

Classifying Lakes to Quantify Relationships Between Epilimnetic Chlorophyll *a* and Hypoxia

Lester L. Yuan · Amina I. Pollard

Received: 8 May 2014 / Accepted: 21 November 2014 / Published online: 4 December 2014
© Springer Science+Business Media New York (outside the USA) 2014

Abstract Excess nutrient loading increases algal abundance which can cause hypoxia in many lakes and reservoirs. We used a divisive partitioning approach to analyze dissolved oxygen profile data collected across the continental United States to increase the precision of estimated relationships between chlorophyll *a* (chl *a*) concentrations and the extent of hypoxia in the water column. Chl *a* concentrations predicted the extent of hypoxia most accurately in lakes that were stratified at the time of sampling with a maximum temperature gradient of at least 1.2 °C/m. Lake elevation, Secchi depth, and lake geometry ratio further refined the specification of groups of lakes with different relationships between chl *a* and the extent of hypoxia. The statistical relationships between chl *a* and the extent of hypoxia that were estimated can be used directly for setting management thresholds for chl *a* in particular types of lakes.

Keywords Lake · Hypoxia · Chlorophyll *a* · Stressor-response · Classification

Introduction

Excess nutrient loading is one of the main causes of ecological degradation in freshwater systems worldwide (Smith

2003). Increased nutrient concentrations in a waterbody can stimulate algal growth, and often, the subsequent decomposition of the algal organic matter can substantially reduce dissolved oxygen concentrations in the water column. These hypoxic conditions are extremely inhospitable to many aquatic species and influence their distribution (Wetzel 2001). Owing to the effects on biota, the occurrence and factors related to hypoxic conditions are of interest to resource managers. For example, a summary of lake status reports indicates that oxygen depletion is identified as the fifth most common reason for degradation, affecting 1.4 million surface acres of lakes across the United States (http://ofmpub.epa.gov/waters10/attains_nation_cy.control).

In individual lakes, detailed process-based models can often accurately predict changes in dissolved oxygen (DO), but the data requirements for these models can be extensive. Process-based models are based on a relatively complete understanding of the mechanisms which control the rate at which DO is depleted from a lake, including physical factors that control mixing, factors that influence algal growth rates, and factors that influence organic matter decomposition rates (Bella 1970; Di Toro et al. 1983; Stefan and Fang 1994). However, models such as these require substantial data for calibration. For example, one of the key input parameters for these models is sediment oxygen demand (SOD), which expresses the rate at which decomposition of sediment organic material depletes dissolved oxygen (Livingstone and Imboden 1996). SOD is difficult to quantify accurately for an entire lake (Bowman and Delfino 1980; Cross and Summerfelt 1987; Rippey and McSorley 2009) and is rarely measured during routine monitoring. So, its value in a model is often assumed based on other studies (del Giorgio and Williams 2005), modeled simply based on estimates of nutrient loading (Chapra and Canale 1991), or modeled explicitly in terms of the

L. L. Yuan (✉)
Office of Science and Technology, Office of Water, U.S.
Environmental Protection Agency, 1200 Pennsylvania Ave NW,
Washington, DC 20460, USA
e-mail: yuan.lester@epa.gov

A. I. Pollard
Office of Wetlands, Oceans, and Watersheds, Office of Water,
U.S. Environmental Protection Agency, 1200 Pennsylvania Ave
NW, Washington, DC 20460, USA

different chemical and biological processes that consume oxygen (Walker and Snodgrass 1986). Other extensive measurements, such as daily meteorological observations, and repeated observations of nutrient concentrations and flows entering and exiting the water body, are also often required for calibrating process-based models (Hamilton and Schladow 1997). Hence, calibrating and running these models for many different lakes is resource intensive (Stefan et al. 1996).

Statistical models can potentially be better suited for guiding management actions for groups of water bodies because they can provide insights into average responses among these water bodies using available data. For example, in the case of DO, a common management action is to specify threshold levels of algal biomass or nutrient concentrations to avoid hypoxic conditions in the majority of lakes in a region. To specify this threshold for a single lake, one might choose to run a process-based model and identify nutrient and chlorophyll *a* (chl *a*) concentrations that maintain DO at levels necessary for aquatic life. However, the limited availability of data usually precludes calibrating and running these models for most lakes in a region. Statistical models can be based on the same underlying scientific knowledge as process-based models (i.e., that decomposition of algal biomass can lead to decreases in dissolved oxygen). However, these models can be calibrated using just the data that are available for the majority of lakes in a region. Then, conclusions can be drawn regarding the average response of the sampled lakes and tempered by an understanding that much of the uncertainty in the estimated relationships is caused by factors that are unmeasured and not included in the model (Reckhow 1988).

Data collected by the National Lakes Assessment (NLA) provide an opportunity to test whether statistical models can provide information that is useful for managing algal abundance to maintain DO at levels that protect aquatic life. The NLA sampled randomly selected lakes and reservoirs across the contiguous United States in 2007 and at each of these lakes, collected an extensive suite of environmental measurements. Included in each sample were vertical profiles of dissolved oxygen and temperature, which we analyzed to better understand large scale patterns in the relationships between epilimnetic algal biomass (as quantified by chl *a* concentration) and oxygen depletion in the lake. We hypothesized that higher concentrations of chl *a* would generally be associated with increases in the extent of hypoxia at these large spatial scales, and that taking into account lake morphological characteristics and other environmental conditions would improve the precision of estimated relationships between chl *a* and hypoxia. Our specific goal for this analysis was to identify different classes of lakes in which chl *a* concentrations were predictive of hypoxic conditions.

Materials and Methods

Data

Data used for this analysis were collected by the NLA in the summer (May–September) of 2007 (US EPA 2010), available at http://water.epa.gov/type/lakes/NLA_data.cfm. Lakes greater than 4 ha and at least 1 m deep were selected from the contiguous United States primarily using a stratified random sampling design, but supplemented by selecting by hand a small number of lakes to serve as relatively undisturbed reference lakes or as repeat samples from the 1972 National Lake Eutrophication Study (Gakstatter et al. 1976).

