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PRIMARY RESEARCH PAPER

Detecting the effect of water level fluctuations on water quality impacting endangered fish in a shallow, hypereutrophic lake using long-term monitoring data

Jacob Kann · Jeffrey D. Walker

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Abstract Water level fluctuations (WLFs) affect phytoplankton dynamics, water quality, and fish populations in lakes and reservoirs around the world. However, such effects are system-specific and vary due to interactions with other external factors such as solar radiation, air temperature, wind, and external phosphorus loading. Utilizing data from a long-term monitoring program (1990–2016), we developed an approach using cross-tabulation contour and conditional probability analyses to detect the effects of WLFs on the frequency of poor water quality impacting native fish in a large, shallow, hypereutrophic lake. Through the incorporation of long-term inter-annual and seasonal variability in climatic factors and cyanobacterial bloom periodicity, our approach detected non-linear WLF effects whereby both high and low-lake levels were associated with higher probabilities of poor water quality conditions stressful to fish including high pH, high un-ionized ammonia, and low dissolved oxygen. Although lake level management may not prevent poor water quality in any given year due to other external factors such as temperature or wind, we determined that seasonally based intermediate lake levels bracketing the long-term median afforded the best water quality conditions for endangered fish during the summer period when poor water quality is most common.

Keywords Water level fluctuations · Shallow lakes · Water quality · Fish health · Long-term monitoring · Cyanobacteria

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J. Kann (✉)
Aquatic Ecosystem Sciences LLC, Ashland, OR 97520, USA
e-mail: jacob@aquatic-ecosciences.com

J. D. Walker
Walker Environmental Research LLC, Brunswick, ME 04011, USA

Introduction

Poor water quality and fish kills are a common occurrence in shallow eutrophic lakes (e.g., Jeppesen et al., 1998; Sayer et al., 2016), and changes in water level can adversely affect water quality critical to fish in lakes and reservoirs throughout the world (Barica, 1978; Miranda et al., 2001; Kangur et al., 2005; Goetz et al., 2014). This is particularly true in waterbodies experiencing cyanobacterial blooms that undergo large cyclic increases and decreases in biomass (Kangur et al., 2005; Kann & Welch, 2005; Kangur et al., 2013; Paerl & Otten, 2013), often leading to

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hypoxia (e.g., Paerl et al., 2016). While external nutrient loads usually determine the timing and magnitudes of cyanobacterial blooms, water level fluctuations (WLFs) can also control water quality in both shallow and deep lakes (Naselli-Flores, 2003; Nõges et al., 2003, 2007; 2010; Scheffer, 2004; Welch & Jacoby, 2004; Zohary & Ostrovsky, 2011; Jeppesen et al., 2015).

By changing lake volume and depth, WLFs can affect water quality both directly by altering physical–chemical processes, as well as indirectly by making conditions more conducive to cyanobacteria growth, which in turn leads to poorer water quality. For example, WLFs directly affect heat budgets (Gorham, 1964) and patterns of water column stability and mixing leading to modification of water temperature and dissolved oxygen (DO) dynamics (Padisák & Reynolds, 2003; Kirillin & Shatwell, 2016). WLFs also directly affect the ratio of sediment bottom area to water volume and thus influence the effect of sediment oxygen demand (SOD) on water column DO (Pace & Prairie, 2005). In addition to these direct effects on water quality, WLFs can also influence cyanobacterial bloom dynamics through changes to nutrient concentrations via sediment resuspension/efflux as well as vertical mixing of the water column (Bakker & Hilt, 2016; Havens & Ji, 2018), and by modifying water column light availability (Nõges et al., 2003). By altering cyanobacterial bloom dynamics, WLFs can thus indirectly affect water quality by causing high pH during growth periods (Kann & Smith, 1999; Kangur et al., 2016), and hypoxia and toxic levels of ammonia during bloom decline periods (Mericas & Malone, 1984; Kann & Welch, 2005; Kangur et al., 2013; Paerl et al., 2016).

The specific effects of WLFs on cyanobacterial blooms and water quality can vary depending on trophic state, lake depth, morphometry, sediment composition, hydraulic residence time, and external nutrient loading (Bakker & Hilt, 2016). In addition, the effects of water level drawdown differ between deep lakes and unstratified, polymictic shallow lakes (sensu Padisák & Reynolds, 2003). In deep lakes that undergo stratification, the primary effects of drawdown include erosion of the thermocline and changes in the euphotic zone (e.g., Naselli-Flores & Barone, 2003; Zohary & Ostrovsky, 2011). In shallow lakes, drawdown may increase both water column light availability (Nõges et al., 2003, 2010) and wind-driven sediment resuspension leading to increased nutrient concentrations (Søndergaard et al., 1992; Jeppesen et al., 2000; Koski-Vähälä & Hartikainen, 2001; Tammeorg et al., 2013, 2015; Bakker & Hilt, 2016). A recent review of case studies showed that water level drawdown resulted in a greater proportion of lakes with increased cyanobacteria levels compared to those with decreased cyanobacteria (Bakker & Hilt, 2016). Similarly, while other drivers may also affect cyanobacteria dynamics, minimizing drawdown was expected to reduce cyanobacteria dominance and phytoplankton biomass (e.g., Yang et al., 2016, 2017). Borics et al. (2013) also concluded that phytoplankton density in shallow polymictic lakes is often inversely proportional to the lake depth, and that raising water levels should be considered for water quality improvement.

Although minimizing drawdown should generally improve water quality critical to fish, local conditions and diverse effects of WLFs (e.g., Bakker & Hilt, 2016; Yang et al., 2016) necessitate system-specific evaluations to determine water level management that improves water quality. Here, we use a long-term monitoring dataset from a large, shallow lake in the northwest United States (Upper Klamath Lake, UKL) as an example for applying graphical and statistical analyses to evaluate the effects of WLFs on water quality. In UKL, algal bloom-driven degradation of water quality has caused extended periods of low DO, elevated pH, and toxic levels of un-ionized ammonia, all of which have been linked to large fish kills and spatial redistribution of endangered sucker species (Perkins et al., 2000; Kann & Welch, 2005; Banish et al., 2009; Rasmussen, 2011).

Conceptually, water level management in UKL has the potential to act either directly on water quality conditions that may elicit fish response (e.g., morbidity, mortality, or movement) or indirectly by minimizing cyanobacterial blooms and subsequent poor water quality (Fig. 1). For example, lake level increases may reduce the effect of recycled phosphorus (P) flux from the sediment by diluting water column P, or by reducing wind-driven sediment resuspension (Laenen & LeTourneau, 1996) in shallow UKL (pathways affecting internal P recycling; Fig. 1). In addition, the ratio of lake-sediment area to lake volume can double in low-lake elevation years compared to higher elevation years (Kann & Welch, 2005) leading to directly proportional effects of SOD

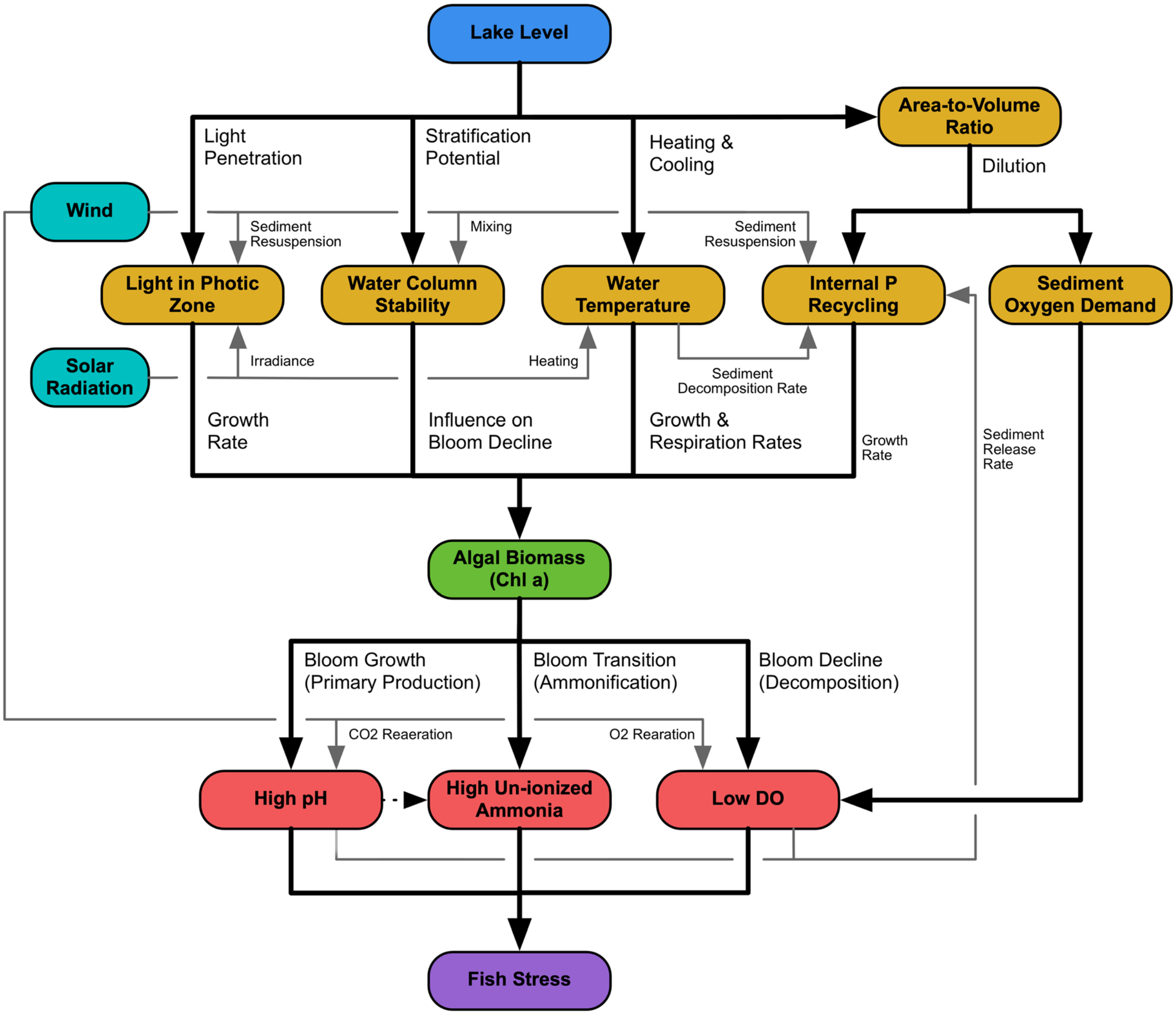

Fig. 1 Conceptual diagram showing interactions and pathways between lake level and water quality in Upper Klamath Lake

