



Assessment of Inland Lake Coldwater Fish Habitat in Isle Royale and Voyageurs National Parks through Analysis of Oxygen and Temperature Data

Natural Resource Report NPS/VOYA/NRR—2022/2457



ON THE COVER

Park staff offloading array data in Little Trout Lake, Voyageurs National Park.
NPS photo.

Assessment of Inland Lake Coldwater Fish Habitat in Isle Royale and Voyageurs National Parks through Analysis of Oxygen and Temperature Data

Natural Resource Report NPS/VOYA/NRR—2022/2457

Jaime F. LeDuc^{1*}, Ryan P. Maki¹, Rick A. Damstra², Jay D. Glase³, Jared T. Myers⁴, and Mark C. Romanski⁵

¹ National Park Service
Voyageurs National Park
360 Highway 11 East
International Falls, Minnesota 56649

**Current address:* Concerned Citizens of Montauk, Inc., 6 South Elmwood Avenue, Montauk, New York 11954

² National Park Service
Great Lakes Inventory and Monitoring Network
2800 Lakeshore Drive East
Ashland, Wisconsin 54806

³ National Park Service
Interior Regions 3, 4, and 5 (Great Lakes, Mississippi, and Missouri Basins)
2800 Lakeshore Drive East
Ashland, Wisconsin 54806

⁴ U.S. Fish and Wildlife Service
2800 Lakeshore Drive East
Ashland, Wisconsin 54806

⁵ Isle Royale National Park
800 East Lakeshore Drive
Houghton, Michigan 49931

September 2022

U.S. Department of the Interior
National Park Service
Natural Resource Stewardship and Science
Fort Collins, Colorado

The National Park Service, Natural Resource Stewardship and Science office in Fort Collins, Colorado, publishes a range of reports that address natural resource topics. These reports are of interest and applicability to a broad audience in the National Park Service and others in natural resource management, including scientists, conservation and environmental constituencies, and the public.

The Natural Resource Report Series is used to disseminate comprehensive information and analysis about natural resources and related topics concerning lands managed by the National Park Service. The series supports the advancement of science, informed decision-making, and the achievement of the National Park Service mission. The series also provides a forum for presenting more lengthy results that may not be accepted by publications with page limitations.

All manuscripts in the series receive the appropriate level of peer review to ensure that the information is scientifically credible and technically accurate.

Views, statements, findings, conclusions, recommendations, and data in this report do not necessarily reflect views and policies of the National Park Service, U.S. Department of the Interior. Mention of trade names or commercial products does not constitute endorsement or recommendation for use by the U.S. Government.

This report is available in digital format from the [Great Lakes Inventory and Monitoring Network website](#) and the [Natural Resource Publications Management website](#). If you have difficulty accessing information in this publication, particularly if using assistive technology, please email irma@nps.gov.

Please cite this publication as:

LeDuc, J. F., R. P. Maki, R. A. Damstra, J. D. Glase, J. T. Myers, and M. C. Romanski. 2022. Assessment of inland lake coldwater fish habitat in Isle Royale and Voyageurs national parks through analysis of oxygen and temperature data. Natural Resource Report NPS/VOYA/NRR—2022/2457. National Park Service, Fort Collins, Colorado. <https://doi.org/10.36967/2294181>

Contents

	Page
Figures.....	v
Tables.....	vii
Abstract.....	ix
Acknowledgments.....	xi
Introduction.....	1
Methods.....	5
Site Description	5
Field Methods.....	5
Estimated Minimum Volumes of Optimal Habitat and Non-lethal Habitat for Lake Trout and Cisco	5
Estimated Duration of Exposure to Sub-optimal Habitat and Non-lethal Habitat	7
Continuous Temperature and Dissolved Oxygen Arrays.....	8
Results.....	9
Estimated Minimum Volumes of Optimal Habitat and Non-lethal Habitat Using Discrete Dissolved Oxygen Data.....	9
Assessment of Optimal Habitat and Non-lethal Habitat Using Continuous Dissolved Oxygen Data.....	18
Discussion.....	21
Conclusions.....	23
Literature Cited	25