At the deepest point of each lake (or in the midpoint of reservoirs), a multiparameter water quality meter was used to measure profiles of dissolved oxygen (DO) concentrations, temperature, and pH at a minimum of 1-m depth intervals. Profiles for shallow lakes were sampled at 0.5-m depth intervals. Temperature gradient (Tgrad), a measure of the magnitude of the thermocline, was computed between all available depths below 0.5 m as the difference in temperature between two successive measurements divided by the difference in the depths of the two measurements. Samples collected in the uppermost 0.5 m were excluded to limit the effects of surface warming on gradient calculations. The maximum observed temperature gradient was then retained for each sample.

At this same location, Secchi depth was measured, and water was sampled using a vertical, depth-integrated methodology that collected a water sample from the photic zone of the lake (to a maximum depth of 2 m). Multiple sample draws were combined in a rinsed, 4-L cubitainer. When full, the cubitainer was gently inverted to mix the water, and a subsample was poured off to obtain a water chemistry sample. After collection, water samples were placed on ice and shipped overnight to the Willamette Research Station in Corvallis, Oregon, which quantified true color, sulfate concentration (SO₄), acid neutralizing capacity (ANC), and chl *a* concentrations (and other analytes that were not considered in this analysis) at pre-specified levels of precision and accuracy (US EPA 2006).

Lake physical characteristics were estimated from mapped data. These characteristics included lake surface area (Area), geographic location (latitude and longitude), elevation (Elev), lake catchment area, and lake perimeter. From these characteristics, we calculated the following composite variables: (1) the drainage ratio, which is defined as the ratio of catchment area to surface area and characterizes the degree to which the lake catchment influences the lake, (2) the shoreline development (SLD), which is defined as the ratio between the perimeter of the lake and the perimeter of circle with the same area as the

lake and characterizes the geometric complexity of the lake shore; and (3) the lake geometry ratio, which approximates the ratio between fetch and maximum depth as $\text{Area}^{0.25}/\text{Depth}$, and has been shown to differentiate lakes that stratify seasonally (low values of the geometry ratio) from lakes that are polymictic (Gorham and Boyce 1989; Stefan et al. 1996).

Variables quantifying the mean annual precipitation (Precip) and maximum monthly average air temperature (Temp) were extracted from 30-year-averaged climatic data (Daly et al. 2008).

Summary statistics of chl *a*, the extent of hypoxia, and the variables used as candidates for classification are shown in Table 1. Candidate variables for classifying lakes were selected based on a general understanding of the environmental factors that can possibly affect the degree to which increased algal abundance is manifested as hypoxia. Chief among these factors was stratification strength, which controls the degree to which vertical diffusion can transport oxygen to the lower depths of a lake. We used maximum observed temperature gradient (Tgrad) as a direct measure of stratification strength at the time of sampling, and included several other variables that are known to influence stratification such as lake depth, lake surface area, and lake geometry ratio. We also included factors that influence warming of the lake, including maximum monthly average air temperature and average

precipitation at the lake location, Secchi depth, and water color, as these also can influence stratification strength. The average air temperature variable had the added potential of influencing water temperature and thus, controlling the saturation concentration of dissolved oxygen in the water. Similarly, water color can influence the degree to which solar radiation warms the water column, and potentially can approximately quantify the concentrations of humic substances in the water and the associated chemical oxygen demand (Vuorenmaa et al. 2006). We included sampling day of the year as a candidate variable, because oxygen depletion in the hypolimnion usually progresses gradually after spring turnover in dimictic lakes (Molot et al. 1992). Finally, we included water chemistry variables (ANC and SO_4) that might influence decomposition rate (Kelly et al. 1984; Holmer and Storkholm 2001).

Statistical Analysis

A variety of approaches have been proposed to measure the severity of hypoxia in lakes and reservoirs (Nürnberg 1995), but we chose simply to quantify the extent of hypoxia as the proportion of samples in which $\text{DO} < 2 \text{ mg/L}$. The value of 2 mg/L was selected as the threshold for hypoxic conditions following standard practice, although many aquatic organisms do suffer adverse effects when DO concentrations decrease below higher threshold concentrations (Vaquer-Sunyer and Duarte 2008). The selection of a simple proportion of depths to quantify the extent of hypoxia was preferable to other analytical approaches [e.g., hypoxic metrics based on the rate of oxygen depletion (Walker 1979; Nürnberg 1995)] because very little temporal data (i.e., DO profiles in time) and no measurements of lake bathymetry were available for the national-scale dataset used in this analysis. Although hypoxia is most frequently observed in the hypolimnion of a lake, we used the entire water column to quantify the extent of hypoxia because a wide variety of lakes were sampled with varying degrees of mixing and stratification. Our simple definition permitted a consistent measurement of the extent of hypoxia across all lakes in the dataset. Also, the selected response variable is directly linked to the loss of habitable areas in the lake for fish and other aquatic organisms.

The relationship between epilimnetic chl *a* concentration and the extent of hypoxia in different lakes was estimated using a generalized linear model, in which the sampling distribution of the response variable (i.e., the proportion of samples that were hypoxic) was modeled as a quasibinomial distribution (McCullagh and Nelder 1989). Use of this sampling distribution properly accounted for the fact that possible values for the extent of hypoxia were bounded by 0 and 1.

To refine the estimated relationships between chl *a* and the extent of hypoxia, we grouped lakes by applying a

Table 1 Summary statistics of analysis variables

Variable	Minimum	Median	Maximum
Acid neutralizing capacity ($\mu\text{eq/L}$)	−41	1,753	74,249
Area ratio	0.7	31.8	45,154.0
Chlorophyll <i>a</i> ($\mu\text{g/L}$)	0	7	271
Color (PCU)	0	11	150
Elevation (m)	0	323	3,403
Lake geometry ratio ($\text{m}^{-0.5}$)	0.65	4.33	101.15
Lake surface area (ha)	4.2	76.0	167,489.6
Latitude (°)	26.94	41.31	48.96
Longitude (°)	−124.63	−94.48	−67.70
Maximum depth (m)	1	7	97
Maximum monthly temperature (°C)	16	29	42
Mean annual precipitation (in/years)	7.5	91.7	268.2
Proportion hypoxic	0.00	0.12	1.00
Sampling day	127	211	290
Secchi depth (m)	0	2	37
Shoreline development	1.02	1.88	28.63
SO_4 ($\mu\text{eq/L}$)	3	201	141,298
Temperature gradient (°C/m)	−1.50	2.10	16.44

variant of classification and regression trees (Breiman et al. 1984) known as TREED analysis (Alexander and Grimshaw 1996). In classification and regression trees, the dataset is partitioned in a stepwise manner such that at each step, the dataset is split into two groups, each of which have different mean values of the response variable. In contrast, in TREED analysis, the dataset is partitioned such that samples included within each of the groups are similar in terms of a functional relationship. In the present analysis, each end node of the tree consisted of the generalized linear regression model that modeled the proportion of hypoxic measurements as a function of chl *a* (as described above), and the dataset was partitioned to minimize the residual deviance in the estimated relationship between chl *a* and the extent of hypoxia across all end nodes. By using a function in the end node rather than a single value, the classification tree can be less complex, and therefore more interpretable (Alexander and Grimshaw 1996).

