>,  $0.69 (\pm 0.07 \text{ SE})$  and  $0.82 (\pm 0.04 \text{ SE})$ ,  $3.7 (\pm 1.3 \text{ SE})$  inds. m<sup>-3</sup>, and  $2.4 (\pm 1.3 \text{ SE})$  inds. m<sup>-3</sup>, respectively.

There were no linear trends for any of the clear-water phase metrics in Lake Mendota (Table 1). In Lake Monona, the clear-water phase magnitude decreased significantly over time, and the clear-water phase maximum date showed a marginally significant trend of occurring earlier over time. For predictors, there were no temporal trends in May 1st water temperature, TP, and *D. pulicaria* proportion, but there were significant increases in *Bythotrephes* density in both lakes (Table 1).

The clear-water phase start date had the highest level of temporal coherence between Lakes Mendota and Monona (Spearman  $r = 0.74$ ). The clear-water phase maximum date and duration had moderate coherence ( $r = 0.51$  and  $0.58$ , respectively), while the coherence of the clear-water phase magnitude was low ( $r = 0.24$ ). For the drivers of the clear-water phase metrics, the temporal coherence of May 1st water temperature between Lakes Mendota and Monona was highest ( $r = 0.86$ ), while *D. pulicaria* proportion and TP were moderately coherent ( $r = 0.61$  and  $0.63$ ).

## Factors affecting the clear-water phase metrics

### Lake Mendota

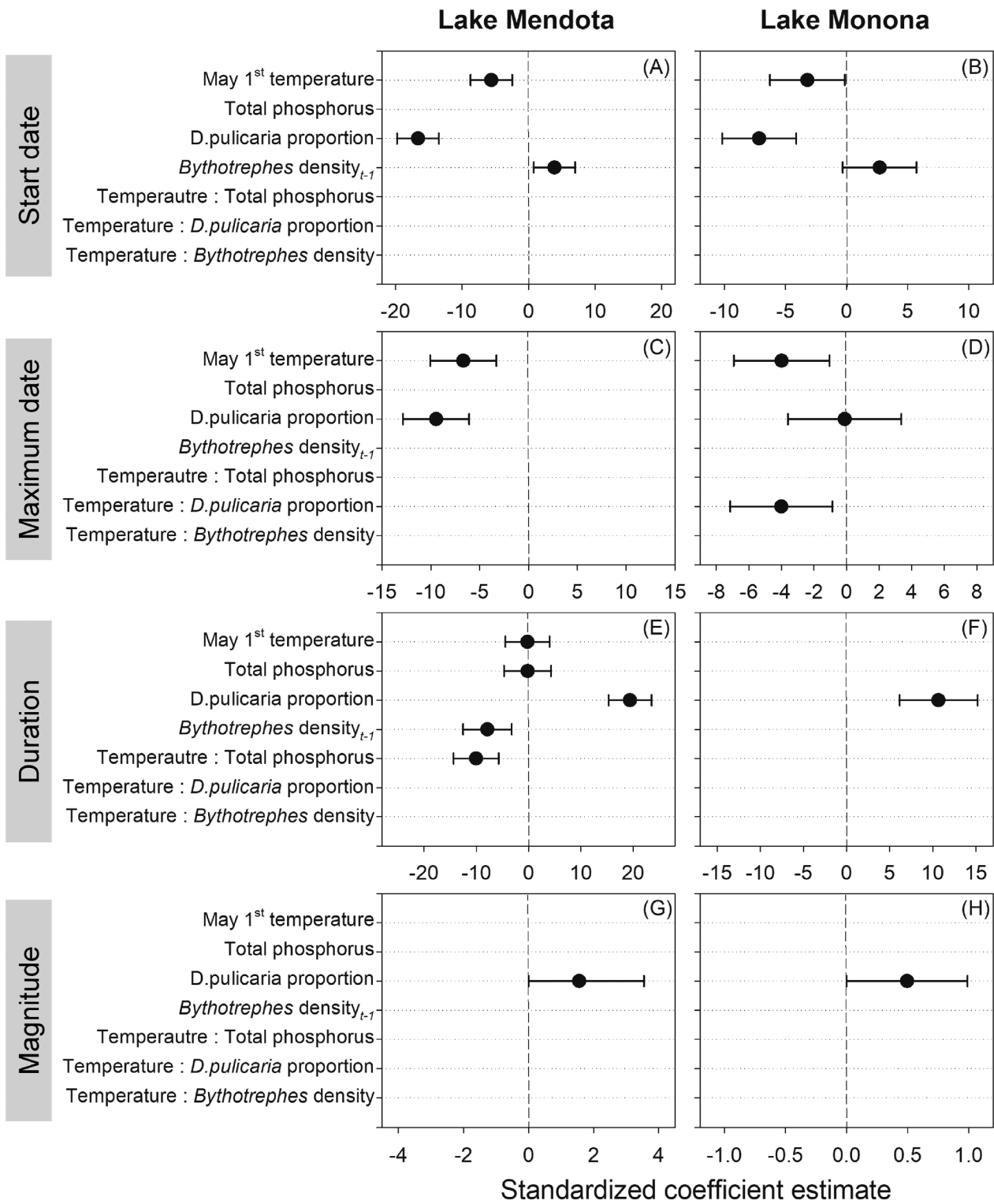
For the clear-water phase start date, May 1st water temperature, *D. pulicaria* proportion, and *Bythotrephes* density<sub>*t*-1</sub> were included in the best model (Table 2, Fig. 3). The start date was significantly earlier with higher May 1st water temperature and higher *D. pulicaria* proportion but was delayed with higher *Bythotrephes* density<sub>*t*-1</sub> (Fig. 4). The best model estimated that the clear-water phase start date was  $4.2 \pm 1.2$  d earlier per 1°C warmer May 1st water temperature. The clear-water phase always started earlier in *D. pulicaria* dominant years (defined as  $\geq 50\%$  *D. pulicaria* proportion) than *D. galeata mendotae* dominant years ( $< 50\%$  *D. pulicaria* proportion) across the range of May 1st water temperatures (Fig. 5B). The three variables selected in the best model also appeared in the second best model and the estimated coefficients were significant. The second best model also included a significant interaction term between TP and May 1st water temperature. When May 1st water temperature was lower, the clear-water phase start date was earlier in higher TP conditions (Fig. 5A).

