

# Modeling oxythermal stress for cool-water fishes in lakes using a cumulative dosage approach

Madeline R. Magee, Peter B. McIntyre, and Chin H. Wu

**Abstract:** Lake warming can negatively impact cool-water fishes through both temperature and oxygen stress. We modeled the joint dynamics of water column temperature and oxygen to quantify oxythermal habitat for yellow perch (*Perca flavescens*) in Fish Lake, Wisconsin, USA. To estimate annual oxythermal stress, we developed a novel metric (cumulative oxythermal stress dosage; COSD) that integrates both stress duration and stress magnitude. We find that COSD better predicts observed perch declines than the published TDO3 metric (temperature at depth where dissolved oxygen is 3 mg·L<sup>-1</sup>), which was developed for cold-water fish. Simulations show increases in COSD between 1911 and 2014, punctuated by a sharp rise since 1989. Extreme COSD years result from the intersection of high maximum daily dosage and prolonged duration exceeding the tolerance threshold. Temperature perturbation experiments to explore future climate scenarios reveal that COSD would increase greatly if the atmosphere warms by >3 °C. Applying the COSD metric broadly to temperate lakes could help direct management efforts toward the ecosystems most likely to serve as climate refugia for cold- and cool-water fishes in the future.

**Résumé :** Le réchauffement des lacs peut avoir une incidence négative sur les poissons d'eau tempérée par le biais de stress associés tant à la température qu'à l'oxygène. Nous avons modélisé la dynamique combinée de la température et de l'oxygène dans la colonne d'eau pour quantifier l'habitat oxythermique pour la perchaude (*Perca flavescens*) dans le lac Fish (Wisconsin, États-Unis). Afin d'estimer le stress oxythermique annuel, nous avons mis au point une nouvelle mesure (le dosage du stress oxythermique cumulatif, COSD), qui intègre la durée et la magnitude du stress. Nous constatons que le COSD prédit mieux les baisses observées des perchaudes que la TDO3 (température à la profondeur où la concentration d'oxygène dissous est de 3 mg·L<sup>-1</sup>), une mesure mise au point pour les poissons d'eau froide. Les simulations montrent des augmentations du COSD de 1911 à 2014 dont une augmentation abrupte depuis 1989. Les années de valeurs extrêmes du COSD découlent de l'intersection de valeurs journalières maximums élevées et d'une longue durée dépassant le seuil de tolérance. Des expériences de perturbation de la température visant à explorer des scénarios de climat futur révèlent que le COSD augmenterait considérablement pour un réchauffement de l'atmosphère de plus de 3 °C. L'application large du COSD aux lacs tempérés pourrait aider à orienter les efforts de gestion vers les écosystèmes les plus susceptibles de servir de refuges climatiques pour les poissons d'eau froide et d'eau tempérée. [Traduit par la Rédaction]

## Introduction

In lakes, water temperature and dissolved oxygen (DO) substantially affect the survival and growth of fish (Fry 1971; Magnuson et al. 1979; Coutant 1990; Jacobson et al. 2010). Fish species are commonly classified by thermal guild, wherein cool- and cold-water species require higher oxygen concentration and lower temperatures than warm-water counterparts (Cahn 1927; Frey 1955; Rudstam and Magnuson 1985). Water temperatures control metabolism, feeding, and growth (Brett 1971; Elliott 1995); impact reproduction and recruitment (Farmer et al. 2015; Feiner et al. 2016); affect predator-prey interactions (Hinz and Wiley 1998; Sharma et al. 2011); and mediate competition (De Staso and Rahel 1994; Reese and Harvey 2002). During the summer stratified season, the temperature needs of cool- and cold-water fish species typically restrict them to the hypolimnion and metalimnion of dimictic lakes. However, decaying organic material can reduce deepwater DO concentrations to stressful or even lethal levels for these species (Nürnberg 1995). Oxythermal habitat refers to the portion of the water column where temperature requirements and DO demands are both met; oxythermal stress reflects condi-

tions that violate one or both needs at a given location. As air temperatures have increased under global climate change, cool- and cold-water fish populations have proven to be highly vulnerable to oxythermal stress (Jacobson et al. 2010; Sharma et al. 2011; Van Zuiden et al. 2016).

Warmer air temperatures negatively impact cool- and cold-water fish species directly through lake warming and indirectly through changes in stratification patterns (Stefan et al. 2001; Casselman 2002; Fang and Stefan 2009; Kraemer et al. 2017). As air temperature increases, so do lake water temperatures in most cases (Fang and Stefan 2009; O'Reilly et al. 2015; Magee et al. 2016), threatening the oxythermal habitat of cool- and cold-water fish populations near their southern ranges (Casselman 2002; Sharma et al. 2011; Herb et al. 2014). Simultaneously, stratification duration and stability also increase with surface warming, thereby isolating the metalimnion and hypolimnion from atmospheric oxygen exchange and reducing their DO concentrations (Fang and Stefan 2009; Ito and Momii 2015). The combination of warmer water temperatures and lower DO under a warming climate is

Received 27 June 2017. Accepted 1 October 2017.

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likely to increase oxythermal stress on fish in lakes that have historically been suitable for cool-water species.

Though the general mechanisms underlying the effects of rising air temperatures on lakes and their fish populations are well understood, predicting the magnitude and pace of those effects relative to air warming is difficult. Warming rates of lake water are not closely tied to warming rates of the overlying atmosphere (O'Reilly et al. 2015), and focusing on temperature alone can overlook critical changes in DO levels. Regression techniques can classify broad suites of lakes by susceptibility to warming or DO depletion (Sharma et al. 2011; Van Zuiden et al. 2016), yet they neglect important processes and may still have problematic misclassification rates. Models that predict water volume or layer thickness between thermal and DO thresholds for particular species (Stefan et al. 2001; Dillon et al. 2003) have not addressed chronic effects of sublethal temperature (Selong et al. 2001; Wehrly et al. 2007) or behavioral thermal regulation (Snucins and Gunn 1995). Newer approaches, such as the TDO3 method (temperature at 3 mg·L<sup>-1</sup> of DO) and its variations (Jacobson et al. 2010; Jiang et al. 2012; Herb et al. 2014), attempt to estimate the availability of water that is both cold and oxygenated to allow for inferences across taxa, thereby simplifying modeling efforts (Jacobson et al. 2010). TDO3-style indices have proven useful for cold-water fish species on a regional scale (Jiang et al. 2012; Herb et al. 2014), but their utility for cool-water species or for assessing the time dynamics of stress have not been tested. Accurately assessing rates of change in oxythermal stress for cool-water fish species is essential for proper management of temperate lakes under increasing air temperatures because many key sportfish are classified within the cool-water guild (e.g., percids, esocids).