Selection of classification variables and specifying the classification tree proceeded as follows. We first set aside a randomly selected 20 % of the dataset as validation data. The remaining 80 % of the dataset was used to calibrate the trees and the associated regression models. For each level of the tree, each candidate classification variable was considered in turn, and approximately 50 values spanning the observed range of that variable were selected as possible splitting values. The dataset was divided into two groups based on each of the possible splitting values, and a single generalized linear regression model relating chl *a* to the extent of hypoxia was fit, specifying group membership as a dummy variable and allowing different values of the regression coefficients for each group. The residual deviance of the model was then computed and retained. This procedure was repeated for each of the classification variables, and the combination of classification variable and splitting value that yielded the greatest reduction in residual deviance was saved. Splitting the dataset and building the classification tree continued recursively using this procedure until any further splits would have reduced the number of samples in a group to less than 60 lakes. This minimum number of samples was established to ensure that sufficient independent samples were available in each group to reliably fit the regression relationship between chl *a* and the proportion of hypoxic measurements (Harrell 2001).

After specifying the largest possible classification tree based on the sample size constraint, trees were then pruned to reduce the potential for overfitting and to improve predictive accuracy. To this end, each pair of end nodes was combined into a single node (i.e., pruned) and the predictive accuracy of the tree when applied to independent validation data was compared to the predictive accuracy of the unpruned tree. When the pruned version of the tree did

not degrade predictive accuracy (where a degradation in predictive accuracy was defined as a minimum of a 1 % change), it was retained and the unpruned version discarded. This process was repeated for all possible pairs of end nodes until further pruning degraded predictive accuracy. To quantify predictive accuracy while pruning, we calculated the root mean square (RMS) prediction error between predicted and observed values of the proportion of hypoxic measurements.

An enormous number of different trees are possible because of the number of candidate classification variables and the number of possible values at which splits can be specified for each of the variables. The stepwise, or “greedy” algorithm described above only minimizes the residual deviance at each level of the tree, an approach that is locally optimal, but may not yield the best global model (Chipman et al. 1998). To more broadly explore the space of possible classification trees, we computed a “bootstrap umbrella of model parameters”, or “bumped” trees (Tibshirani and Knight 1999), by fitting 200 classification trees to bootstrap replicates of the original calibration dataset. For each bumped tree, we fit the quasibinomial regression model relating chl *a* to the proportion of hypoxic measurements, using group membership as a dummy variable. We then evaluated the resulting trees in terms of the residual deviance of the model and by calculating the RMS predictive accuracy when applied to the independent validation data. From the set of bumped trees, we selected a final classification tree that exhibited the best predictive performance.

All statistical calculations were performed with R (R Core Team 2013). Regression trees were fit by adapting scripts provided in the partykit library (<http://CRAN.R-project.org/package=partykit>).

Results

A total of 1,157 distinct lakes were included in the profile data provided by the NLA. Approximately 10 % of these lakes were visited more than once, and to avoid over-weighting these lakes in the statistical analysis, we only included samples collected on the first visit to each of these lakes in the analysis. The DO probe failed for 56 of these profiles, and water quality data was not collected in an additional 67 lakes, leaving 1,034 dissolved oxygen profiles with complete covariate information. In 74 of these profiles, fewer than 2 samples were collected at depths below 0.5 m and computing a temperature gradient was not possible, leaving a total of 960 samples for analysis. We randomly selected 194 of these samples and designated them as validation data, and used the remaining data to calibrate the models.

In a generalized linear model fit using all of the calibration data, the proportion of hypoxic samples was significantly associated with chl *a* concentration, with the logit-transformed proportion of hypoxic samples increasing by 0.36 (95 % confidence intervals: 0.19–0.53) for every unit increase in log-transformed chl *a*. Substantial variability was observed about the mean relationship (Fig. 1), and the quasi- R^2 value indicated that this “no-classification” model only accounted for 2 % of the variability in the proportion of hypoxic samples. The RMS prediction accuracy was 0.26 (units of proportion of hypoxic samples) when this model was applied to validation data.

Several models selected by bumping improved on the greedy classification tree in terms of the quasi- R^2 value and prediction accuracy, and the performance of all candidate classifications improved on the no-classification case (Fig. 2). To better understand the relative importance of different classification variables, we examined all 24 splits in the dataset selected by the 5 best performing trees, and observed that Tgrad was selected 10 times. Lake geometry ratio and maximum monthly air temperature were each selected 3 times, and Secchi depth and lake surface area were each selected twice. Elevation, mean annual precipitation, maximum depth, and ANC were each selected once as classification variables. In 3 out of the 5 best performing trees, five distinct groups of lakes were identified, and we selected the five-group scheme with the lowest RMS error as our final classification scheme, which exhibited the best predictive accuracy when applied to the validation data (Fig. 3). Lakes with an observed temperature gradient of less than or equal to 1.2 °C/m were identified as the first distinct group (Group 2). In the group of lakes with maximum temperature gradients exceeding 1.2 °C/m, those lakes located at elevations greater than 1,580 m were