For the clear-water phase maximum date, the best model included May 1st water temperature and *D. pulicaria* proportion (Table 2, Fig. 3). May 1st water temperature and *D. pulicaria* proportion led to significantly earlier clear-water phase maximum dates (Fig. 4). The best model estimated that the clear-water phase maximum date was  $5.0 \pm 1.3$  d earlier per 1°C warmer May 1st water temperature. Like the clear-water phase start date, the clear-water phase maximum date was always earlier in *D. pulicaria* dominant years than

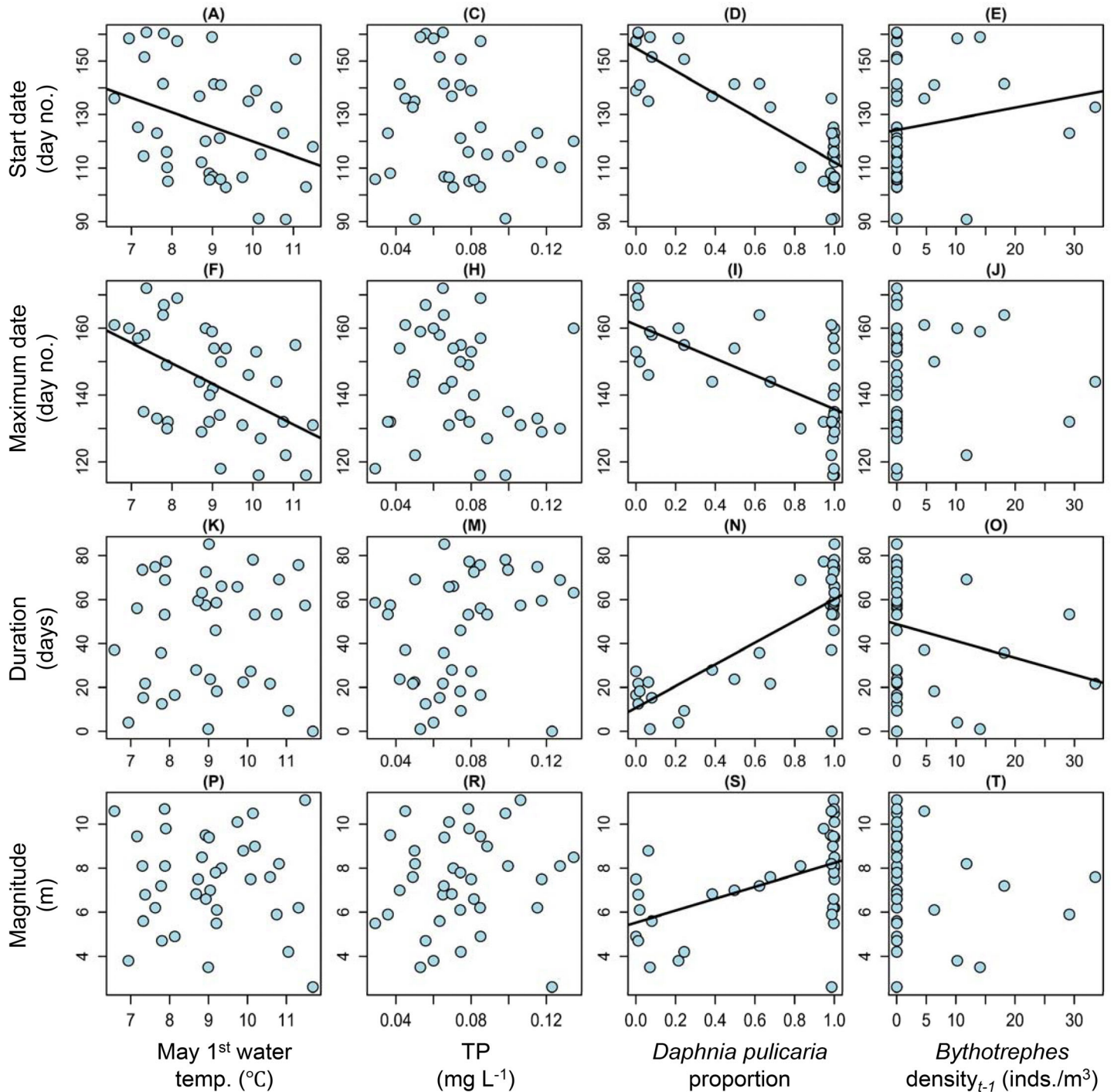
**Table 2.** Top-ranked models predicting the start date, maximum date, and magnitude of the clear-water phase in Lakes Mendota and Monona (1980–2017). Values for each explanatory variable represent the standardized estimated coefficients ( $\pm$  SE) and thus differ from non-standardized results reported in the text (empty cells indicate variables not included in a particular model). Significant effects ( $p < 0.05$ ) are shown in bold. \*Marginally significant ( $0.05 < p < 0.1$ ).

