Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

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Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2017-0043.R3
Manuscript Type:	Article
Date Submitted by the Author:	07-Jun-2017
Complete List of Authors:	Lyons, John; Wisconsin Department of Natural Resources, Parks, Timothy; Wisconsin Department of Natural Resources Minahan, Kristi; Wisconsin Department of Natural Resources Ruesch, Aaron; Wisconsin Department of Natural Resources
Is the invited manuscript for consideration in a Special Issue? :	N/A
Keyword:	LAKES < Environment/Habitat, CLIMATE CHANGE < General, EUTROPHICATION < General, TEMPERATURE < General, FRESHWATER FISHES < General

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Evaluation of oxythermal metrics and benchmarks for the protection of cisco (*Coregonus artedii*) habitat quality and quantity in Wisconsin lakes

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Abstract: The cisco (*Coregonus artedii*) requires cold, well-oxygenated water and is threatened by climate warming and lake eutrophication, especially at the southern edge of its range in the Laurentian Great Lakes region. In this paper, a method is described to assess the quality, quantity, and variability of suitable cisco habitat. Two metrics are proposed to characterize existing cisco oxythermal habitat in this region: water temperature in the water column at a dissolved oxygen of 6 mg/L (TDO6), and “cisco layer thickness” (CLT), the vertical extent of the water column within which water temperature is $\leq 22.8^{\circ}\text{C}$ and dissolved oxygen is ≥ 6 mg/L. It is proposed that values of TDO6 = 22.8°C and CLT = 1 m be used as benchmarks to identify cisco lakes with potentially stressful oxythermal habitat. Long-term summer data from 14 Wisconsin cisco lakes with a wide range of limnological characteristics indicated that TDO6 varied from 4.2 – 27.5°C and CLT from -6.2 – 66.7 m. Cisco abundance across lakes was greater at lower values of TDO6 and higher values of CLT, and non-attainments of the proposed benchmarks were most likely in lakes with remnant or extirpated cisco populations. Non-attainment of benchmarks could occur from late June through September, and three or more samples across the entire summer would be required to have a reasonable probability of detecting a non-attainment in TDO6 or CLT within any given year. Across years, to detect a single year of non-attainment with an 80% level of confidence, two years of sampling would be sufficient for CLT and three years for TDO6; to detect more than one non-attaining year, three years of sampling for CLT and six years of sampling for TDO6 would be required. Despite relatively high temporal variation in some lakes, the proposed metrics and benchmarks appear to have value for assessing cisco oxythermal habitat in the Great Lakes region.

INTRODUCTION

The cisco (*Coregonus artedii*) is a lake-dwelling, ecologically and societally important fish species of temperate and arctic North America that requires cold, well-oxygenated water to survive (Becker 1983). In stratified lakes at or near the southern edge of their range in the Laurentian Great Lakes region, cisco are usually limited to cooler hypolimnetic or metalimnetic waters in the summer and are vulnerable to physiological stress and mortality if dissolved oxygen concentrations in these waters become too low (Cahn 1927; Frey 1955; Colby and Brooke 1968; Rudstam and Magnuson 1985). Particularly during long summers and in productive lakes, the upper portion of the water column may become too warm and the lower portion too deficient in dissolved oxygen, and cisco may be “squeezed” into a relatively narrow layer of the water column where oxythermal conditions are suitable (Hile 1936; Fry 1937; Frey 1955; McLain and Magnuson 1988; Jacobson et al. 2008a). In extreme cases, suitable habitat may disappear and cisco may suffer fish kills or even be eliminated from the lake. Broad-scale trends in greater lake warming associated with climate change and declines in summer hypolimnetic and metalimnetic dissolved oxygen concentrations from increasing eutrophication caused by human activities have been blamed for reducing summer habitat quality and quantity and for causing losses of cisco populations (Frey 1955; Evans et al. 1996; Jacobson 2008b; Kumar et al. 2013; Honsey et al. 2016; Fang et al. 2016). Many more cisco populations are projected to disappear if, as expected, these trends continue into the future (Sharma et al. 2011; Fang et al. 2012a, b; Jacobson et al. 2013; Herb et al. 2014; Fang et al. 2016). However there may be opportunities to mitigate habitat loss by improving deep-water dissolved oxygen levels through the reduction of incoming nutrient loads (Chapra and Canale 1991; Burns et al. 2005; Jacobson et al. 2013).

Although it has long been known that cisco require both cold water temperatures and high dissolved oxygen levels, it is only relatively recently that the simultaneous effects of temperature and dissolved oxygen on cisco survival have been fully quantified (Jacobson et al. 2008a, 2010). Field and laboratory studies have shown that cisco prefer water temperatures of 12.5-16.5°C, avoid temperatures above 20-21°C if possible, and have an upper lethal limit of 23.8-26.0°C when dissolved oxygen levels are near saturation (Cahn 1927; Fry 1937; Frey 1955; Colby and Brooke 1969; Engel and Magnuson 1976; Edsall and Colby 1970; Edsall and DeSorcie 2002; Jacobson et al. 2008a). Cisco prefer dissolved oxygen levels above 6 mg/l, avoid levels below 4-4.5 mg/l if possible, and have a lower lethal limit of about 3 mg/l (Rudstam and Magnuson 1985; McLain and Magnuson 1988; Evans et al. 1996; Aku et al. 1997; Jacobson et al. 2010; Fang et al 2012b; Hrycik et al. 2016).

Upper limits for temperature and lower limits for dissolved oxygen are related; cisco can survive at higher temperatures when dissolved oxygen is higher and can tolerate lower dissolved oxygen levels when temperature is lower (Rudstam and Magnuson 1985; Jacobson et al. 2008a). Based on combinations of temperature and dissolved oxygen at which cisco mortality was observed in Minnesota lakes, this relationship has been shown to be curvilinear, with an estimated upper thermal limit for adult cisco of 23.8°C at 8 mg/L dissolved oxygen, 23.3°C at 6 mg/L, 22.0°C at 3 mg/L, and 19.5°C at 1 mg/L (Jacobson et al. 2008a).

