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Drivers and Management Implications of Long-Term Cisco Oxythermal Habitat Decline in Lake Mendota, WI

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Abstract

Cisco (*Coregonus artedi*) are an important indicator species for cold-water lake habitats in the Great Lakes region, and many populations have been extirpated at their southern range limit over the last century. Understanding the roles of climate and water quality in these extirpations should inform protection of cold-water fishes. Using the water temperature at the depth where dissolved oxygen falls to 3 mg L^{-1} (TDO3) as a metric, we investigated the roles of climate and water quality as drivers of habitat availability for cisco in Lake Mendota, WI, USA from 1976 to 2013. We find that summer (Jun−Aug) air temperatures, spring (Mar−May) phosphorus load, and spring inflow influence summer TDO3. Warm air temperatures lead to the greatest increases in TDO3, whereas reduced phosphorus loads can reduce TDO3, thus alleviating oxythermal stress. Under air temperatures expected under the A1B climate change scenario, a 25% reduction in phosphorus load would stabilize TDO3 at current levels, while a 75% reduction in phosphorus loading would be required to expand oxythermal habitat. Costs of these reductions are estimated to range from US$16.9 million (−25%) to US$155–167 million (−75%) over a 20-year period but may be feasible by expanding upon current watershed phosphorus reduction initiatives if sustained funding were available. Identifying targeted reductions will become increasingly important throughout the region as warmer temperatures and longer stratification reduces cool- and cold-water fish habitat in many Midwestern lakes under the expected future climate.

Keywords Climate change · Fisheries management · Phosphorus reductions · Cisco · Lake Mendota

Introduction

Cisco (*Coregonus artedi*), a cold-water fish species, serve as an important forage fish for top predators in Canadian and northern United States lakes (Jacobson et al. 2010; Van Zuiden et al. 2016) such as walleye (*Sander vitreus*), northern pike (*Esox lucius*), and muskellunge (*Esox masquinongy*). They require cold, well-oxygenated water to survive and reproduce (Cahn 1927; Frey 1955; Jacobson et al. 2008); hence, inland cisco are found primarily in large, deep lakes (Rudstam and Magnuson 1985; Jacobson et al. 2008). Their susceptibility to temperature and oxygen (oxythermal) stress make cisco a good indicator of reductions in cold-water habitat under climate warming and eutrophication (Jacobson et al. 2008).

During the summer, cisco seek thermal refuge in the hypolimnion, but are forced to move shallower as hypolimnetic dissolved oxygen (DO) decreases during the stratified season (Ficke et al. 2007; Jacobson et al. 2008). In extreme cases, suitable habitat may be eliminated completely by absence of DO from below and warm temperature from above. The lakes of southern Wisconsin lie near the southern edge of cisco's range (Becker 1983; Lyons et al. 2000), and ongoing extirpations suggest that

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remaining populations are at considerable risk (Sharma et al. 2011; Herb et al. 2014; Van Zuiden et al. 2016).

Cultural eutrophication can reduce cisco habitat (Jacobson et al. 2010; Honsey et al. 2016) because increased primary production (Carpenter 2005) leads to organic material decomposition that depletes hypolimnetic oxygen (Ito and Momii 2015). Jacobson et al. (2010) found that phosphorus (P) plays a pivotal role in availability of cold-water fish habitat in Minnesota lakes, and Latta (1995) concluded that ciscoes have been extirpated from at least 14% of Michigan lakes as a result of eutrophication. In Indiana, which includes the southern extent of the cisco range (Frey 1955), appropriate habitat is scarce (Clingerman et al. 2013), and cisco persist only in the most oligotrophic lakes (Honsey et al. 2016).

Climate change can exacerbate the impacts of cultural eutrophication (De Stasio et al. 1996; Jacobson et al. 2010; Herb et al. 2014). Lake ecosystems worldwide are becoming both warmer (Perroud and Goyette 2010; O'Reilly et al. 2015) and more strongly stratified (Hetherington et al. 2015; Kraemer et al. 2015), which reduces the availability of cold-water habitats by isolating deeper, colder water from well-oxygenated surface waters (Santiago et al. 2016; Van Zuiden et al. 2016). At the same time, climate change is expected to increase the frequency of heavy rain events in Wisconsin (Kucharik et al. 2010; IPCC 2013), which can transport P-rich soil into lakes (Lathrop 2007; Carpenter et al. 2015). Indeed, the majority of P inputs into lake ecosystems result from high flow events (Duan et al. 2013; Carpenter et al. 2015). Moreover, the combination of warmer air temperatures and decreasing wind speeds increases the duration of summer stratification (Kerimoglu and Rinke 2013; Magee et al. 2016), thereby isolating the hypolimnion and increasing the likelihood of hypoxia (De Stasio et al. 1996; Fang et al. 2012). The combination of epilimnetic warming and hypolimnetic oxygen depletion driven by climate change and cultural eutrophication is believed to result in cisco extirpation from lakes that were historically suitable for cisco and other cold-water fishes.

Lake Mendota, WI, USA lies at the southwestern edge of the species' range, yet has historically supported a large cisco population (Lyons et al. 2000). Temperature and DO tolerance thresholds have restricted these fish to a narrow "cisco layer" (Rudstam and Magnuson 1985; Lathrop et al. 1992) of approximately 4 m in the lower epilimnion, which has allowed cisco to survive through most summers (Rudstam and Magnuson 1985; Lathrop et al. 1992). However, mass mortality in 1987 reduced the population by >90% (Lathrop et al. 1992; McDermot and Rose 2000), and it has never recovered (Lathrop et al. 1992; Kitchell 1992). Since that time, average air temperatures have increased significantly (Kucharik et al. 2010; Magee et al. 2016), and extensive efforts have been undertaken to control eutrophication of the lake (Lathrop 2007; Lathrop and Carpenter 2014). In light of its small but sustained cisco population (NTL LTER 2012a) and historical records of summer fish mortalities (Lathrop et al. 1992), Lake Mendota represents an ideal site to investigate the relative role of climate changes and cultural eutrophication as controls on cisco habitat availability. Furthermore, reduced P loading could potentially be utilized to increase the amount of oxythermal habitat available to cisco and other cold-water fishes.