Clear-water phase metrics	Factors										AICc	$\Delta$ AICc	$w_i$	
	May 1st water temperature	Total phosphorus	<i>D. pulicaria</i> proportion	<i>Bythotrephes</i> density <sub><i>t</i>-1</sub>	May 1st water temperature × phosphorus	May 1st water temperature × <i>D. pulicaria</i> proportion	May 1st water temperature × <i>Bythotrephes</i> density <sub><i>t</i>-1</sub>							
Lake Mendota														
Start date	-5.59±1.59		-16.6±1.6	3.89±1.58								268.9	0.00	0.26
	-5.89±1.52	1.07±1.67	-16.3±1.5	5.59±1.76	4.06±1.76							269.0	0.04	0.25
Maximum date	-6.68±1.73		-9.47±1.73									275.0	0.00	0.30
	-7.14±1.76		-9.32±1.72	2.07±1.74								276.1	1.16	0.17
Duration	-0.22±2.15	-0.19±2.30	19.4±2.1	-7.88±2.38	-10.4±2.2							301.0	0.00	0.53
	0.07±2.14	-0.25±2.29	19.8±2.2	-8.43±2.4	-11.4±2.3	2.86±2.41						302.6	1.58	0.24
Magnitude			1.11±0.31									156.4	0.00	0.23
	-0.27±0.31		1.09±0.32									157.5	1.18	0.13
	-0.34±0.32		1.10±0.31	-0.34±0.31								157.6	1.23	0.12
			1.17±0.31									157.6	1.28	0.12
Lake Monona														
Start date	-3.21±1.56		-7.16±1.55	2.71±1.54*								285.3	0.00	0.17
	-3.41±1.53		-5.60±1.82	3.04±1.52*								285.4	0.10	0.16
	-3.12±1.60*		-7.19±1.60									286.0	0.67	0.12
	-3.28±1.59		-5.90±1.89									286.9	1.61	0.08
			-6.67±1.61	2.62±1.61								287.1	1.82	0.07
Maximum date	-3.99±1.50		-0.11±1.78									282.3	0.00	0.20
	-4.01±1.47		0.11±1.75	2.21±1.46								282.6	0.29	0.18
	-4.13±1.45		-0.26±1.74	1.88±1.46								283.2	0.94	0.13
	-3.69±1.50	-1.92±1.54	0.43±1.82									283.3	1.08	0.12
Duration			10.7±2.3									313.4	0.00	0.25
			10.6±2.3	-3.39±2.27								313.5	0.16	0.23
		2.50±2.32	10.4±2.3									314.6	1.27	0.13
Magnitude			0.49±0.25*									145.0	0.00	0.18
	-0.29±0.25		0.45±0.25*									146.1	1.16	0.10
		-0.26±0.25	0.52±0.25									146.4	1.40	0.09
												146.5	1.51	0.08
												146.9	1.92	0.07