Using these findings, Jacobson et al. (2010) proposed a metric to assess summer oxythermal habitat quality for cisco and other coldwater fishes in lakes, the water temperature (T) at the depth in the water column at which the dissolved oxygen (DO) was at a certain level, termed TDOX, where X was the dissolved oxygen concentration (Figure 1). The maximum annual temperature value for TDOX provides a measure of the relative habitat quality of a lake for coldwater species and the likelihood of lethal or sublethal impacts, with lower maximum TDOX temperatures indicating better oxythermal habitat. In Minnesota a value of 3 mg/L dissolved oxygen was used for analyses, and hence there the metric was termed TDO3. A TDO3 value of 22.0°C represents a lethal oxythermal limit for cisco (Jacobson et al. 2008a).

The TDOX concept has obvious value for assessing and tracking current oxythermal habitat conditions for cisco and other coldwater fishes throughout the Great Lakes region. The TDO3 metric used in Minnesota focuses on potentially lethal conditions, but by applying a higher dissolved oxygen concentration, the TDOX concept can also be used to identify sublethal oxythermal habitat. In Wisconsin, water quality standards for coldwater fishes are set at no more than 22.8°C (73°F) for water temperature and no less than 6 mg/L for dissolved oxygen to avoid potential sublethal effects (Wisconsin Administrative Codes, Wisconsin Department of Natural Resources, Chapters NR102.04 [4] [b] and NR102.25 [2]). From these standards and what is known of the preferred and avoided water temperatures and dissolved oxygen levels for cisco, a TDO6 of 22.8°C is a logical benchmark for identifying lakes with potentially stressful or sublethal oxythermal habitat conditions for cisco.

Although TDOX metrics are correlated with the amount of suitable habitat for cisco and other coldwater fishes, they are not direct measures of habitat quantity, and lakes with the same TDOX values could have unequal amounts of suitable cisco habitat because of differences in bathymetry and productivity. The actual quantity of suitable cisco habitat in

the water column of a stratified lake is determined by the shallowest depth at which the water temperature is sufficiently cold and the deepest depth at which the dissolved oxygen concentration is sufficiently high, which Frey (1955) termed the “cisco layer”. The greater the cisco layer thickness (CLT), the more suitable habitat would be potentially available for cisco. Accordingly, based on the Wisconsin water quality standards and what is known of the preferred and avoided water temperatures and dissolved oxygen levels for cisco, a CLT useful for assessing sublethal oxythermal habitat can be defined quantitatively as the portion of the water column in which the water temperature is at or below 22.8°C and the dissolved oxygen concentration is equal to or greater than 6 mg/L (Figure 1). The annual minimum CLT is a direct measure of the relative amount of cisco habitat present, with higher values indicating more suitable habitat. Based on a preliminary examination of oxythermal data from 133 current or former Wisconsin cisco lakes, a CLT value of 1 m or lower can be recommended as another benchmark for identifying cisco populations that currently have sublethal oxythermal conditions (WDNR, unpublished data).

Studies from the Great Lakes region (e.g., Frey 1955; Evans et al. 1996; Aku et al. 1997; Bowlby et al. 2016; Magee and Wu 2016) indicate that cisco habitat quality and quantity may fluctuate substantially within and among years in response to weather variations. The date during the summer on which cisco habitat quantity and quality are at their lowest may also change from year to year. This temporal variation needs to be better understood before either TDO6 or CLT can be used effectively as water quality metrics. The uncertain timing during the summer of the occurrence of maxTDO6 and minCLT also mandates development of appropriate sampling protocols that ensure an acceptable likelihood of detecting non-attainments of the benchmarks.

With the above in mind, the goal of this study was to develop a methodology for assessing the quality and quantity of oxythermal habitat for cisco in lakes that have (or recently had) populations. Quantitative assessment of oxythermal habitat quality and quantity will result in a better understanding of the current suitability of lakes in the Great Lake region to support cisco and will help identify those lakes that might benefit from management. The four study objectives were to: 1) characterize spatial and temporal variation in TDO6, maximum TDO6, CLT, and minimum CLT values across a group of Wisconsin cisco lakes that encompassed a wide range in surface area, depth, productivity, and location in the state and that were generally representative of many cisco lakes in the Great Lakes region; 2) determine the magnitude and frequency at which TDO6 and CLT failed to attain the proposed benchmarks; 3) assess how TDO6 and CLT related to cisco relative

abundance; and 4) develop practical and effective sampling guidelines for accurately assessing attainment of the TDO6 and CLT benchmarks.

METHODS

Several criteria were used to select lakes for analyses. To be included, lakes had to have at least nine years in which there were water temperature and dissolved oxygen vertical profiles measured in the deepest area of the lake on at least two dates each summer (21 June to 21 September) during the period 1981-2015. For each profile, at least eight concurrent measurements of water temperature and dissolved oxygen had to have been made between the surface and the bottom using appropriately calibrated electronic meters. Lakes also had to have valid records of cisco occurrence since 1981 and at least one year with three or more nights of standardized overnight vertical gill net sampling with a gang of seven net panels of different mesh sizes that stretched from the surface to the bottom to determine cisco relative abundance. This sampling protocol has been shown to be effective at assessing cisco occurrence and relative abundance in Wisconsin lakes (Rudstam 1984). Relative abundance was categorized as High = mean of > 25 cisco per net gang per net night, Moderate = 10-25, Low = 1-10, and Remnant or Extirpated = 0-1. Vertical profile data were obtained from: U.S. Geological Survey (USGS), Wisconsin Water Science Center, Middleton, Wisconsin, (http://waterdata.usgs.gov/wi/nwis/dv?referred_module=qw&search_criteria=county_cd&submitted_form=introduction; accessed 14 November 2016); Northern Temperate Lakes – Long Term Ecological Research program (NTL-LTER), funded by the National Science Foundation, Physical Limnology Dataset of the Primary Study Lakes, 1981-Present, University of Wisconsin-Madison, Center for Limnology (<https://lter.limnology.wisc.edu/datacatalog/search>; accessed 14 November 2016); and Wisconsin Department of Natural Resources (WDNR) data collected by the authors, other WDNR staff, cooperators, and public volunteers (<http://prodoasint.dnr.wi.gov/swims/login.jsp;jsessionid=klQhXQjJXyH2JSmM2J5SdF7GQG6v6klJyQr5KBTvFwTv6TW2hZcp!1173890563>; accessed 14 November 2016). Vertical gill net data were obtained from NTL-LTER and WDNR.