and recycled P flux per unit volume (Livingstone & Imboden, 1996). Superimposed on the WLF-water quality linkages are external factors such as solar radiation, wind, and watershed P loading. Although these external factors are not directly affected by WLFs, they can interact via numerous pathways to influence both the frequency and year-to-year variability of poor water quality in UKL (e.g., Kann & Welch, 2005). Because climatic factors are not manageable and external P reductions are being addressed by other watershed restoration efforts, this study specifically focused on the effect of WLFs on the frequency of poor water quality in UKL.

Due to the complex relationships between the physical, chemical and biological processes in shallow lakes such as UKL, analyses to evaluate the effects of WLFs on water quality dynamics must not only account for site-specific factors, but also variability induced by other external drivers. For UKL, a primary strength of our analysis is the availability of 27 years of long-term water quality monitoring data that incorporates wide variability in inter-annual and seasonal climatic factors and bloom periodicity (e.g., pathways including temperature, wind, light, and algal growth and decay; Fig. 1). Based on the conceptual WLF pathways (Fig. 1), our goal was to test the hypothesis that poor water quality conditions adversely affecting endangered fish would vary seasonally as a function of lake level. Specifically, we utilized cross-tabulation contour and conditional probability analyses along with significance testing to determine whether the frequencies of high algal biomass and stressful levels of pH, un-ionized ammonia, or dissolved oxygen were related to lake levels over the long-term period of record (1990–2016). If such relationships were detected, a secondary goal was to determine lake-level management targets that would reduce the probability of poor water quality events adversely affecting endangered UKL suckers.

Materials and methods

Study area

Upper Klamath (UKL) and Agency Lakes comprise a large (surface area 270 km^2), shallow (mean depth 2.1 m) lake system located in southern Oregon in the Pacific Northwest U.S. (Fig. 2). Both lakes are hypereutrophic and the phytoplankton community is seasonally dominated by blooms of the nitrogen-fixing cyanobacterium *Aphanizomenon flos-aquae* Ralfs ex Bornet et Flahault (Kann, 1998; Kann & Smith, 1999). Historically, paleolimnological studies indicate that these blooms were not always dominant in UKL, and that *A. flos-aquae* increased in response to land-use alterations that included timber harvest, drainage of wetlands, agricultural activities, and hydrologic modifications such as water diversions and channelization (Snyder & Morace, 1997; ODEQ, 2002). Paleolimnological coring studies showed increases in indicators (e.g. Ti, Al, tephra, and charcoal) of watershed erosion to UKL in the 20th century, as well as the appearance of *Aphanizomenon* akinetes circa the late 1800s (Bradbury et al., 2004; Eilers et al., 2004; Simon & Ingle, 2011).

Nutrient load reduction to UKL (particularly for P) has been identified as an important means of reducing algal biomass and improving water quality conditions that affect native fish species in UKL (ODEQ, 2002). Total Maximum Daily Load modeling efforts predicted that reductions of external anthropogenic P loads would result in decreased in-lake water column and sediment P, chl-a, and pH levels (Wherry et al., 2015; Wherry & Wood, 2018). Efforts to reduce external P loads were initiated in the 1990s and included restoration of wetlands (Stevens & Tullos, 2011; Wong et al., 2011), stream channels, and riparian zones. However, there is often a delay in the response of in-lake P following such restoration measures given the time needed to restore the ecological structure and functioning of previously degraded systems (Hamilton, 2012; Mueller et al., 2015; Van Meter & Basu, 2015), as well as the slow depletion of legacy P remaining on former crop or grazing lands (Duff et al., 2009; Wong et al., 2011; Sharpley et al., 2013). Thus, additional measures such as water level management are of interest in conjunction with restoration efforts to reduce P loads and improve water quality in UKL.

Although historically a natural lake, the hydrology of UKL has been significantly altered by hydroelectric power diversions, irrigation diversions and returns, deforestation, and, most dramatically, by the construction of the Link River Dam at the lake outlet in 1921. During construction of the dam, channels were cut into a natural basalt reef at the lake's outlet that historically prevented minimum elevations from falling below 1261.8 m (Fig. 3a). Following construction of the dam, water levels were often lowered by as much as 1.5 m in dry years and the range of annual WLFs approximately doubled from 0.5–1.0 to 0.75–1.75 m (Fig. 3a). Due to the shallowness of UKL, these WLFs translate to large relative changes in mean depth. For example, annual mean depth minima during dry years ($\sim$ 1 m) were approximately 45% lower compared to pre-dam annual minima ($\sim$ 1.75 m). Thus, unlike many dams that are designed to increase water level and lake storage, the Link River dam permits higher elevations to be maintained longer into the early summer period, followed by lake levels lower than were historically possible as the summer algal growing season progresses. Lake surface elevations in UKL dropped below the historical minimum of 1261.8 m in every year during the current study period (1990–2016), except 1997 and 1999 (Fig. 3b).

Establishment of critical periods and primary water quality thresholds

Historical spatially weighted daily mean lake surface elevations for UKL were obtained for the January 1, 1990 to December 31, 2016 study period (USGS Station 11507001; USGS, 2017). Missing values were estimated for 43 days (out of 9862 total) by linearly interpolating between the two nearest observations. Water quality data collected at seven continuously

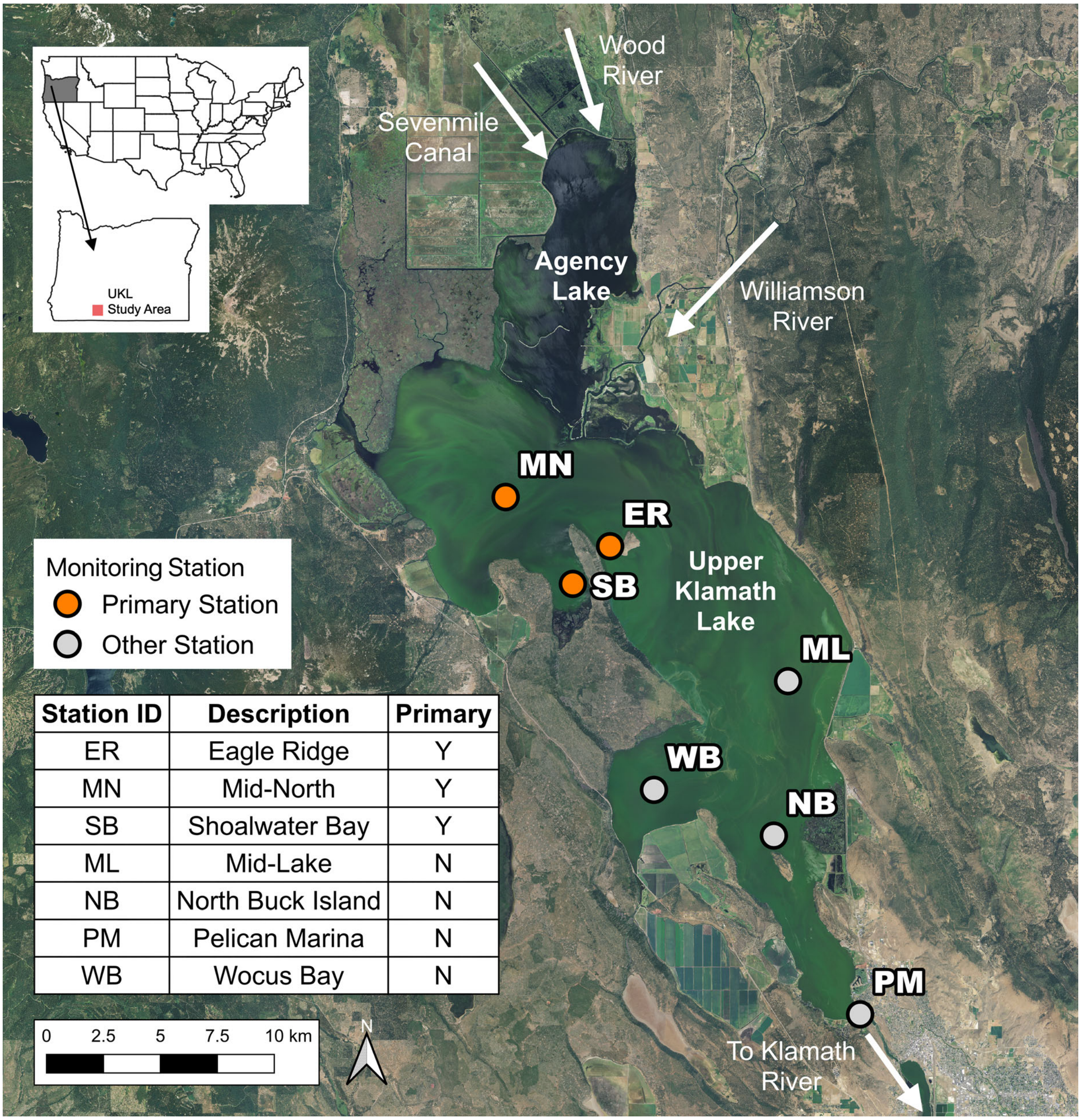

Fig. 2 Satellite image showing the location of Upper Klamath Lake and long-term monitoring stations, and visible surface accumulations of *Aphanizomenon flos-aquae*, the primary UKL bloom former. Imagery Source: Oregon Imagery Explorer (http://imagery.oregonexplorer.info), 2012 NAIP Survey

monitored stations within UKL were obtained from the Klamath Tribes Long-Term Monitoring Network for the same period, 1990–2016 (Fig. 2). Water samples were collected approximately biweekly (14-days) from late-April through October in all years except 1990 when samples were collected weekly. For each sampling event, depth-integrated grab samples were analyzed for chl-a and ammonia–nitrogen (Eaton et al., 1995), and vertical profiles were collected for DO, temperature, and pH at approximately 1-m intervals through the water column. Sample collection and analysis followed the Klamath Tribes standard operating procedures (Klamath Tribes, 2013a, b; Kann, 2017).