The goals of this paper were three-fold. First, we sought to quantify how year-to-year changes in cisco habitat extent are associated with meteorological and water quality parameters by modeling water temperature and DO over 38 years. Second, we aimed to develop a simple multiple regression model to characterize temporal variability in cisco habitat. Finally, we determined how future warming might reduce cisco oxythermal habitat in Lake Mendota and assess the potential for P load management to offset the effects of climate change.

Methods

Site Description

Lake Mendota (43°6′N; 89°24′W is near the southern edge of cisco range and has extensive historical datasets including frequent water quality observations. It is a dimictic, eutrophic, drainage lake in an urbanizing agricultural watershed (Carpenter and Lathrop 2008) with a surface area of 3940 ha, a mean depth of 12.8 m, a maximum depth of 25.3 m, a shoreline length of 33.8 km, and a maximum fetch of 9.8 km (Robertson and Ragotzkie 1990). The mean flushing rate is 0.23 yr^{-1} (Lathrop and Carpenter 2014). Stratification typically lasts from May to September, with mean summer surface temperature of 22.4 °C and hypolimnetic temperature range from 11 to 15 °C. Secchi depth during the summer is ~3 m (Lathrop et al. 1996; Magee et al. 2016).

Modeling Lake Hydrodynamics

The model used in this paper is a physics-based, one-dimensional model of hydrodynamics, lake ice, and water quality. Specifically, DYRESM-WQ-I (Magee et al. 2016) is based on the DYRESM-WQ model (Dynamic Reservoir Simulation Model—Water Quality model) (Hamilton and Schladow 1997); with an additional ice model included that enables simulation of water temperature, ice cover, and water quality parameters year-round. The lake is represented by horizontal Lagrangian layers with uniform properties that may change in thickness. The hydrodynamic component includes algorithms for mixed layer processes, inflow, outflow, and hypolimnetic mixing (Hamilton and Schladow 1997). The ice model is a three-component ice and snow model based on the MLI model of Rogers et al. (1995) with alterations to two-way coupling of the water and ice components and the addition of a time-dependent sediment heat flux for all horizontal layers. A full description of the hydrodynamic and ice model can be found in Magee et al. (2016). The water quality model simulates phytoplankton production and loss, nutrient cycling, and the DO budget. Hamilton and Schladow (1997) describe the phytoplankton and nutrient subroutines in detail. The model is configured for three functional groups of phytoplankton: a non-nitrogen fixing genus of cyanobacteria represented by *Microcystis*, chlorophytes plus chrysophytes, and diatoms. Mortality is incorporated into the phytoplankton parameters. Bacterial respiration processes in the hypolimnion are captured through the sediment oxygen demand.

Calibration of the hydrodynamic and ice cover components of the model for Lake Mendota were previously conducted for the period 2010–2013 by Magee et al. (2016). Evaporative fluxes are included in DYRESM-WQ-I; we assume that the wind-driven equations in the model are appropriate without further validation. DO was calibrated for Lake Mendota through trial-and-error adjustment of chemical and phytoplankton parameters within the bounds of published values and assigned ranges and values for DYRESM-WQ-I until a satisfactory performance was achieved for range and temporal pattern of DO based on traditional goodness-of-fit metrics. Initial phytoplankton and chemical parameters before calibration were obtained from Kara et al. (2012) and Snortheim et al. (2017), who similarly calibrated Lake Mendota using DYRESM-CAEDYM and GLM-FABM-AED, respectively, with appropriate conversions between model units. Final calibrated chemical and phytoplankton parameters are provided in Supplementary Materials S1 and S2. Parameters not specifically listed are taken as default values from DYRESM-WQ (Hamilton and Schladow 1997). To validate the model, we used three goodness-of-fit measures to evaluate model predictions against observations: Spearman's rank correlation coefficient (Rho), normalized mean absolute error (NMAE), and root-mean-squared error (RMSE). Statistics were calculated for observed and predicted data at times and depths when observations were made.

The final model was initialized on 8 April 1976 and run until 31 December 2013. Simulation period was chosen based on available input and observation data, particularly P load data, which was available starting in 1976. Initial conditions were based on observed water temperatures at that time, and an average of April chemical and biological observations collected from NTL-LTER (2012b).

Linear Regression

Multiple linear regression (MLR) was used to test which of the meteorological and water quality drivers most strongly affect oxythermal habitat availability, and to assess whether a simple MLR equation is an adequate stand-in for hydrodynamic modeling when seeking to assess changes in oxythermal habitat for cold-water fishes in Midwestern lakes. The meteorological drivers were calculated separately for spring (March, April, May; MAM) and summer (June, July, August; JJA), and included: air temperature, wind speed, relative humidity, and total precipitation. Air temperature, wind speed, and relative humidity were averaged over each season; precipitation values were summed. Water quality drivers included: spring, summer, and annual (November−November) total P loads; spring, summer, and annual inflow volumes; spring and summer Secchi depths; and summer water level. P loads and inflow volumes were sums for each period, while water level and Secchi depths were averaged.

To determine the ideal MLR, we ran through combinations of all the identified driver parameters that include at least one of the following: P load (spring, summer, or annual), summer water level, or inflow volumes (spring, summer, or annual). We chose to require at least one of these water quality variables so that a minimum of one variable within the MLR model could be conceivably adjusted by a lake or watershed manager at the local level to improve oxythermal habitat conditions within the lake. P load reductions could be achieved through best management practices within the watershed; changes in inflow volume could be achieved through alterations in land use and land management; and water level could be controlled by Dane County through the Tenney Lock at Lake Mendota's outflow. The final model was selected based on a balance of RMSE, adjusted R^2, and the small-sample-size corrected version of the Akaike information criterion (AICc).