The data analysis had five sequential steps. First, vertical profile data were used to calculate the two metrics. On each sampling date, the depth in the vertical profile at which the water temperature was 22.8°C and the depth at which

dissolved oxygen was 6 mg/L were determined by linear interpolation between measurements (Figure 1). The CLT for that date was the difference between these two depths. Values could be negative if the depth at which the dissolved oxygen was 6 mg/L was shallower than the depth at which the temperature was 22.8°C. The water temperature at the depth at which the dissolved oxygen was 6 mg/L, TDO6, was also determined by linear interpolation. If all depths had dissolved oxygen concentrations more than 6 mg/L, then the TDO6 was the coldest water temperature observed in the vertical profile. Summary statistics for TDO6 and CLT were calculated for each lake.

Second, the most stressful oxythermal conditions were identified. For each summer and for each lake, the maximum TDO6 (maxTDO6) and minimum CLT (minCLT) values were determined. Because there is evidence that water temperature and stratification duration have increased over the last 50-100 years for at least three of the lakes in our dataset (Fish, Mendota, Monona; Magee and Wu 2016) and such an increase could influence patterns of temporal variation, we also used correlation analysis to test for time trends in maxTDO6 and minCLT over the study period.

Third, the frequency and timing of potentially stressful oxythermal habitat were analyzed. The number of samples each year that did not meet the proposed benchmarks, $\text{TDO6} \leq 22.8^{\circ}\text{C}$ and $\text{CLT} \geq 1$ m, hereafter termed non-attainments, were determined and expressed as a percentage of the total summer samples. The dates on which non-attainments occurred were noted. The number of years in which there was at least one non-attainment was also determined as a percentage of the total years with data.

Fourth, variation in oxythermal habitat conditions was related to cisco population status. Summary statistics for TDO6, maxTDO6, CLT, and minCLT and the percentages of samples and of years with non-attainments were compared across the study lakes to determine how variable the two measures of oxythermal habitat were and how they were related to cisco relative abundance. We used a one-way ANOVA with a Student-Newman-Keuls multiple comparisons test (SAS/STAT software: http://www.sas.com/en_us/software/analytics.html#statistical-analysis; accessed 16 Dec 2016) to determine whether there were differences in TDO6 or CLT among the four cisco relative abundance categories.

Fifth and finally, data on variation in the two oxythermal metrics were used to develop sampling guidelines for detecting non-attainments of the proposed benchmarks. We summarized the distributions of dates on which TDO6 and CLT non-attainments occurred across all lakes and years. We used these distributions to determine the probability of detecting

non-attainments under three existing summer sampling protocols: a single vertical profile collected between 28 July and 27 August, as recommended for estimating TDO3 in Minnesota lakes (Jacobson et al. 2010); a total of three vertical profiles collected in July, August, and September, which is the schedule followed by the USGS and many of the public volunteers and cooperators who collect data for WDNR; and a total of seven biweekly samples from late June through late September, which is the usual sampling regime employed by NTL-LTER. Based on these probabilities, we discuss sampling guidelines to estimate non-attainments of the TDO6 and CLT benchmarks.

RESULTS

Fourteen lakes met the criteria for inclusion in the study (Table 1). These were located across a broad area of the state (from 42.59°N to 46.30°N and 88.46°W to 91.55°W) and encompassed wide ranges of surface area (51-3,983 ha), maximum depth (12.5-72.0 m), lake geometry ratio [Gorham and Boyce 1989] 1.03-3.40), and productivity (satellite-derived trophic state index [TSI; Carlson 1977] 31.0-57.6 – oligotrophic to eutrophic). The lake geometry ratio relates lake surface area to depth, and lakes with values less than 2.0 tend to have strong summer stratification. Four lakes had high (H) cisco relative abundance, three had moderate (M) abundance, three had low (L) abundance, and four had remnant or extirpated (R/E) populations.

Values of TDO6 and CLT varied substantially across lakes and within and among years. Individual summer TDO6 values were as low as 4.2°C in Trout Lake (H) on 5 September 1989 and as high as 27.5°C in Fish Lake (R/E) on 9 July 2012 (Table 2). Annual maxTDO6 was as cool as 4.6°C in Big Green Lake (H) in 2013 and as warm as 27.5°C in Fish Lake in 2012. Fish Lake had the greatest range in TDO6 values across all samples, 21.8°C, and Big Green Lake the lowest, 7.3°C. Lake Geneva (H) had the greatest range in maxTDO6 across all years, 16.3°C, and Fish Lake the lowest, 4.6°C (Table 2; Figure 2). Individual summer CLT values were as large as 66.7 m in Big Green Lake on 24 June 2008 and as small as -6.2 m in Lake Mendota (R/E) on 31 July 1988 (Table 3). Annual minCLT was as large as 52.5 m in Big Green Lake in 2014 and as small as -6.2 m in Lake Mendota in 1988. Lake Geneva had the widest range in CLT and minCLT values, 43.0 m and 27.6 m, and Little St. Germain Lake (L) the narrowest, 6.0 m and 5.6 m (Table 3; Fig. 2). Within individual years, the range of TDO6 values was as low as 0.4°C for Big Green Lake in 2005 and as high as 21.2°C for Fish Lake in 2007 and 16.0°C for Lake Geneva in 1998

(Fig. 3). Ranges in CLT values within a year were as low as 0.3 m in Little St. Germain Lake in 1997 and as high as 30.7 m in Big Green Lake in 2009 and 30.0 m in Lake Geneva in 2012.