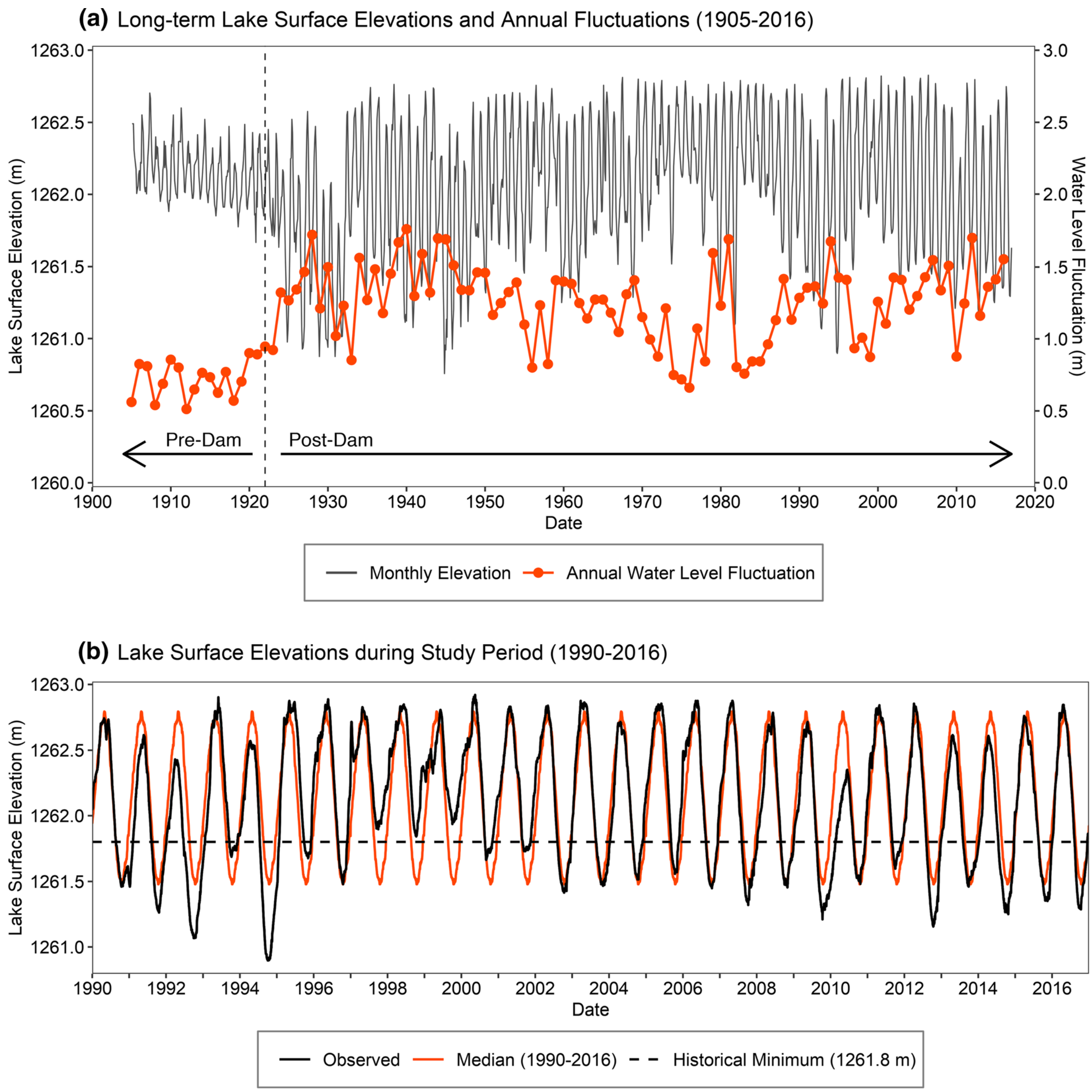

Fig. 3 Historical (1905–2016) Upper Klamath Lake minimum monthly surface elevation shown with annual water level fluctuations (**a**), and daily mean lake surface elevation and period of study median, 1990–2016 (**b**). Annual water level fluctuations computed as the difference between annual maximum and minimum elevations

For this study, we focused on four primary water quality variables: DO, pH, un-ionized ammonia (calculated from measured total ammonia with pH and temperature corrections; USEPA, 2013), and chl-a. Three of these variables (DO, pH, and un-ionized ammonia) can directly cause high stress to endangered fish species in UKL (Loftus, 2001). The fourth variable (chl-a) does not directly cause high stress but was included in this study to represent changes in algal biomass associated with bloom formation and decline. For DO and pH, mean values were calculated over the bottom 1 m of each vertical profile and will be referred to as "Bottom DO" and "Bottom pH". Because suckers are oriented to and generally feed near the lake bottom (Banish et al., 2009), these metrics were considered more directly related to sucker stress than mean values over the entire water column. Analyses were performed utilizing data from three long-term stations representing the adult sucker habitat zone located in the north-western portion of the lake (Banish et al., 2009): Eagle Ridge (ER), Mid-North (MN), and Shoalwater Bay (SB) (Fig. 2). The remaining stations (ML, NB, PM, WB) were used to evaluate the spatial sensitivity of the results.

For each variable, the analyses were based primarily on samples collected during a critical period, which is defined as the seasonal portion of the year when the highest (or lowest for DO) concentrations most often occur. The start and end of each critical period was determined by calculating the rolling 14-day exceedance frequencies for a range of threshold concentrations based on individual samples from all years. One of these thresholds was selected as the primary threshold and represented the concentration above (or below for DO) which conditions were stressful for native fish. The primary thresholds were 4.0 mg/l for bottom DO and 9.75 for bottom pH (high stress thresholds identified for UKL suckers; Loftus, 2001), 200 μg/l for chl-a (the concentration at which pH values tend to exceed 9.75; Kann & Smith, 1999), and 200 μg/l for un-ionized ammonia (the sub-lethal level identified for juvenile UKL suckers; Meyer et al., 2000). Although toxicity from elevated un-ionized ammonia varies with pH and temperature (Loftus, 2001), this threshold was based on pH levels and temperatures common in UKL, and therefore, represented an average stress threshold. For each variable, the critical period was selected as the period containing the largest peaks in concentrations and exceedance frequencies among all thresholds, and for which the exceedance frequency of the primary threshold was greater than approximately 10%. Although the concentrations and exceedance frequencies remained elevated outside the critical period for some variables, to be consistent across the four variables and to match the typical length of the bloom growth and decline phases in UKL, each critical period was limited to a maximum duration of 1½ months.

Cross-tabulation contour plots

Cross-tabulation contour (CTC) plots were constructed to graphically represent the relationship between water quality conditions and lake elevation during the summer algal growth period. The CTC plots build upon non-parametric cross-tabulation analyses commonly used to determine exceedance frequencies of water quality variables such as chl-a, cyanobacterial toxins, phosphorus, or pH, as a function of another driving variable (e.g., Heiskary & Walker, 1988; Havens, 1994; Walker & Havens, 1995; Kann & Smith, 1999; Lindon & Heiskary, 2009). The CTC plots were constructed using a contouring algorithm to depict how both the mean concentrations and exceedance frequencies of primary water quality thresholds varied seasonally and as a function of lake elevation. This algorithm, the details of which are provided in the Electronic Supplementary Material, was used to generate a continuous gridded surface where each grid cell was color-coded to represent expected water quality conditions (either mean concentration or exceedance frequency) over varying lake levels (y-axis) and day of the year (Julian day; x-axis).

The sensitivity of the primary CTC plots with respect to either any 1 year of data or any one monitoring site (i.e., the spatial sensitivity) was evaluated by generating a series of alternative CTC plots for each water quality variable using temporal and spatial subsets of the primary dataset. To evaluate the influence of any 1 year of data, a series of 27 CTC plots were generated by leaving out 1 year of data at a time. To evaluate spatial sensitivity, we compared the CTC plot based on the three adult sucker habitat stations (ER, MN, SB) to alternative CTC plots based on samples from each of those sites individually as well as from all seven long-term sites combined (ER, MN, SB, ML, NB, PM, WB; Fig. 2) to determine how well the results for the adult sucker habitat zone compared to the lake as a whole.