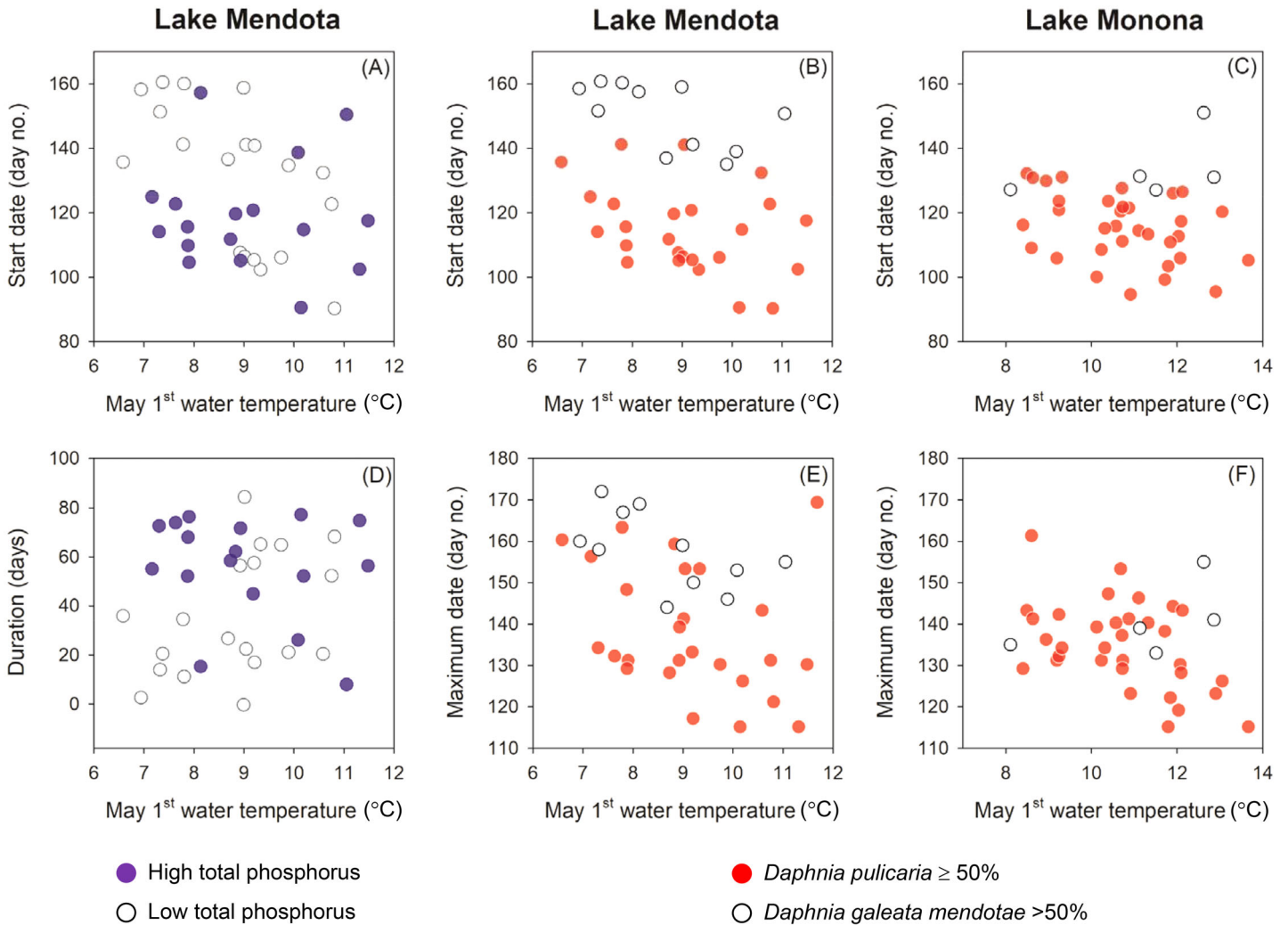
**Fig. 3.** The standardized coefficient (solid circle) and 95% confidence interval (bar) of each predictor in the best model for explaining variations in the clear-water processes (left panels; Lake Mendota, right panels; Lake Monona). No circle and bar indicate that the variable was not included in the best model (see Table 1).



**Fig. 4.** Relationships between all drivers and clear-water phase metrics in Lake Mendota. The solid line or asterisk indicates that the relationship between the variables is significant or marginally significant in the top-ranked models (Table 2).

*D. galeata mendotae* dominant years, although May 1st water temperatures was associated with earlier clear-water phase maximum dates regardless of food web structure (Fig. 5E). The second model included these two variables and *Bythotrephes* density<sub>t-1</sub>, but the estimated coefficient of *Bythotrephes* density<sub>t-1</sub> was not significant.

The best model for the clear-water phase duration included May 1st water temperature, TP, *D. pulicaria* proportion, *Bythotrephes* density<sub>t-1</sub>, and the interaction between May 1st water temperature and TP (Table 2, Fig. 3). *D. pulicaria* proportion increased the clear-water phase duration significantly, while the clear-water phase duration was shorter with higher



**Fig. 5.** The response of the clear-water phase metrics to the interaction effects between drivers. The different response of the clear-water phase start date (A) and duration (D) of Lake Mendota to May 1<sup>st</sup> water temperature between low (below median) and high (above median) TP condition. The different responses of the clear-water phase start and maximum dates to May 1<sup>st</sup> water temperature between dominant *Daphnia* species in Lake Mendota (B, E) and Lake Monona (C, F). Note that > 50% *D. galeata mendotae* (open circles) matches with < 50% *D. pulicaria* proportion.

*Bythotrephes* density<sub>*t*-1</sub> (Fig. 4). When May 1<sup>st</sup> water temperature was lower, the clear-water phase duration was longer in higher TP conditions (Fig. 5D). The interaction between May 1<sup>st</sup> water temperature and *D. pulicaria* proportion was also included in the second model, but the estimated coefficient was not significant.

The model including *D. pulicaria* proportion alone was selected as the best model for the clear-water phase magnitude (Table 2, Fig. 3). The clear-water phase magnitude increased with higher *D. pulicaria* proportion (Fig. 4). *D. pulicaria* proportion was also included in the next three top-ranked models and the estimated coefficients were significant (Table 2). May 1<sup>st</sup> water temperature, *Bythotrephes* density<sub>*t*-1</sub>, and the interaction between May 1<sup>st</sup> water temperature and *D. pulicaria* proportion also appeared in the second model, although the estimated coefficients were not significant.