Relatively few time trends were evident for maxTDO6 or minCLT for the 14 lakes over the study period. For maxTDO6, there were strong increasing trends for Little St. Germain Lake ($r = 0.71$; $p = 0.0203$), Middle Eau Claire Lake (L) ($r = 0.57$; $p = 0.006$) and Sparkling Lake (M) ($r = 0.43$; $p = 0.0136$) and a marginal increasing trend for Lower Eau Claire Lake (L) ($r = 0.39$; $p = 0.0685$). The other 10 lakes had no significant trends in maxTDO6. For minCLT, there was a strong trend towards reduced habitat quantity for Middle Eau Claire Lake ($r = -0.49$; $p = 0.0211$) and marginal trends for less habitat in Lower Eau Claire Lake ($r = -0.41$; $p = 0.0536$) and Fish Lake (R/E) ($r = -0.47$; $p = 0.0777$). The other 11 lakes had no significant trends in minCLT.

Non-attainments of the oxythermal benchmarks varied substantially among lakes. Eight of the 14 lakes never were warmer than the benchmark for TDO6 and six never had a lower habitat quantity than the benchmark for CLT (Table 4). Of those lakes that did not attain the benchmarks, the percentage of total samples with TDO6 greater than 22.8°C ranged from 3.8% in Middle Eau Claire Lake (L) to 56.6% in Lake Monona (R/E) and the percentage of years with maxTDO6 above 22.8°C ranged from 9.1% in Middle Eau Claire Lake to 100% in Fish Lake (R/E). The percentage of total samples with CLT less than 1 m ranged from 3.3% in Lake Geneva (H) to 72.2% in Lake Beulah (R/E) and the percentage of years with minCLT below 1 m ranged from 11.1% in Lake Geneva to 100% in Lake Monona and Fish Lake.

Overall, lower cisco relative abundance was associated with higher values for TDO6 and maxTDO6 and lower values for CLT and minCLT (Tables 2, 3; Figure 4). Lakes with remnant or extirpated cisco populations or with low cisco relative abundance did not differ in TDO6 but had warmer TDO6 values than lakes with moderate cisco relative abundance which in turn had warmer TDO6 values than lakes with high cisco relative abundance ($F = 31.60$, $P < 0.001$). Similarly, lakes with remnant or extirpated cisco populations or with low cisco relative abundance did not differ in CLT but had lower CLT values than lakes with moderate cisco relative abundance which in turn had lower CLT values than lakes with high cisco relative abundance ($F = 33.70$; $P < 0.001$). Non-attainments of the proposed Wisconsin benchmarks for TDO6 and CLT also generally corresponded to cisco relative abundance (Table 4). All four lakes with remnant or extirpated cisco populations commonly exceeded a TDO6 of 22.8°C and fell below a CLT of 1 m, often by substantial margins (Tables 2-4). Two of three

lakes with low cisco relative abundance occasionally did not attain the TDO6 and CLT benchmarks, but all three lakes with moderate cisco relative abundance always attained the benchmarks. Of the four lakes with high cisco relative abundance, none were warmer than the benchmark for TDO6, but two were sometimes less than the benchmark for CLT by a relatively small amount.

The timing of non-attainments of the TDO6 and CLT benchmarks varied across years (Figure 5). Non-attainments were most frequent from mid-July through early September but could occur between late June and late September. Based on the overall distribution of non-attainments in Figure 5, 75.8% of the TDO6 and 61.8% of the CLT non-attainments would be likely to occur during the midsummer sampling period (28 July through 27 August) recommended for Minnesota lakes (Jacobson et al. 2010), but the chances of a single sample in that period detecting a non-attainment would range from only 9.6-14.7% with a median of 13.0% for TDO6 and from only 9.8-14.7% with a median of 13.4% for CLT. With three monthly samples in July, August, and September, the probability of detecting a non-attainment would vary from 12.4-37.5% with a median of 32.3% for TDO6 and 17.4-37.1% with a median of 28.1% for CLT. With seven biweekly samples from late June through late September, the probability of detecting a non-attainment of TDO6 would vary from 45.8-54.2% with a median of 50.0% and the probability of detecting a non-attainment of CLT would vary from 39.6-61.5% with a median of 50.6%. In other words, with a single midsummer sample, the odds of detecting a non-attainment for TDO6 or CLT in any particular year if it occurred would be on the order of one in eight, with three monthly samples the odds would be roughly one in three or one in four, and with seven biweekly samples the odds would be one in two.

DISCUSSION

Based on our findings, the metrics TDO6 and CLT appear to be useful in characterizing the quality and quantity of oxythermal habitat for cisco in lakes, and the benchmarks proposed, 22.8°C for TDO6 and 1 m for CLT, seem appropriate for identifying thresholds beyond which cisco populations may be negatively impacted. Use of these metrics and benchmarks should allow better characterization and classification of cisco habitat suitability within and across lakes and help identify and prioritize lakes where management actions might need to be taken to conserve cisco populations.