Figures

	Page
Figure 1. Voyageurs National Park showing Little Trout, Mukooda, and Locator lakes highlighted in purple.	1
Figure 2. Isle Royale National Park showing Richie Lake highlighted in purple.....	2
Figure 3. Heat plots showing oxythermal habitat in Little Trout Lake, Voyageurs National Park, for each open water season 2011–2019.	12
Figure 4. Heat plots showing oxythermal habitat in Mukooda Lake, Voyageurs National Park, for each open water season 2015–2019.....	14
Figure 5. Heat plots showing oxythermal habitat for Cisco in Richie Lake, Isle Royale National Park, for each open water season 2010–2013 and 2015–2019.....	17
Figure 6. Heat plots based on continuous temperature and dissolved oxygen data collected in Little Trout, Mukooda, Locator, and Richie lakes in 2019.	19

Tables

	Page
Table 1. Oxythermal (dissolved oxygen and temperature) habitat suitability for Lake Trout and Cisco.....	2
Table 2. Stage storage table for Little Trout Lake, Voyageurs National Park, Minnesota.	6
Table 3. Estimates of the minimum volumes of optimal and non-lethal habitat, and whether Lake Trout were exposed to sub-optimal and lethal habitat in Little Trout Lake, Voyageurs National Park, Minnesota.	10
Table 4. Estimates of the minimum volumes of optimal and non-lethal habitat, and whether Cisco were exposed to sub-optimal and lethal habitat in Little Trout Lake, Voyageurs National Park, Minnesota.	11
Table 5. Estimates of the minimum volumes of optimal and non-lethal habitat, and whether Lake Trout were exposed to sub-optimal and lethal habitat in Mukooda Lake, Voyageurs National Park, Minnesota.	13
Table 6. Estimates of the minimum volumes of optimal and non-lethal habitat, and whether Cisco were exposed to sub-optimal and lethal habitat in Mukooda Lake, Voyageurs National Park, Minnesota.	13
Table 7. Estimates of the minimum volumes of optimal and non-lethal habitat, and whether Cisco were exposed to sub-optimal and lethal habitat in Locator Lake, Voyageurs National Park, Minnesota.	16
Table 8. Estimates of the minimum volumes of optimal and non-lethal habitat, and the duration of exposure to sub-optimal and lethal habitat for Cisco in Richie Lake, Isle Royale National Park, Michigan.	16

Abstract

Voyageurs National Park (VOYA) and Isle Royale National Park (ISRO) are the only U.S. national parks to protect a series of boreal lakes on the Canadian (Precambrian) Shield. Lakes within both parks are home to coldwater fish, including Lake Trout (*Salvelinus namaycush*) and Cisco (*Coregonus artedii*). Predictions for future climate scenarios suggest that coldwater fish habitat could be threatened by elevated temperatures, prolonged periods of stratification, deepening of the thermocline, and diminished oxygen concentrations in the hypolimnion. The persistent threat of warming in VOYA and ISRO suggests there is a need for a robust coldwater fish-habitat monitoring program in support of coldwater fish conservation.

The objective of this study was to assess combined oxygen and temperature (oxythermal) conditions and the availability of habitat suitable to sustain populations of coldwater fish in Little Trout, Mukooda, and Locator lakes in VOYA, and Richie Lake in ISRO. Continuous water temperature data and both discrete and continuous dissolved oxygen data from each study lake were used to determine the following for Lake Trout and Cisco for each study year: 1) the minimum volume of optimal habitat available, and the percent of the total lake volume this represents; 2) the minimum volume of non-lethal habitat available, and the percent of the total lake volume this represents; 3) the duration of exposure to sub-optimal habitat; and 4) the duration of exposure to lethal habitat. A secondary objective was to consider the merits of using continuous oxygen monitoring to improve assessments of available coldwater fish habitat and oxythermal stress.