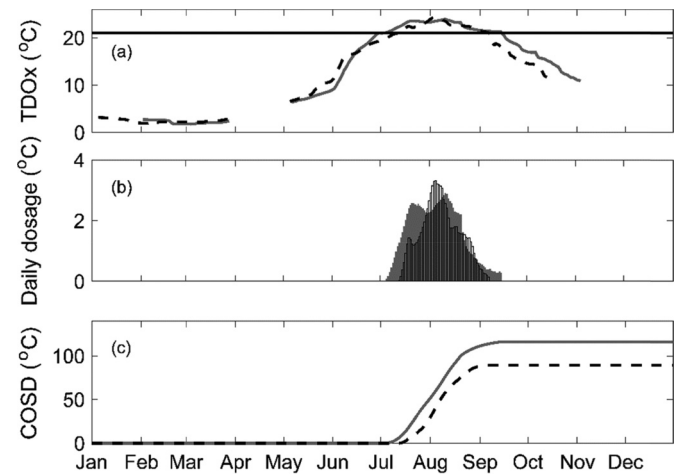
The goal of this paper is to develop an integrative metric for quantifying oxythermal stress throughout the year and apply this metric to investigate the effects of long-term air temperature increases on yellow perch (*Perca flavescens*), a cool-water species. We build upon the TDO3 concept to create a new metric that quantifies cumulative oxythermal stress dosage (COSD) across the year and compare the dynamics of COSD with TDO3 for the same lake (Jacobson et al. 2010; Jiang et al. 2012; Herb et al. 2014). We use a one-dimensional hydrodynamic water quality model to calculate COSD and TDO3 values from simulated daily temperature and DO profiles. Applying this approach to both historical and future air temperature scenarios enables us to investigate how oxythermal stress of yellow perch has been and may be further affected by atmospheric warming.

## Methods

### Study site

Fish Lake (43°17'N, 89°39'W) is a dimictic, eutrophic seepage lake located in northwestern Dane County, Wisconsin, USA. There are no stream inlets or outlets, although nearby Mud Lake may overflow into Fish Lake during large storm events. Fish Lake has a surface area of 87.4 ha, mean depth of 6.6 m, maximum depth of 18.9 m, and a shoreline length of 4.3 km. The lake water level rose gradually by 2.75 m from 1966 to 2001 due to increased groundwater recharge from increased infiltration of snowmelt (Krohelski et al. 2002). Fish Lake was chosen as a study site because it has a monitored yellow perch population, long-term water temperature and DO observations, and regional climate data to extend model simulations across 20 years. Its isolated nature also removes confounding issues of fish movement upstream or downstream to escape inhospitable conditions.

**Fig. 1.** (a) Application of the cumulative oxythermal stress dosage (COSD) approach for 2005 (grey solid) and 2006 (black dashed) on Fish Lake, Wisconsin. Daily TDO3 values (temperature at depth where dissolved oxygen is 3 mg·L<sup>-1</sup>) are calculated as described in Jacobson et al. (2010) and Jiang et al. (2012), where the solid black line shows the temperature threshold value for yellow perch (21 °C). (b) Daily TDO3 dosages exceeded the threshold value during the summer season for both 2005 (light grey) and 2006 (dark grey). (c) The COSD represents a running total of daily TDO3 during the year for 2005 (grey solid) and 2006 (black dashed).



### Fish abundance

Yellow perch abundance was derived from data collected by the North Temperate Lakes — Long Term Ecological Research (NTL-TER) program (<https://lter.limnology.wisc.edu/data/filter/5698>) between 1995 and 2015. Sampling occurred between 14 August and 8 September using a boom-style electrofishing system. Four electrofishing transects were performed annually until 1997, after which the number of transects was reduced to three. The same transects locations were used every year, and each transect consisted of 30 min of current output with the boat moving parallel to shore. Catch per unit effort (CPUE) is shown in online Supplementary material, Fig. S1<sup>1</sup>.

### Oxythermal stress metrics

We developed a new metric of oxythermal stress (COSD) by building upon two previously developed approaches: the TDO3 metric (Jacobson et al. 2010) and degree-day methods (Chezik et al. 2014). TDO3, which represents water temperature at the depth where DO equals 3 mg·L<sup>-1</sup>, is calculated from daily temperature and DO profiles (see Jacobson et al. (2010), their figure 1; and Jiang et al. (2012), their figure 4). This method can be applied to any threshold DO concentration, based on fish species of interest, so we will refer to the generalized metric as TDOx. In the Jiang et al. (2012) TDO3 approach, lakes were characterized based on the peak of the 31-day moving average for the year (hereinafter referred to as peak average TDO3; Fig. S2b<sup>1</sup>). The degree-day approach sums the cumulative degrees above a threshold daily value, yielding an integrative metric across longer periods of time.

In the COSD approach, TDOx is determined for each day of the year (Fig. 1a), and the magnitude of exceedance (°C) of a species-specific temperature threshold is calculated as an index of stress dosage for each day (Fig. 1b). Thus, COSD is the cumulative total of the TDOx exceedance dosage for the year (Fig. 1c). This cumulative approach combines the intensity of daily stress, as determined by the peak average TDO3 method (Jiang et al. 2012), with the dura-

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0260>.

tion of stress as in degree-day calculations and other similar approaches (Stefan et al. 2001; Dillon et al. 2003).

### Temperature and DO thresholds

Suitable fish habitat in the water column is determined jointly by water temperature and DO with respect to species-specific thresholds. Laboratory investigations with yellow perch show that its preferred temperature during summer depends on the size of the fish (McCauley and Read 1973). Reported upper temperature preferences range from 21.4 to 24.2 °C for young fish (McCauley and Read 1973; Neill and Magnuson 1974; Cherry et al. 1977) and from 20 to 21 °C for older fish (Ferguson 1958; McCauley and Read 1973; Reutter and Herdendorf 1974). Upper lethal temperature limits are reported between 29 °C (Eaton et al. 1995) and 34 °C (McCormick 1976). However, these studies do not consider the chronic effects of temperature, and fish exposed to sublethal temperatures during acute tests may experience delayed mortality during longer exposure times (Selong et al. 2001). For this study, we use a conservative temperature of 21 °C (as in Rudstam and Magnuson 1985) as the threshold for calculating TDOx dosage.