Variation in TDO6 and CLT

Values for TDO6 and CLT were highly variable over time in some Wisconsin lakes. Within these lakes, TDO6 and CLT changed both seasonally and annually. Within-year variation was apparently driven by short-term weather fluctuations. Typically, as the summer progressed, the amount of dissolved oxygen in the hypolimnion declined, decreasing the depth at which dissolved oxygen equaled 6 mg/L and contributing to a reduced CLT and a higher TDO6 later in the summer. However, in some years in some larger lakes, the depth at which dissolved oxygen equaled 6 mg/L increased later in the summer, possibly from strong winds that partially circulated and deepened the upper part of the metalimnion, leading to an increase in CLT (e.g., Gorham and Boyce 1989). Conversely, in other lakes the deepening of the metalimnion from strong winds drove water warmer than the threshold of 22.8°C deeper, reducing CLT and increasing TDO6. Major fluctuations in epilimnion water temperatures over the course of the summer also affected TDO6 and CLT. In some lakes in some years, particularly in northern Wisconsin, the epilimnion was below 22.8°C for most of the summer, and thus suitable for cisco, and maxTDO6 and minCLT values were determined largely by a short warm period when the epilimnion temperature peaked. Epilimnion temperature peaks could occur as early in the summer as late June or early July, particularly in the south, or as late as early September.

Variation in maxTDO6 and minCLT6 across years appeared to be driven by longer-term fluctuations in climate. Years such as 2012 with relatively early spring warming and warm summer temperatures, which led to earlier and longer lake stratification (Magee and Wu 2016; Wisconsin State Climatology Office; <http://www.aos.wisc.edu/~sco/>; last accessed 22 November 2016), tended to have warmer values for maxTDO6 and smaller values for minCLT (Fig. 2). Conversely, years such as 2013 with later spring warming and cool summer temperatures, which led to later and shorter lake stratification, tended to have cooler values for maxTDO6 and larger values for minCLT. There was limited evidence of the effects of long-term climate warming on cisco oxythermal habitat with only four of 14 lakes having a warming time trend in maxTDO6 and three lakes having a decreasing thickness trend in minCLT over the study period. Interestingly, two lakes that have had documented increases in summer temperature and stratification duration over the last 50-100 years, Mendota and Monona (Magee and Wu 2016), did not show significant trends in maxTDO6 or minCLT over the 20-30 years of this study.

This implies that high within and among-year variability in these two metrics may obscure the relatively subtle time trends that are visible for other thermal measures over longer time periods. Statistical modeling from Minnesota indicates that TDO3 values are likely to increase in the future in many lakes as a result of climate change and land-use change (Jacobson et al. 2008b, 2010; Fang et al. 2012b; Jiang et al. 2012; Jacobson et al. 2013; Herb et al. 2014), suggesting that TDO6 values will also increase and CLT values will decline. Although our analyses provide no prediction of future conditions, continued long-term oxythermal habitat monitoring using the TDO6 and CLT metrics in Wisconsin lakes can help test and refine climate- and land-use-change modeling projections.

Magnitude and frequency of non-attainment of benchmarks

The occurrence and severity of benchmark non-attainments also varied substantially across lakes and over time, as would be expected given the high temporal and spatial variation in maxTDO6 and minCLT. Some lakes never had non-attainments whereas others had non-attainments nearly every summer. The timing of benchmark non-attainments also varied, ranging from late June to early September. Lakes with frequent non-attainments also had non-attainments of greater magnitude than lakes for which non-attainments were rare. Non-attainment frequency and severity were negatively correlated with cisco relative abundance (see next section), indicating that the benchmarks were meaningful for cisco conservation and management. However, variation in the occurrence and timing of non-attainments poses a challenge to the development and implementation of effective monitoring strategies and to the use of the benchmarks as possible water quality standards to help conserve at-risk cisco populations (see subsequent section).

Relation of TDO6 and CLT to cisco relative abundance

Cisco relative abundance was generally higher in lakes with cooler values for maxTDO6 and larger values for minCLT. Lakes with remnant or extirpated cisco populations regularly failed to attain the TDO6 and CLT benchmarks, whereas lakes with low to high cisco relative abundance only occasionally or never went beyond the benchmarks. Jacobson et al. (2010) found that the related metric TDO3 was negatively related to cisco relative abundance in Minnesota lakes. Previous studies have

shown that the water temperature benchmark, 22.8°C, was below, and the dissolved oxygen benchmark, 6 mg/L, was above the potentially lethal values for cisco (Edsall and Colby 1970; Rudstam and Magnuson 1985; Aku et al. 1997; Edsall and DeSorcie 2002; Jacobson et al. 2008a). However, both were set at levels where non-attainments could indicate sub-lethal conditions. Nonetheless, the occurrences of a few minor non-attainments of the proposed benchmark for CLT (Table 3, 4) and single years with values that equaled the benchmark for TDO6 for two lakes, Geneva and Oconomowoc, with high cisco relative abundance (Table 2) show that small and infrequent non-attainments of the benchmarks do not preclude a strong cisco population.

Guidelines for assessing TDO6 and CLT

Although TDO6 and CLT appear to be good indicators of cisco oxythermal habitat quality and quantity, their often substantial fluctuations in values within and across years make it challenging to design a cost-effective sampling program. A single mid-summer vertical profile may be insufficient to document non-attainments of the proposed benchmarks, with a detection likelihood of less than 15%. Increasing the number of vertical profiles improves this likelihood, but even a biweekly summer sampling program, seven times as much effort as a single sample, will have a probability of only 50% within any given year. Also, a single year of data may be inadequate to determine the oxythermal habitat conditions that matter most for a cisco population. Cisco populations may be limited by the warmest TDO6 and the smallest CLT across years rather than the average values, and a single year of data might not encompass occasional years with stressful oxythermal conditions (e.g., Lathrop et al. 2002). From our data, some of the lakes with remnant or extirpated cisco populations had years in which non-attainments of the TDO6 and CLT did not occur, and a set of profiles collected from one of those years could give a misleading picture of cisco oxythermal habitat quality and quantity.