Oxythermal habitat conditions varied greatly among the four study lakes, ranging from fully suitable in two lakes (Little Trout and Mukooda), in which optimal habitat was available throughout the monitoring period each year, to uninhabitable in one lake (Richie Lake). The band of non-lethal habitat in Locator Lake in early fall appeared to be small and continued increase in atmospheric temperature could exert even greater pressure on the coldwater fish population of this lake. Considering projected climate warming, the variability in oxythermal habitat conditions among lakes and years, and the high conservation value of native coldwater fish populations, continuous oxygen and temperature monitoring throughout the water column is warranted in lakes with populations of coldwater fish in VOYA and ISRO. Adding continuous oxygen monitoring to the existing continuous temperature monitoring will ensure that low oxygen conditions are recorded, including during the late summer and fall period. Late summer and fall are when a constriction of available coldwater fish habitat is apparent but is outside of the time frame of the discrete oxygen measurements made annually during routine water quality monitoring. Monitoring of oxythermal habitat will provide resource managers with essential information to manage for sustained populations of native coldwater fish.

Acknowledgments

We would like to thank A. LaBounty and R. Key for GIS suggestions and guidance, and D. VanderMeulen and A. Egan for their technical input. We appreciate T. Gostomski's assistance with formatting and figures. We are also grateful for the hard work that Isle Royale and Voyageurs National Park staff and volunteers put into constructing, deploying, retrieving, and offloading the temperature arrays throughout the years. The authors are grateful for funding support from the NPS Natural Resource Condition Assessment Program which made this project possible.

Introduction

Lake surface temperatures have risen globally over the past 30 years (O'Reilly et al. 2015). Climate scientists predict a further 1°C–7°C increase in inland lake surface water temperatures by the end of the 21st century for the Great Lakes Region (Ficke et al. 2007). Higher water temperatures are expected to be accompanied by lower dissolved oxygen (DO) concentrations in most lakes (Wetzel 1983). Impacts of warming lake temperatures and decreased DO concentrations on coldwater fishes range from increased stress and metabolic rates, to complete loss of suitable habitat and extinction (Ficke et al. 2007, Eby et al. 2014). Suitable habitat is all non-lethal habitat available to coldwater fish (this includes optimal habitat when available). There is concern that climate change could lead to the elimination of many coldwater fish populations, especially along the southern edge of their distribution, an area that includes Voyageurs National Park (VOYA) (Figure 1) and Isle Royale National Park (ISRO) (Figure 2). Both VOYA and ISRO have inland lakes with species of coldwater fish that are vulnerable to changes in temperature and oxygen concentrations. This report summarizes an assessment of oxythermal habitat (i.e., habitat that is bound by an upper temperature and a lower DO concentration) for Lake Trout (*Salvelinus namaycush*) and Cisco (*Coregonus artedii*) in Little Trout and Mukooda Lakes at VOYA and Cisco in Locator Lake at VOYA and Richie Lake at ISRO.