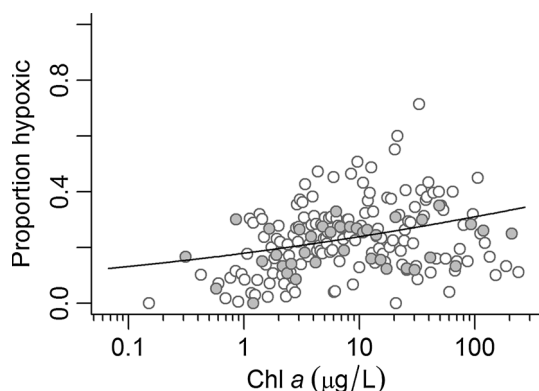


Fig. 1 Relationship between chlorophyll *a* (chl *a*) concentration and the proportion of hypoxia. Each symbol represents the average proportion of hypoxia of 5 lakes with the indicated chl *a* concentration. Solid line is the generalized linear regression fit. Open circles calibration data. Grey filled circles validation data

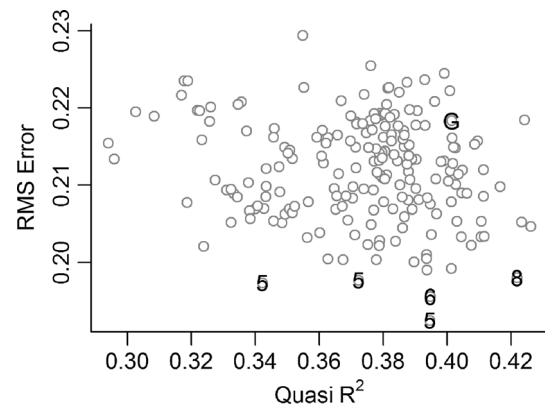


Fig. 2 Relationship between RMS prediction error and Quasi- R^2 for different bumped trees. *G* greedy tree. Arabic numbers number of distinct groups in models with the 5 lowest RMS errors

assigned to a distinct group (Group 9). Lower elevation lakes were then classified based on lake geometry ratio (Group 8) and Secchi depth (Group 6 and 7).

When the selected classification scheme was included as a dummy variable, the generalized linear regression model accounted for substantially more of the variability in the proportion of hypoxic measurements than the no-classification model, increasing the quasi- R^2 from 2 to 39 %. The proportion of hypoxic measurements increased with increased epilimnetic chl *a* in all groups of lakes, but the rate of increase (i.e., the regression slope) was greatest in Group 7 (Fig. 4, Table 2). In Group 6 lakes, which were similar to Group 7 with respect to all classification variables except for Secchi depth, the proportion of hypoxic measurements increased at a much slower rate. However, the mean proportion of hypoxic samples in Group 6 (Secchi ≤ 2.2 m) was generally greater than that in Group 7 (Secchi > 2.2 m) at the same chl *a* concentration (Fig. 4). The magnitudes of the regression slopes for Group 8 and 9 lakes were similar.

The accuracy of the predictions of the probability of hypoxia varied across different groups, with the most accurate predictions observed in Groups 2 and 7 (Table 2), corresponding to lakes in which the extent of hypoxia was generally low (Group 2) and lakes in which a strong relationship between chl *a* and the extent of hypoxia was observed (Group 7). A comparison of the proportion of the water column that was predicted to be hypoxic, normalized to the same concentration of chl *a*, provided an indication of the prevalence of hypoxia in different groups of lakes at similar levels of algal abundance. This predicted extent of hypoxia varied strongly across different lake classes (Table 2). Groups 6 and 7 had the highest predicted extents of hypoxia at chl *a* = 10 µg/L, while the predicted extent in Group 2 was substantially lower than other groups.

Fig. 3 Final five-node tree.
Variables as defined in Table 1

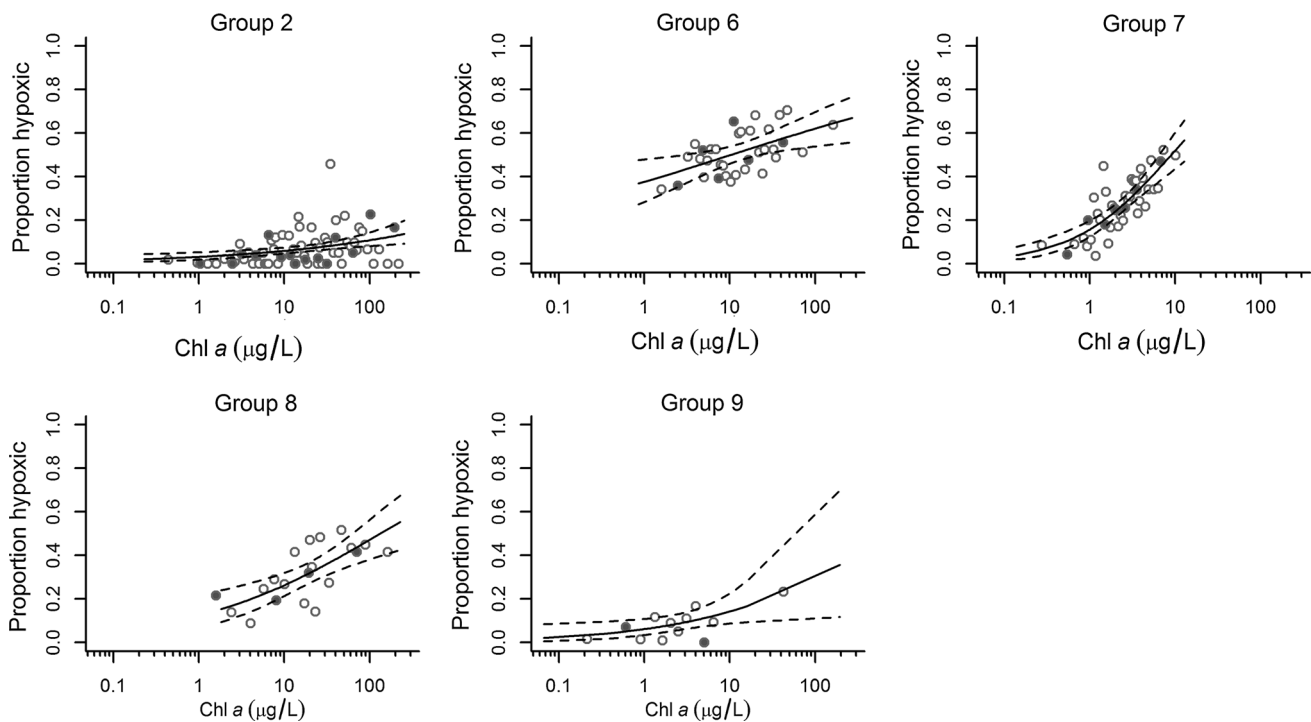
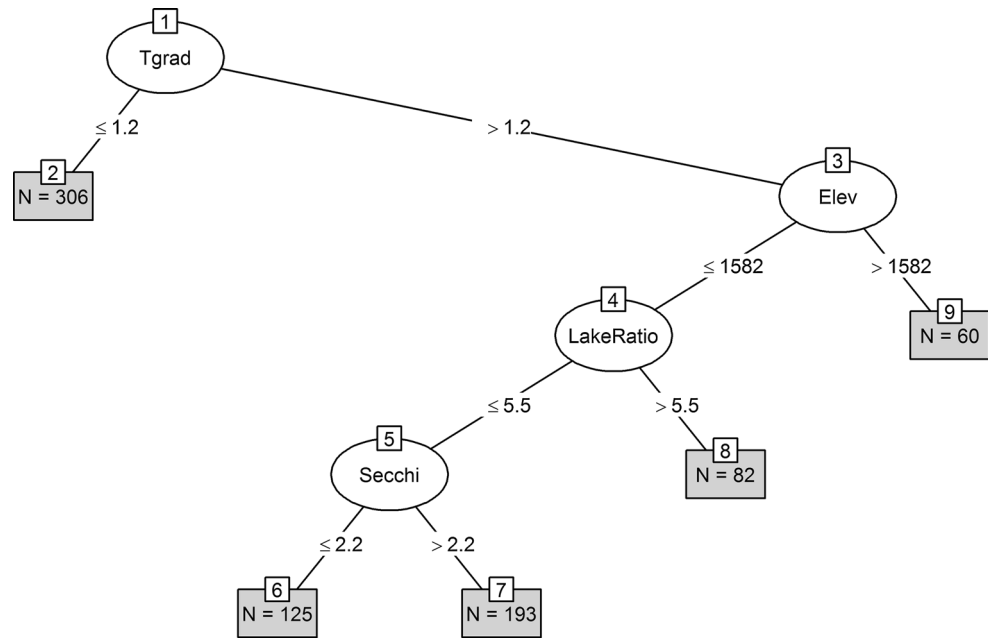