A clear and accurate assessment of the quality and quantity of oxythermal habitat for cisco and other coldwater fishes in stratified lakes can potentially be a long-term enterprise. Multiple vertical profiles would need to be taken each summer to have a reasonable chance of determining whether the TDO6 or CLT benchmarks were not attained for that year. We recommend at least once-monthly samples in July, August, and September and ideally biweekly samples. Multiple years of data would also likely be required to determine if the proposed benchmarks were being met. Based on the lowest rate of

annual non-attainments of the proposed benchmarks in lakes with remnant or extirpated Cisco populations, 44.4% for maxTDO6 and 77.8% for minCLT for Lake Beulah, and using binomial sampling probabilities (attaining vs. not; <http://vassarstats.net/binomialX.html>; last accessed 20 Dec 2016), a sampling period of at least five years for TDO6 and two years for CLT would be needed to have an approximately 95% likelihood of detecting at least one non-attainment. If an 80% likelihood of detection were sufficient then sampling could be reduced to three years for TDO6 and two years for CLT. If the goal was to detect more than one year with non-attainments, since even lakes with high cisco relative abundance may have infrequent and small non-attainments (e.g., Lake Geneva), then more years of sampling would be needed, at least nine years for TDO6 and four years for CLT for a 95% likelihood of detection and six and three years, respectively, for an 80% likelihood. Bear in mind that these are worst-case sampling recommendations, designed for detecting non-attainments in lakes with infrequent non-attainments of short duration. Lakes with regular and long periods of non-attainment (e.g., Lake Monona, Fish Lake) as well as lakes with good oxythermal conditions and typical metric values far from benchmark levels (e.g., Big Green Lake, Trout Lake) could be characterized with only two to three years of data.

Although the required sampling for assessing attainment may be long-term in some lakes, it is likely feasible within the scope of the types of monitoring programs used to assess state or provincial water quality standards. For example, Wisconsin assessments for total phosphorus and chlorophyll-a require at least two years of monitoring with at least three samples per year (WDNR, unpublished data), and water temperature and dissolved oxygen measurements could be taken simultaneously to meet the requirement for 80% confidence of detecting a single year of CLT non-attainment. Moreover, the sampling techniques and instrumentation for collecting oxythermal data are inexpensive and simple to use, and could therefore be collected through volunteer efforts, as was the case for several of the lakes we examined in this study. Alternatively, the deployment of monitoring buoys that can continuously track the water temperature and dissolved oxygen throughout water column provides a powerful new approach for assessing oxythermal habitat conditions over time (e.g., Matthews and Effler 2009) that is worth exploring. The cost of these buoys is declining and their reliability is improving, and they may eventually be more cost-effective than direct human sampling in many situations (Marcé et al. 2016).

Implications for cisco conservation

Suitable oxythermal habit is critical for cisco survival, but actual long-term data on oxythermal conditions in cisco lakes are surprisingly scarce. Despite the fact that Wisconsin has at least 188 documented cisco lakes (WDNR, unpublished data) and a long history of lake thermal and dissolved oxygen monitoring (e.g., Beckel and Egerton 1987), only 14 lakes met the criteria for inclusion in this study. Although difficult to determine, based on our discussions with biologists in other states and provinces, we suspect that long-term data on oxythermal conditions in cisco lakes are also limited elsewhere in the Great Lakes region. Thus, beyond that which we analyzed, there may be relatively little available information to assess within- and among-year temporal variation in the TDO6 (or TDO3) and CLT metrics and benchmarks. Fortunately, the 14 Wisconsin lakes we studied experienced a variety of climatic conditions and encompassed a wide range of lake morphological and trophic conditions such that they were representative of cisco lakes more generally in the Great Lakes region. Indeed, the attributes of the 14 study lakes overlapped with at least 96% of the surface areas, maximum depths, lake geometry ratios, and trophic states for the other 174 cisco lakes in Wisconsin (WDNR, unpublished data), the 648 documented cisco lakes in Minnesota (Jacobson et al. 2010), the 44 cisco lakes in Indiana (Honsey et al. 2016), the 153 cisco lakes in Michigan (Latta 1995), and 73 of the many cisco lakes in Ontario (Jackson and Harvey 1989). Certainly, however, long-term data from more lakes and from other areas would be valuable and would help better define the ranges and temporal variation of the TDO6 and CLT metrics and benchmarks. We urge investigators outside Wisconsin to look for or to begin to collect appropriate long-term data to examine further the utility of these measures for characterizing oxythermal habitat quality and quantity.

Cisco are an important indicator species in deep lake ecosystems in the Great Lakes region, and therefore the development of effective metrics for assessing lake oxythermal habitat is essential for protecting cisco and other coldwater fish populations on the southern margins of their geographic range. With advancing climate change, it is generally infeasible to mitigate habitat loss through the direct control of lake temperatures and stratification duration. However, adoption of watershed-scale and lakeshore best-management practices for controlling nutrient inputs may result in improved hypolimnetic and metalimnetic dissolved oxygen levels, thereby potentially offsetting rising water temperatures and preventing increased oxythermal stress. In small lakes with particularly valuable coldwater species populations, direct re-oxygenation of the hypolimnion might also be possible (e.g., Aku et al. 1997). The TDO6 and CLT metrics and benchmarks can act as an early warning system for lakes facing potential oxythermal habitat challenges for their coldwater species and

can help prioritize implementation and track responses to nutrient management or hypolimnetic oxygenation efforts across lakes.

ACKNOWLEDGEMENTS

We are grateful to staff of the Wisconsin Department of Natural Resources, U.S. Geological Survey, and University of Wisconsin-Madison, Center for Limnology, National Science Foundation-funded Long-Term Ecological Research Program, and to Wisconsin citizen volunteers for collecting and making available the data used in this study. We thank Mark Gahler, Corinna Gries, Dick Lathrop, Noah Lottig, Rachel Preacher, and Alex Smith for assistance in accessing and compiling the vertical profile data, and Ashley Beranek and Brian Weigel for helpful discussions on establishing benchmark values. Pete Jacobson and Madeline Magee provided valuable comments on an earlier draft of this manuscript. Analyses were funded in part by Federal Aid in Sportfish Restoration, Project WI F-95-P, and the Wisconsin Department of Natural Resources, appropriations 401-GPR and 441-FED-Nonpoint-Grant.