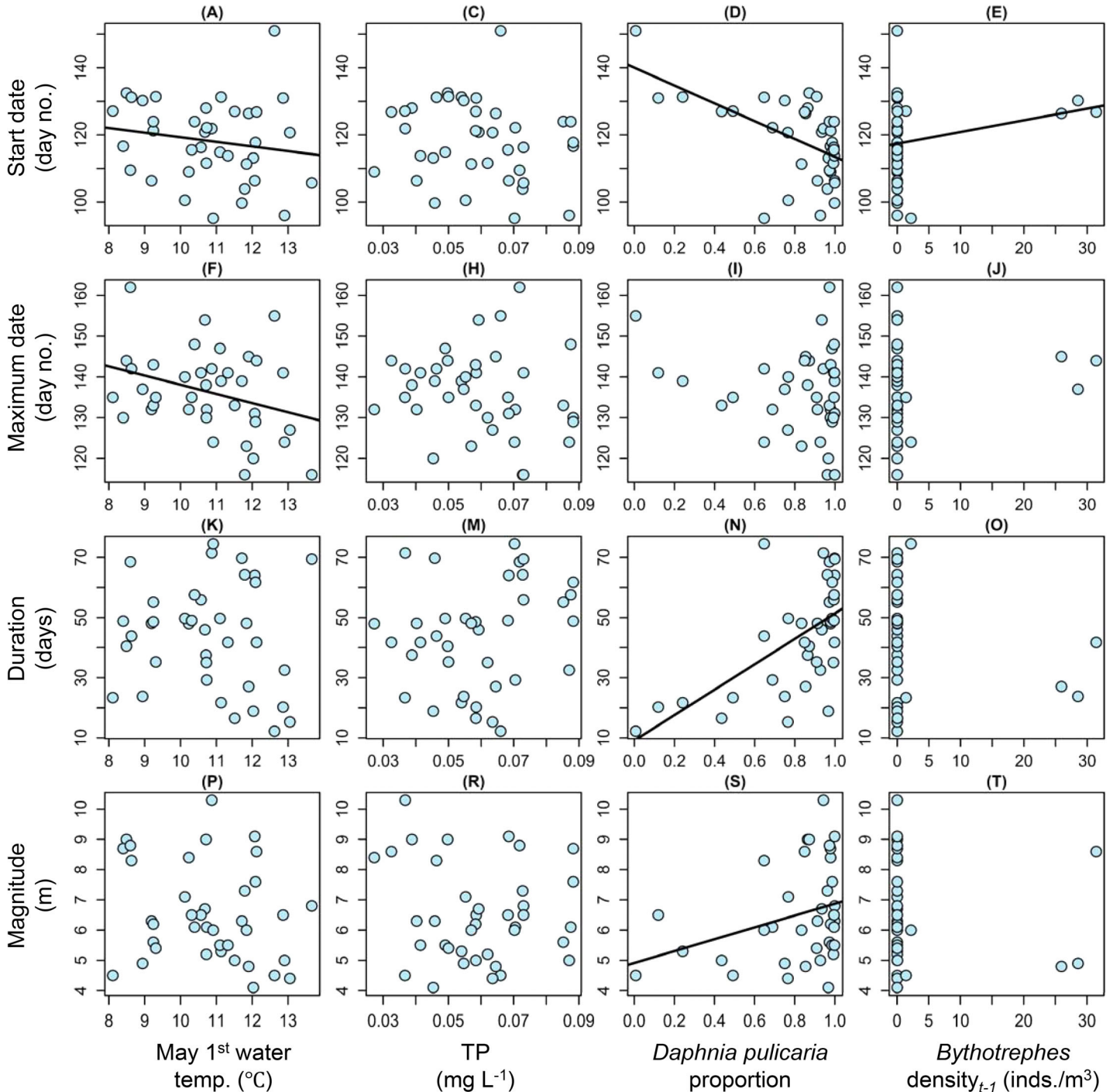
Over the time of this study, Lake Mendota had three major “food web periods”; 1980–1987 (before biomanipulation), 1988–2009 (during biomanipulation and before *Bythotrephes* invasion), and 2010–present (after *Bythotrephes* invasion) (Walsh et al. 2017). We compared the clear-water phase metrics across the three food web periods (Supporting Information Fig. S9). The clear-water phase start and maximum dates were earlier during the biomanipulation, but these dates were later after *Bythotrephes* invasion. Although the clear-water phase duration and magnitude were longer and larger, respectively, during the biomanipulation; after *Bythotrephes* invasion these metrics reverted to the conditions before the biomanipulation.