Significance of observed patterns

We used the non-parametric Kruskal–Wallis test (Helsel & Hirsch, 2002) to determine if the patterns observed in the CTC plots were statistically significant, meaning there was a sufficiently small probability of these patterns occurring if the sample values were randomly generated and independent of lake elevation. For each water quality variable, the statistical tests were performed using only samples collected during the critical period of that variable and by grouping those samples into five discrete lake elevation bins. Since UKL elevations decline over the season in each year (Fig. 3b), the bins were based on the relative (i.e., seasonally detrended) lake elevation computed as the difference between the daily elevation and the 1990–2016 median elevation for each day of the year (ESM Fig. 1). Using relative elevations thus avoided loading the lowest elevation bin with a greater proportion of samples collected later in a given critical period when lake levels were often lower in general. The five bins were delineated using relative elevation quantiles in 20% increments so that each bin contained an equal number of samples. The bins were designated as “Low” (relative elevation ranging from − 0.76 to − 0.16 m), “Below Average” (− 0.16 m to − 0.06 m), “Average” (− 0.06 m to 0.075 m), “Above Average” (0.075 m to 0.19 m), and “High” (0.19 m to 0.49 m).

If the Kruskal–Wallis tests resulted in significant *P* values (less than 0.05 was considered highly significant; between 0.05 and 0.1 was considered somewhat significant) indicating that the distributions across the five relative elevation groups were not identical, the post hoc Conover–Iman test was performed to determine which pairs of specific bins were significantly different (Conover & Iman, 1979). The p values calculated by the Conover–Iman test were adjusted using the Holm correction to control the familywise error rate associated with multiple comparisons (Holm, 1979). Choosing the number of bins for these tests involved trade-offs between having too few bins that fail to capture variability in water quality among elevation bins, and too many bins that reduce the statistical power of the test by having fewer samples within each bin. Therefore, sensitivity of the statistical test results to bin size was evaluated using alternative numbers of relative elevation bins (three to eight bins) in addition to the five bins used for the primary analysis.

Conditional probability plots

In addition to the Kruskal–Wallis tests, which were performed on discrete relative elevation bins, we also generated conditional probability plots that provide continuous relationships between the frequency of water quality exceedances and relative lake elevation. Conditional probability plots have been used in other studies to depict relationships between water quality variables and various controlling factors (Paul & McDonald, 2005; USEPA, 2006; Paul et al., 2008). For example, Paul & Munns (2011) identified thresholds of biological effects based on varying pollutant levels, and Hollister & Kreakie (2016) evaluated the probability of exceeding health advisories based on microcystin concentrations over varying chl-a concentrations. In both of these examples, the relationship between the two variables was based on a cumulative frequency statistic and assumed to be monotonic. However, for UKL the relationship between water quality and lake elevation was not assumed to be monotonic because poor water quality occurred at both high and low lake elevations for some variables. Therefore, a modified version of the method used in those studies was developed whereby a rolling (instead of cumulative) conditional probability was computed over a sliding window of relative elevation. Specifically, the conditional probability of a water quality variable (Y) exceeding its primary threshold (Y^*) was calculated from samples having a relative elevation (X) within a window of width (w) and center (X^*):

$$P\left(Y > Y^* | X^* - \frac{w}{2} < X < X^* + \frac{w}{2}\right)$$

For each variable, the conditional probabilities were calculated over a series of rolling windows with centers (X^*) ranging from the minimum to the maximum observed relative elevation at 0.05 m increments and using a fixed width (w) of 0.5 m. The conditional probabilities were then plotted as a series of points showing the computed probability of each rolling window interval and positioned at the center of that window. Uncertainty ranges were generated using the bootstrap method by resampling each relative elevation window 1,000 times with replacement and calculating the 90% confidence intervals of the resulting distribution of computed probabilities (Hollister et al., 2008).

Identifying seasonal lake-level targets to reduce risk of poor water quality

To evaluate the overall risk of poor water quality relative to lake elevation over the course of the season, we combined the CTC plots of all four variables into a single CTC plot using the maximum exceedance frequency among the four variables on each Julian day and elevation increment. The combined CTC plot thus shows the highest probability of poor water quality over the season irrespective of which of the four variables was associated with that maximum probability. We then identified the range of lake levels that had the lowest combined probability of poor water quality relative to the minimum achievable probability on selected days. To account for alternative levels of risk tolerance, two sets of lake-level ranges were identified based on combined probabilities within fixed ranges of 5% or 10% relative to the minimum achievable probability on the selected dates. The specific steps to identify each set of lake-level ranges are described in the Electronic Supplementary Material.

Results

Bloom periodicity and critical water quality periods

In general, two phases of *Aphanizomenon* blooms, each lasting approximately 1½ months, tended to occur in any given year in UKL (ESM Fig. 2). Although the magnitude and timing of blooms varied from year to year, the first phase encompassed a period of active growth and the development of high levels of algal biomass from late-May through July. The second phase consisted of a period of bloom decline from mid-July through August, sometimes extending into September. Water quality associated with these bloom phases included high pH during the initial biomass increase and low DO during bloom decline as biomass decomposed and oxygen input via photosynthesis diminished (Fig. 4a, b, c, d, g, h). Un-ionized ammonia levels also increased during and following the blooms, and highest values usually occurred during the transition from active growth to bloom decline during late-June to mid-July (Fig. 4e, f). These increases in un-ionized ammonia levels were due to ammonification as organic matter accumulation was coupled with decreased DO during bloom decline periods. In some years, a secondary bloom re-growth phase occurred during August or September (ESM Fig. 2); however, these secondary blooms were generally smaller in magnitude than the primary blooms ocurring earlier in the season.

Given that water quality is tied to bloom periodicity, and that lake level effects may differ between algal biomass, pH, un-ionized ammonia, or DO, the critical period for each variable was selected based on the seasonal patterns in both concentration and exceedance frequencies (Fig. 4). In general, each critical period included the primary peaks in the exceedance frequencies of the various thresholds, as well as the period during which the exceedance frequency of the primary threshold was predominantly greater than $\sim$ 10%. Although the exceedance frequencies remained elevated past the end of the critical period in some cases, we limited the periods to a maximum duration of 1½ months (which is the typical duration of each bloom growth and decline phase; ESM Fig. 2) to ensure consistency among the four variables. For example, the exceedance frequency of the primary chl-a threshold (200 µg/l) remained slightly greater than 10% into August and September due to secondary biomass increases (Fig. 4b). However, the initial bloom peak and decline clearly occurred prior to the end of July (ESM Fig. 2), and exceedances of the 9.75 primary pH threshold, which is controlled directly by algal photosynthesis in UKL (Kann & Smith, 1999), declined below 10% by the end of July (Fig. 4d). Thus, for chl-a and pH, we defined the critical period as being from June 15th to July 31st, which represents the typical period of initial bloom formation (Fig. 4a–d). For un-ionized ammonia, the critical period was defined from June 25th to August 7th representing the typical transition period from active bloom growth to bloom decline (Fig. 4e, f). For DO, even though exceedance frequency of the primary threshold (4 mg/l) remained somewhat elevated (10–20%) during September, concentrations generally showed an increasing trend after September 1st (Fig. 4g). Thus, to capture the primary period of seasonally decreasing DO due to bloom decline we defined the critical period as July 15th to August 31st (Fig. 4g, h).

Relationships between water quality and lake elevation

CTC plots

The CTC plots provide graphical representations of the seasonal water quality patterns for chl-a, pH, un-ionized ammonia, and DO at varying lake levels (Fig. 5). Although the specific patterns varied among the four variables, the CTC plots generally showed that poorest water quality tended to occur at the highest and/or lowest lake elevations. Furthermore, poor water quality (indicated by the yellow-to-red

