

Lake water level response to drought in a lake-rich region explained by lake and landscape characteristics

K. Martin Perales, Catherine L. Hein, Noah R. Lottig, and M. Jake Vander Zanden

Abstract: Climate change is altering hydrologic regimes, with implications for lake water levels. While lakes within lake districts experience the same climate, lakes may exhibit differential climate vulnerability regarding water level response to drought. We took advantage of a recent drought (~2005–2010) and estimated changes in lake area, water level, and shoreline position on 47 lakes in northern Wisconsin using high-resolution orthoimagery and hypsographic curves. We developed a model predicting water level response to drought to identify characteristics of the most vulnerable lakes in the region, which indicated that low-conductivity seepage lakes found high in the landscape, with little surrounding wetland and highly permeable soils, showed the greatest water level declines. To explore potential changes in the littoral zone, we estimated coarse woody habitat (CWH) loss during the drought and found that drainage lakes lost 0.8% CWH while seepage lakes were disproportionately impacted, with a mean loss of 40% CWH. Characterizing how lakes and lake districts respond to drought will further our understanding of how climate change may alter lake ecology via water level fluctuations.

Résumé : Les changements climatiques modifient les régimes hydrologiques, ce qui a des conséquences sur les niveaux de l'eau des lacs. Si les lacs au sein d'une même région sont exposés au même climat, ils pourraient toutefois présenter différentes vulnérabilités climatiques en ce qui concerne la réaction des niveaux d'eau à la sécheresse. Nous avons tiré parti d'une sécheresse récente (~2005–2010) pour estimer les variations de superficie, de niveau d'eau et de position des rives de 47 lacs dans le nord du Wisconsin en utilisant l'orthoimagerie de haute résolution et des courbes hypsographiques. Nous avons élaboré un modèle qui prédit la réaction des niveaux d'eau à la sécheresse, afin de cerner les caractéristiques des lacs les plus vulnérables dans la région, qui indiquent que les lacs fermés de faible conductivité se trouvant à haute élévation dans le paysage et caractérisés par peu de milieux humides environnants et des sols très perméables présentent les plus grandes baisses des niveaux d'eau. Afin d'examiner les changements potentiels dans la zone littorale, nous avons estimé la perte d'habitats de débris ligneux grossiers (HDLG) durant la sécheresse et relevé que les lacs ouverts perdent 0,8 % de leurs HDLG, alors que les lacs fermés subissent un impact disproportionné, présentant une perte moyenne de 40 % de leurs HDLG. La caractérisation de la réaction des lacs et des régions de lacs à la sécheresse rehaussera la compréhension de l'incidence possible des changements climatiques sur l'écologie des lacs découlant des fluctuations des niveaux d'eau. [Traduit par la Rédaction]

Introduction

Water levels in lentic systems can fluctuate at multiple temporal scales for a variety of reasons, including climatic factors, water extraction, and artificial regulation (i.e., dams). The broader ecological implications of water level fluctuations are poorly understood, though recent studies suggest that large changes, such as those produced by prolonged drought, can have strong influences on the ecological interactions within these systems (Evtimova and Donohue 2016; Leira and Cantonati 2008; Zohary and Ostrovsky 2011). In this context, climatic phenomena such as drought exert their influence at regional scales. Yet individual lakes and their watersheds within a region have different abiotic and biotic attributes and as a result may differ with regard to how water levels respond to drought (Webster et al. 1996). This is an example of how individual ecosystems may differ with regard to climate vulnerability (Johnson et al. 2005; Markovic et al. 2017). Understanding which ecosystems are most vulnerable to climate change is an important step in mitigating impacts (Weißhuhn et al. 2018). Two key questions that need to be explored are as follows: Which ecosystems are most vulnerable? What are the ecological consequences of this heterogeneity in vulnerability? In this study we will evaluate water level response to a multiyear drought and

associated impacts on littoral habitat as a way of assessing ecosystem vulnerability to climate change.

Climate change is leading to a warmer climate, characterized by more extreme precipitation events and more frequent droughts (Alexander et al. 2006; Sheffield and Wood 2008; Dai 2011; Donat et al. 2013). It is difficult to predict the consequences of these weather extremes, but there are clear implications for net basin supply and fluctuating water levels (Schindler et al. 1990; Watras et al. 2014). While water levels fluctuate naturally, future climate regimes may push water levels outside of the historical range of conditions (Sherwood and Fu 2014). There is evidence suggesting that the frequency and magnitude of water level fluctuations in North American lakes are changing, as illustrated by recent changes in water level oscillations and record low water levels due to a multiyear drought (Assel et al. 2004; Gronewold and Stow 2014; Watras et al. 2014).

The potential for ecosystem-specific responses under a changing climate poses serious challenges in predicting impacts, especially if there are strong differences in water level responses. Previous studies of lake districts have found that water levels in individual lakes can have heterogeneous responses to drought, with some systems responding more strongly than others (Webster

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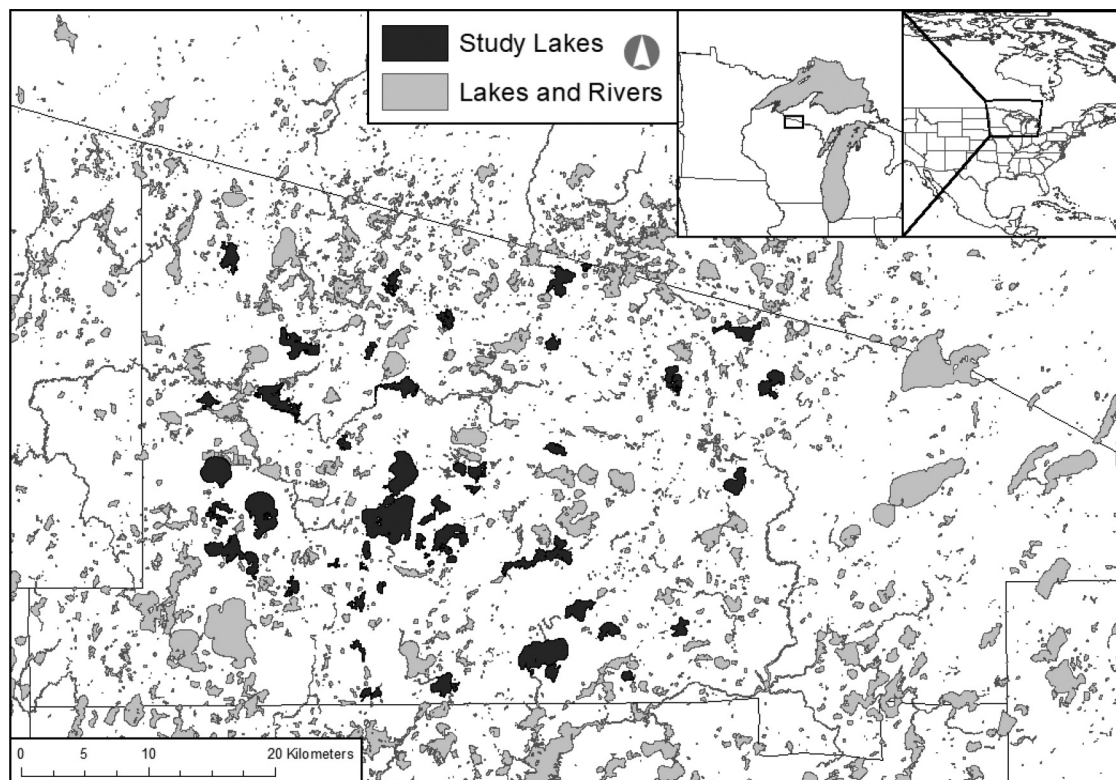
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Fig. 1. Map of Vilas County, Wisconsin, USA, showing the location of lakes included in the study. Study lakes are shown in black and other lakes and rivers are shown in gray. Map was created using ArcGIS 10.6.1 using data from the Wisconsin Department of Natural Resources (WDNR 2011, 2017) and Environmental Systems Research Institute (Esri 2012, 2015).