#### Lake Monona

For the clear-water phase start date, May 1<sup>st</sup> water temperature, *D. pulicaria* proportion, and *Bythotrephes* density<sub>*t*-1</sub>

comprised the best model (Table 2, Fig. 3). The clear-water phase start date was significantly earlier with higher *D. pulicaria* proportion and with higher May 1st water temperature (Fig. 6). The best model estimated that the clear-water phase start date was  $2.2 \pm 1.1$  d earlier per  $1^\circ\text{C}$  increase in the May 1st water temperature. The clear-water phase start date

was also delayed with higher *Bythotrephes* density<sub>t-1</sub> and the estimated coefficient was marginally significant. May 1st water temperature, *D. pulicaria* proportion, and *Bythotrephes* density<sub>t-1</sub> were included in top-ranked models and these estimated coefficients were significant or marginally significant. Top-ranked models also included the interaction between May 1st water



**Fig. 6.** Relationships between all drivers and clear-water phase metrics in Lake Monona. The solid line or asterisk indicates that the relationship between the variables is significant or marginally significant in the top-ranked models (Table 2).

temperature and *D. pulicaria* proportion, but these estimated coefficients were not significant.

The model including May 1st water temperature, *D. pulicaria* proportion, and the interaction between these two variables was selected as the best model for the clear-water phase maximum date (Table 2, Fig. 3). The clear-water phase maximum date was significantly affected by May 1st water temperature (Fig. 6) and the best model estimated that the clear-water phase start date was  $6.2 \pm 3.6$  d earlier per  $1^\circ\text{C}$  increase in May 1st water temperature. However, the effect of May 1st water temperature on the clear-water phase maximum date differed depending on *D. pulicaria* proportion. The clear-water phase maximum date of the years with low relative abundances of *D. pulicaria* was not responsive to the May 1st water temperature (Fig. 5D). The three variables selected in the best model were included in all top-ranked models, but the estimated coefficient of *D. pulicaria* proportion was not significant. Although TP, *Bythotrephes* density<sub>*t*-1</sub>, and the interaction between May 1st water temperature and *Bythotrephes* density<sub>*t*-1</sub> also appeared in top-rank models, these estimated coefficients were also not significant.

For the duration of the clear-water phase, *D. pulicaria* proportion alone comprised the best model (Table 2, Fig. 3). The duration was significantly longer with higher *D. pulicaria* proportion (Fig. 6). *D. pulicaria* proportion appeared in the second and third models. Although the third model included *Bythotrephes* density<sub>*t*-1</sub>, the coefficient was not significant.

The best model for the clear-water phase magnitude included *D. pulicaria* proportion only, and the estimated coefficient was marginally significant ( $p = 0.057$ ) (Table 2, Fig. 3). The clear-water phase magnitude was greater with increasing *D. pulicaria* proportion (Fig. 6). *D. pulicaria* proportion was again included in the second and third models, and those estimates were marginally significant ( $p = 0.085$ ) and significant, respectively. The intercept-only model was selected as the fourth model. May 1st water temperature and TP were appeared in top-ranked models, but were not significant.

## Discussion

Our analysis of long-term data (1980–2017) shows that climate and food web structure (including the impact of *Bythotrephes* invasion) influence the timing, strength, and duration of the clear-water phase in Lakes Mendota and Monona (Figs. 4, 6). Our findings emphasize the consistency of the drivers affecting the clear-water phase despite notable differences in size and food web structure of these two adjacent eutrophic lakes. Earlier studies have demonstrated that climate conditions can shift the clear-water phase start or maximum dates (Straile 2000; Winder and Schindler 2004b; Droscher et al. 2009), but did not explicitly consider the effect of food web structure. In contrast, previous studies on Lake Mendota showed that trophic cascades can influence the clear-water phase, but did not consider the effect of climate.

Our results are consistent with Scheffer et al.'s (2001) model showing that both climate and trophic cascade via fish predation on *Daphnia* influence the clear-water phase. Furthermore, *Bythotrephes* invasion affected the timing of the onset of the clear-water phase in Lakes Mendota and Monona and its duration in Lake Mendota. To our knowledge, our study is the first to show that climate variability and food web structure may affect different aspects (start date, maximum date, duration, and magnitude) of the clear-water phase.

## Climate affects the clear-water phase start and maximum dates

May 1st water temperature affected the start and maximum dates of the clear-water phase in both lakes but did not influence its duration and magnitude (Table 2). The clear-water phase start date was  $4.2 \pm 1.2$  and  $2.2 \pm 1.1$  d earlier per  $^\circ\text{C}$  in Lakes Mendota and Monona, respectively, and the clear-water phase maximum date was  $5.0 \pm 1.3$  and  $6.2 \pm 3.6$  d earlier per  $^\circ\text{C}$  in Lakes Mendota and Monona, respectively. These effects were smaller than have been observed in other lakes (ca. 9 d per  $^\circ\text{C}$  in MullerNavarra et al. 1997; ca. 9 d per  $^\circ\text{C}$  in Winder and Schindler 2004b; ca. 6 d per  $^\circ\text{C}$  in Wagner and Benndorf 2007), but are similar to the result from a simulation model (Scheffer et al. 2001) that predicted 3 to 7 d per  $^\circ\text{C}$  in a lake with moderate fish density. Considering there were no long-term trends in water temperature nor in the clear-water phase start or maximum dates between 1980 and 2017 (Table 1, Figs. 1, 2), our findings indicate that the phenological timings of the clear-water phase may respond dynamically to climate variability.