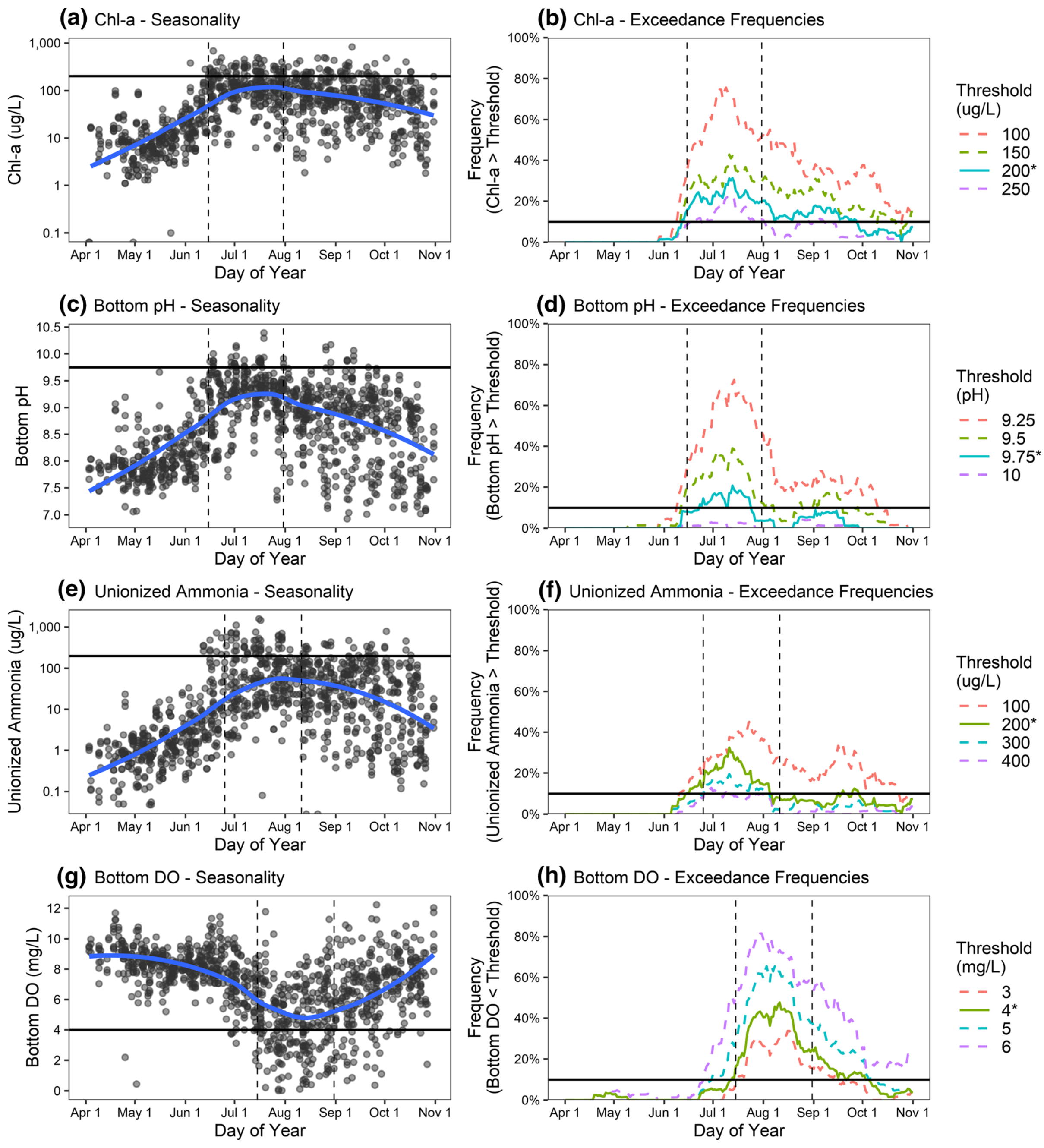

Fig. 4 Seasonal trends and designated critical periods (vertical-dashed lines) for chl-a (**a**, **b**), bottom pH (**c**, **d**), un-ionized ammonia (**e**, **f**), and bottom dissolved oxygen (**g**, **h**) during the study period (1990–2016). Concentration panels (**a**, **c**, **e**, **g**) are shown with primary water quality thresholds (black solid lines) and the LOESS trend (blue lines) based on individual samples for all stations and years (circles). Exceedance frequency trends (**b**, **d**, **f**, **h**) are based on the 14-day centered moving average of the percent of sample events with values above (or below for DO) varying thresholds (* denotes primary threshold) and include a horizontal line denoting the 10% limit used in part to delineate critical periods

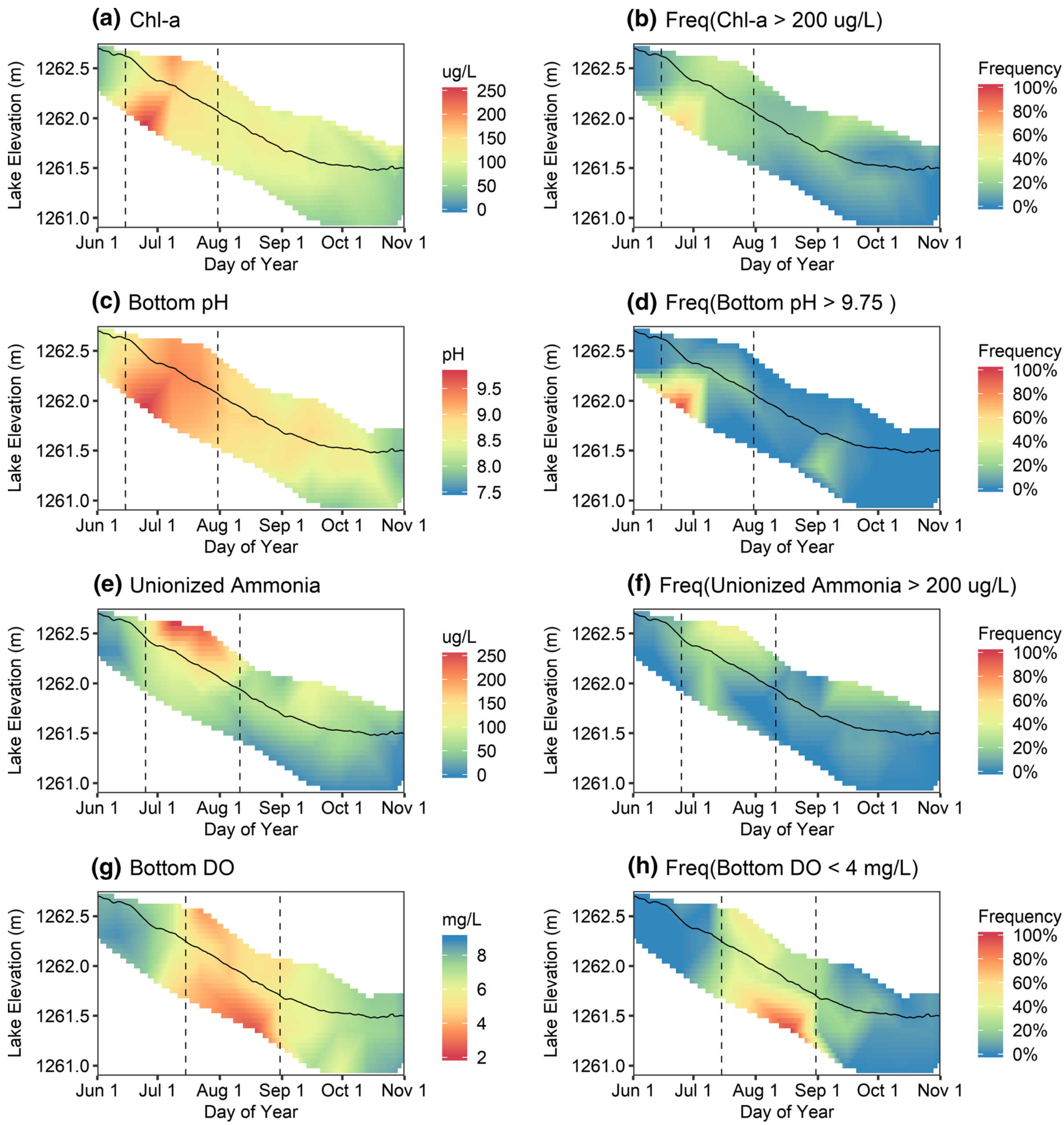

Fig. 5 Cross-tabulation contour plots for chl-a, pH, un-ionized ammonia, and DO concentration and associated frequency metrics

colors; Fig. 5) primarily occurred within the critical period of each variable (vertical-dashed lines; Fig. 5) confirming that each critical period delineation accurately represented the portion of the year when poor water quality was most common.

For both chl-a and bottom pH, the highest concentrations and exceedance frequencies occurred at low lake elevations (i.e., below the median) during the first half of the critical period from June 15th to July 7th (Fig. 5a–d). Later in the critical period, high-chl-a concentrations and frequencies as well as high bottom pH levels also occurred at elevations above the median, though they were not as high as those at the low elevations (Fig. 5a–c). For un-ionized ammonia, the highest concentrations and exceedance frequencies occurred at high-lake elevations over the entire critical period (Fig. 5e, f). And lastly, the lowest bottom DO concentrations and highest exceedance frequencies of low DO occurred at the lowest elevations in mid-August (Fig. 5g, h). Although less extreme than at lower elevations, low bottom DO concentrations and high-exceedance frequencies also occurred at high elevations during the critical period. Collectively, the CTC plots indicate that lake elevations near the long-term median provide the best opportunity for good water quality by avoiding extreme high or low elevations at which the highest (or lowest for DO) concentrations and exceedance frequencies tended to occur.

With the exception of chl-a, the lake level-water quality patterns observed during respective critical periods in the primary CTC plots were insensitive to any one year of data or to which station or combination of stations was used to generate the plots (ESM Figs. 3 to 10). For chl-a, the high-exceedance frequencies that occurred at low elevations in the CTC plots were sensitive to the lowest elevation year of 1992; however, excluding the 1992 data still showed that elevated chl-a occurred at lower June–July lake elevations but with lower probability than when 1992 was included. In addition, the chl-a pattern was more pronounced at station SB, and the DO pattern of higher exceedance frequencies occurring at both high and low elevations was more pronounced at station ER. Although un-ionized ammonia showed higher exceedance frequencies at high elevation in September at station ER, this pattern occurred outside of the critical period.

Significance of observed patterns

Kruskal–Wallis testing showed statistically significant ($P < 0.05$) differences among the five relative elevation bins for bottom pH, un-ionized ammonia, and bottom DO, and generally confirmed the lake elevation-water quality patterns observed in the CTC plots (Fig. 6). Among these three variables, the post hoc Conover–Iman test revealed significant ($P < 0.05$) pairwise differences between the low and both the high and average elevation bins for bottom pH (Fig. 6b), between the below average and both the average and above average elevation bins for un-ionized ammonia (Fig. 6c), and between the below average and both the high and low bins for DO (Fig. 6d). Although slightly less significant ($P = 0.0574$), the post hoc test also showed a difference between the low and above average bins for un-ionized ammonia. In addition, lower un-ionized ammonia concentrations were observed in the highest elevation bin, a pattern not evident in the CTC plots. For both pH and un-ionized ammonia, significance levels were relatively insensitive to the number of elevation bins (ESM Figs. 12–13), while for DO they were somewhat sensitive (ESM Fig. 14) with significant results ($P < 0.10$) using 5, 6, or 7 bins but not 3, 4, or 8 bins. These results may indicate that too few bins do not capture sufficient variability in the data, especially since the relationship is non-linear and adjacent low and high DOs are canceled out if the bins are too large. Moreover, statistical power is reduced with a greater numbers of bins (e.g., 8 bins) having fewer samples per bin.