et al. 1996). Lakes are embedded in heterogeneous landscapes, each with their own unique watersheds, which may lead adjacent ecosystems to respond differently to the same driver (Cardille et al. 2004; Soranno et al. 1999). Understanding the relationship between the abiotic factors that make up these watersheds and water level responses may allow us to better anticipate how lakes will respond to future drought and consequently help us identify the most vulnerable lakes in a region.

While we understand that not all lakes may respond strongly to drought, for those that do, changes in water levels can strongly influence the structure and function of lake ecosystems (Evtimova and Donohue 2016; Zohary and Ostrovsky 2011). For instance, lowered water levels can affect water chemistry and clarity (Gafny and Gasith 1993; Webster et al. 2000; Lisi and Hein 2019), play a role in the community assembly of aquatic macrophytes and macroinvertebrates (Chase 2007; Coops et al. 2004; Quinlan and Mulamootil 1987), affect mercury bioaccumulation in piscivorous birds and fishes (Watras et al. 2020), alter food web structure (Hansen et al. 2018), and impact littoral fish communities (Henderson 1985; Gafny et al. 1992; Gasith et al. 2000; Gaeta et al. 2014; Glassic and Gaeta 2019). In a north temperate lake, lowered water levels corresponded to a loss of >75% coarse woody habitat (CWH), which led to considerable changes in littoral fish predator–prey dynamics, species composition, and growth rates (Gaeta et al. 2014).

To understand how lakes and lake districts respond to changing hydrologic regimes, we quantified responses of north temperate lakes to a recent multiyear drought. First, we empirically estimated changes in lake area, water level, and shoreline position change on 47 lakes in the Northern Highlands Lake District of northern Wisconsin using high-resolution orthoimagery and hypsographic curves. We developed a statistical model relating water level fluctuations to lake and landscape characteristics, which allowed us to identify characteristics of lakes that are more responsive to drought. We then used this statistical model to predict the water

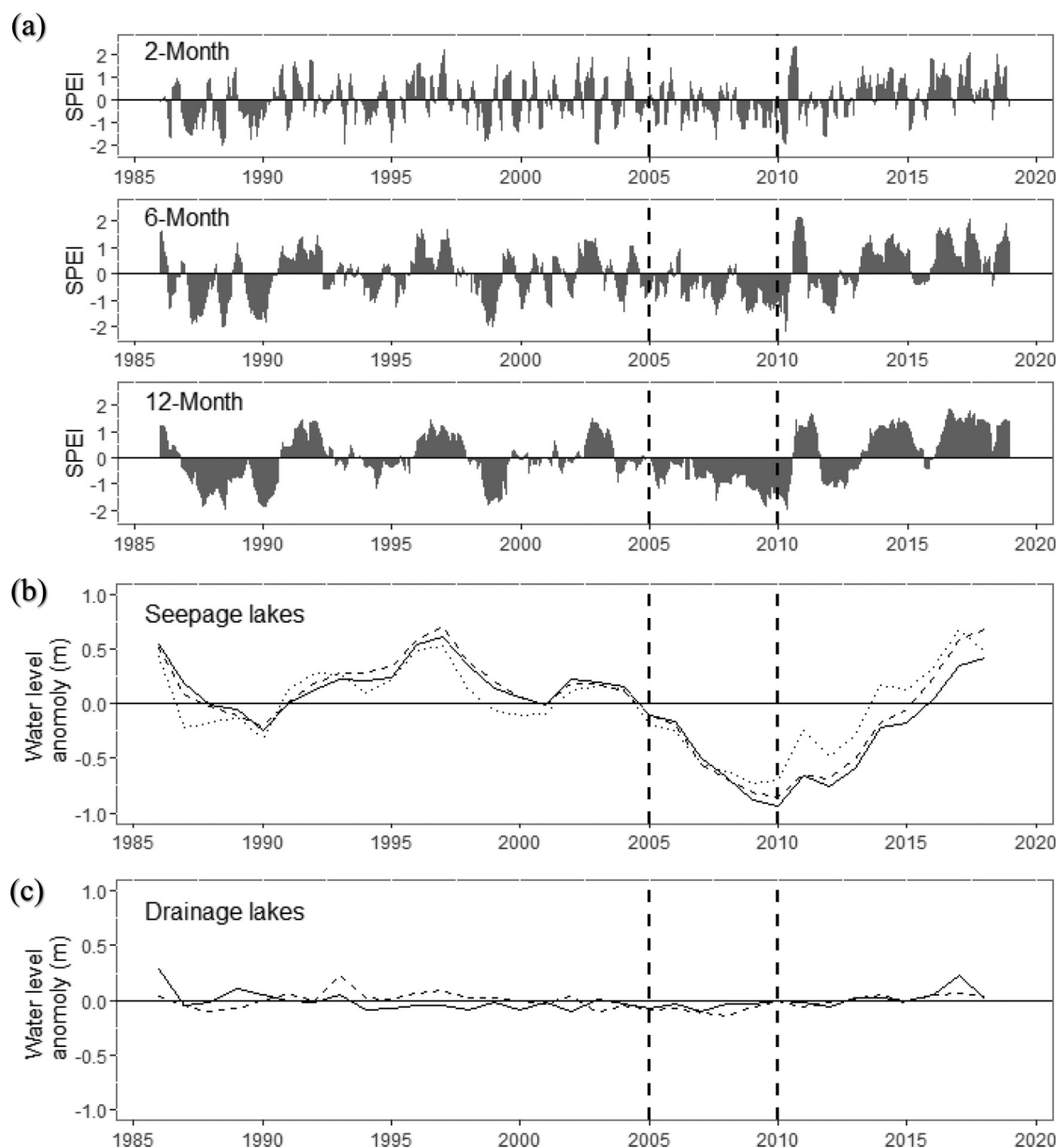
level changes for lakes in the region. This allowed us to explore the extent that drought might affect whole lake districts. Finally, we used our regional estimates of water level changes to estimate changes in littoral CWH, a critical habitat feature of littoral zones.