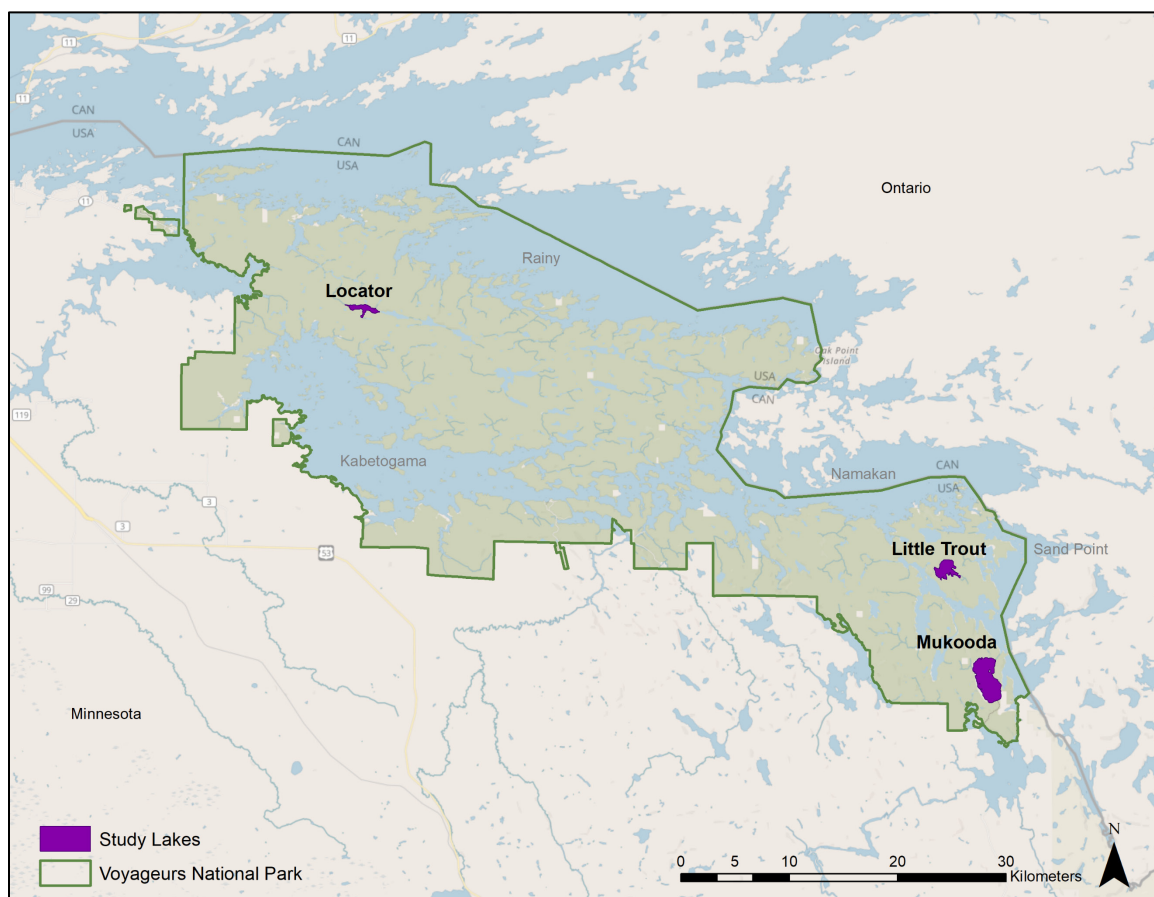


Figure 1. Voyageurs National Park showing Little Trout, Mukooda, and Locator lakes highlighted in purple.