Despite higher chl-a concentrations and exceedance frequencies at low elevations shown in the CTC plots, chl-a levels during the critical period were not significantly ($P > 0.10$) different among the five relative elevation bins (Fig. 6a). In addition, sensitivity to the number of relative elevation bins does not provide strong evidence for a significant relationship between chl-a and lake level during the June 15th to July 31st critical period (ESM Fig. 11). Lack of significance for chl-a may be due to the high variability in algal bloom timing (ESM Fig. 2), as well as the complex causes for secondary blooms that may obscure any relationship associated with the initial bloom.

Conditional probability analysis

The conditional probability analyses reflect the general patterns observed in the CTC plots whereby lower exceedance probabilities of the primary thresholds occurred at intermediate elevations for both chl-a and bottom DO, at high elevations for pH, and at low elevations for un-ionized ammonia (Fig. 7). The probability of pH > 9.75 monotonically declined from 37% at $-$ 0.4 m to 0% at the highest relative elevation of 0.5 m (Fig. 7b). Although pH exceedance probabilities at the lowest relative elevations ($<$ 0.75 to $-$ 0.40 m) were greater than at higher elevations, they exhibited larger variability and wider confidence bands due to a fewer number of samples and because those samples only occurred in two specific years (1992 and 2014) when algal biomass and pH

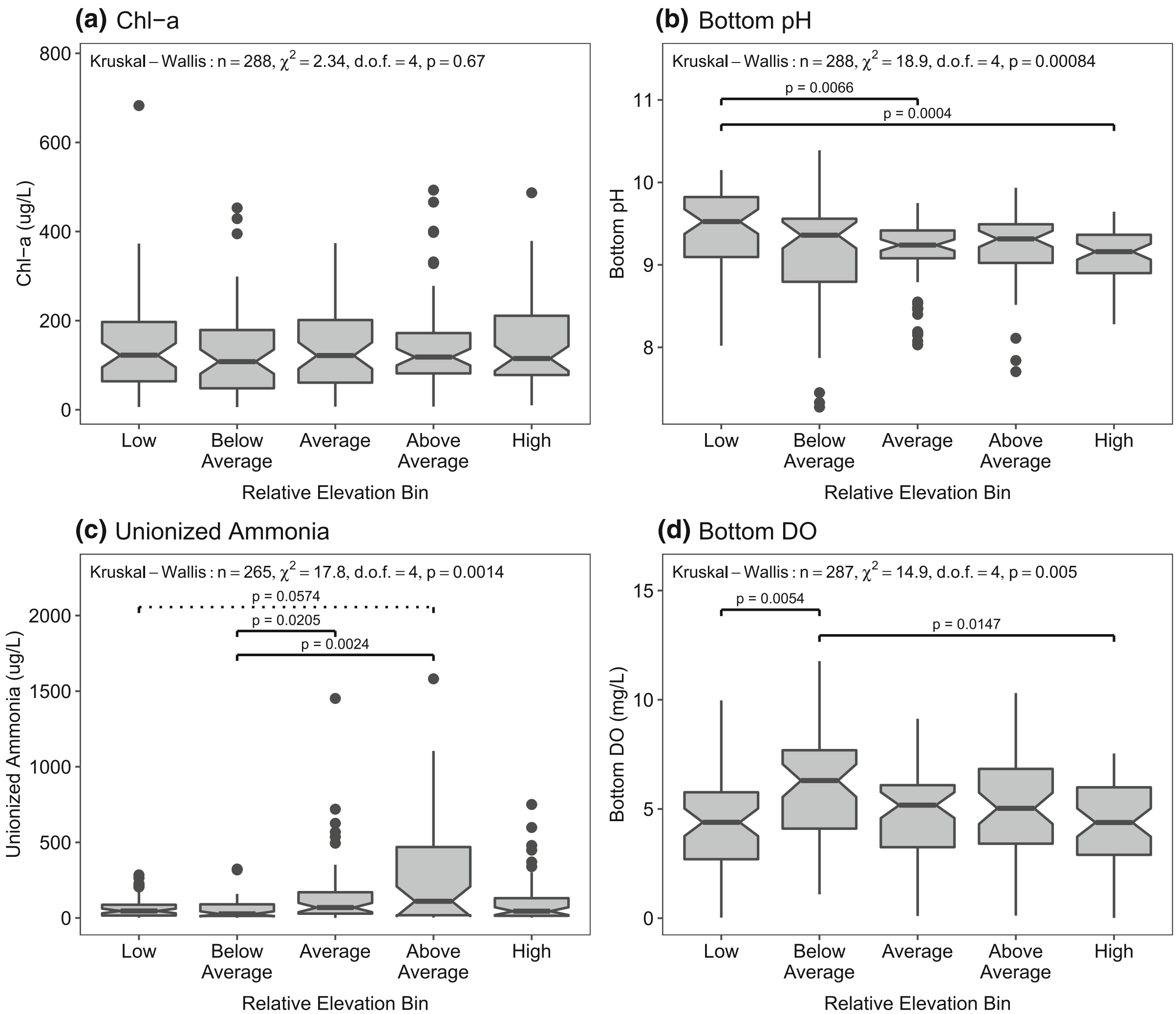

Fig. 6 Notched box-and-whisker plots and Kruskal–Wallis test results for chl-a (**a**), bottom pH (**b**), un-ionized ammonia (**c**), and bottom DO (**d**). Box mid-line = median, lower/upper notches = 95% confidence interval of median, lower/upper hinges = 25th and 75th percentiles, lower/upper whiskers = minimum/maximum values within 1.5 times interquartile range (IQR) of median, circles = values more than 1.5 * IQR from median. Horizontal brackets link relative elevation bins showing significant (solid line: $P < 0.05$, dashed line: $P < 0.10$) differences based on Conover-Iman pair-wise comparisons among all relative elevation bins

atypically declined early in the season (ESM Fig. 2). For un-ionized ammonia, the probability of exceeding 200 μg/l increased from a range of 8–14% at the lowest relative elevations (− 0.65 to − 0.25 m) to nearly 30% at 0.3 m, and similar to the bin pattern for the Kruskal–Wallis test then decreased to 20% at the highest elevation (0.5 m; Fig. 7c). The probability of bottom DO < 4 mg/l increased from 29% at a relative elevation of − 0.25 m (which is slightly below the median) to nearly 50% at the lowest relative elevation (− 0.60 m) and to 47% at the highest relative elevation of 0.5 m (Fig. 7d).

Identifying seasonal lake level targets to reduce the risk of poor water quality

Since lake-level effects differed among the four water quality variables, determination of lake levels that minimize the overall risk of poor water quality required an approach that incorporated multiple trade-offs. For example, during overlapping critical

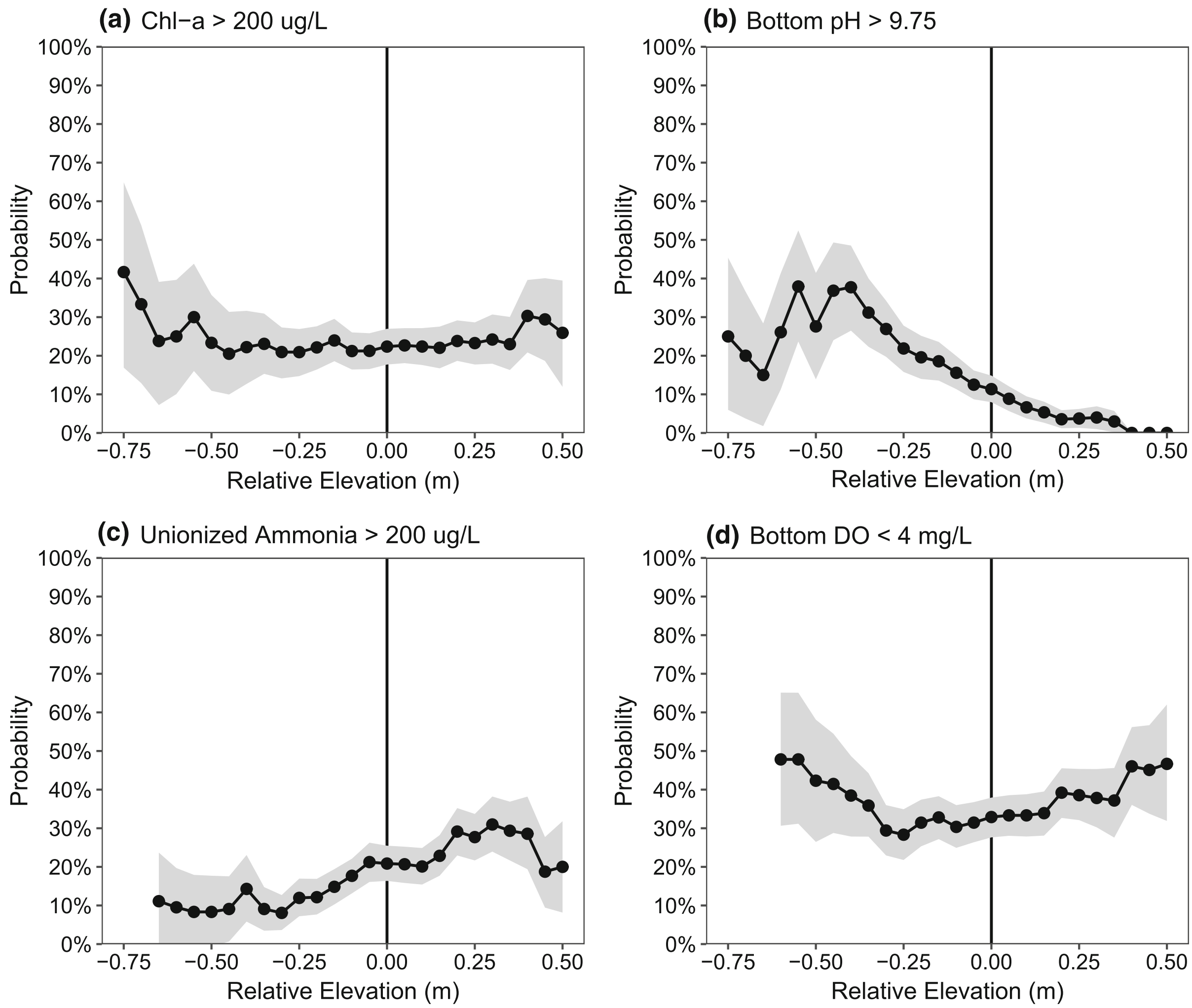

Fig. 7 Conditional probability plots shown with 90% confidence intervals (gray band) for chl-a (**a**), bottom pH (**b**), un-ionized ammonia (**c**), and bottom DO (**d**)