We tested a range of DO thresholds from 2 to 6 mg·L<sup>-1</sup> to calculate COSD (Fig. S3<sup>1</sup>). To inform the final selection of an appropriate DO threshold by using the observed dynamics of perch populations, we compared COSD values for each year with both the percentage change and absolute change in CPUE from the prior year. We identified 3 years (2002, 2005, 2012) during the study period as having especially large declines in yellow perch abundance compared with prior years, suggesting that they are potentially informative with respect to DO threshold selection (Fig. S1<sup>1</sup>). We elected not to consider years that had large percentage decreases but low absolute change in CPUE arising from low CPUE in multiple consecutive years. DO thresholds of 3 and 4 mg·L<sup>-1</sup> both identified 2002, 2005, and 2012 as years with highest COSD values (Fig. S3<sup>1</sup>). For this paper, we chose to use a threshold of 3 mg·L<sup>-1</sup>, which has been identified as the acute lethal limit for multiple cool-water fish species (Frey 1955; US EPA 1986).

### Model input data

#### Meteorological data

Meteorological data used as model input consists of daily solar radiation, air temperature, vapor pressure, wind speed, cloud cover, total precipitation, and snowfall. Air temperature, wind speed, vapor pressure, and cloud cover were computed as daily means, while solar radiation, precipitation, and snowfall were computed as daily sums. Meteorological data were taken from Robertson (1989), who constructed a continuous daily meteorological data set for Madison, Wisconsin, from 1884 to 1988 by adjusting for changes in site location, observation time, and surface roughness. More recent data were drawn from the National Climate Data Center weather station (NCDC, NOAA) at the Dane County Regional Airport (Truax Field) in Madison. All data can be obtained from <http://www.ncdc.noaa.gov/>, except solar radiation, which is available from <http://www.sws.uiuc.edu/warm/weather/>. Additional adjustments were made to wind speed data based upon changes in observational techniques occurring in 1996 (McKee et al. 2000) by cross-calibration between the Truax Field site and the Atmospheric and Oceanic Science Building at the University of Wisconsin–Madison (<http://metobs.ssec.wisc.edu/data/>). Magee et al. (2016) detail this adjustment.

#### Water level data

Water level in Fish Lake has gradually increased by 2.75 m from 1966 to 2001 (Krohelski et al. 2002). To account for this water level increase, we used USGS water level data from 1966 to 2003 ([www.waterdata.usgs.gov](http://www.waterdata.usgs.gov)) to estimate inflow and outflow from surface runoff and groundwater inflow using the water budget approach of balancing inflows, outflows, precipitation, evaporation, and

lake level changes. For early years of simulation, lake level observations were not available, so we assumed the long-term mean was applicable. Surface runoff accounted for two-thirds of inflowing water while groundwater inflow contributed one-third of total inflow over the period 1990–1991 (Krohelski et al. 2002). Thus, throughout the simulation period we attributed two-thirds of inflowing water to surface runoff, with runoff temperature estimated from air temperatures as in Magee et al. (2016), and one-third of inflow as groundwater, with temperatures estimated as the long-term mean of all available groundwater temperature measurements (Hennings and Connelly 2008).

#### Air temperature perturbation scenarios

To explore changes in COSD in response to hypothetical increases in air temperature, we simulated five scenarios: +1, +2, +3, +4, and +5 °C perturbations applied to daily mean air temperatures observed from 1995 to 2014. For each scenario, all meteorological inputs other than air temperature remained the same as in the original simulation, except snowfall was converted to rainfall if air temperature rose above 0 °C on the day of precipitation. Additionally, the water balance was maintained such that simulated daily water levels match the historical record.

### Model description

#### Temperature model

To model hydrodynamics in Fish Lake, we used DYRESM-WQ-I, a one-dimensional lake-ice and water quality model based on the DYRESM-WQ (Dynamic Reservoir Simulation Model – Water Quality) model (Hamilton and Schladow 1997) with an additional ice model that simulates water temperature and ice cover year-round. Discrete horizontal Lagrangian layers of uniform properties that vary in thickness are employed to simulate vertical water temperature, salinity, and density (Imberger et al. 1978). A detailed description of the hydrodynamic and ice models can be found in Magee et al. (2016) and Magee and Wu (2017).

#### Dissolved oxygen model

The ecological model in DYRESM-WQ-I includes subroutines for phytoplankton production and loss, nutrient cycling, and DO dynamics. Detailed descriptions of the phytoplankton and nutrient subroutines are found in Hamilton and Schladow (1997). DO concentrations are calculated as the sum of oxygen sources and sinks: surface transfer, inflows and outflows, phytoplankton photosynthesis and respiration, biochemical oxygen demand, sediment oxygen demand, and nitrification. At the surface layer, the saturation concentration of DO is determined from water temperature according to the equation given by Mortimer (1981), as described in Hamilton and Schladow (1997). Oxygen flux at the air–water interface is based on a gas transfer velocity that varies by wind velocity. The model produces daily phytoplankton chlorophyll *a* concentrations in each layer of the water column and then estimates the implications for DO dynamics from photosynthesis and respiration using fixed carbon:chlorophyll ratios and oxygen:carbon stoichiometry (Hamilton and Schladow 1997). Biochemical oxygen demand is modeled by considering the detrital mass of phytoplankton in terms of its equivalent oxygen consumption. In the euphotic zone, oxygen demand in the sediments is assumed to be fully offset by benthic primary production; below the euphotic zone, a modification of the sediment oxygen model of Walker and Snodgrass (1986) is used (Hamilton and Schladow 1997). A stoichiometric factor is used to convert nitrate produced to oxygen consumed during nitrification (Wlosinski et al. 1995; Hamilton and Schladow 1997).

#### Model calibration

The model was calibrated for the period 1995–2010 using observed water temperature and DO profiles in the deepest part of Fish Lake (81 dates), as well as observed water levels and ice cover

**Table 1.** Coefficient of determination ( $R^2$ ) from linear regression, Spearman's rank correlation coefficient (Spearman's Rho), and normalized mean absolute error (NMAE) value for temperature and dissolved oxygen (DO) simulated and observed data.

Variable	No. of observations	$R^2$	Spearman's Rho	NMAE
Temperature	5523	0.79	0.83	0.022
DO	5466	0.62	0.78	0.20

dates. The hydrodynamic and water temperature calibrations are described in detail by Magee and Wu (2016, 2017). DO was calibrated through trial-and-error adjustment of chemical and phytoplankton parameters within the ranges of published values for DYRESM-WQ until satisfactory performance was achieved based on goodness-of-fit metrics. Final phytoplankton and chemical parameters are provided in Table S1<sup>1</sup>. The model was run from 1911 to 2015 to capture the full period where we have model driver data, as well as encompassing the range of years with perch abundance records.