Observation Data

We compiled data on meteorology, inflow rates, P loading, and water column temperature and oxygen profiles for Lake Mendota to calibrate our hydrodynamic model. Meteorological data included daily means of air temperature, vapor pressure, wind speed, cloud cover, and daily totals of solar radiation, rainfall, and snowfall. Meteorological datasets (1884–1988) were described in detail by Robertson (1989), and accounted for shifts in sampling location, observation time, and surface roughness (Robertson 1989). More recent radiation data were gathered from http://www.sws.uiuc.edu/warm/weather, and other data were appended from the National Climate Data Center weather station at the Dane

County Regional Airport (Truax Field; http://www.ncdc.noaa/gov). Wind speeds were adjusted based on changes in observational techniques in 1996 (McKee et al. 2000) as described in Magee et al. (2016).

Volumetric inflow rates of three major tributaries (Yahara River, Station #05427850; Pheasant Branch, Station #05427948; and Spring Harbor, Station #05427965) were acquired from USGS stream gage data (http://waterdata.usgs.gov/wi/nwis/sw/) at a daily frequency for the duration of the model period. Daily discharge ($m^3\,d^{-1}$) from 1975 to 1997 were calculated from gate/lock/bypass pipe USGS ratings and local governmental daily operational records. From 1998 to 2003, daily outflow was estimated from the relationship between measured downstream Lake Waubesa outlet data and Lake Mendota outlet data. After 2003, daily outflow measurements were obtained from the USGS stream gage data (http://waterdata.usgs.gov/wi/nwis/uw/?site_no=05428000).

River water temperatures have been recorded at the Yahara River inlet since 2002 and are assumed to be the same for all three inflowing streams. Prior to 2002, daily river temperatures were estimated from air temperatures (Hsieh 2012). River temperatures and weekly average air temperatures from 2002 to 2009 were linearly correlated ($r^2 = 0.86$) when air was > 0 °C but required a second-order polynomial when air temperatures were below freezing ($r^2 = 0.68$).

Daily total P loadings ($g\,d^{-1}$) were estimated from 1976 to 1990 following Lathrop et al. (1998). For 1990–2013, the Yahara River at the Windsor Site (usgs.gov) was used as a proxy for loading into the lake using the equation: total load = 4.5 × Yahara River load ($r^2 = 0.97$; Walsh et al. 2016). Total nitrogen (N) loads were estimated by assuming a constant mass ratio of N:P in inflows as in Kara et al. (2012). Lake Mendota salinity is low, so inflow salinity was set to zero.

Water temperature profiles were collected for 1976–2013 from Robertson (1989) and the NTL-LTER (NTL LTER 2012b). Vertical resolution was normally 1 m but varied from 0.5 to 5 m before NTL-LTER sampling efforts began in 1995. Available water temperature profiles ranged from only one or two profiles per year to multiple profiles for a given day. DO profiles were collected from 1995 to 2013 by the NTL-LTER (2012b) at approximately 2-week intervals and 1 m vertical resolution during the open water season and once per year under the ice.

Oxythermal Habitat Metric

To quantify the oxythermal habitat available to cisco in Lake Mendota, we use the water temperature at the shallowest depth where DO drops below $3\,mg\,L^{-1}$ (TDO3; Jacobson et al. 2010). TDO3 is derived from temperature and DO profiles generated by our model for each day of the summer stratified season. A threshold DO of $3\,mg\,L^{-1}$ was chosen by Jacobsen et al. (2010) because it constitutes the approximate lethal threshold for cold-water fishes, including cisco (Frey 1955; US EPA 1986). Originally, TDO3 was developed for use in presence−absence models for multiple species across many lakes. Jacobson et al. (2008) used temperature and DO profiles at the time of cisco fish kills to estimate a lethal maximum TDO3 of 22 °C in Minnesota lakes, which we adopt as the threshold indicating no remaining oxythermal habitat for cisco in Lake Mendota.

To evaluate long-term changes in habitat availability, we choose TDO3 over earlier approaches (Fang and Stefan 2000; Stefan et al. 2001; Dillon et al. 2003) because it quantifies the squeeze created jointly by high temperature and low DO. The TDO3 method has been extensively validated for cold-water fish in Midwestern US lakes. Low TDO3 values represent better oxythermal habitat for cisco, while higher TDO3 values indicate a decreased band of habitable depths. We focused on the maximum TDO3 observed each year during the stratified period, rather than averaging TDO3 values (Jacobson et al. 2010; Jiang et al. 2012; Herb et al. 2014), to maximize sensitivity to periods when the entire lake would be inhospitable.

Future Oxythermal Stress and Management Responses

To evaluate the sensitivity of cisco oxythermal habitat to potential changes in meteorology and water quality in the future, we perturbed the key drivers of oxythermal habitat identified by MLR analysis (summer air temperature, spring P load, and spring inflow). Drivers were perturbed individually and in combination to explore possible climate and water quality scenarios. Air temperatures were permuted in units of 1 °C across a range of −2 to +5 °C, reflecting the expectation of future warming (IPCC 2013). All other parameters were varied in 25% increments across a range from −50 to + 50%. Groundwater and surface water inflow temperatures were adjusted simultaneously under air temperature scenarios, but meteorological inputs were held constant except that precipitation switched between rainfall and snowfall as temperatures crossed 0 °C. For all scenarios outflow was adjusted to maintain simulated lake water levels that matched the time dynamic evident in historical records.