Methods

Study area — Northern Highlands Lake District

Our study lakes were in Vilas County, Wisconsin, USA, in the Northern Highlands Lake District (Fig. 1). The Northern Highlands Lake District is a forested lake-rich region located in northern Wisconsin and the upper peninsula of Michigan, USA. The Northern Highlands Lake District was formed by glacial forces and is set in a low relief, pitted outwash plain characterized by kettle lakes, moraines, drumlins, and eskers (Magnuson et al. 2006). Roughly a third of the landscape is made up of lakes and wetlands, making it one of the highest concentrations of kettle lakes in the world (Carpenter et al. 2007). Most lakes in this region are seepage lakes and are not connected to other lakes via streams and rivers, whereas drainage lakes are (Riera et al. 2000). The hydrologic flow system in this region is dominated by groundwater flow, and all lakes interact with the groundwater to some degree (Pint et al. 2003). Hydrologic budgets are highly variable among lakes and are related to the relative position of a lake in the regional hydrologic flow system (Kratz et al. 1997). Typically, lakes that are located higher in the landscape tend to be smaller and more reliant on precipitation and (or) groundwater inputs, whereas lakes lower in the landscape tend to be larger drainage lakes (Riera et al. 2000). Wisconsin's Northern Highlands Lake District has experienced drier summers and wetter winters, with an overall reduction in annual precipitation, although future precipitation projections are uncertain (Kucharik et al. 2010). Further, recent changes in the long-term oscillations of lake levels has resulted in record low water levels for the region (Gronewold and Stow 2014; Watras

Fig. 2. (a) Time series of the Standardized Precipitation–Evapotranspiration Index (SPEI) using the Thornthwaite method (Vicente-Serrano et al. 2010; Beguería et al. 2014) and (b, c) mean annual water level anomalies (m) for NTL-LTER lakes. The two comparison years (2005 and 2010) are indicated by the vertical dashed lines. (a) Time series of the SPEI show multiple wet and dry periods with a notable multiyear dry period from ~2005 to 2010. (b) The time series for seepage lake water level anomalies highlight relatively high temporal variation with some among-lake differences (solid = Big Muskellunge Lake, dashed = Crystal Lake, dotted = Sparkling Lake), whereas (c) drainage lake water level anomalies show relatively little temporal variation (solid = Allequash Lake, dashed = Trout Lake). Precipitation data used to calculate SPEI are from the Oregon State University PRISM Climate Group (PRISM Climate Group 2019) and from coordinates 46.0759°N, 89.5862°W.



et al. 2014). Neighboring lakes with similar land use have responded differently to past droughts despite experiencing almost identical weather and climate (Webster et al. 1996). During the last drought cycle, water levels were near long-term means in 2005 and decreased to record lows around 2010 (Fig. 2b; Watras et al. 2014). This region experiences wet and dry periods on a decadal scale, and water levels have since rebounded to record or near record highs as of 2020 (Fig. 2b; Gronewold and Rood 2019; Watras et al. 2020). It is reasonable to think that lake water level variability will increase given that precipitation and temperatures are both projected to increase in the Great Lakes area, and both parameters affect water levels in the opposite direction (Notaro et al. 2015). In general, this region has poor spatial and temporal

coverage of water level data, but there is extensive water level data for seven lakes monitored by North Temperate Lakes Long Term Ecological Research program (NTL-LTER) since 1981 (Fig. 2). This leaves us with a poor understanding of the spatial (i.e., among-lake) heterogeneity of responses to drought. Thus, we view this drought as a natural experiment and focus on a relatively small geographic area to explore how lakes in a heterogeneous landscape respond to drought.

Quantify change in lake surface area, water level, and shoreline distance due to drought

To characterize how north temperate lakes respond to drought, we hand-digitized lake shorelines using a geographic information

Table 1. Summary statistics of data used to parameterize the final generalized least squares model and used to estimate water level responses to drought in the region, along with data sources.

Predictor	Observed data, mean $\pm$ SD (min., max.)	Modeled data, mean $\pm$ SD (min., max.)	Data source
Hydrology type	22 drainage, 25 seepage	142 drainage, 200 seepage	NTL-LTER: Wisconsin lake historical limnological parameters 1925–2009
Percent wetland buffer	26.5 $\pm$ 12.5 (5.9, 55.4)	27.7 $\pm$ 13.2 (0.5, 72.3)	Soranno et al. 2017; Homer et al. 2015
Elevation (m)	497.6 $\pm$ 9.1 (485.0, 523.6)	499.4 $\pm$ 11.1 (476.1, 538.0)	Soranno et al. 2017
Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	61.6 $\pm$ 39.7 (12.8, 164.1)	48.0 $\pm$ 35.9 (9.9, 170)	NTL-LTER: Wisconsin lake historical limnological parameters 1925–2009
Soil permeability (inches $\cdot$ hour $^{-1}$ $\times 100$) ^a	822 $\pm$ 247 (182, 1032)	730 $\pm$ 329 (146, 1032)	Wisconsin Department of Natural Resources 24k Hydro — value-added geodatabase

Note: Only the variables included in the most parsimonious model are summarized.

^a1 inch = 2.5 cm.