While the coherence of May 1st water temperature was high (0.86), the start and maximum dates of the clear-water phase responded differently to May 1st water temperature between Lakes Mendota and Monona and the estimated slopes for Lake Mendota were higher than those of Lake Monona (Table 2). Our results suggest that Lake Mendota might have greater sensitivity of the clear-water phase timings (rate of change per unit temperature). However, these results need to be interpreted carefully, as our models estimated the effect of water temperature on a specific date, whereas the plankton communities may be at different successional stages in the two lakes on that date.

Previous studies of European lakes found that warmer early spring water temperatures increased *Daphnia* biomass, which in turn resulted in an earlier onset of the clear-water phase, although in early summer *Daphnia* biomass was lower with higher water temperature (Straile 2000; Straile and Adrian 2000). Winder and Schindler (2004b) reported that spring *Daphnia* densities did not correlate with spring water temperature in Lake Washington, but that water temperature affected the timing of peak *Daphnia* density. The egg development and growth rates of *Daphnia* species increase with water temperature (Bottrell et al. 1976). In our study, there was no significant relationship between May 1st water temperature

and May–June averaged *D. pulicaria* or *D. galeata mendotae* biomass (data not shown). Relationships between water temperature and clear-water phase state dates were similar in *D. pulicaria* and *D. galeata mendotae* dominant years (Fig. 5). Thus, our results suggest that clear-water phase timing is related to the timing of peak *Daphnia* populations in response to spring water temperatures, but not to *Daphnia* biomass.

### Food web impacts “all” clear-water phase metrics:

#### Importance of *D. pulicaria*

The relative abundance of *D. pulicaria* influenced all four clear-water phase metrics in Lake Mendota, and three of these metrics in Lake Monona (Table 2, Figs. 4, 6). Higher *D. pulicaria* proportions were associated with earlier start and maximum clear-water phase dates, lengthened the clear-water phase duration, and strengthened the clear-water phase magnitude. Standardized coefficients for the start and maximum dates for Lake Mendota and the start date for Lake Monona were greater for the proportion of *D. pulicaria* than for May 1st water temperature, highlighting the effect of food web structure on the timing, duration, and magnitude of the clear-water phase.

Our results are consistent with previous studies on Lake Mendota (Rudstam et al. 1993; Lathrop et al. 1996, 1999; Kasprzak et al. 1999; Walsh et al. 2017) which found that the clear-water phase was later and shorter when small-bodied *D. galeata mendotae* was dominant (i.e., lower *D. pulicaria* proportion). *D. galeata mendotae* dominance results from size-selective predation because larger-bodied *D. pulicaria* are consumed selectively by zooplanktivorous fishes. The physiological differences between *D. galeata mendotae* and *D. pulicaria* may be also related to shifts in the timing, duration, and magnitude of the clear-water phase. Because *D. pulicaria* has a higher grazing rate and population growth rate at cold temperature and a lower incipient food threshold (Threlkeld 1979; Rudstam et al. 1993; Johnson and Kitchell 1996), *D. pulicaria* can dominate earlier in spring. *D. galeata mendotae* is also less resistant to starvation than *D. pulicaria* (Kitchell 1992). When zooplanktivory is high, the dominance of *D. galeata mendotae* in spring and early summer can shorten the clear-water phase duration. The functional difference between *Daphnia* species with regard to the clear-water phase is supported by studies on other lakes. Hairston et al. (2005) reported that the change in the dominant *Daphnia* species from *Daphnia exilis* and *Daphnia curvirostris* to *D. galeata mendotae* and *D. pulicaria* led to earlier, higher magnitude of clear-water phases even though overall abundance and biomass of *Daphnia* decreased. Thus, our study underscores the functional role of *Daphnia* species in the clear-water phase.

The clear-water phase maximum date for Lake Monona was earlier with higher May 1st water temperature, but the effect was not observed in *D. galeata mendotae* years (Fig. 5F). Although this is possibly because so few *D. galeata mendotae* years occurred in Lake Monona, one possible explanation for this result is earlier development of inedible phytoplankton,

such as cyanobacteria, in warmer conditions. Given that cyanobacteria starts to grow earlier in warmer conditions, the maximum date, which is the middle or latter of the clear-water phase, might be variable in *D. galeata mendotae* years. However, future experimental and observational work should address the interaction effect between food web and climate variability.

#### *Bythotrephes* impacts at high density

With increasing *Bythotrephes*<sub>t-1</sub> density, the clear-water phase start date of Lakes Mendota and Monona was more delayed and the clear-water phase duration of Lake Mendota only was shorter in the following year. *Bythotrephes* and planktivorous fish can have different impacts on the clear-water phase. In Lake Erie as well as Lakes Mendota and Monona, *Bythotrephes* is reported to dominate in fall, while the predation pressure by planktivorous fish on *Daphnia* is high in summer (Berg and Garton 1988). Walsh et al. (2017) showed that in Lake Mendota, winter *D. pulicaria* densities decreased after the invasion of *Bythotrephes* in late summer 2009. Predation by higher *Bythotrephes* density on *Daphnia* populations in the fall and winter might delay the development of *Daphnia* populations of the following spring, leading to delay the clear-water phase start date and shorten the clear-water phase duration. However, further work is needed to assess potential mechanisms of *Bythotrephes*' impact on *Daphnia* resting egg production and overwintering success of *Daphnia*.