periods for pH and un-ionized ammonia, low lake levels that minimize the risk of high un-ionized ammonia would increase the risk of stressful pH levels. To address these trade-offs, the combined CTC plot depicts the overall water quality pattern over varying lake levels by reflecting both the high (i.e., hot spots that are evident on the individual CTC plots; Fig. 5b, d, f, h) and low exceedance probabilities among all four variables on any given day of the season (Fig. 8). During some portions of the target period, no single lake level was clearly associated with an overall minimum risk because the combined exceedance probabilities were relatively uniform over a wide range of lake levels (e.g., 1262.25–1262.65 m on June 15th; Fig. 8). Thus, the targeted lake levels on the selected days (black circles; Fig. 8) denoted by the fixed upper and lower bounds (red 5% and blue 10% polygons; Fig. 8) account for seasonal changes in risk (i.e., lower risk levels occurring early in the season, highest risk level occurs in the middle of the season) as well as instances when there was little change in risk over a range of lake elevations. The target lake elevations (Table 1) associated with the 5% (red) and 10% (blue) polygons, therefore, avoid areas representing the highest probability of poor water quality (red areas; Fig. 8), which generally correspond to the highest and lowest lake elevations at various points over the season.

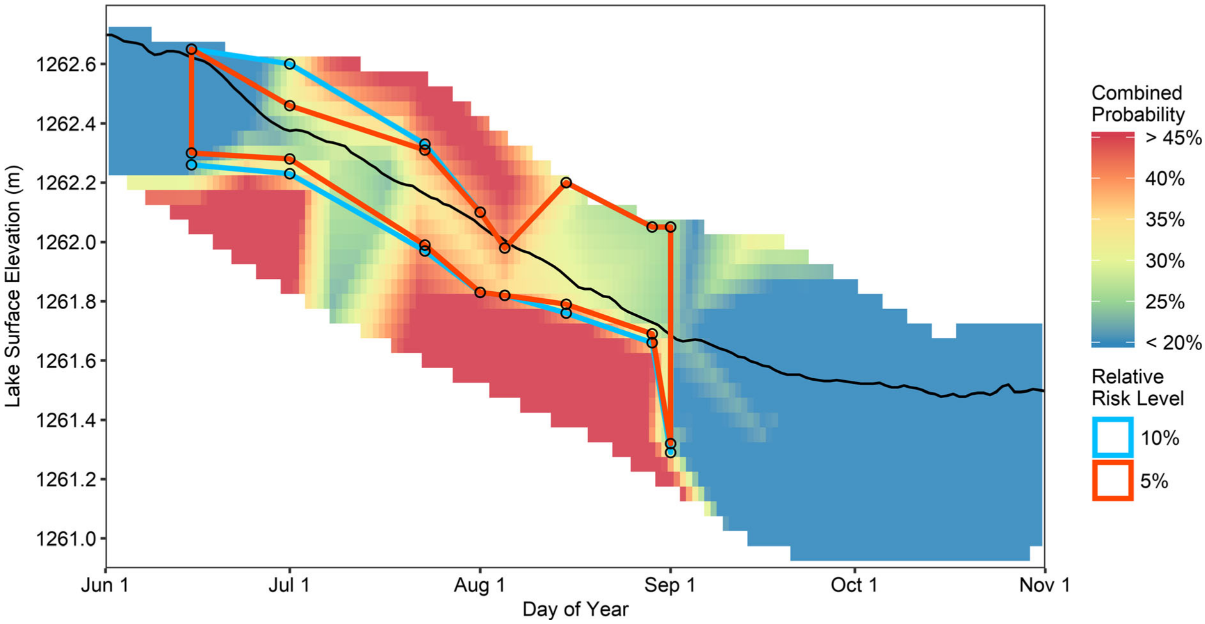

Fig. 8 Cross-tabulation contour chart of combined exceedance probability across all four variables with median lake elevation (black line) and target lake level ranges corresponding to relative risk tolerance levels of 5 and 10% (red 5% and blue 10% polygons) on selected dates (black circles)

Table 1 Minimum risk level and target lake level ranges for relative risk tolerances of 5 and 10% on selected dates

Target date	Minimum risk		Target lake level ranges	
	Combined probability (%)	Lake level (m)	5% risk tolerance	10% risk tolerance
June 15	10.5	1262.35	1262.30–1262.65 m	1262.26–1262.65 m
July 1	23.9	1262.35	1262.28–1262.46 m	1262.23–1262.60 m
July 23	34.1	1262.15	1261.99–1262.31 m	1261.97–1262.33 m
August 1	35.1	1261.95	1261.83–1262.10 m	1261.83–1262.10 m
August 5	35.7	1261.85	1261.82–1261.98 m	1261.82–1261.98 m
August 15	29.3	1262.05	1261.79–1262.20 m	1261.76–1262.20 m
August 29	25.3	1261.75	1261.69–1262.05 m	1261.66–1262.05 m
September 1	21.6	1261.35	1261.32–1262.05 m	1261.29–1262.05 m

Discussion

For shallow UKL, relatively small WLFs on the order of 1–2 m translate to large differences in mean depth and volume, and thus WLFs have the potential to influence algal blooms, water quality, and fish response through multiple causal pathways (Fig. 1). However, whether the effects of WLFs on cyanobacteria blooms and subsequent water quality are observable depends on the stochastic nature of climatic controlling factors such as wind and temperature that can act to obscure these effects. Algal biomass levels in large shallow polymictic lakes, in particular, are sensitive to natural physical drivers (e.g., Scheffer, 2004). Such physical drivers also affect lake water quality, as do the dynamics of plankton and fish communities (Kangur et al., 2013; Mackay et al., 2014; Jeppesen et al., 2015; Kangur et al., 2016). Havens et al. (2017) showed the mediating effect of climatic cycles on lake depth and subsequent cyanobacteria blooms, and the substantial effect of temperature and vertical mixing on bloom formation and water quality on lakes in general has been well demonstrated in a number of studies (Huisman et al., 1999, 2004; Reynolds, 2006; Moreno-Ostos et al., 2009; Paerl et al., 2016; Havens & Ji, 2018). Specifically for UKL, Kann & Welch (2005) showed the effect of wind speeds on water column stability and subsequent DO concentrations.

Given the various pathways by which WLFs could both directly and indirectly affect water quality in UKL (Fig. 1), we hypothesized that the frequency of poor water quality events adversely affecting endangered fish would vary seasonally and as a function of lake level. We found evidence to support this hypothesis through a series of analyses using a long-term (27-year) monitoring dataset that incorporated wide inter-annual variation in physical and biological conditions. Collectively, the CTC plots, conditional probability analyses, and Kruskal–Wallis tests provided strong evidence that both high and low lake levels were associated with higher probabilities of exceeding fish stress thresholds in UKL at various points in the season. Lake levels near the long-term median generally provided the overall lowest risk of poor water quality.

Our results were consistent with previous analysis showing that indicators of poor water quality (specifically, those associated with morbidity and mortality of endangered suckers) were tied to the periodicity of large cyanobacterial blooms (Kann & Smith, 1999; Perkins et al., 2000; Kann & Welch, 2005; Banish et al., 2009). High chl-a and bottom pH levels generally occurred at the lowest lake elevations between June 15th and July 15th when the initial algal bloom tended to occur in most years. In contrast, high levels of un-ionized ammonia tended to occur at high lake elevations between June 25th and August 7th as the bloom reached its peak magnitude. Although more extreme at low lake elevation, high frequencies of bottom DO less than 4 mg/l showed a non-linear pattern, occurring at both high elevations from July 15th to August 15th and at low elevations from August 1st to August 31st during the period of bloom decline.

While the CTC plots revealed that poor water quality tended to be associated with either high or low lake elevations, the Kruskal–Wallis tests, with the exception of chl-a, confirmed that these observed patterns were statistically significant during the respective critical period of each variable. Although the Kruskal–Wallis test result for chl-a was not statistically significant, conditional probability analyses reflected a pattern similar to the low lake elevation-high chl-a pattern observed in the CTC plots. These high chl-a levels occurred only at the lowest relative lake elevations (< -0.6 m) and were due to 1 year (1992), which had the lowest June elevation of the 27-year study period. Combined with the statistically significant decline in the frequency of stressful pH levels with increased lake elevation, these analyses show that lake levels equal to or above the 1990–2016 median during the June 15th to July 31st critical period were associated with reduced probability of poor water quality.