### Model evaluation

We used three statistical measures to evaluate model output against observed data (Table 1): linear coefficient of determination ( $R^2$ ), Spearman's rank correlation coefficient (Rho), and the normalized mean absolute error (NMAE; Alewell and Manderscheid 1998). Statistics were calculated for observed and predicted data at times and depths when observations were made. Temperature and DO profiles (1 m intervals) were obtained for Fish Lake from the NTL-LTER program (<https://lter.limnology.wisc.edu/data/filter/5721>). Profile frequencies were biweekly during spring and summer, monthly during fall, and once annually under the ice.

The model consistently produced surface water levels within 0.2 m (~1%) of observed values. Water temperature dynamics also were reproduced well (Fig. 2a). Observed and predicted temperatures were highly correlated ( $R^2 = 0.79$ , Rho = 0.83; Table 1), and the NMAE was small (0.022; Table 1). Similarly, DO was well estimated throughout the water column (Fig. 2b), although there were under-predictions of DO in the epilimnion year-round (Fig. 2e) and occasionally in the hypolimnion during spring and fall mixing (Fig. 2f). During the stratified period, both the magnitude and timing of hypoxic conditions in the hypolimnion were reproduced well. Goodness-of-fit metrics were poorer for DO than for water temperature, but still highly correlated ( $R^2 = 0.67$ , Rho = 0.78; Table 1) with low NMAE (0.20; Table 1).

### Breakpoint analysis

Breakpoint analysis for COSD and peak average TDO3 values was performed in R Studio ([www.rstudio.com](http://www.rstudio.com)) using the "segmented" package (Muggeo 2003, 2008).

## Results

### COSD as a predictor of fish stress

The years identified as highly stressful based on COSD calculated for a temperature threshold of 21 °C and DO threshold of 3 mg·L<sup>-1</sup> were different from those indicated by peak average TDO3 following Jiang et al. (2012) (Fig. 3). Comparing COSD with the percentage and absolute changes in CPUE of yellow perch from the prior year shows that the three highest COSD values occurred in the years with the greatest perch declines (2002, 2005, 2012; Fig. 3a, Fig. S1<sup>1</sup>). Substantial perch declines were never observed in years with COSD values lower than in 2002; 2008 had the fourth highest COSD value (92.8 °C), but perch declined only 10.5% compared with the previous year. These results indicate that large COSD values are generally associated with declining perch populations, presumably because of oxythermal stress. In comparison, the two highest TDO3 values were calculated for 2012 and 2005, but 6 years (1996, 1999, 2001, 2006, 2008, 2010) had values higher

than 2002 yet exhibited smaller declines in perch CPUE (Figs. 3b and 3c). The TDO3 method underestimated the oxythermal stress that occurred in 2002 because thermal limits were exceeded only modestly yet for a sustained period (Fig. S4<sup>1</sup>). Thus, COSD appears to be a more sensitive metric for predicting yellow perch population declines than the peak average TDO3 values.

As a cumulative metric, similar COSD values can arise from either low daily TDO3 maintained over a period of months or a few weeks of extreme daily TDO3. For example, 2006 had a COSD of 89.6 °C resulting from high daily dosages over a period of nearly 2 months, while COSD of 89.5 °C arose in 2010 from extreme daily dosages that were maintained for just 1 month (Fig. S4<sup>1</sup>). In our 20-year record from Fish Lakes, numerous combination of exceedance duration and dosage were observed (Fig. 4). Statistically, the number of thermal exceedance days (TDO3 > 21 °C) is a somewhat better predictor of high COSD than the maximum daily exceedance dosage in each year (Fig. 4b), but the mean and maximum exceedance dosage showed similar patterns across years (Fig. 4c).

### Long-term changes in oxythermal stress

During the 20-year period for which perch CPUE is available (1995–2014), there is no significant trend in COSD or peak average TDO3. The mean COSD was 64.6 °C (SD = 30.7 °C), and the mean TDO3 was 22.6 °C (SD = 0.74 °C). However, extending the modeling period to 1911 (Fig. 5) using historical meteorological data (see Magee and Wu 2016) reveals long-term changes in both COSD and peak average TDO3. COSD increased significantly (values of 3.7 °C·decade<sup>-1</sup>;  $p < 0.01$ ) largely driven by substantially higher COSD values after 1989. Before 1989, only 21 of 79 years had COSD greater than 0 °C, suggesting that oxythermal stress was unusual. Using 2002 as a COSD benchmark (95.6 °C) due to its association with the first major perch decline in the CPUE record from 1995 to 2014, only 1955 exceeded that threshold COSD (97.2 °C) prior to 1989. In contrast, 3 of the 4 exceedance years occur after 2000, suggesting a general rise in exceedance with time.