Our results suggest that the effect of *Bythotrephes* density on the clear-water phase is weaker in Lake Monona compared to Lake Mendota. The average density of *Bythotrephes* (2009–2017) was higher in Lake Mendota (16.0 inds. m<sup>-3</sup>) than Lake Monona (11.2 inds. m<sup>-3</sup>). Walsh et al. (2018) found that *D. pulicaria* biomass declined in Lakes Mendota and Monona after *Bythotrephes* invasion, but to a much greater extent in Lake Mendota. Because Lake Monona has been managed as a “panfish” or zooplanktivore lake while managing Lake Mendota as a “gamefish” or piscivore lake (i.e., strict regulations on harvest of piscivorous fishes) (Lathrop et al. 2002; Walsh et al. 2017), *Bythotrephes* may be controlled by planktivorous fish, such as bluegill, in Lake Monona. Further, warmer temperatures in Lake Monona might exceed thermal tolerances for *Bythotrephes* (Garton et al. 1990).

#### Effect of TP concentration on the clear-water phase

The interaction between water temperature and TP influenced the start date and duration of the clear-water phase in Lake Mendota (Table 2). In years with high TP, the clear-water phase start date was earlier and the clear-water phase duration was longer even when May 1st water temperature was low (Fig. 5A,D). These effects of TP conditions were not evident when May 1st water temperature was high. According to the PEG model (Sommer et al. 1986), in eutrophic lakes, nutrient limitation occurs in the periods of spring

phytoplankton blooms (mostly small and edible algae) and summer phytoplankton blooms (mostly large and inedible algae), whereas nutrient limitation does not occur during the clear-water phase. Whereas Winder and Schindler (2004b) reported that the timing of spring phytoplankton bloom and clear-water phase were delayed more with higher TP, Thackeray et al. (2013) demonstrated that higher phosphorus advanced the peak timing of phytoplankton biomass, and earlier phytoplankton blooms further advanced the timing of peak *Daphnia* population. Moreover, Luecke et al. (1990) reported that high food availability allowed spring *Daphnia* populations to expand rapidly, particularly in cooler water temperature conditions. Thus, our results suggest that when water temperature is low, TP might indirectly affect the initial stage of the clear-water phase by altering the peak timing and biomass of phytoplankton.

#### Future clear water phase characteristics and management implication

Changes in the timing, duration, and magnitude of the clear-water phase can ultimately lead to the alteration of summer water quality and plankton community dynamics (Leavitt 1992; Lathrop et al. 1996). Our study underscores the role of food web management, including both control of *D. pulicaria* proportion and *Bythotrephes* density, for the water quality of our two study lakes. In Lake Mendota, the clear-water phase metrics during the biomanipulation project (1988–1992) and subsequent years clearly differed from before and after the biomanipulation (Fig. 1 and Supporting Information Fig. S9). Although these results suggest that the biomanipulation project can change the clear-water phase and improve spring water quality, Walsh et al. (2017) demonstrated that *Bythotrephes* invasion soon after the biomanipulation decreased *D. pulicaria* and changed water quality. Maintaining piscivore stocking would be needed to increase *D. pulicaria* proportion by limiting total planktivory by fishes. Because there is little evidence of predator control of *Bythotrephes* by planktivorous fish in these lakes (Walsh et al. 2017), future studies should investigate whether piscivore stocking has had a positive effect on *Bythotrephes* and identify potential food web management options to reduce *Bythotrephes* populations. Our study also suggests that any food web management efforts should also consider the time-lag effects of *Bythotrephes* (i.e., *Bythotrephes* density of the previous year) in the clear-water phase.

How will the clear-water phase of Lakes Mendota and Monona change in the future? The timing, duration, and magnitude may be variable and unpredictable. Magnuson et al. (2000) showed that interannual variability in ice phenology dates has increased since 1950 in the Northern Hemisphere lakes including Lake Mendota. Although we detected the impacts of *Bythotrephes* invasion on the clear-water phase metrics, exotic zebra mussel (*Dreissena polymorpha*), which has recently invaded both study lakes, could increase clarity of the

lakes independent of fluctuations in *Daphnia* (Reed-Andersen et al. 2000). The ecological impacts of such invasive species change considerably over time (Strayer et al. 2006). These uncertainties make the prediction of the clear-water phase more complex. Thus, future studies should explore the temporal changes in the relative strengths of and interactions among the drivers. One important strength of our study is the use of biweekly long-term monitoring data over 38 yrs. Maintaining long-term monitoring and comparing multiple lakes will improve the future predictions for the phenological patterns of the clear-water phase and help manage water quality under multiple and changing pressures.

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### Conflict of Interest

None declared.

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