Among the drivers considered in this study, nutrient loading presents a unique opportunity to adapt an existing management framework to enhance oxythermal habitat availability for cold-water fishes. We were particularly interested in (i) understanding whether management of P loads could offset the effects of future climate warming on Lake Mendota, and (ii) the associated economic costs. To

Table 1 Spearman's rank correlation coefficient, NMAE, and RMSE values for simulated temperature and dissolved oxygen compared to values observed in Lake Mendota

Variable	Number of observations	Spearman's rho	NMAE	RMSE
Epilimnetic temperature	5,658	0.99	0.0017	1.01
Hypolimnetic temperature	12,259	0.92	0.0017	1.54
Individual temperature	24,518	0.97	0.0004	1.59
Epilimnetic DO	1,484	0.58	0.013	0.87
Hypolimnetic DO	2,756	0.84	0.021	0.86
Individual DO	5,514	0.88	0.0055	0.93

Separate comparisons are shown for epilimnion-averaged, hypolimnion-averaged, and individual depth measurements where each observation represents a distinct depth-time combination

NMAE normalized mean absolute error, *RMSE* root-mean-squared error

quantify the equivalency of warming and nutrient loading in terms of habitat available to cisco, we used downscaled air temperature projections for Madison, Wisconsin for 2055 (WICCI 2011). The air temperature projections are based on 14 global circulation models, and we chose the A1B emissions scenario to address the most likely case (WICCI 2011). Seasonal warming is projected to be +4.4 °C for winter, +3.3 °C for spring, +2.7 °C for summer, and +3.6 °C for autumn. As before, water balance was forced to adhere to historical lake water level records, precipitation was snowfall or rainfall based on a 0 °C threshold, and inflowing water temperatures were adjusted in concert with air temperatures. We calculated the net response of TDO3 under the future A1B scenario to 10, 25, 50, 75, or 90% reductions in P based on historic concentrations from 1976 to 2013.

We estimated the economic investment required to achieve each level of P load reduction using the *Yahara CLEAN Engineering Report* (Strand Associates 2013). The report details a list of action items that result in a 50% P loading reduction to Lake Mendota, the cost of each item (Table 4.01-2 in Strand Associates 2013), and a maximum implementation plan representing an 86% load reduction based on elimination of 97% of direct drainage sources (Table 4.05-1 in Strand Associates 2013). The cost efficiency (in US$ per kg P reduction) and nonmonetary factors associated with each potential P reduction method are also provided in the report. These figures enabled us to estimate the economic cost of each load reduction target over a 20-year period in terms of present-day value. In addition, we calculated both the most- and least-cost effective combinations of efforts that would achieve the target load reduction, thereby bracketing potential costs.

Results

Model Evaluation

The process-based model reproduced the observed data reasonably well (Table 1 and Fig. 1). Observed and predicted temperature values were closely related, and both NMAE and RMSE were small. Epilimnion temperatures had higher correlations and smaller RMSE than hypolimnion temperatures, indicating that the model reproduces observed values more accurately for the epilimnion (Fig. 1a, b). Through the year, both thermocline depth and duration of stratification are simulated accurately (Fig. 1c). Modeled and observed DO profiles were highly correlated, and NMAE and RMSE were both small (less than 1 mg L^{-1}). During the summer, epilimnetic DO was under-estimated by the model (Fig. 1b, d). The depth of DO depletion in the water column was reproduced well; however, the model suggested that hypolimnetic deoxygenation and re-oxygenation occur earlier than observed (Fig. 1d).

Historical Characterization of Oxythermal Niche

Maximum annual TDO3 varied widely during the period 1976–2013 (Fig. 2). The mean TDO3 value was 23.59 °C, the maximum was 27.10 °C, and the minimum value was 19.80 °C. During the study period, the yearly maximum TDO3 value increased significantly ($p < 0.001$) at a rate of 0.92 °C decade^{-1} (Fig. 2). In Lake Mendota, there was a large cisco mortality event in 1987, which seemed to correspond to the largest simulated TDO3 (24.84 °C) up to that time. After 1987, TDO3 values declined for approximately 5 years before increasing steadily up to the present. Further comparisons between TDO3 and cisco monitoring data were not fruitful because cisco were functionally extirpated by the high mortality in 1987 (Supplementary Materials S5).

MLR of Meteorological and Water Quality Variables

Model validation metrics indicated that TDO3 response was best represented by the following linear equation:

$$\mathrm{TDO3} = -4.26 + 0.59 \times \ln(\mathrm{P}) + 0.62 \times T + 2.03 \times \ln(Q),$$

where TDO3 is the annual maximum, P is the spring P loading (kg total P) into the lake (standard error = 0.26),