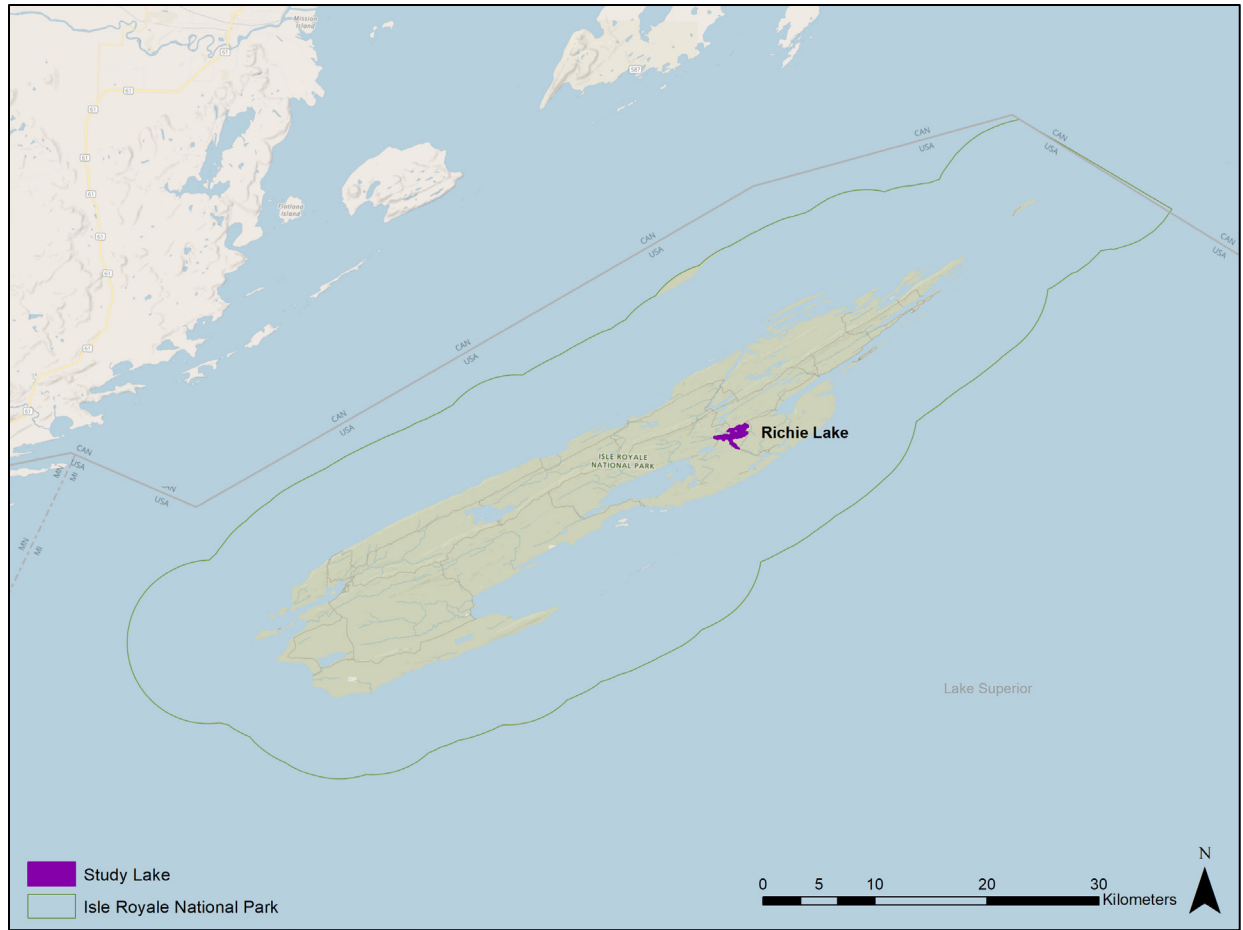


Figure 2. Isle Royale National Park showing Richie Lake highlighted in purple.

The habitat requirements for coldwater fishes (i.e., oxythermal habitat) are defined by cold water and high DO concentrations (Table 1; Plumb and Blanchfield 2009). Lake Trout non-lethal habitat is defined as areas with water temperatures $\leq 15.5^{\circ}\text{C}$ and DO concentrations ≥ 4 mg/L (Martin and Olver 1976, Evans et al. 1991, Blanchfield 2009), while Lake Trout optimal habitat is defined as water with temperatures $\leq 10^{\circ}\text{C}$ and DO concentrations ≥ 6 mg/L (Evans et al. 1991, Dillion et al. 2003). Cisco non-lethal habitat is defined as areas with water temperatures $\leq 20^{\circ}\text{C}$ and DO concentrations ≥ 3 mg/L (Jacobson et al. 2008, Fang et al. 2012), while Cisco optimal habitat is defined as water with temperatures $\leq 11^{\circ}\text{C}$ and DO concentrations ≥ 3 mg/L (Fang et al. 2012).

Table 1. Oxythermal (dissolved oxygen and temperature) habitat suitability for Lake Trout and Cisco.