Fig. 4 Relationships between proportion of samples that were hypoxic and chl *a* concentration for different groups of lakes. Each symbol represents the average proportion of hypoxia of 5 lakes with the indicated chl *a* concentration. Open circles calibration data, filled

circles validation data, solid line mean regression relationship, dashed lines approximate 90 % confidence intervals on mean relationship. Lake groups as indicated in Fig. 3

Discussion

Our analysis identified groups of lakes within which epilimnetic chl *a* concentrations accurately predicted the extent of hypoxia, and as such, these relationships can

provide useful information for managing algal biomass to protect aquatic life that depend on adequate concentrations of dissolved oxygen. Our findings were generally consistent with a conceptual understanding of how increased algal abundance affects dissolved oxygen concentrations in

Table 2 Characteristics of relationships between chl *a* and proportion hypoxic for different groups of lakes

Group	Regression slope (95 % confidence intervals)	RMS error	Predicted proportion of hypoxic samples at chl <i>a</i> = 10 µg/L
2	0.66 (0.23, 1.11)	0.16	0.06
6	0.50 (0.09, 0.92)	0.23	0.50
7	1.76 (1.14, 2.41)	0.17	0.52
8	0.92 (0.38, 1.49)	0.26	0.26
9	0.93 (−0.03, 1.88)	0.15	0.14

terms of (1) the observed relationships between chl *a* and the extent of hypoxia, and (2) the variables selected to identify discrete classes of lakes. First, the strong associations between chl *a* and the extent of hypoxia in certain lakes are consistent with the idea that increased algal abundance contributes organic matter to a lake, which depletes oxygen while decomposing. Others have observed similar relationships between epilimnetic chl *a* and DO concentrations from field data within a region (Jones et al. 2011), and process-based models have yielded similar observations (Stefan et al. 1996).

Chl *a* in this study provided an instantaneous measurement of algal biomass, but for this analysis we assumed that this measurement was an indicator of the long-term primary productivity of the lake and the lake trophic status, which, in turn, would be expected to be strongly associated with the accrual of organic material in lake sediments and sediment oxygen demand. Others have adopted a similar interpretation of grab samples, assuming, for example, that instantaneous measurements of TP were indicative of long-term lake nutrient conditions and oxygen demand in the hypolimnion (Chapra and Canale 1991; Molot et al. 1992). These assumptions, while consistent with a general understanding of lake processes, require further detailed studies to quantify the variability of relationships between epilimnetic chl *a* and SOD (Borsuk et al. 2001). For example, with our dataset we were unable to consider how interannual changes in chl *a* would manifest in changes in SOD, and how quickly reductions in chl *a* would result in reductions in SOD.

Instead of the more common approach of modeling linkages between phosphorus and DO (Molot et al. 1992), we chose to focus on chl *a* as a predictor of the extent of hypoxia, because it provides a direct measure of algal biomass. Therefore, the causal path linking it to hypolimnetic hypoxia includes fewer steps (and variables) than the pathway linking nutrients concentrations to hypoxia. In other words, by modeling the relationship between chl *a* and hypoxia, we eliminated the uncertainty associated with modeling changes in algal biomass as a function of nutrient concentration. The resulting models can therefore

potentially be applied to a broader variety of lakes. Separate models can be used to predict changes in chl *a* as a function of nutrient concentrations or nutrient loading (Reckhow 1988), and these models can better account for differences among lakes that influence the nutrient–chlorophyll relationship (Yuan and Pollard 2014).