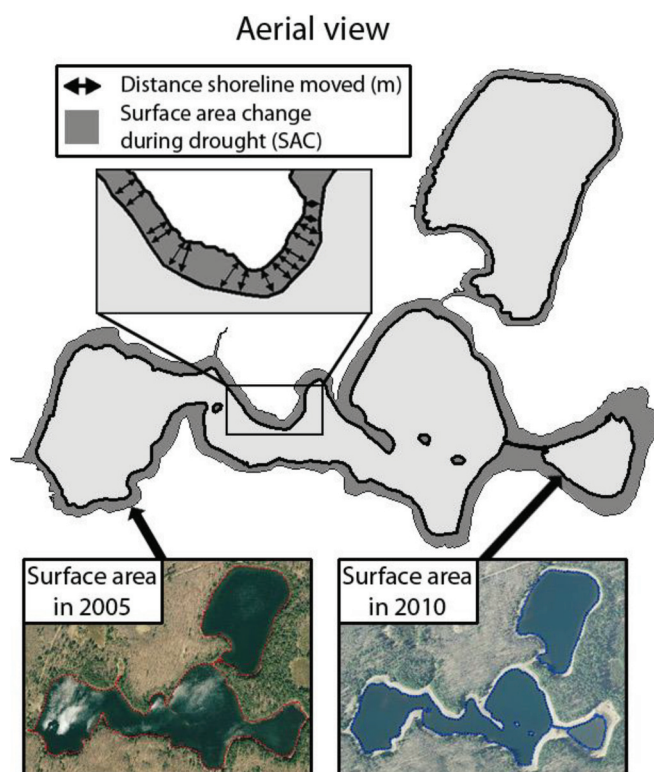
system and one-foot (1 foot = 30.5 cm) resolution orthoimagery collected in 2005 and 2010 ($n = 47$ lakes), which correspond to the mean and low water level years for this region, respectively (Fig. 2; Watras et al. 2014). Imagery was collected by the Vilas County Land Information Office during spring before leaf-out (April or May), which facilitated delineation and digitization of lake shorelines (VCLIO 2015). All digitization was done at a fixed map scale of 1:800 in ArcMap 10.6.1 (Esri 2018). The 47 lakes were selected based on the availability of previously digitized bathymetry maps and are representative of lakes in the region in terms of lake and landscape characteristics (Table 1). This approach was taken because there was little water level data taken during the drought. The study lakes ranged in size from 9 to 1564 ha ($\bar{x} = 196$ ha), slightly acidic to slightly basic (pH 5.5–8.5), and varied in maximum depth from 3 to 35 m ($\bar{x} = 13$ m).

Lake surface area for the high and low water level years was calculated from the digitized lake polygons in ArcMap. We used three metrics to express the change lakes underwent during drought conditions from 2005 to 2010. First, percent surface area change is the relative change in surface area due to the drought. Surface area change is the difference in surface area (ha) between 2005 and 2010, expressed as a percentage of 2005 surface area (Fig. 3; $\frac{\text{Area 2005} - \text{Area 2010}}{\text{Area 2005}} \times 100$). Second, we estimated the change in the lake surface elevation in metres, hereinafter referred to as water level change (WLC). To do this, the changes in lake surface area were converted to changes in water level using relative surface area to depth relationships (i.e., hypsographic curves) derived from digitized bathymetric maps from the Wisconsin Department of Natural Resources. To test the validity of using hypsographic curves to convert changes in relative surface area to changes in water level, we compared these estimates with water level gauge data for seven lakes that are monitored as part of the NTL-LTER. WLCs on NTL-LTER lakes were calculated by averaging April and May water level data, or June data if neither existed, and finding the difference from years 2005 and 2010 in metres. Our estimated WLC was consistent with observed WLC for the seven NTL-LTER lakes (slope = 0.97, intercept = -0.02 , $p < 0.001$, $r^2 = 0.915$). Third, we calculated the perpendicular shift of the wetted shoreline between the high and low water periods, expressed in metres, hereinafter referred to as shoreline position change (Fig. 3). To do this, we selected 500 random points around the perimeter of each lake polygon for the high-water level year, and for each point, we measured the nearest distance to the counterpart lake polygon for the low-water level year (Fig. 3). Shoreline position change is the mean of the 500 measured distances.

Statistical analysis

We developed a statistical model to predict water level response to drought using lake and landscape characteristics (Table 1). We then used this model to scale up the water level response to the region. An exhaustive model selection procedure with seven

Fig. 3. Approach used to measure change in surface area (% SAC) and shoreline position change (SPC) in metres. For illustrative purpose, the shoreline of Camp Lake at two time periods, overlaid each other, are shown. The outer polygon is the aerial extent in 2005, the inner polygon is the aerial extent in 2010, and the dark grey area represents the area lost during the drought from 2005 to 2010. SAC is the difference in surface area (ha) between 2005 and 2010, divided by the area in 2005, expressed as a percentage. The arrows in the inset map represent the distance the shoreline moved during the drought. The mean of these distances is SPC. Map was created using ArcGIS 10.6.1 using data created by authors and base map data from Vilas County Land Information Office (VCLIO 2015). [Colour online.]



covariates and a single pairwise interaction term was conducted using Bayesian information criterion (BIC) to identify the optimal statistical model for WLC (Burnham and Anderson 2002). Lake area (hectare) and shoreline development factor were included in the model selection procedure to account for any potential differences due to lake morphometry. Shoreline development factor is an index of how irregular the shoreline is

$\left(\frac{\text{length of lake perimeter}}{2 \times \sqrt{\pi \times \text{Area}}} \times 100; \text{Wetzel 2001}\right)$. We a priori selected an additional five predictor variables that we hypothesized were indicative of a lake's reliance on precipitation, groundwater, and surface waters (i.e., a lake's hydrologic budget; Magnuson et al. 2006; Webster et al. 1996). Further, our variables were included in the model selection procedure if they were relatively static or changed slowly at longer time scales and were readily available for other lakes in the region. Hydrology type is a two-level factor: drainage versus seepage lakes. Drainage lakes are downstream of other lakes and are connected via surface waters, while seepage lakes have no surface water connections with other lakes or have only an outlet. Percent wetland buffer is the percentage of the land in a 500 m buffer around a lake that is made up of woody wetlands, defined as "areas where forest or shrubland vegetation accounts for greater than 20% of vegetative cover and the soil or substrate is periodically saturated with or covered with water" (Homer et al. 2015). Perennial wetlands are not included in this percentage. Elevation is elevation above mean sea level in metres. Conductivity is an indicator of the concentration of ionic compounds dissolved in water ($\mu\text{S}\cdot\text{cm}^{-1}$). Soil permeability is the ability of soil within the immediate lakeshed to conduct water ($\text{inches}\cdot\text{hour}^{-1} \times 100$; 1 inch = 2.5 cm).