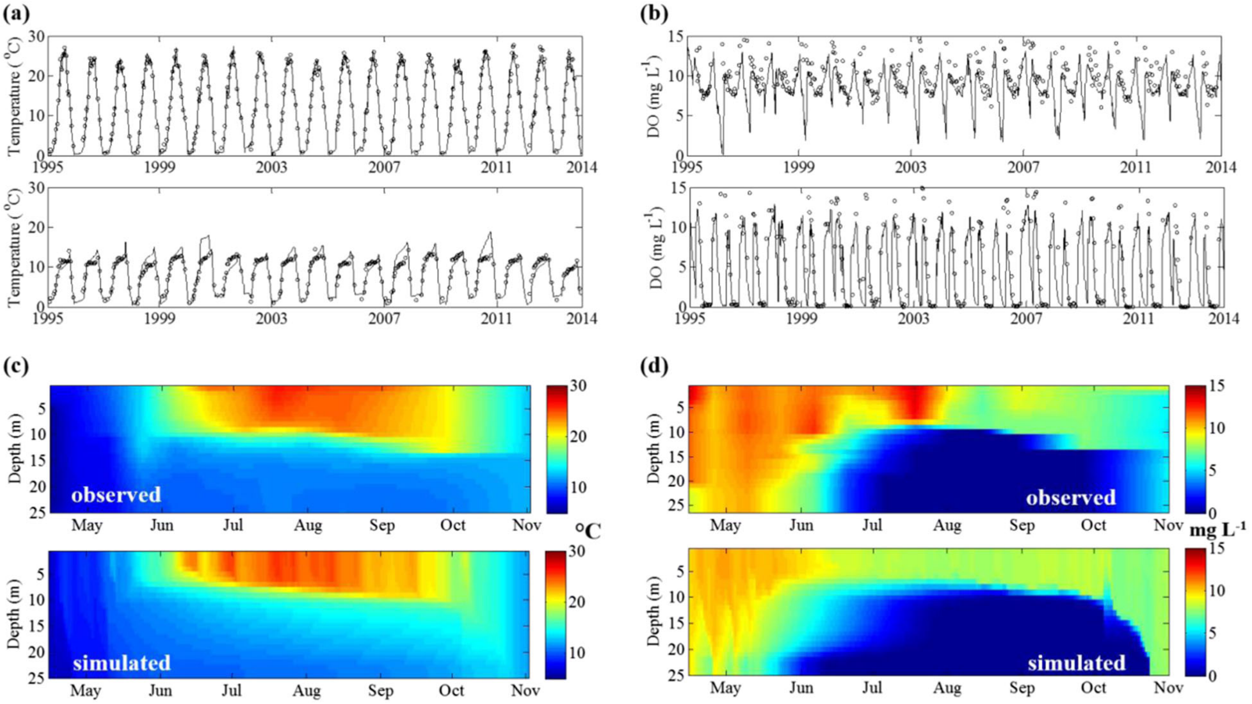
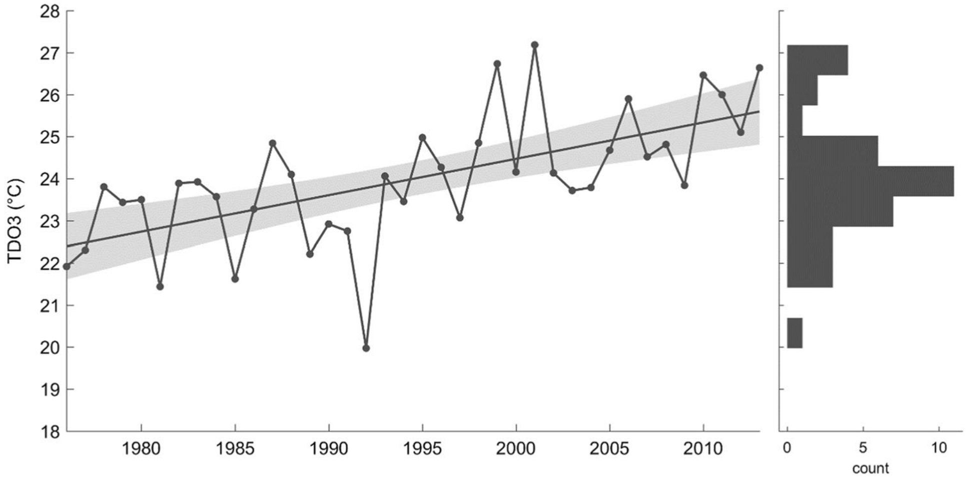


Fig. 1 Comparisons of volumetrically averaged simulated (solid line) and observed (circles) **a** temperatures and **b** dissolved oxygen in the epilimnion (top) and hypolimnion (bottom) of Lake Mendota for the period 1995–2013. Temperature comparison from 1975 to 1995 is not shown for brevity but showed comparable patterns. Interpolated observed (upper) and simulated (lower) time series of temperature **c** and dissolved oxygen **d** profiles for depths 0–25 m from 15 April to 1 November 2005 illustrate the squeeze of oxythermal cisco habitat late in the stratified season

Fig. 2 Maximum annual TDO3 from 1976 to 2013 for Lake Mendota, indicating that cisco have lost all oxythermal habitat for at least 1 day during every year since 1993. The mode in the frequency histogram of TDO3 values during this period exceeds the 22 °C limit for cisco, and maximum annual TDO3 has increased at a rate of 0.92 °C decade^{-1} ($p = 1.45 \times 10^{-5}$). The gray band indicates the 95% confidence interval around the trendline



and T (°C) is the summer (JJA) average air temperature (SE = 0.01) and Q is the spring inflow (1000 m^3) into Lake Mendota (SE = 0.48). Analysis of the residual plots shows linearity, normality, and homoscedasticity and the model had the second lowest RMSE, second-highest R^2, and lowest AICc criterion of all the models tested (Supplementary Material S3). MLR analysis between the meteorological and water quality drivers with TDO3 show that summer (JJA) air temperature, ln-transformed spring (MAM) P load, and ln-transformed spring (MAM) inflow were all significant predictors of the annual maximum TDO3 value ($p < 0.01$ for each variable; $N = 38$). Higher P loads, summer air temperatures, and spring inflow are all associated with higher TDO3, and together explain 76% of the variance. Spring P load and inflow are themselves closely correlated ($r = 0.79$, $p < 0.001$), perhaps reflecting mutual dependence on precipitation even though spring precipitation and inflow are not correlated ($r = 0.05$, $p = 0.76$).

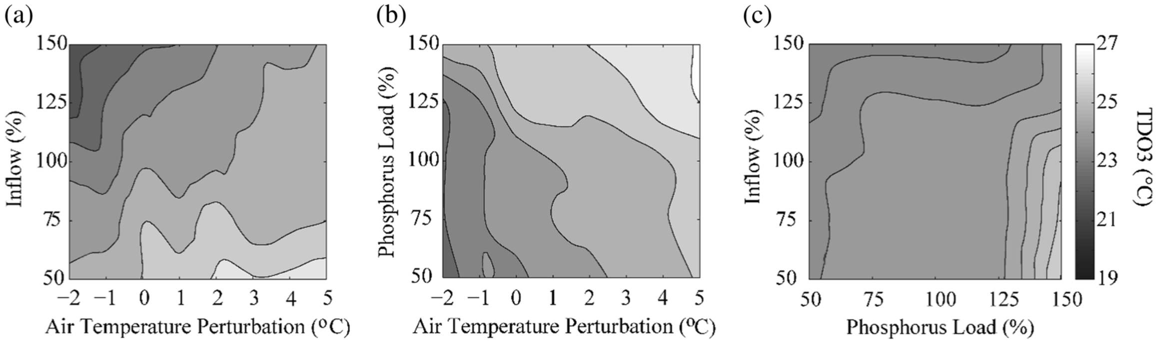


Fig. 3 Response surfaces illustrating the sensitivity of maximum annual TDO3 in Lake Mendota to pairwise factorial combinations of simulated change in three key drivers: **a** air temperature and inflow volume, with constant phosphorus loading; **b** air temperature and phosphorus loading, with constant inflow volume; and **c** phosphorus loading and inflow volume, with constant air temperature