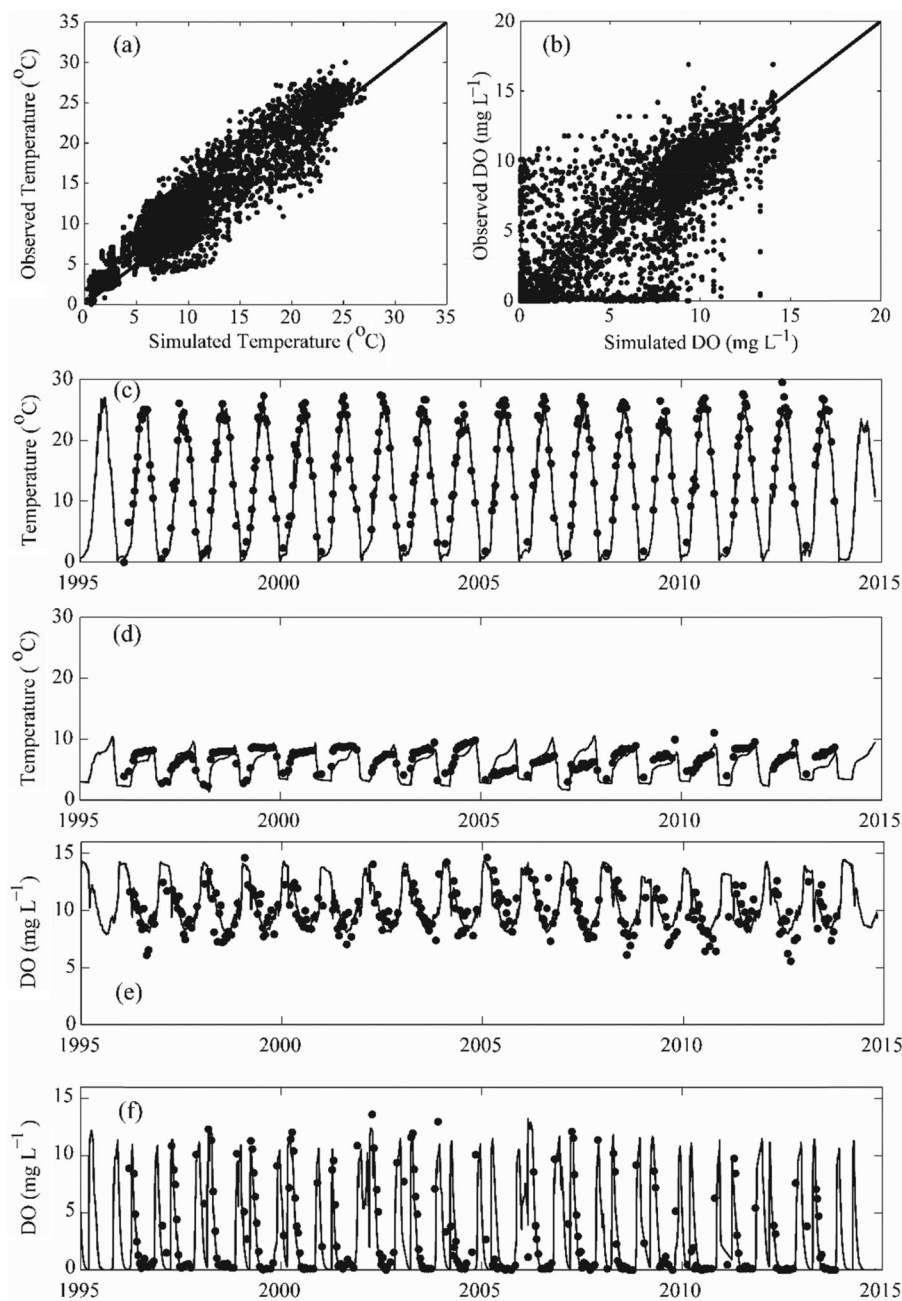
The peak average TDO3 also increased significantly over the 104-year simulation period (0.62 °C·decade<sup>-1</sup>;  $p < 0.01$ ). The trend in peak average TDO3 is more consistent than for COSD (Fig. 5). However, there are two distinct phases of rising peak TDO3: the first occurring before 1930 and the second contemporaneous with the sharp increase in COSD starting after 1984.

Water temperature and DO measurements for validation are not available before 1995; therefore, our ability to realistically recreate historical water temperature and DO values is unknown, especially considering the large change in water levels over the period. Nonetheless, the longer simulation period suggests that there have been enormous changes in both COSD and TDO3 through time in Fish Lake. By extension, we infer that yellow perch oxythermal habitat availability has become scarcer over the last century, including complete elimination for prolonged periods during 3 years over the last two decades (2002, 2005, 2012).

### Air perturbation scenarios

Simulation of the oxythermal consequences of increasing air temperatures (+1 to +5 °C) consistently yielded higher COSD and peak average TDO3 with warming temperatures (Fig. 6). July–September (JAS) averaged air temperatures were most highly correlated with COSD values ( $r = 0.62$ ,  $p < 0.01$ ) and TDO3 values ( $r = 0.53$ ,  $p < 0.01$ ) in comparison with other 3-month air temperature means. For each 1 °C increase in JAS air temperature, COSD increases by 22.55 °C ( $p < 0.01$ ), while peak average TDO3 increases by 0.49 °C ( $p < 0.01$ ). As air temperatures increase, both the mean COSD increases and the range across years becomes broader (Figs. 6–7). Together, these shifts yield dramatically higher probability of problematic COSD with air temperature warming. Beyond a perturbation of +3 °C, the mean COSD value exceeds 92 °C, which was the highest COSD value observed (in 2008) that did not result in notable perch declines. Whereas the +2 °C perturbation

**Fig. 2.** Simulated and observed (a) water temperature and (b) dissolved oxygen (DO) values for Fish Lake from 1995 to 2014. Each point compares modeled and observed temperatures (a) and DO concentrations (b) for one date and lake depth. Volumetrically averaged simulated (solid lines) and observed (black circles) values are shown for water temperatures in the (c) epilimnion and (d) hypolimnion water temperatures and DO in the (e) epilimnion and (f) hypolimnion.



scenario yields only 40% of years (8 of 20) that exceed COSD of 92 °C, 65% (13 of 20) of years exceed that threshold under the +3 °C perturbation.

### Discussion

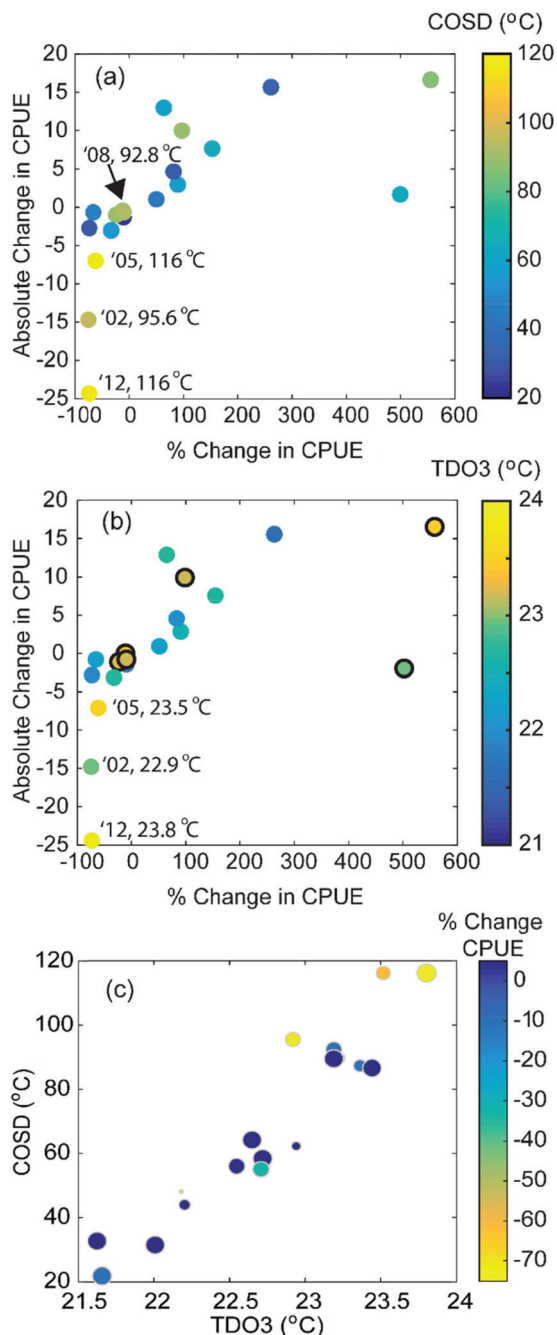
The constraints on habitat availability for cold- and cool-water fishes imposed by summer water temperatures and DO patterns have long been recognized (Hasler 1947; Rudstam and Magnuson 1985; Magnuson et al. 1990), inspiring the development of the TDO3 index (Jacobson et al. 2008, 2010; Jiang et al. 2012). Peak average TDO3 is well designed to assess the rise of oxythermal stress in a general way, focusing on the average stress over a specified duration. To provide a more time-integrated perspective, we designed the COSD index to reflect the summed dosage of oxythermal stress. Conceptually,