Based on preliminary analysis and a log-likelihood ratio test, we included hydrology type as a variance covariate to meet homogeneity of variance assumptions ($L = 8.06$, $df = 2$, $p = 0.0045$). Thus, we parameterized a generalized least squares model (Zuur et al. 2009). This allowed the models to have different variances per level of hydrology type. WLC was log+1-transformed. Because most lakes had negative responses during the drought, the sign for WLC was changed and a constant was added so all values were ≥ 0 prior to transformation. Marginal- R^2 value was calculated for the generalized least squares model (Nakagawa and Schielzeth 2013). Moran's I was calculated for the selected model to test for spatially autocorrelated residuals (Gittleman and Kot 1990; Zuur et al. 2009). All statistical analyses were done in R (version 3.4.3; R Project for Statistical Computing, Vienna, Austria; R Core Team 2019).

Estimating regional water level and CWH responses to drought

To estimate how lakes in Vilas County respond to drought more broadly, we predicted WLC on hundreds of lakes using the WLC statistical model and regionally available lake and landscape characteristic data. Because our analysis did not include very small lakes or wetlands, the regional lake responses were estimated only for lakes that had a depth > 3 m and an area > 8 ha ($n = 342$ lakes). To explore potential implications of WLC on lake littoral zones, we estimated the proportion of littoral CWH lost from each lake in the county during the drought using published data on the distribution of littoral CWH in a lake without lakeshore development (Gaeta et al. 2014). Although CWH density declines with increasing lakeshore development (Christensen et al. 1996), we assumed a constant CWH density at 0–3 m depth across all lakes. This allowed us to evaluate the potential impact of WLCs on CWH density apart from other drivers.

Results

Lake responses to drought

Lake responses to drought varied widely among lakes (Fig. 4). Most lakes (43 of 47) lost water during the drought. On average, percent surface area change was $-4.0\% \pm 5.3\%$ ($\bar{x} \pm \text{SD}$), with the maximum response being a loss of 26.6%. The mean WLC was -0.4 ± 0.5 m, and 41% of lakes had declines in water levels of more than 0.5 m. Mean shoreline position change was -4.9 ± 5.3 m. Lake responses were highly variable and exhibited a bimodal pattern, largely explained by hydrology type (Fig. 4). Seepage lakes responded more strongly and with more variability than drainage

lakes. Seepage lakes lost, on average, 8.2 times more surface area and water level than drainage lakes in response to the drought (mean percent surface area change = $-7.4\% \pm 6.0\%$ versus $-0.9\% \pm 1.5\%$; mean WLC = -0.8 ± 0.4 m versus -0.1 ± 0.2 m). Shorelines receded 7.4 times further in seepage lakes than in drainage lakes (mean shoreline position = -9.1 ± 4.7 m versus -1.2 ± 2.1 m).

Statistical model predicting WLC

Our statistical model reveals the relationship of potential drivers to a lake's response to drought. We developed statistical models predicting WLC in response to drought from lake and landscape variables. The most parsimonious model predicting log WLC included five of the seven covariates and an interaction term between soil permeability and conductivity (BIC = -37.6, $\Delta\text{BIC} = 2.7$, marginal- $R^2 = 0.85$).

$$\begin{aligned} \log \text{WLC} = & -3.19 + 0.278 \times \text{seepage} \\ & + 0.00254 \times \text{conductivity} + 0.00060 \times \text{soil permeability} \\ & + 0.0064 \times \text{elevation} - 0.00495 \times \text{percent wetland buffer} - \\ & \text{conductivity} \times \text{soil permeability} \times 0.000005 \end{aligned}$$

The residuals of the final WLC model are not spatially autocorrelated, indicating that the covariates included in the model adequately explained the spatial variability in log WLC (Moran's $I = 0.0019$, $p = 0.39$). The results of the statistical model indicate that lakes with the greatest water level declines are low-conductivity seepage lakes found high in the landscape with little surrounding wetland and highly permeable soils (Fig. 5).

Regional water level response to drought

There were strong spatial patterns and high among-lake variability in modeled WLC among the 342 suitably sized lakes in Vilas County (Fig. 6). Some of this heterogeneity is explained by hydrology type, with seepage and drainage lakes representing two defined peaks in the frequency distribution of WLC (Fig. 6a). However, each lake type had broad, overlapping distributions of WLC, reflecting the among-lake variability in lake and landscape characteristics that predict response to drought. At the county-wide scale, the responses of both drainage and seepage lakes to drought are spatially structured, with lakes toward the center of Vilas County responding more strongly than the northwest and far east, again reflecting differences in landscape characteristics (Fig. 6b).