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Table 1. Characteristics of the 14 Wisconsin lakes included in this study. Satellite TSI = Trophic State Index (Carlson 1977), based on satellite estimates of lake water clarity (WDNR, unpublished data), is a measure of relative lake productivity, with higher values indicating higher productivity. Cisco abundance classes are based on mean catch rates in standardized vertical gill net sampling during summer stratification from 1981-2015 (WDNR and NTL-LTER, unpublished data: High > 25 cisco per net gang per night, Moderate 10-25, Low 1-<10, Remnant or Extirpated 0-<1). Sparkling Lake had moderate cisco catches in the early 1980's, but by the 1990's cisco had been eliminated by invasive non-native rainbow smelt (*Osmerus mordax*) (McLain and Magnuson 1988; Sharma et al. 2011).

Lake	Latitude	Longitude	Lake		Satellite	Vertical		Year range
			Surface	Maximum		geometry	profile	
Lake	Latitude	Longitude	area (ha)	depth (m)	TSI	ratio	data source	Year range
Cisco Abundance High								
Geneva	42.59°N	89.36°W	2130	41.2	49.6	1.64	USGS	1997-2004
Big Green	43.82°N	88.99°W	2973	72.0	40.2	1.03	USGS	2004-2014
Trout	46.03°N	89.67°W	1544	31.0	31.0	2.02	NTL-LTER	1982-2013
Oconomowoc	43.10°N	88.46°W	310	18.9	45.1	2.22	USGS	1986-2015
Cisco Abundance Moderate								
Big Muskellunge	46.02°N	89.62°W	376	21.3	35.3	2.07	NTL-LTER	1981-2013
Sparkling	46.01°N	89.70°W	51	19.5	35.0	1.37	NTL-LTER	1981-2013
Lac Court Oreilles	45.89°N	91.44°W	2039	27.4	41.3	2.45	WDNR	2005-2013
Cisco Abundance Low								
Little St. Germain	45.93°N	89.45°W	397	16.2	55.6	2.76	USGS	1991-2003
Middle Eau Claire	46.30°N	91.52°W	365	20.1	40.3	2.17	WDNR	1988-2014

Lower Eau Claire	46.28°N	91.55°W	325	12.5	44.4	3.40	WDNR	1986-2014
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Cisco Population Remnant or Extirpated

Beulah	42.82°N	88.39°W	338	17.7	46.9	2.42	USGS	2007-2015
Mendota	43.11°N	89.41°W	3983	25.0	54.7	3.18	NTL-LTER	1982-2013
Monona	43.07°N	89.36°W	1325	19.5	57.6	3.09	NTL-LTER	1995-2013
Fish	43.29°N	89.56°W	87	18.9	50.6	1.62	NTL-LTER	1999-2013

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Table 2. Summary statistics for the temperature in the water column at which dissolved oxygen was 6 mg/L (TDO6) and the annual summer (21 June through 21 September) maximum value for this temperature (maxTDO6) for the 14 study lakes across all years. Values that are warmer than the proposed TDO6 benchmark of 22.8°C are in italics and boldface. For the TDO6 columns, N refers to the total number of summer samples across all years, and for the maxTDO6 columns, N refers to the number of years. Min = minimum, 25th = 25th percentile, Med = Median (50th percentile), 75th = 75th percentile, and Max = maximum.

Lake	TDO6 (°C)						maxTDO6 (°C)					
	N	Min	25th	Med	75th	Max	N	Min	25th	Med	75th	Max
Cisco Abundance High												
Geneva	61	5.5	7.0	8.1	9.1	22.8	18	6.5	8.1	13.3	20.6	22.8
Big Green	35	4.4	4.6	4.9	5.6	11.7	11	4.6	4.8	5.2	6.0	11.7
Trout	207	4.2	5.9	6.8	7.7	14.1	32	5.9	6.8	8.2	9.3	14.1
Oconomowoc	72	6.7	10.4	15.7	19.7	22.8	30	11.3	16.0	19.4	21.6	22.8
Cisco Abundance Moderate												
Big	212	7.2	10.0	11.9	14.9	21.1	33	10.9	14.4	16.3	18.2	21.1
Muskellunge												
Sparkling	213	5.0	6.0	6.7	7.6	19.4	33	5.9	7.0	7.8	8.6	19.4
Lac Courte	35	8.5	17.1	19.1	20.4	21.3	9	17.4	20.1	20.3	21.0	21.3
Oreilles												
Cisco Abundance Low												
Little St.	24	8.1	9.8	11.4	14.2	18.5	10	9.7	13.8	14.3	18.2	18.5
Germain												
Middle Eau	53	4.1	8.3	11.9	17.4	23.5	22	8.3	11.4	17.1	18.9	23.5

Claire

Lower Eau	61	9.2	18.7	20.0	21.9	25.0		23	19.2	19.7	21.9	22.6	25.0
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Claire

Cisco Population Remnant or Extirpated

Beulah	18	8.7	21.8	22.6	24.4	25.9		9	20.7	22.2	22.7	24.4	25.9
Mendota	209	11.1	18.8	21.2	22.7	26.7		32	20.9	23.0	23.9	25.0	26.7
Monona	116	14.7	21.7	23.1	24.1	27.4		19	22.0	24.0	24.9	26.2	27.4
Fish	87	5.7	20.8	23.1	24.8	27.5		15	22.9	24.5	25.3	26.5	27.5

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Table 3. Summary statistics for the thickness of the water column that had a water temperature less than or equal to 22.8°C and a dissolved oxygen greater than or equal to 6 mg/L (CLT) and the annual summer (21 June through 21 September) minimum value for this thickness (minCLT) for the 14 study lakes across all years. Negative values indicate that the depth at which the temperature was less than 22.8°C was deeper than the depth at which the dissolved oxygen was greater than 6 mg/L. Values that are smaller than the proposed CLT benchmark of 1 m are in italics and boldface. For the CLT columns, N refers to the total number of summer samples across all years, and for the minCLT columns, N refers to the number of years. Min = minimum, 25th = 25th percentile, Med = Median (50th percentile), 75th = 75th percentile, and Max = maximum.