the difference is analogous to comparing chronic versus acute exposure to a toxin; both are relevant to survival, but failure to exceed an acute toxicity threshold cannot be interpreted as a lack of lethal stress. Indeed, our comparisons with yellow perch CPUE from Fish Lake suggest that both sustained exposure to oxythermal stress and acute exposures represent bottlenecks on cool-water fish populations. Thus, COSD offers a complementary perspective to TDO3 that may help elucidate the ongoing impact of lake warming and eutrophication on cold- and cool-water fish species.

### COSD as a habitat metric

Because COSD integrates both exceedance dosage and number of exceedance days, the broad gradient of COSD values calculated

**Fig. 3.** (a) COSD and (b) peak average TDO3 (using the same method as Jiang et al. 2012) in relation to the absolute and percent change in CPUE of yellow perch in Fish Lake for different years. A temperature threshold of 21 °C was used to indicate thermal stress in both cases. (c) Percent change in CPUE from the previous year in relation to COSD and peak TDO3. Black outlines of data points in panel (b) represent years where peak average TDO3 exceeded the threshold (22.9 °C), associated with major declines of perch in 2002. [Colour online.]



for Fish Lake could arise in multiple ways (Fig. 4). The largest COSD values result from years with both high maximum daily dosage and high number of exceedance days, whereas years with high values for either mean exceedance dosage or number of exceedance days only result in moderate COSD values. In principle, one could match records of fish population declines with both exceedance days and exceedance dosage to discern which component best predicts the impact of oxythermal stress, but our calcu-

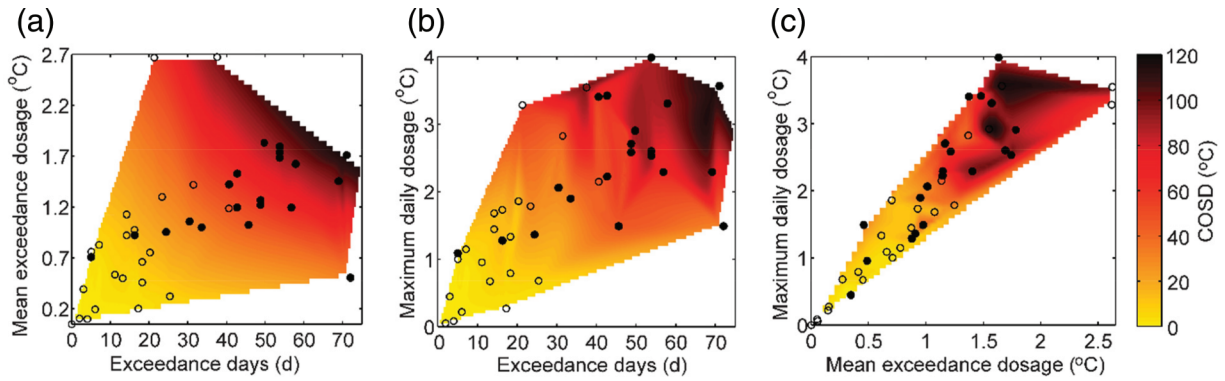
lations for Fish Lake indicate that the extreme COSD associated with large decreases in perch populations emerge from the combination of acute stress (>2 °C) and prolonged duration (>50 days; Fig. 4b). Toxicological research suggests that a parallel phenomenon of high acute stress and prolonged duration both play critical roles in biological response. For example, Onukwufer et al. (2014) found that hypoxia duration and cadmium exposure jointly influence mitochondrial bioenergetics of rainbow trout (*Oncorhynchus mykiss*), and Vehniäinen et al. (2007) found that both the cumulative dose and short-term intensity of ultraviolet radiation mediated impacts on mortality of larval northern pike (*Esox lucius*). For COSD, we find that the relationship between mean exceedance dosage and maximum daily dosage is less variable than the dosage–exceedance duration relationships (Fig. 4c). Generally, as mean exceedance dosage increases, the range of values of maximum daily dosage also increases, and vice versa. Thus, higher COSD values are associated with both higher mean exceedance dosage and higher maximum daily dosages, but very high COSD values appear to be more closely related to maximum daily dosage.

COSD and peak average TDO3 values are highly correlated for both the 20-year study period ( $r = 0.95$ ,  $p < 0.01$ ) and the 104-year extended period ( $r = 0.71$ ,  $p < 0.01$ ). In general, years with high (low) TDO3 values also have high (low) COSD values, reflecting the fact that COSD is a summation of daily TDO3 throughout a year. However, there are some years with key differences between the two values due to the duration of high temperature and low DO conditions during the stratified period. For example, comparing 2005 and 2006, both have similar peak average TDO3 (23.5 versus 23.2 °C; 1.3% difference) but substantially different COSD (116.2 versus 89.6 °C; 22.9% difference). Most of the difference in COSD between these 2 years is due to the extended period when daily TDO3 values exceeded the 21 °C threshold during 2005 compared with 2006 (Fig. 1). Whereas oxythermal stress duration was 30% longer in 2005 (73 versus 56 days), the peak daily TDO3 was only 13% higher in 2006 (3.31 versus 2.92 °C in 2005). Thus, the difference in stress duration is the driving term when disparities in COSD arise despite similar TDO3.