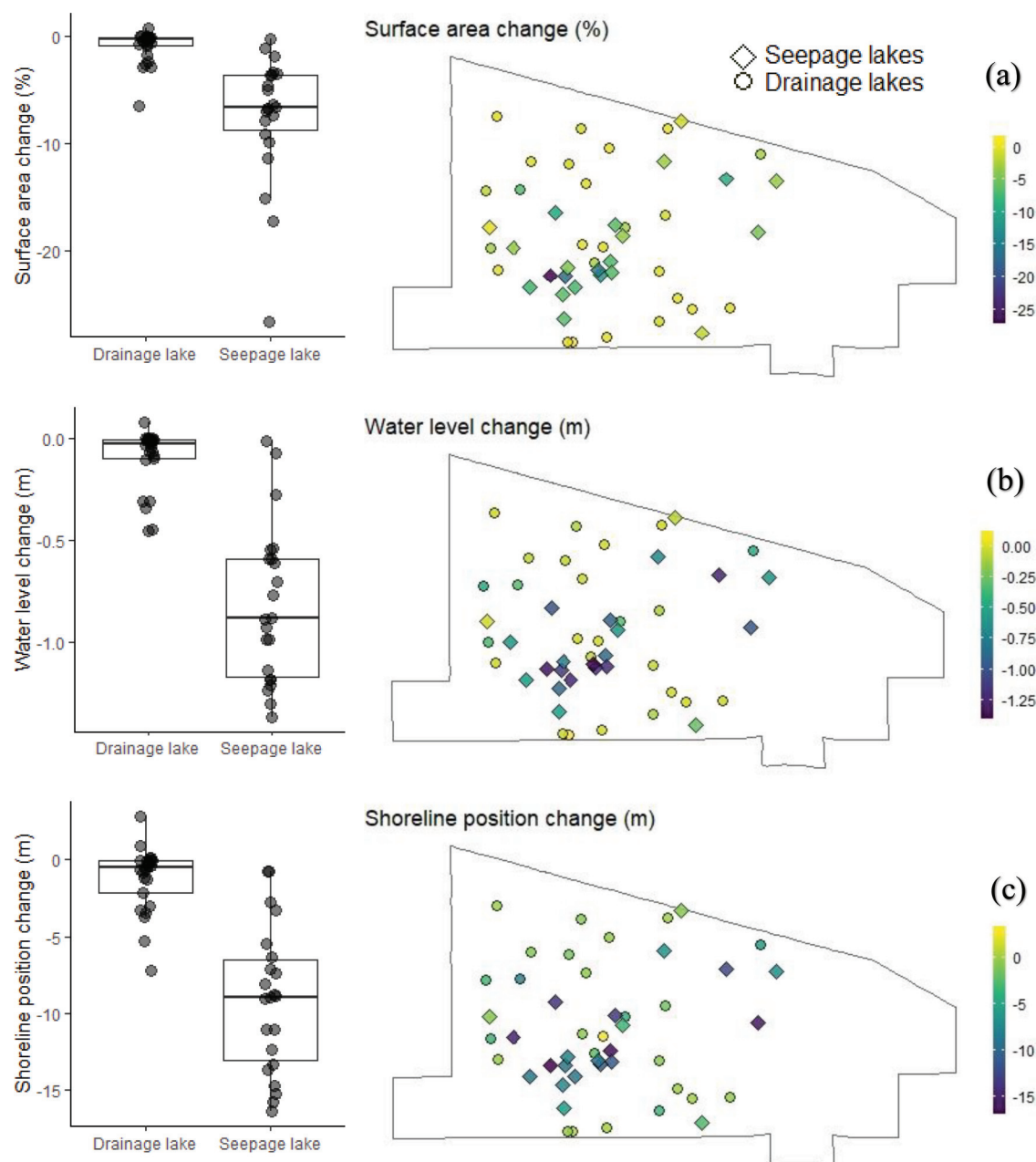
Impact of drought on littoral zone CWH

With the use of a published water level and CWH relationship for Little Rock Lake in the Northern Highlands Lake District (modified from Gaeta et al. 2014; Fig. 7a), we estimated the proportion of littoral CWH lost from each lake during the drought. Overall, lakes in the region lost an average of 23.7% of littoral CWH. The frequency distribution for the estimated percent loss of littoral CWH is right-skewed for drainage lakes, whereas seepage lakes appear to be distributed evenly across a wide range (Fig. 7b). On average, drainage lakes were estimated to have lost relatively little littoral CWH ($\bar{x} = 0.8\%$, $\text{SD} = 3.34\%$, $n = 142$), whereas seepage lakes were estimated to have lost considerably more habitat ($\bar{x} = 39.9\%$, $\text{SD} = 22.9\%$, $n = 200$). CWH losses for drainage lakes ranged from 0% to 26%, while seepage lake losses ranged from 0% to 83%.

Discussion

We documented considerable variation in lake hydrologic response to a recent multiyear drought, with some lakes responding dramatically and others not (Fig. 4). These findings are important in that they highlight the potential for adjacent ecosystems within a small geographic region to respond differently to the same driver. We quantified water level responses to drought using a combination of high-resolution orthoimagery, hypsographic curves, and a statistical model. Moreover, the statistical model was used to predict lake-specific water level response to

Fig. 4. Jitter-box plots showing observed lake responses to drought by lake hydrology type and maps showing spatial patterns in lake responses in Vilas County, Wisc. (diamonds = seepage lakes, circles = drainage lakes). Response variables include (a) percent surface area change, (b) water level change (m), and (c) shoreline position change (m). Box plots show first and third quartiles, along with the median. The whiskers are quartiles $\pm 1.5 \times$ interquartile range. Colour intensity of each point represents observed changes. [Colour online.]



drought using readily available lake and landscape characteristic data, namely hydrology type, conductance, soil permeability, and the amount of surrounding wetland (Fig. 5; Table 1). We used this model to estimate water level response to drought for lakes across the region, which indicated that certain regions and lakes will respond to drought more strongly than others (Fig. 6). Finally, to explore potential consequences of drought for a region, we estimated the proportion of littoral CWH that was lost for each lake during the drought. We estimated that drainage lake littoral zone habitat was mostly unaffected, whereas seepage lakes were disproportionately impacted (Fig. 7b).

Water level declined during the drought in most lakes, with seepage lakes responding more strongly and more variably than drainage lakes. The high variability of percent surface area

change, WLC, and shoreline position change among seepage lakes showed that hydrology type alone is insufficient for predicting lakes' hydrologic responses to drought (Fig. 4). Lake and landscape characteristics were crucial for quantifying variability in lake responses to drought. Similar to the hydrologic responses we observed, Webster et al. (1996) also found stronger chemical and water level responses to drought in seepage than in drainage lakes. Webster et al. (2000) further found heterogeneous chemical responses to drought in the groundwater-dominated lakes of the Northern Highlands Lake District as compared with other more surface-water-dominated lake districts, with these among-lake differences being mediated by the heterogeneous groundwater system (Webster et al. 2000). Our study shows that lake and landscape characteristics can be useful for understanding the magni-

Fig. 5. Model simulations showing water level change (m) prediction and 95% confidence intervals (gray lines) for each variable in the model for drainage (dashed) and seepage (solid) lakes while holding all other variables constant. The variable of interest (i.e., the x axis) was allowed to vary across the range of observed data while other variables were held constant at their mean. The predictions and confidence intervals are back-transformed to facilitate interpretation.