The current findings, in terms of the selected classification variables, also were consistent with the well-established conceptual understanding of the processes that influence the transport of dissolved oxygen within the lake (Wetzel 2001). The importance of seasonal stratification in limiting the vertical transport of oxygen from the surface layer to the deep waters of a lake has been well established (Bella 1970). In the current analysis, two distinct measurements of stratification were selected to classify lakes: (1) Tgrad, a measurement of stratification strength at the time of sampling, and (2) lake geometry ratio, a measurement of lake morphological characteristics that influence stratification. The combination of these two measures appears to provide an effective approach for accounting for the effect of stratification on hypoxia, as a high value of Tgrad suggests that the deep waters are isolated from vertical transport of oxygen, allowing oxygen demand at these depths to deplete dissolved oxygen, while a low value of the lake geometry ratio indicates that characteristics of lake morphology are conducive to maintaining this stratification. Hence, in these lakes, a strong relationship between chl *a* and the extent of hypoxia was observed. In other lakes that were stratified at the time of sampling (Group 8), the average extent of hypoxia was less than in Groups 6 and 7 (Table 2). Lake geometry ratio in these lakes suggested that they were polymictic. Therefore, stratification observed at the time of sampling may have existed for only a short period of time, and observed DO concentrations likely reflect the effects of both depletion and occasional mixing of DO rich water from shallower depths, which reduces the extent of hypoxia compared to lakes that are stratified for longer periods of time.

The linkage between lake geometry ratio and seasonal stratification has been observed in other studies. In analysis of mid-North American lakes, a lake geometry ratio of $2.9 \text{ m}^{-0.5}$ was found to delineate between lakes that seasonally stratify and lakes that do not consistently stratify or do not stratify at all (Gorham and Boyce 1989). Subsequent analysis of a large set of temperature profiles collected from Missouri reservoirs suggested that somewhat higher values of the lake geometry ratio more accurately identified reservoirs that seasonally stratify (Jones et al. 2011). Our finding of a threshold in lake geometry ratio at $5.5 \text{ m}^{-0.5}$ is consistent with this previous work, especially given the broader spatial representation of our dataset.

Other factors selected as classification variables were also generally consistent with an understanding of the

mechanisms by which hypoxia is established in a lake. The strong effect of Secchi depth on the relationship between chl *a* and the extent of hypoxia might be attributed to differences in the input of allochthonous organic material to the lake. More specifically, when comparing lakes with similar chl *a* concentrations, the high turbidity associated with lower Secchi depths may be caused by non-algal seston, which in turn, is often associated with high loadings of organic material (Bergström and Jansson 2000; Jones and Knowlton 2005). This allochthonous material may provide a source of organic material in addition to that provided by algal growth (Carpenter et al. 2002), which may explain the weaker relationship between chl *a* and the extent of hypoxia observed in this group of lakes. Lakes at high elevations were also identified as a distinct group (Group 9, Fig. 3), and these lakes would tend to stratify later in the summer because of lower air temperatures, and therefore, we would expect a lesser extent of hypoxia and a weaker association between hypoxia and epilimnetic chl *a*, compared to lower elevation lakes (Livingstone et al. 1999).

Some candidate classification variables that have been associated with the extent or strength of hypoxia in other studies were not selected here. For example, in seasonally stratified lakes, oxygen depletion occurs progressively over time, and the day of the first observation of hypoxia often is a function of different lake characteristics (Molot et al. 1992). Hence, we expected that the sampling day of the year would account for some differences in the relationship between hypoxia and chl *a*. The lack of importance of sampling day suggests that differences among lakes in physical characteristics were stronger determinants of hypoxia at the large spatial scale considered in this analysis.

For this analysis, we quantified the extent of hypoxia as the proportion of all water column samples for which DO <2 mg/L, but typically, hypoxia is observed in the hypolimnion, and the proportion of the hypolimnion that is hypoxic may provide a more informative assessment of the effects of reduced DO on aquatic life. The primary threshold at $T_{grad} = 1.2\text{ }^{\circ}\text{C/m}$ identified by the present analysis is very close to the typical metalimnion identifier of $1\text{ }^{\circ}\text{C/m}$ (Wetzel 2001) and provides a convenient means of selecting lakes that were stratified at the time of sampling, and within those lakes, we estimated the extent of hypolimnetic hypoxia as the proportion of samples at depths below the location of the maximum observed temperature gradient for which DO <2 mg/L (Fig. 5). As would be expected, a strong relationship was observed between the extent of hypoxia observed in the water column and that observed in the hypolimnion, and further, the extent of hypolimnetic hypoxia was generally greater than the extent of hypoxia computed using the entire water

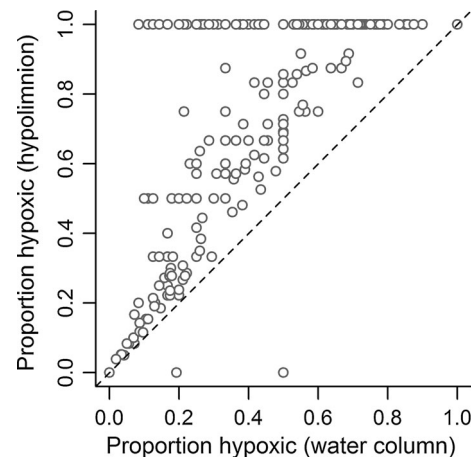


Fig. 5 Comparison of proportion of hypoxia in the water column with proportion of hypolimnetic hypoxia. Dashed line shows the 1:1 relationship

column. Indeed, in a large number of lakes, the entire hypolimnion was hypoxic. Because the hypolimnion can often provide temperature refugia for cold- and cool-water fish (Stefan et al. 1996), the relationship between the extent of hypoxia in the entire water column and the occurrence of complete hypolimnetic hypoxia may be particularly important when considering the effects of hypoxia on certain fish species. A further refinement of this work would be to compare temperature profiles with DO profiles to identify lakes that become inhospitable to certain cold-water fish species because of the “squeeze” between the warm epilimnion and the hypoxic hypolimnion.

As discussed earlier, statistical models provide a means of estimating relationships that can be used for managing groups of lakes, and while the predictions from these models may not be as accurate as predictions of process-based models calibrated for individual lakes, use of statistical models provides several unique advantages. First, the uncertainty in statistically estimated relationships can be explicitly quantified and incorporated into management decisions. As shown in the analysis, the accuracy of predictions varied substantially among lake classes and substantial uncertainty about the estimated mean relationship between chl *a* and the proportion of hypoxic measurements was still observed in certain lake groups. This uncertainty might arise from factors for which data were not available and were not included in the analysis. For example, other models have explicitly linked lake water volume and the associated dissolved oxygen in that water to oxygen demand to predict the temporal evolution of the dissolved oxygen profile and the ultimate extent of hypoxia (Livingstone and Imboden 1996). However, data on lake bathymetry were not available in the current study, and we were unable to quantify lake volume at different depths. So, in this statistical analysis, the uncertainty associated

with the lack of bathymetric data and data on other potentially influential factors is inherently incorporated in the confidence and prediction intervals in the estimated relationships, and managers can use these intervals to inform decisions. In other groups of lakes, chl *a* simply might not accurately predict the occurrence of hypoxia, information which is also useful for management decisions.