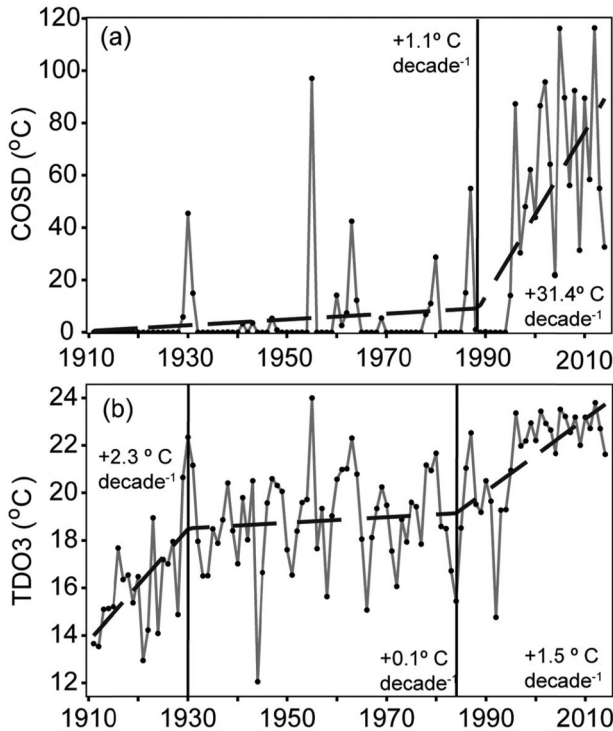
By considering the average of the most stressful 31 days, peak average TDO3 calculations may readily underestimate oxythermal stress in two ways. First, prolonged stress lasting greater than 31 days is not accounted for, yet chronic exposure to elevated temperatures or depressed DO is an important dimension of habitat suitability and species performance (Wehrly et al. 2007). This phenomenon is illustrated more broadly by comparing 2002 with other years (1996, 1999, 2001, 2006, 2008, 2010) that had higher TDO3 values but lower COSD values (Fig. 3). Looking at the daily exceedance dosage (Fig. S4<sup>1</sup>), it is apparent that oxythermal stress in years with low exceedance dosages but long exceedance duration (e.g., 2002) may not appear stressful using the TDO3 method. This can occur in years with prolonged stratification and shallower thermoclines, both of which are becoming more common in lakes worldwide under climate warming (Kraemer et al. 2017). Under that scenario, hypolimnetic hypoxia prevails for a longer period, thereby extending the long exceedance duration, while a shallower thermocline results in cooler hypolimnion and metalimnion temperatures, yielding a lower exceedance dosage.

The second scenario under which TDO3 may underestimate oxythermal stress is when short periods of extreme stress are averaged with days of less harsh conditions, thereby diluting the stress intensity indicated by the peak average TDO3 method even when temperatures exceed lethal limits for acute exposure. This can occur in years when there is a short period of extreme temperatures in late summer, the period of greatest oxygen stress in the water column, resulting in brief exposure to a high thermal exceedance dosage until air temperatures cool. The COSD method would capture the period of extreme stress, but the TDO3 method would indicate a less stressful year because the extreme stress period would be averaged with less stressful conditions.

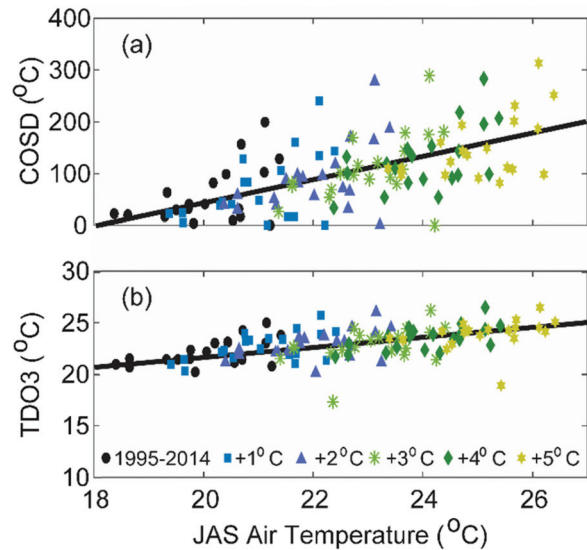
**Fig. 4.** Heatmap of COSD values showing the relationship between the number of exceedance days (number of days when daily TDO3 > 21 °C) and (a) the mean daily temperature dosage above the 21 °C threshold (mean of TDO3 values greater than 21 °C) or (b) maximum daily temperature dosage (maximum TDO3 exceedance dosage in the year). (c) The mean and maximum exceedance dosage are closely associated across observed COSD values. Filled circles represent individual simulation years between 1995 and 2015; open circles represent 1 simulation year with COSD greater than 0 °C between 1911 and 1994. [Colour online.]



**Fig. 5.** Annual values of (a) COSD and (b) peak average TDO3 from 1911 to 2014. Dashed lines represent trends in different periods, and solid vertical lines identify statistical breakpoints. Fitted rates of change are indicated during each period.



**Fig. 6.** Simulated values of (a) COSD and (b) peak average TDO3 for 120 scenarios of July, August, and September (JAS) mean air temperatures. The first 20 years (dark circles) represent the air temperature conditions during the 1995–2014 period; the remaining years representing air temperature increases of +1, +2, +3, +4, and +5 °C. Solid lines represent the linear rate of change in oxythermal stress with increasing JAS air temperatures. [Colour online.]



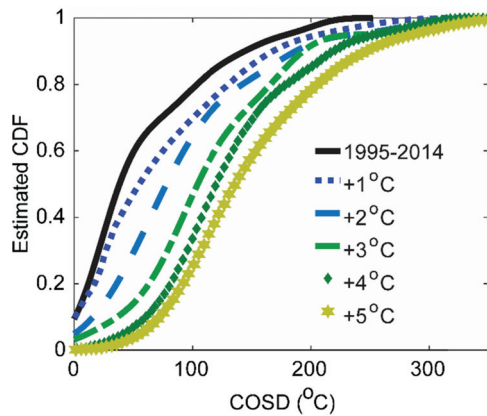
In addition to the limitations of peak average TDO3 for describing oxythermal stress within a year, its averaging approach is not conducive to describing year-to-year and longer-term changes. The duration of exposure to stressful conditions is likely to become increasingly important for developing management responses and mitigation strategies to sustain cool- and cold-water fishes as climate change continues. The advantage of the COSD method lies in characterizing the degree of environmental stress by combining the short-term intensity and long-term duration of inhospitable conditions, thereby providing a more representative metric of oxythermal stress both during a year and across years.