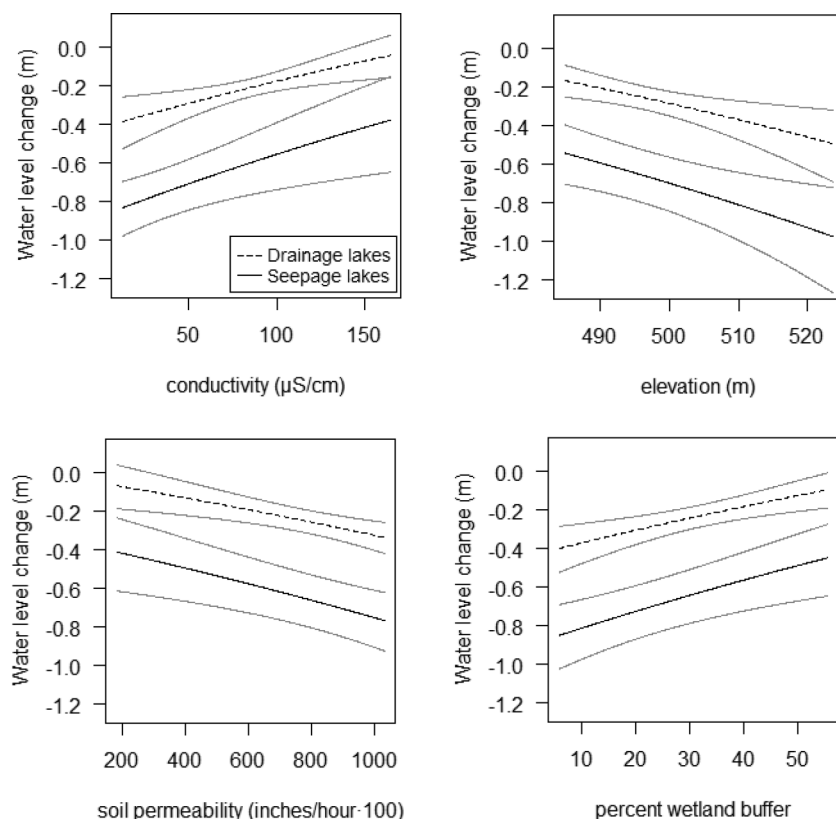
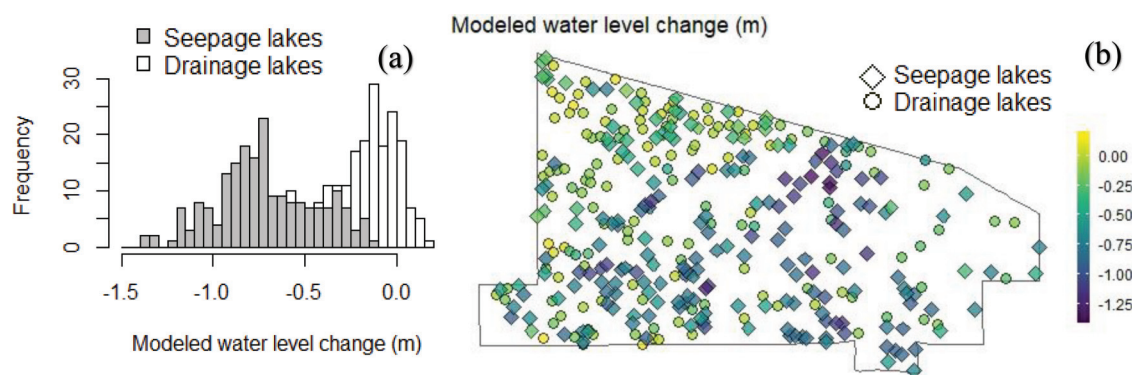


Fig. 6. Modeled water level change (m) for the 342 suitably sized lakes for which data were available in Vilas County, Wisc. (a) Stacked frequency distributions for water level change shows among-lake variability (gray = seepage lakes, white = drainage lakes). (b) Map shows spatial pattern in lake water level change (diamonds = seepage lakes, circles = drainage lakes). Colour intensity of each point represents modeled water level change (m). See online Supplemental material¹ for modeled surface area change (%) and shoreline position change (m) maps and histograms. [Colour online.]



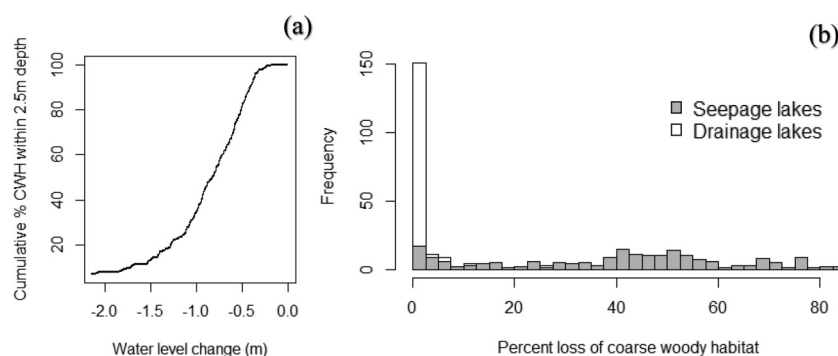
tude and variability of water level responses to drought for lakes in groundwater-dominated lake districts.

The lake and landscape variables included in the most parsimonious model are indicative of a system's vulnerability to drought, but also a lake's relative position in the landscape (Winter 2001; Magnuson et al. 2006). Lakes higher in the landscape are more sensitive to drought and changes in precipitation than lakes lower in the landscape (Cheng and Anderson 1994). Drainage lakes rep-

resent the lakes lowest in the landscape and are the least responsive to changes in precipitation. Meanwhile, seepage lakes can be more variable in terms of their position in the landscape and, thus, more variable in response to droughts (Cheng and Anderson 1994). The among seepage lake variability is ultimately tied to a lake's hydrologic budget. Thus, the lake and landscape variables we use to predict drought response also serve as proxies for a lake's position in the landscape and hydrologic budget. For exam-

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0270>.

Fig. 7. Linking water level change and coarse woody habitat (CWH) in lakes. (a) The relationship between water level (m) and the proportional loss of CWH in the littoral zone of Little Rock Lake, Wisc. (plot modified from Gaeta et al. 2014). This relationship between CWH and water level from Little Rock Lake was used as the basis for estimating how modeled changes in water level would affect littoral zone CWH. (b) Frequency distribution of the estimated percent loss of CWH in Vilas County lakes in response to the 2010 drought. Seepage lake littoral zones were disproportionately impacted compared with drainage lakes.



ple, our model indicates that higher elevation lakes with lower conductivity are more responsive to droughts (Fig. 5; Cohen et al. 2006). Lakes found higher in the landscape tend to have lower conductivity, indicating a greater reliance on precipitation (Kratz et al. 1997). Conversely, higher conductivity often indicates greater net groundwater contributions to a lake's hydrologic budget because groundwater is more ion-rich than precipitation. In general, groundwater levels are related to precipitation, but the response is integrated over longer time periods (Smail et al. 2019). Thus, a lake that relies more on precipitation will respond more quickly and more dramatically to dryer conditions than a lake that relies more on groundwater.