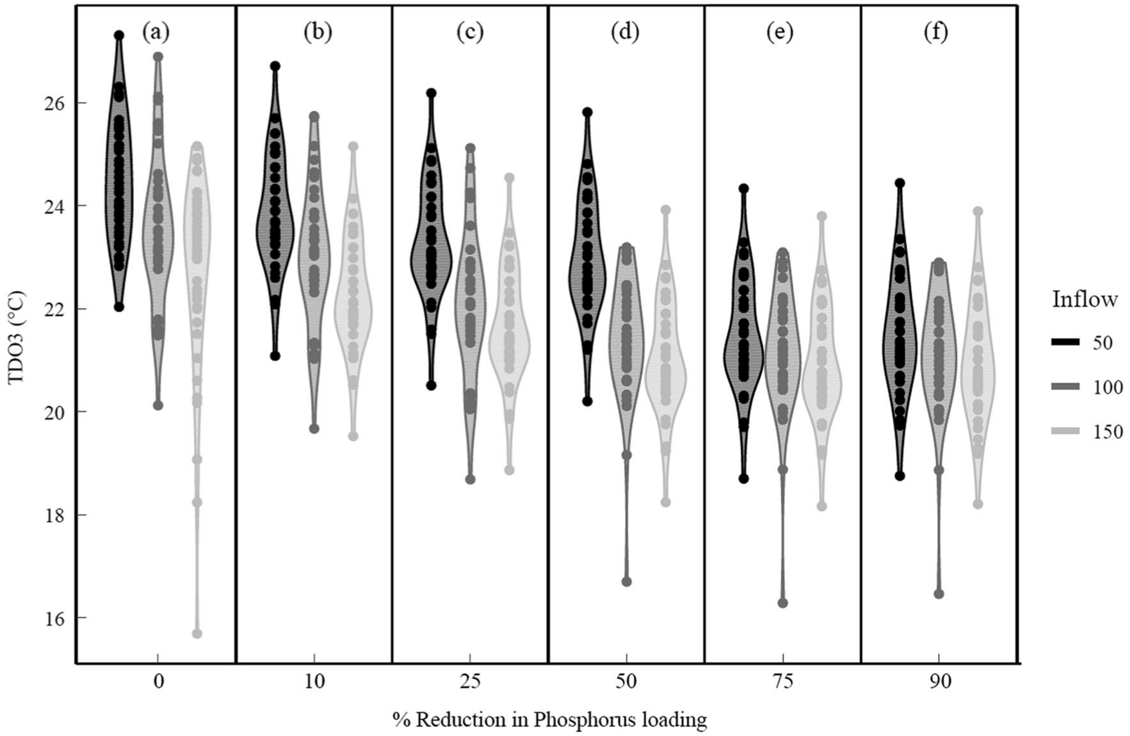


Fig. 4 Frequency distribution of maximum annual TDO3 for scenarios of reduced phosphorus loading (0, 10, 25, 50, 75, and 90% reductions) under the A1B climate scenario, illustrated for three scenarios of inflow volume to Lake Mendota: 50% of current inflow (dark gray); 100% of current inflow (medium gray); and 150% of current inflow (light gray). Individual markers show projected TDO3 for 1 simulation year; the width of the bubbles indicate overall data density across years

Sensitivity of TDO3 to Perturbations

The average maximum TDO3 for the 38 simulation years under each scenario run (e.g., +1 °C temperature + 75% of P load perturbation) reveals no interactive effects between inflow and P loading, but slight nonlinearity in TDO3 responses to jointly permuting air temperature and either inflow or P load (Fig. 3). Importantly, multiple driver combinations result in the same TDO3 values, as implied by the MLR results.

Phosphorus Loading Reductions

Under the A1B climate scenario, TDO3 values decrease as P load decreases for all inflow scenarios (Fig. 4). Under the A1B scenario with identical inflow and P load as the present, 34 of 38 years (89.5%) have TDO3 values that exceed the cisco threshold value of 22 °C. For P loads in line with present levels, reduced inflow (50% inflow scenario) is expected to experience TDO3 above the threshold value, whereas enhanced inflow (150%) has only 28 of 38 years

(74%) above the threshold. While P loading reduction scenarios (10–90%) predict lower TDO3 values for both reduced inflow and enhanced inflow scenarios, none of the scenarios offset the effects of the A1B warming projections to keep TDO3 below the threshold value in every year. The number of years with maximum TDO3 < 22 °C is never more than 8 (21%) under any scenario; hence, this may be considered the best case plausible under A1B rates of warming. To achieve even that modest level of success, P loads would need to be reduced by 75% under current inflow patterns (Fig. 4d) or by 50% if inflow were to increase to 150% of current inflow (Fig. 4d). Based on P load reduction strategies, we determined that P load reductions of 50–75% would cost between US$70 million and US$167 million over a 20-year period.