While sensitivity of COSD to both stress intensity and duration is an advantage over peak average TDO3, several limitations must also be recognized. First, in lakes where DO levels are generally

high and water temperatures are low, COSD values do not exceed 0 °C, unlike peak TDO3 values, which are always above zero unless the lake has no anoxic conditions (i.e., if DO is always above 3 mg·L<sup>-1</sup>). This is an artifact of the temperature threshold that must be exceeded before stress is attributed to a day. Using the temperature threshold assigns a penalty only to days that exceed the preferred or optimal growth temperature, which may be problematic in variable ecosystems where temperatures frequently fluctuate above and below threshold values. Zero values for some years may complicate assessment of long-term trends and changes when using COSD, in comparison with nonzero values of stress from the peak average TDO3 method. Thus, the simplicity of the TDO3 derivation may make trends easier to interpret through time and across lakes. Second, the TDO3 method can be used to analyze stress for multiple fish species within and across lakes without any additional analysis (Jacobson et al. 2010; Jiang et al. 2012; Herb et al. 2014), whereas COSD values must be recalculated based on specific temperature and DO thresholds for each

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**Fig. 7.** Cumulative distribution functions (CDF) for annual COSD values under six air temperature scenarios: the original daily air temperature from 1995 to 2014 and perturbations reflecting +1, +2, +3, +4, and +5 °C increases throughout that period. [Colour online.]



fish species of interest. With these limitations of COSD in mind, we view cumulative metrics as a complement rather than replacement for TDOx analyses.

### Management implications of air temperature changes

Air temperature perturbation scenarios show a strong association between probability of high COSD and expected atmospheric warming (Fig. 7). As air temperatures increase, cool-water fish like yellow perch will continue to experience population declines in Fish Lake. Beyond a 3 °C increase, the COSD that exceeds dosages associated with recorded perch collapses will become the norm. With a 5 °C increase, exceeding the COSD threshold for declines is expected in >75% of years.

While projections of future temperatures remain quite uncertain (WICCI 2011; Fan et al. 2015), these statistics suggest a substantial likelihood of extirpation of yellow perch and other cool-water species from Fish Lake under even moderate warming projections. From 1981 to 2014, air temperatures in Madison, Wisconsin, increased at a rate of 0.334 °C·decade<sup>-1</sup> (Magee et al. 2016), and mean annual air temperatures are expected to reach +3.6 °C over baseline by the year 2055 (WICCI 2011; Karmalkar and Bradley 2017). It is important to note that our analysis of historical CPUE data indicates large drops in perch populations after a single extreme COSD, but our temperature perturbation analysis indicates that repeated high COSD is likely to become commonplace by the middle of this century (Fig. 7). Fish populations are remarkably robust to individual years with anomalous high temperatures (Casselman 2002; Jacobson et al. 2008), but an unrelentingly and inhospitable oxythermal stress regime is likely to exceed their capacity for demographic resilience (Sharma et al. 2011; Herb et al. 2014; Van Zuiden et al. 2016).

Moreover, our analysis did not account for changes in precipitation or wind speed, both of which are likely to change in the future. Precipitation in all seasons has been increasing in the Fish Lake watershed (Kucharik et al. 2010), and yearly mean precipitation is expected to continue to increase, albeit with large uncertainty (WICCI 2011; Fan et al. 2015). Increased precipitation may benefit yellow perch habitat by increasing lake levels, creating more vertical habitat within the lake. However, summer precipitation projections have more uncertainty, and warmer precipitation coupled with increased atmospheric heat input could offset any gains in oxythermal habitat arising from increased annual precipitation. Wind speeds in Madison, Wisconsin, have been decreasing, which enhance epilimnetic warming and extend the duration of stratification (Magee and Wu 2016). Increases in both epilimnetic temperatures and hypolimnetic DO deficits are expected with longer stratification duration, and these hydrodynamic shifts

are likely to exacerbate the general effects of atmospheric warming on COSD. Wind speed is difficult to project — both increases and decreases have been observed regionally (Klink 2002; Pryor et al. 2009) and globally (Pryor et al. 2005; Jiang et al. 2009) in recent history — so the potential influence of future wind patterns on COSD remains uncertain.

In addition to the general loss of oxythermal habitat with atmospheric warming, the population dynamics of cool-water fishes in temperate lakes may reflect a variety of factors that cannot readily be included in ecosystem models. For example, juvenile perch sometimes use hypoxic profundal zones as a refuge from predators (Vejřík et al. 2016), which may suggest the capacity of young perch to violate the COSD threshold assumed in our model. Warmer overwinter temperatures, which were not investigated in our models, can alter the number of female perch that spawn and the fatty acid composition of eggs (Feiner et al. 2016). As a consequence, short, warm winters are often followed by recruitment failures due to production of smaller eggs, lower hatching rates, and smaller larvae (Farmer et al. 2015). Ongoing climate change is resulting in shorter, warmer winters throughout central North America (Ning and Bradley 2015; Ning et al. 2015; Fan et al. 2015), which may exacerbate the effect of summer oxythermal stress on cool-water fish populations. Accounting for such influences in addition to COSD represents a frontier in understanding and predicting the responses of fish populations to climate change.

This study presents a new perspective for quantifying oxythermal habitat of cool-water fishes in the context of broad air temperature changes. The COSD approach developed here suggests that both sustained and acute exposure to oxythermal stress conditions will impact cool-water fish populations under changing climate and highlights the ongoing impact of lake warming and eutrophication. Given the expected changes in air temperatures into the future, our results suggest a substantial likelihood of yellow perch extirpation from Fish Lake and other similar lakes even under moderate warming projections.

### Acknowledgements

We thank Richard Lathrop, John Magnuson, Paul Hanson, Katherine McMahon, Paul Block, Jordan Read, and Andrew Rypel for insightful comments on earlier versions of the manuscript. Financial support was provided by the NSF-LTER program (No. DEB-1440297, NTL-LTER), University of Wisconsin Water Resources Institute USGS 10(B) Research grant, the University of Wisconsin Office of Sustainability SIRE Award Program, and the Department of Interior Northeast Climate Science Center. The project described in this publication was supported in part by Grant or Cooperative Agreement No. G12AC00001 from the United States Geological Survey. Its contents are solely the responsibility of the authors and do not necessarily represent the views of the Northeast Climate Science Center or the USGS.

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