However, groundwater flow is dynamic and made up of regional and local flow paths, of which local flow paths are more responsive to changes in precipitation (Anderson and Cheng 1993; Webster et al. 2000). The other lake and landscape characteristics can be used to infer a lake's reliance on these different flow paths (Winter 2000). For example, highly permeable soils may be an indicator of more responsive groundwater tables because highly permeable soils are better able to transmit water (van der Kamp and Hayashi 2009). Lakes with more permeable soils nearby might indicate a lake is more likely to rely on more transient groundwater inputs that are more responsive to changes in precipitation. Further, wetlands also represent the buffering capacity of groundwater on water levels, indicating areas where the water table is consistently near the surface (Hayashi et al. 2016). Thus, our models can be used to identify lakes that are most vulnerable to droughts. In general, our statistical model indicates that low-conductivity seepage lakes that are high in the landscape with highly permeable soils and little wetland nearby showed the greatest water level declines in response to drought (Fig. 5). The beauty of these lake and landscape variables is that they are easy to measure and can serve as qualitative indicators of drought vulnerability.

An important contribution of this study was using our statistical model and regionally available lake and landscape characteristic data to "scale up" and estimate drought responses for lakes across the region and thus explore lake response to drought at the regional level rather than just for our individual study lakes. This approach allowed us to explore spatial characteristics of drought responses. According to our modelled WLC for the region, seepage lakes in northwestern Vilas County were not as affected by drought as compared with all other seepage lakes. Drainage lakes showed similar spatial patterns, which reflect differences in lake and landscape characteristics. The northwest corner of Vilas County has less permeable soils, while the central and southern portion of the county has patches of more permeable soils. Further, scaling up allowed us to generate frequency distributions of

lake responses to drought, which show that most seepage lakes respond strongly to drought (Fig. 6; see online Supplemental material¹ for regional estimates of loss in terms of percent change in water column). For example, water level decreases of >0.5 m occurred in 76.5% of seepage lakes, while only 1.4% of drainage lakes responded as strongly. These strong differences among seepage and drainage lakes is not trivial; most of the lakes in this region are seepage lakes with high potential for water level fluctuations to affect lake ecosystems.

A recent study in the Northern Highlands Lake District documented considerable ecological consequences of drought-induced habitat loss, and our study indicates that habitat loss may be prevalent across the region (Fig. 7b). Gaeta et al. (2014) documented strong responses in the littoral fish community of Little Rock Lake, a small seepage lake in northern Wisconsin, during the 2005–2010 drought. This lake's surface area shrank by 17% resulting in 76% loss of littoral CWH and altered predator–prey dynamics. The abundance of yellow perch (*Perca flavescens*), a ubiquitous prey fish species in this region, declined below the sampling detection limit as water levels declined and stranded CWH on shore. Density of largemouth bass (*Micropterus salmoides*), a predatory fish, increased initially as yellow perch abundance began to decline, but then sharply fell, presumably because the prey species became less abundant. We estimated that the amount of CWH lost in Vilas County lakes during this drought was highly variable, but that on average, seepage lakes lost ~40% of CWH (Fig. 7b). Most yellow perch were already gone at ~40% CWH loss in Little Rock Lake, suggesting that our regional estimate of CWH losses is indeed important to littoral fish communities. Further, loss of CWH in the littoral zone has been implicated in altering foraging and spawning behavior, home ranges, diet composition, and growth rates of littoral fish (Schindler et al. 2000; Sass et al. 2006; Ahrenstorff et al. 2009; Lawson et al. 2011). Thus, in addition to the many ways in which drought affects lakes, drought-mediated CWH loss may be an additional driver of littoral communities.

While most studies focus on the negative impacts of water level fluctuations, it is important to recognize that hydrologic variation in lentic ecosystems is to be expected and may be important for maintaining biodiversity and ecosystem processes (Wantzen et al. 2008a, 2008b). Multiyear drought, followed by wetter years, can be strong drivers of biotic communities. For example, waterfowl and estuarine fish populations fluctuate depending on the intensity and periodicity of wet and dry periods (Johnson et al. 2005; Sommer et al. 2007). However, the role of these multiyear wet and dry periods on structuring lentic biotic communities are not as well resolved, especially for temperate systems that do not undergo extreme desiccation. It is challenging to understand the ecological implications of this hydrologic variation. How do lakes

with little versus large hydrologic variation differ from one another? Given the strong ecological responses documented as water levels drop (Leira and Cantonati 2008), hydrologic variation may be a strong driver in certain lakes. Another unresolved facet of research is how biotic communities respond as water levels rebound in natural lakes. Are ecological responses symmetrical? For our example, do prey fish rebound when CWH is inundated once again or do new dynamics emerge? Is the long-term population viability of fish different among these lakes? The lakes that are the most variable are also isolated from other, more stable systems. These levels of hydrologic variation likely set the tone for ecological processes taking place in and around a lake. While many questions abound regarding the specific ecological consequences of hydrologic variation among lakes, our study indicates that some lake ecosystems are more strongly driven by climate and hydrology than others.

While our study focuses on drought-induced WLCs at the regional scale for north temperate lakes, we note that this study is part of a much larger body of literature documenting water level responses to climate and other factors such as water use and groundwater extraction. There are numerous examples of lake level responses to drought being quite extreme (Tweed et al. 2009; Wine et al. 2019). In semi-arid regions of China and the Mongolian plateau, drought has desiccated many hundreds of lakes, and many have dried completely (Liu et al. 2013; Tao et al. 2015). Smol and Douglas (2007) similarly documented that many small ponds in the Canadian Arctic crossed “the final ecological threshold” of complete desiccation as a result of climate warming. In Oklahoma, changes in precipitation patterns in combination with groundwater extraction has led to smaller waterbodies disappearing and sustained surface area losses in larger waterbodies (Zou et al. 2017). These studies highlight not only the overall potential for dramatic changes in lake levels as a result of shifting climate and water withdrawals, but also the potential for dramatic consequences for ecosystem services and human well-being (Brauman et al. 2007; Banerjee et al. 2013).

In conclusion, we believe the value of this study is not only the magnitude of, but also the high degree of variability of lake level responses to drought that we documented. The latter, in particular, will aid in the identification of which lakes are most vulnerable to change by future drought. Our ability to define lakes with large hydrologic variation may allow us to identify lakes that will exhibit the most dramatic responses to future drought and climate change. Because we expect the same lakes to respond similarly to future drought, the modelled drought responses can serve as indices of vulnerability to drought. Many lakes in the Northern Highlands Lake District region are small seepage lakes (Riera et al. 2000), whose littoral communities will likely change in response to future multiyear drought, especially as the frequency and magnitude of climatic cycles change (Watras et al. 2014). Our study suggests that drought may be a strong driver of hydrologic and biotic change in lakes at a regional scale. Understanding and quantifying the heterogeneity of lake responses to drought are key steps in anticipating how lakes may respond to climate change.

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