Discussion

TDO3 values in Lake Mendota have increased significantly between 1976 and 2013, possibly explaining the mass mortality of cisco in 1987 and their subsequent failure to recover. Regression analysis indicates that annual maximum TDO3 is associated with summer air temperatures, spring phosphorus loads, and spring inflow volumes. The MLR model is not robust enough to explore scenarios of future TDO3, but the process-based model does indicate major reductions from present-day P loads will be required to offset changes in projected warming and precipitation to maintain TDO3 at its current level. The high cost of such P reductions suggests poor prospects for recovery of cisco populations in Lake Mendota. However, a 50% loading reduction, which is the target of a current P loading initiative in the Yahara watershed, would make a significant contribution to achieving efforts necessary for cisco recovery and offset changes in oxythermal stress caused by a warmer climate.

Evaluation of Process-Based Model

For the duration of the simulation, predicted water temperatures, stratification timing, and thermocline depth matched observed values quite well (Fig. 1; Table 1). The process-based model performed as well or better than previous studies of temperate lakes. For instance, Perroud et al. (2009) found RMSE values for water temperature of 1.7°–4.0 °C for a variety of model formulations including the Hostetler model, DYRESM, SIMSTRAT, and FLake, while Fang and Stefan (1996) had standard errors of 1.37 °C for the open water season. Our Spearman's rho and NMAE values are comparable to those of Kara et al. (2012) for Lake Mendota.

Simulated dissolved oxygen concentrations also agreed well with observed data (Fig. 1b, d). The majority of model error occurs in epilimnetic DO, but performance was satisfactory for this study because cisco habitat availability depends primarily on hypolimnetic DO. NMAE values compare well with those from Kara et al. (2012) and Snortheim et al. (2017) for Lake Mendota, and are considerably better than NMAE values for DO reported by Bruce et al. (2006) and Gal et al. (2009). However, Spearman's rho values here are lower than those from Gal et al. (2009) and Kara et al. (2012). Most importantly for TDO3 calculations, our model simulated the depth of DO depletion in the water column accurately during the summer (Fig. 1d).

Predictive Ability of MLR Compared to Process-Based Model

The MLR approach adequately predicts the average TDO3 in a lake by focusing on key climatological and nutrient drivers of temperature and DO, yet is too imprecise to forecast year-to-year changes in TDO3 reliably. In both the historical scenario and expanded sensitivity analysis scenarios (Table 2; Supplementary Materials S4, S6) the MLR equation fitted to results from our process-based model only performs modestly well at predicting TDO3 when compared to the process-based model in both the historical scenario and the expanded sensitivity analysis scenarios. The MLR model forecasted annual maximum TDO3 within 1 °C of the mechanistic model 49% of years for each simulation scenario (e.g. historical scenario and sensitivity perturbation

Table 2 Frequency with which the multiple linear regression (MLR) model predicts whether the mechanistic model (DYRESM-WQ-I) would indicate maximum annual TDO3 above versus below the 22 °C threshold value for cisco in Lake Mendota in scenarios of future climate change and phosphorus loading

	TDO3 from MLR	TDO3 from DYRESM-WQ-I	
		TDO3 < 22 °C	TDO3 > 22 °C
All modeled values	TDO3 < 22 °C	2477 (44.26%)	1153 (20.60%)
	TDO3 > 22 °C	1167 (20.85%)	799 (14.28%)
Scenario-averaged values	TDO3 < 22 °C	105 (37.23%)	81 (28.72%)
	TDO3 > 22 °C	52 (18.44%)	44 (15.60%)

Percent characterization is given in parenthesis. The MLR approach correctly predicts exceedance or nonexceedance of the threshold 58.5% of the time for all scenario years and 52.8% of the time for the average of all years within a single scenario scenarios; Table 2). With respect to cisco habitat thresholds, MLR matched the process-based model above or below the 22 °C threshold 58% of the time. Performance of the MLR approach did not improve when forecasting average TDO3 values for sensitivity scenario simulations only matching the process-based model 52% of the time. A longer calibration period with larger variability in driver input might improve MLR performance. Additionally, because we have few years that are below the 22° TDO3 threshold, there may be a bias in the MLR model under future conditions to overestimate TDO3. Few years with TDO3 values below the threshold reflect the fact that this lake has become marginal habitat for cold-water fishes. Both the MLR model and the process-based model are affected by this limitation of real data at low-stress conditions, but comparisons between models are focused on the range of oxythermal regimes that are relevant for predicting hospitable conditions for cold-water fish; thus cross-comparisons between the two are not impacted. Our data limitations likely produce a conservative estimate of stress conditions under alternative scenarios because if reslult bias exists, it is toward higher stress conditions.

One notable difference between MLR and the process-based model is the importance of inflow volume to the lake. Contrary to results from MLR, surface plots (Fig. 3) indicate that increased inflow volumes result in decreases in maximum TDO3 values. This may be due to the high correlation between inflow volumes and phosphorus loadings in the measured data. High inflow correlates with high P load since the majority of P loadings come from these large inflow events (Carpenter et al. 2015). In the sensitivity analysis, there is a lower correlation between inflow volume and P load ($r = 0.30$, $p < 0.001$) compared to the historical condition ($r = 0.79$, $p < 0.001$). The process-based model can test the impact of inflow and P load independently from one another. Altering the data to keep inflow volume and/or P load consistent with the historical distribution while changing the other variable shows that increases in inflow volume can reduce TDO3 under an unchanged P load because of the decrease in flushing time with larger inflow volume, more quickly removing P from the lake than during lower flow scenarios. Such scenarios may be possible through agricultural best management practices such as stream buffers, conservation tillage, and terracing that mitigate P transfers to surface water despite increases in runoff (Sharpley et al. 2006). In this case, increased precipitation would cause increased inflow, but best management practices would prevent a larger P load from entering the lake after large precipitation events.