Although the effect of WLFs on pH should be similar to that of chl-a due to the controlling effect of photosynthesis on pH (Kann & Smith, 1999), the discrepancy in the results between the two variables may reflect that pH is an indicator of lake productivity that is less variable than chl-a, and that pH is directly related to lake levels via other mechanisms. One mechanism is the direct effect of productivity on pH, which should be reduced at higher elevations due to a smaller lake area-to-volume ratio compared to lower elevations. Mechanistically, at a given areal rate of productivity, the volumetric productivity rate is expected to be lower at higher lake volume corresponding to higher lake elevation. For example, Brylinsky & Mann (1973) noted that while shallow and deep lakes have similar production per unit area under a given energy and nutrient regime, shallow lakes are expected to have higher production per unit volume. Similarly, Fee (1979) indicated that while areal primary productivity generally remains similar in lakes of differing trophic status, volumetric primary productivity is lower in lakes with greater mean depth. A similar effect was previously observed in the UKL system whereby higher pH levels were predicted at a given chl-a level in the shallower Agency Lake relative to UKL (Kann & Smith, 1999). The effect of lake level on pH was also shown for Lake Võrtsjärv in Estonia, a large, shallow, eutrophic lake that is very similar in area (270 km^2 vs. 266 km^2) and mean depth (2.8 m vs. 2.2 m) to UKL. In that case, a lake level increase of 1.5 m (corresponding to a mean depth increase of about 1 m) resulted in a decrease in available light, algal production, biomass, and pH (Nõges & Järvet, 1995; Nõges et al., 1997, 2003).

The net effect of lake level on un-ionized ammonia during the initial bloom growth phase likely occurred through two opposing mechanisms: (1) higher lake levels being associated with lower pH levels decreases the fraction of total ammonia in the toxic un-ionized form; and (2) higher lake levels reduce both wind-driven vertical mixing and light penetration to off-bottom waters causing reduced photosynthetic oxygen production fostering further ammonification and subsequent ammonia buildup. Thus, if the goal is to improve water quality for fish in UKL, lake-level management must balance the increased probability of high pH at lower lake levels, with increased probability of high ammonia at higher lake levels during the period of peak bloom magnitude

Likewise, the non-linear effect of lake level on DO (at intermediate lake levels the probabilities of bottom DO less than 4 mg/l were lower than those at both the highest and lowest elevations) during the July–August period of bloom decline likely resulted from multiple offsetting mechanisms. At higher lake levels, the ratio of bottom sediment area (as a source of sediment oxygen demand, SOD) to lake volume decreases and is, therefore, expected to result in lower consumption of DO over the entire water column. Conversely, SOD is expected to exert a greater effect on water column DO at lower lake levels due to a higher sediment area-to-volume ratio. Although the positive relationship between DO consumption and the ratio of sediment area to water volume is well established (e.g., Pace & Prairie, 2005), this effect may be offset by wind-driven reaeration of the water column because lower lake levels allow for greater reaeration rates and thus higher DO, while higher lake levels tend to increase water column stability (Kann & Welch, 2005) which reduces reaeration and decreases DO. Furthermore, there is an increase in the percent of the water column in the photic zone at lower lake levels (for a given light extinction rate) allowing for more photosynthetically-produced oxygen, but less light penetration to greater depth at higher lake levels with reduced off-bottom oxygen production. Thus, although a smaller lake volume can increase the effect of SOD and lead to decreased water column DO, this effect can be offset by greater reaeration and light penetration resulting from decreased depths. Nõges & Nõges (1999) also noted increased light and improved mixing that was associated with higher DO concentration in shallow compared to deep conditions in Lake Võrtsjärv. Our results indicate that the net effect of these processes leads to the highest probability of DO greater than the high stress level for target fish when the lake is maintained at intermediate levels, which balance the offsetting effects during the bloom decline phase.

Maintenance of intermediate lake levels would not necessarily prevent low DO events from occurring in any given year since extended periods of low wind speed, high temperatures, or large bloom decline can cause low DO even when the lake is maintained at these intermediate lake levels. These mechanisms are well established in UKL (e.g. Kann & Welch, 2005). In general, water column DO has been shown to reach very low levels during calm periods in shallow lakes, especially following the rapid decline of cyanobacterial blooms (Barica, Barica, 1978; Kangur et al., 2005, 2016). Nevertheless, the results here show that over the long-term period of record, which includes a variety of wind and bloom decline conditions, the probability of achieving a low DO event at intermediate depths (25–30%) was nearly half the probability at either the lowest or highest elevation groupings (40–50%).

As noted above, the stochastic nature and inter-annual variability of external factors may act to decrease the signal-to-noise ratio and can thus obscure the effects of WLFs on water quality in UKL. Failure to account for these as well as the seasonally dynamic and controlling effect of bloom periodicity has likely led several earlier studies to come to alternative conclusions with regard to these lake level effects. For example, using a dataset consisting of nine years of data, NRC (2004) concluded that the annual growing season means of chl-a, pH, and DO were not related to lake level based on seasonally aggregated scatter plots. However, the expected effect of increased lake level on blooms via reducing water column light (Fig. 1; sensu Nõges et al., 2003) and decreasing resuspension of internally recycled P (Fig. 1.; sensu Tammeorg et al., 2013, 2015) is only expected to operate during active algal growth periods such as the critical period of June 15th to July 31st identified in this study, but not during periods of bloom decline when algal biomass and pH are expected to be largely independent of lake level. Therefore, the scatter plots utilizing data outside the algal bloom-driven critical period likely obscures lake elevation relationships with water quality, as well as the type of non-linear DO pattern observed in our study.

Considering the complex interactions involving lake levels, sucker habitats, phosphorus loading, mixing, phytoplankton blooms, and toxic conditions, another early review of lake level effects in UKL concluded that even if no strong direct correlation was observed due to noise caused by the complexity of the system, there is credible evidence of a connection between lake level and the welfare of endangered suckers in UKL (IMST, 2003). Although no overarching variable or combination of variables was revealed, a subsequent multivariate study that did consider some of the complex interactions found evidence that both water temperature and lake level appeared to be important variables in explaining the variability of minimum DO concentrations observed in UKL (Morace, 2007). Utilizing a much longer dataset containing a large number of samples, and methods that accounted for bloom periodicity using variable-specific critical periods within which to evaluate lake level effects (e.g., CTC plots and conditional probability analyses with statistical confirmation), our study was able to demonstrate a clear effect of lake elevation on water quality.

Since lake level effects differed among the four water quality variables, determining specific target lake levels over the period of algal bloom and decline required making a set of assumptions regarding overall management constraints, goals, and acceptable levels of risk. The intermediate target lake level ranges bracketing the long-term median based on 5 and 10% risk tolerance levels for selected dates (Fig. 8; Table 1) provide a basis for management and operational decisions with the goal of reducing the probability of poor water quality negatively impacting endangered suckers in UKL. Alternative target lake level ranges could also be generated based on other chosen risk tolerance levels, and ultimately, specification of target lake levels would require consideration of broader management goals and acceptable risk tolerance levels, as well as other factors such as sucker habitat availability and operational constraints. Nevertheless, the results presented here provide a quantitative basis for making these decisions.

The techniques presented here provide an approach for detecting the effect of lake levels on water quality using long-term datasets. As noted by others (e.g., Dodds et al., 2012; Lindenmayer et al., 2012), utilization of long-term monitoring data allows for the incorporation of complex ecological dynamics across a wide range of hydrologic and climatic conditions and is, therefore, important for quantifying the complex non-linear interactions that are common in many ecosystems. Moreover, increased water abstraction along with expected changes in temperature and precipitation patterns due to global climate change could exacerbate the effects of eutrophication in lakes that are already eutrophic (e.g., Jeppesen et al., 2015) and may cause extended periods of shallow lake depth that can hinder long-term water quality improvement expected from external P reduction efforts (Ji & Havens, 2019). Therefore, understanding the role of WLFs in water quality and fisheries dynamics is critical for integrating climate resiliency into future lake management efforts.

Conclusions

Considering the complexity of the theoretical basis for the effect of WLFs on water quality in UKL (Fig. 1), and the potential for non-linear relationships, we utilized a series of techniques (e.g., CTC plots and conditional probability plots) to evaluate the effect of WLFs on water quality within the context of seasonality and without prior assumptions regarding linearity. Although the results varied by parameter and over the course of the season, we found that water quality varied as a function of lake level, and our analyses revealed that the highest probabilities of poor water quality were associated with both high and low lake levels. To account for both seasonal changes in risk as well as instances when the risk is relatively uniform over a range of lake elevations, we determined a range of target lake levels associated with reduced probability of exceeding critical water quality thresholds during the June 15th to September 1st core period when poor water quality conditions were most common. Lake level target ranges based on risk tolerance levels of 5 and 10% generally followed intermediate lake levels (spanning the long-term median lake level), and avoided relatively high and low lake levels that were associated with a high risk of poor water quality among all four variables.

Although maintenance of the target lake levels over the long-term would be expected to reduce the frequency of poor water quality negatively affecting and preventing the recovery of endangered native fishes in UKL, lake level management alone may not necessarily prevent poor water quality or a fish kill in any given year due to effects of other climatic drivers that can affect water quality (e.g., higher or lower than average temperature or wind).

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Compliance with ethical standards

Conflict of interest Analyses were completed as part of research to evaluate water levels necessary to support fish populations for the Klamath Tribes. Jacob Kann was previously employed by and has received research funding from the Klamath Tribes.

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