Lake	CLT (m)						minCLT (m)					
	N	Min	25th	Med	75th	Max	N	Min	25th	Med	75th	Max
Cisco Abundance High												
Geneva	61	0.0	12.6	19.9	29.7	43.0	18	0.0	10.9	12.5	17.8	27.6
Big Green	35	30.1	48.5	54.1	60.8	66.7	11	30.1	39.4	42.3	48.8	52.5
Trout	207	9.0	18.9	23.6	28.2	33.7	32	9.0	14.0	15.9	18.1	23.9
Oconomowoc	72	0.0	1.5	4.4	7.5	15.8	30	0.0	0.3	1.7	3.6	9.7
Cisco Abundance Moderate												
Big	212	2.3	9.7	11.5	12.4	19.0	33	2.3	3.8	6.4	9.3	11.2
Muskellunge												
Sparkling	213	4.8	12.3	13.4	14.0	17.0	33	4.8	7.3	8.8	12.3	13.5
Lac Courte	35	1.0	5.2	8.5	9.8	17.7	9	1.0	1.5	4.1	5.9	9.4
Oreilles												
Cisco Abundance Low												
Little St.	24	2.0	5.0	6.4	7.4	8.0	10	2.0	3.1	6.2	6.4	7.6

Germain

Middle Eau	53	-1.4	6.7	10.8	12.5	16.9		22	-1.4	5.4	6.7	10.8	14.2
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Claire

Lower Eau	61	-1.3	3.7	7.0	8.5	12.3		23	-1.3	0.1	1.9	6.6	8.5
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Claire

Cisco Population Remnant or Extirpated

Beulah	18	-1.4	-1.0	0.0	5.1	11.3		9	-1.4	-1.0	-0.3	0.2	5.7
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Mendota	209	-6.2	0.1	2.5	10.2	15.6		32	-6.2	-1.6	-0.9	-0.1	6.4
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Monona	116	-4.6	-1.0	-0.2	3.7	10.1		19	-4.6	-2.9	-1.9	-0.8	0.4
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Fish	87	-5.5	-1.0	-0.2	2.6	11.5		15	-5.5	-1.9	-1.4	-0.9	0.0
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Table 4. Overall percentages of summer samples and of years in which there were non-attainments of the proposed benchmarks for TDO6 and maxTDO6 ($\leq 22.8^{\circ}\text{C}$) and CLT and minCLT ($\geq 1\text{ m}$).

Lake	Samples not attaining (%)		Years not attaining (%)	
	TDO6	CLT	maxTDO6	minCLT
Cisco Abundance High				
Geneva	0	3.3	0	11.1
Big Green	0	0	0	0
Trout	0	0	0	0
Oconomowoc	0	19.4	0	33.3
Cisco Abundance Moderate				
Big Muskellunge	0	0	0	0
Sparkling	0	0	0	0
Lac Courte Oreilles	0	0	0	0
Cisco Abundance Low				
Little St. Germain	0	0	0	0
Middle Eau Claire	3.8	7.6	9.1	18.2
Lower Eau Claire	6.5	19.4	17.4	43.5
Cisco Population Remnant or Extirpated				
Beulah	38.9	72.2	44.4	77.8
Mendota	24.4	42.6	78.1	96.9
Monona	56.6	68.1	94.7	100

Fish	55.7	67.0	100	100
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Figure legends

Fig. 1. Hypothetical water temperature (filled circles) and dissolved oxygen (filled triangles) vertical profiles from two stratified lakes, the top (a) with good values for TDO6 and CLT and the bottom (b) with non-attainments of the TDO6 and CLT benchmarks. The depths at which water temperature (Temp) equals 22.8°C and dissolved oxygen (DO) equals 6 mg/L are shown with dashed lines, the temperature for TDO6 is indicated by an open circle, and the thickness of the CLT is portrayed with a shaded area.

Fig. 2. Examples of the most and least extreme fluctuations across years for maxTDO6 (top panel) and minCLT (bottom panel).

Fig. 3. Examples of the least and two most extreme fluctuations within a lake across a single summer for TDO6 (top panel) and CLT (bottom panel).

Fig. 4. Mean values and error bars indicating two times the standard error of the mean for TDO6 (top panel) and CLT (bottom panel) for the four cisco relative abundance group (R/E = remnant or extirpated). Within a panel, means with different letters were significantly different, but means with the same letter were not.

Fig. 5. Frequency histogram of the day of the summer (June 21 to September 21; in 7-day bins that start on the day of the x-axis label) during which non-attainments of the TDO6 and CLT benchmarks ($\leq 22.8^{\circ}\text{C}$; $\geq 1\text{ m}$) occurred, pooled across all lakes and years and expressed as a percentage of all samples with non-attainments (N = 177 for TDO6 and 265 for CLT).

Figure 1 - Hypothetical temperature-dissolved oxygen depth profiles showing TDO6 and CLT.

Figure 2 - Least and most extreme fluctuations across years for maxTDO6 and minCLT.

406x312mm (120 x 120 DPI)

Figure 3 - Least and most extreme fluctuations within years for TDO6 and CLT.

406x312mm (120 x 120 DPI)

Figure 4 - TDO6 and CLT values for lake groups with different cisco abundances.

406x312mm (120 x 120 DPI)

Figure 5 - Frequency of occurrence of non-attainments for TDO6 and CLT during summer.

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