Overall, the MLR approach is useful for managers interested in general changes to oxythermal habitat, habitat on a large numbers of lakes, or oxythermal habitat in lakes with limited data to drive a process-based model; but process-based models are necessary when needing to identify year-to-year variability with accuracy and for identifying important mechanisms in management options that make one choice more successful than another. The MLR approach captured general changes to oxythermal habitat with changes in meteorological and water quality drivers, although it was unable to project habitat when altering the drivers outside the range of historical norms (e.g. reducing P load while increasing flow). This approach would be particularly useful as a first cut when needing to triage management actions on many cisco lakes across a large gradient of meteorological and water quality characteristics, where it is not feasible to develop and calibrate process-based models. To tease out differences, especially in year-to-year variability of oxythermal habitat as drivers are altered outside the historical norms, the process-based model becomes necessary to fully understand the impacts of management strategies.

Effect of Climate and Water Quality Changes on TDO3

Our simulations demonstrate sensitivity of TDO3 to perturbations in climate and water quality drivers, indicating that future conditions in Lake Mendota will be closely tied to the rate of climate change and nutrient loading. For instance, a 1 °C rise in air temperature would increase TDO3 by ~0.46 °C, a 10% increase in P load yields a 0.27 °C increase in TDO3, and a 10% increase in inflow volume results in a 0.10 °C decrease in TDO3 (Fig. 3). Interestingly, TDO3 is more sensitive to air temperature and P loading than inflow volumes.

Warmer air temperatures increase TDO3 directly through increasing water temperatures in the epilimnion (Livingstone 2003; Kirillin 2010; Magee et al. 2016) as well as indirectly through increased stratification duration (Cahill et al. 2005; Magee et al. 2016). P loading increases TDO3 by a completely different pathway. Boosting phytoplankton primary productivity leads to higher oxygen demand in the hypolimnion during the stratified season. Additionally, phytoplankton growth rates are temperature dependent (Litchman et al. 2007; Jöhnk et al. 2008), so hypolimnetic deoxygenation can be further accelerated by warming together with increased P loading, which is captured in the process-based model.

Precipitation was not a strong driver for year-to-year differences in TDO3, lake inflow is a strong driver. Future changes in precipitation may indirectly effect TDO3 through alterations in inflow volume into the lake. Similarly, runoff management efforts in the watershed may have consequences for cisco habitat by reducing or increasing direct runoff into the lake, especially during spring months. Surprisingly, we did not find wind speeds to be significantly correlated with TDO3 values in the lakes, despite its significant correlation to both thermal characteristics (Magee et al. 2016) and anoxia (Snortheim et al. 2017) in Lake Mendota. This may be due to the limited hypolimnetic oxygen habitat for cisco during the study period. Because productivity in the lake is so high the vertical extent of our chosen 3 mg L^{-1} threshold reaches the thermocline or nearly to the thermocline in most years (see Fig. 1d for an example) regardless of wind speed or stratification duration. Variability in depth of the 3 mg L^{-1} threshold in the lake appears to be driven by P load rather than wind speed. Since DO availability limits ciscos to the thermocline waters variability in epilimnion, water temperatures may be the main driver of variability in annual maximum TDO3. Thus, air temperature and P load are significant drivers in year-to-year variability, while wind speeds account for little variability in maximum annual TDO3 values.

Response to Reduced P Loading

A series of initiatives within the Lake Mendota watershed and larger Yahara chain of lakes have sought to reduce P loading aiming to improve water quality (Lathrop et al. 1998; Lathrop and Carpenter 2014), and our models provide context for interpreting the magnitude of decrease needed to benefit cold-water fishes. Under the A1B scenario, the effectiveness of P loading reductions depends on the flow of water through the system (Fig. 4). For current inflow conditions, offsetting the expected warming would require a 25% reduction in P load to merely maintain TDO3 at current (1976–2013) levels (Fig. 4c). However, increasing habitable conditions for cisco would require even greater changes in P load—roughly a 75% reduction (Fig. 4e). There is currently a goal to reduce P loading into Lake Mendota by 50% with the aim to improve water quality in the Yahara Chain of Lakes system (Jones et al. 2010; Dane County et al. 2011). During the historical period, only 13% (5 of 38) years were below the 22 °C TDO3 threshold, but if 50% loading reductions were implemented as many as 68% of years could be below the 22 °C threshold if inflow volumes remained consistent with the historical period, which is an improvement over the historic period.

The estimated cost of P loading reductions in the watershed is high, but current P loading reduction initiatives may make improvements to cisco habitat economically feasible. The best-case cisco habitat condition comes at P load reduction of 75% (Fig. 4e), which we estimate to cost between US$155 million and US$167 million over a 20-year period (US$7.75 million – US $8.35 million per year). This cost is unlikely to be economically feasible in the name of cisco habitat conservation. However, the current 50% loading reduction initiative has an estimated cost of US$70 million over a 20-year period (Strand Associates 2013). While current P loading reduction initiatives would not prevent oxythermal stress conditions from occurring during every year, they would offset loss of cisco habitat in the lake at no additional cost above the already proposed management efforts for the watershed.

Implications for Cisco Conservation

To manage cisco habitat in Midwestern lakes, we need to buffer against predicted changes through a suite of approaches. Changing climate and cultural eutrophication have virtually eliminated refuge habitat for cisco during the summer in Lake Mendota. According to our models, summer air temperature, spring P load, and spring inflow are the key factors driving loss of oxythermal habitat in Lake Mendota. While we can do little locally to reduce summer air temperatures, local P loading reductions can be a strong component of this management strategy. Such work will require partnerships across sociopolitical boundaries and other organizational structures, which can be difficult to align and coordinate (Paukert et al. 2017). However, building upon the interests of local and regional stakeholders in improving water quality in the Yahara chain of lakes may offer opportunities to use broader watershed efforts to enhance conservation of cisco. This possibility for Lake Mendota is emblematic of a broader need to combine modeling of long-term oxythermal habitat availability with assessment of other management efforts to identify lakes where cisco and the game fish that forage upon them may be protected by aligning conservation-oriented investments with those made by other stakeholders.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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