Second, statistical models such as the ones described here can provide a means of determining which environmental factors, among many candidates, are associated with changes in the relationships of interest. In the present analysis, we examined existing literature to identify many candidate factors that have been observed to influence the occurrence of hypoxia in lakes and reservoirs, and we included a broad array of candidate classification variables in the analysis (Table 1). Our analysis provided insights into which factors most strongly influence relationships between chl *a* and the extent of hypoxia at the continental spatial scale of this study. At this scale, lake stratification status as quantified by temperature gradient and lake geometry ratio was most important in determining the strength of the relationship between chl *a* and the extent of hypoxia. In particular, a temperature gradient in the water column of at least 1.2 °C/m seemed necessary to reduce the vertical transport of oxygen enough to allow oxygen demand to reduce dissolved oxygen concentrations to hypoxic levels. We further observed that the most accurate predictions of the extent of hypoxia were possible in two types of lakes: (1) unstratified lakes ($T_{\text{grad}} \leq 1.2$ °C/m) in which the extent of hypoxia was generally low, and (2) stratified lakes with high Secchi depths and low lake geometry ratios, in which the extent of hypoxia was strongly predicted by chl *a* concentration. These findings can directly inform management decisions and provide the bases for new hypotheses that can guide future investigations in the factors controlling lake hypoxia.

Third, statistical models are often criticized for being only applicable to the range of conditions included in the data used to estimate the relationships (Livingstone and Imboden 1996). In the present analysis, we used data collected from lakes across the contiguous US that were selected to provide a statistically valid representation of the full population of lakes. Hence, results from the present analysis should be generally applicable to any lake or reservoir in the contiguous US. As the availability of large-scale monitoring data increases worldwide (Carvalho et al. 2008), issues regarding the range of applicability should become less relevant.

The present analysis defined several classes of lakes in which we can expect strong relationships between epilimnetic chl *a* and hypoxia. As noted above, though, several different classification schemes yield similar improvements in predictive accuracy, but we have focused discussion on

only one representative scheme with the best predictive accuracy. The final selection of an appropriate classification scheme to inform management decisions for a particular region may incorporate other factors, including the availability of data for certain classification variables and alignment with existing classifications. Regardless of the classification scheme that is selected, the more precise relationships that are estimated after classification provide a means of setting thresholds for chl *a* concentration that directly link to maintaining dissolved oxygen conditions that support aquatic life. These thresholds are broadly applicable to lakes with the same characteristics as those specified within a particular class, and hence, provide regionally applicable values. Overall, we believe that the relationships shown here provide information that is immediately relevant to the task of managing the effects of nutrients on aquatic resources.

Acknowledgments The authors thank B. Walsh and S. Whitlock for reviewing an earlier draft of this paper. The views expressed in this paper are those of the authors and do not reflect the policy of the US Environmental Protection Agency.

References

- Alexander WP, Grimshaw SD (1996) Treed regression. *J Comput Graph Stat* 5:156–175. doi:[10.1080/10618600.1996.10474702](https://doi.org/10.1080/10618600.1996.10474702)
- Bella DA (1970) Dissolved oxygen variations in stratified lakes. *J Sanit Eng Div* 96:1129–1146
- Bergström A-K, Jansson M (2000) Bacterioplankton production in humic lake örträsket in relation to input of bacterial cells and input of allochthonous organic carbon. *Microb Ecol* 39:101–115. doi:[10.1007/s002480000007](https://doi.org/10.1007/s002480000007)
- Borsuk ME, Higdon D, Stow CA, Reckhow KH (2001) A Bayesian hierarchical model to predict benthic oxygen demand from organic matter loading in estuaries and coastal zones. *Ecol Model* 143:165–181. doi:[10.1016/S0304-3800\(01\)00328-3](https://doi.org/10.1016/S0304-3800(01)00328-3)
- Bowman GT, Delfino JJ (1980) Sediment oxygen demand techniques: a review and comparison of laboratory and in situ systems. *Water Res* 14:491–499. doi:[10.1016/0043-1354\(80\)90215-8](https://doi.org/10.1016/0043-1354(80)90215-8)
- Breiman L, Friedman J, Stone CJ, Olshen RA (1984) Classification and regression trees. Chapman and Hall/CRC, Boca Raton
- Carpenter SR, Kitchell JF, Pace ML (2002) Pathways of organic carbon utilization in small lakes: results from a whole-lake ¹³C addition and coupled model. *Limnol Ocean* 47:1664–1675
- Carvalho L, Solimini A, Phillips G et al (2008) Chlorophyll reference conditions for European lake types used for intercalibration of ecological status. *Aquat Ecol* 42:203–211. doi:[10.1007/s10452-008-9189-4](https://doi.org/10.1007/s10452-008-9189-4)
- Chapra SC, Canale RP (1991) Long-term phenomenological model of phosphorus and oxygen for stratified lakes. *Water Res* 25:707–715. doi:[10.1016/0043-1354\(91\)90046-S](https://doi.org/10.1016/0043-1354(91)90046-S)
- Chipman HA, George EI, McCulloch RE (1998) Bayesian CART model search. *J Am Stat Assoc* 93:935. doi:[10.2307/2669832](https://doi.org/10.2307/2669832)
- Core Team R (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Cross TK, Summerfelt RC (1987) Oxygen demand of lakes: sediment and water column bod. *Lake Reserv Manag* 3:109–116. doi:[10.1080/07438148709354766](https://doi.org/10.1080/07438148709354766)

- Daly C, Halbleib M, Smith JJ et al (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int J Climatol* 28:2031–2064. doi:[10.1002/joc.1688](https://doi.org/10.1002/joc.1688)
- Del Giorgio PA, le Williams PJB (eds) (2005) *Respiration in aquatic ecosystems*. Oxford University Press, Oxford
- Di Toro DM, Fitzpatrick JJ, Thomann RV (1983) Documentation for water quality analysis simulation program (WASP) and model verification program (MVP). <http://udspace.udel.edu/handle/19716/1450>. Accessed 21 Aug 2014
- Gakstatter JH, Allum MO, Omernik JM (1976) Lake eutrophication: results from the national eutrophication survey. Environmental Protection Agency, U.S
- Gorham E, Boyce FM (1989) Influence of lake surface area and depth upon thermal stratification and the depth of the summer thermocline. *J Gt Lakes Res* 15:233–245. doi:[10.1016/S0380-1330\(89\)71479-9](https://doi.org/10.1016/S0380-1330(89)71479-9)
- Hamilton DP, Schladow SG (1997) Prediction of water quality in lakes and reservoirs. Part I: model description. *Ecol Model* 96:91–110. doi:[10.1016/S0304-3800\(96\)00062-2](https://doi.org/10.1016/S0304-3800(96)00062-2)
- Harrell FE (2001) *Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis*. Springer, New York
- Holmer M, Storkholm P (2001) Sulphate reduction and sulphur cycling in lake sediments: a review. *Freshw Biol* 46:431–451. doi:[10.1046/j.1365-2427.2001.00687.x](https://doi.org/10.1046/j.1365-2427.2001.00687.x)
- Jones JR, Knowlton MF (2005) Chlorophyll response to nutrients and non-algal seston in Missouri reservoirs and oxbow lakes. *Lake Reserv Manag* 21:361–371. doi:[10.1080/07438140509354441](https://doi.org/10.1080/07438140509354441)
- Jones JR, Knowlton MF, Obrecht DV, Graham JL (2011) Temperature and oxygen in Missouri reservoirs. *Lake Reserv Manag* 27:173–182. doi:[10.1080/07438141.2011.583713](https://doi.org/10.1080/07438141.2011.583713)
- Kelly CA, Rudd JWM, Furutani A, Schindler DW (1984) Effects of lake acidification on rates of organic matter decomposition in sediments. *Limnol Oceanogr* 29:687–694
- Livingstone DM, Imboden DM (1996) The prediction of hypolimnetic oxygen profiles: a plea for a deductive approach. *Can J Fish Aquat Sci* 53:924–932. doi:[10.1139/f95-230](https://doi.org/10.1139/f95-230)
- Livingstone DM, Lotter AF, Walker IR (1999) The decrease in summer surface water temperature with altitude in Swiss Alpine lakes: a comparison with air temperature lapse rates. *Arct Antarct Alp Res* 31:341. doi:[10.2307/1552583](https://doi.org/10.2307/1552583)
- McCullagh P, Nelder JA (1989) *Generalized linear models*, 2nd edn. Chapman and Hall/CRC, Boca Raton
- Molot LA, Dillon PJ, Clark BJ, Neary BP (1992) Predicting end-of-summer oxygen profiles in stratified lakes. *Can J Fish Aquat Sci* 49:2363–2372. doi:[10.1139/f92-260](https://doi.org/10.1139/f92-260)
- Nürnberg GK (1995) Quantifying anoxia in lakes. *Limnol Oceanogr* 40:1100–1111
- Reckhow KH (1988) Empirical models for trophic state in South-eastern US lakes and reservoirs. *JAWRA J Am Water Resour Assoc* 24:723–734. doi:[10.1111/j.1752-1688.1988.tb00923.x](https://doi.org/10.1111/j.1752-1688.1988.tb00923.x)
- Rippey B, McSorley C (2009) Oxygen depletion in lake hypolimnia. *Limnol Oceanogr* 54:905–916
- Smith VH (2003) Eutrophication of freshwater and coastal marine ecosystems a global problem. *Environ Sci Pollut Res* 10:126–139. doi:[10.1065/espr2002.12.142](https://doi.org/10.1065/espr2002.12.142)
- Stefan HG, Fang X (1994) Dissolved oxygen model for regional lake analysis. *Ecol Model* 71:37–68. doi:[10.1016/0304-3800\(94\)90075-2](https://doi.org/10.1016/0304-3800(94)90075-2)
- Stefan HG, Hondzo M, Fang X et al (1996) Simulated long-term temperature and dissolved oxygen characteristics of lakes in the north-central United States and associated fish habitat limits. *Limnol Oceanogr* 41:1124–1135
- Tibshirani R, Knight K (1999) Model search by bootstrap “bumping”. *J Comput Graph Stat* 8:671–686. doi:[10.1080/10618600.1999.10474842](https://doi.org/10.1080/10618600.1999.10474842)
- US EPA (2006) *Survey of the nation’s lakes. Laboratory methods manual*. Office of Water and Office of Research and Development, Washington
- US EPA (2010) *National lakes assessment: a collaborative survey of the nation’s lakes*. Office of Water and Office of Research and Development, Washington
- Vaquier-Sunyer R, Duarte CM (2008) Thresholds of hypoxia for marine biodiversity. *Proc Natl Acad Sci* 105:15452–15457. doi:[10.1073/pnas.0803833105](https://doi.org/10.1073/pnas.0803833105)
- Vuorenmaa J, Forsius M, Mannio J (2006) Increasing trends of total organic carbon concentrations in small forest lakes in Finland from 1987 to 2003. *Sci Total Environ* 365:47–65. doi:[10.1016/j.scitotenv.2006.02.038](https://doi.org/10.1016/j.scitotenv.2006.02.038)
- Walker WW (1979) Use of hypolimnetic oxygen depletion rate as a trophic state index for lakes. *Water Resour Res* 15:1463–1470. doi:[10.1029/WR015i006p01463](https://doi.org/10.1029/WR015i006p01463)
- Walker R, Snodgrass W (1986) Model for sediment oxygen demand in lakes. *J Environ Eng* 112:25–43. doi:[10.1061/\(ASCE\)0733-9372\(1986\)112:1\(25\)](https://doi.org/10.1061/(ASCE)0733-9372(1986)112:1(25))
- Wetzel RG (2001) *Limnology: lake and river ecosystems*, 3rd edn. Academic Press, San Diego
- Yuan LL, Pollard AI (2014) Classifying lakes to improve precision of nutrient–chlorophyll relationships. *Freshw Sci* 33:1184–1194. doi:[10.1086/678465](https://doi.org/10.1086/678465)