Species	Non-Lethal Temperature ($^{\circ}\text{C}$)	Non-Lethal DO (mg/L)	Optimal Temperature ($^{\circ}\text{C}$)	Optimal DO (mg/L)
Lake Trout	≤ 15.5	≥ 4	≤ 10	≥ 6
Cisco	≤ 20	≥ 3	≤ 11	≥ 3

Fishery assessments conducted by the Minnesota Department of Natural Resources (MN DNR) have documented the presence of both Lake Trout and Cisco in Little Trout and Mukooda lakes, and the presence of Cisco in Locator Lake (MN DNR 2012, 2018, 2019). However, reduced catch rates of Lake Trout captured by both MN DNR and the National Park Service (NPS) in Little Trout Lake over the last decade have raised concerns that the species has been extirpated. No Lake Trout were detected during surveys completed in 2012, 2014, and 2018 (MN DNR 2019). The duration and variability of ice-free periods is increasing from year to year in VOYA (Breneman and Seeley 2011), likely indicating a loss of coldwater fish habitat. Although factors such as interspecific competition and predation may have contributed to the decline in Lake Trout in Little Trout Lake, a 2015 Natural Resources Condition Assessment (Mechenich et al. 2015) and studies of fish communities of VOYA and ISRO referenced concerns about climate change impacts to coldwater species in Little Trout, Mukooda, and Locator lakes at VOYA (Kallemeyn 2000, Kallemeyn et al. 2003, Gorman et al. 2014).

At ISRO, Cisco were found in fisheries surveys conducted in the 1920s at Richie Lake (Koelz 1931, Hubbs and Lagler 1949), but only one Cisco was captured during surveys conducted in the late 1990s in Richie Lake (Kallemeyn 2000). No cisco were captured in a subsequent assessment in 2012, suggesting the species may have been extirpated from this lake. Richie Lake has undergone unprecedented changes in diatom, cyanobacterial, and fish communities that are likely linked to inter-annual extremes in thermal structure driven by climate change (Edlund et al. 2017). In 2007, a major cyanobacteria bloom occurred, which pervaded the water column and resulted in thick floating mats and slicks of cyanobacteria. As a result, the lake experienced anoxic conditions in waters below 5 meters depth due to oxygen demand following a cyanobacteria die-off (Elias and VanderMeulen 2008). Another major bloom occurred in July and August of 2010 (and Elias and Damstra 2011). Lesser cyanobacteria blooms occurred in 2012 and 2013 (Damstra et al. 2014, Fuller et al. 2017). Since 2014, there have been minor cyanobacteria blooms in three out of six years (NPS Great Lakes Network, unpublished data, May–August 2014–2019).

In Gorman et al.'s (2014) assessment, the Minnesota Climate Change Model (MCCM) was applied to classify lakes as either refuge or non-refuge lakes for coldwater fish species, and to assess which lakes will likely hold adequate oxythermal habitat for coldwater fish through the end of the 21st century (Jacobson et al. 2010, 2013; Fang et al. 2012; Jiang et al. 2012). The MCCM classification was also used to identify inland lakes that would likely support “heritage species,” defined as species with limited distributions that represent early post-glacial colonizers (Gorman et al. 2014). Five VOYA lakes (Cruiser, Little Trout, Locator, Mukooda, and War Club) met the MCCM criteria for refuge lakes and contained heritage coldwater fish species. Gorman et al. (2014) concluded that there was insufficient oxythermal habitat near the lake bottom in Little Trout, Mukooda, or Locator lakes, but that there was adequate oxythermal habitat at higher strata in the hypolimnions based on the persistence of coldwater fish in the lakes. Gorman et al. (2014) found that four lakes in ISRO met the refuge lake criteria and had heritage coldwater fishes (Desor, Richie, Sargent, and Siskiwit), but only Siskiwit had sufficient oxythermal habitat at the lake bottom. Gorman et al. (2014) speculated, based on recent Richie Lake fisheries surveys failing to capture Cisco, that Cisco in Richie Lake may have been extirpated due to early stages of climate warming.

Our primary objective in this study was to assess oxythermal habitat and its suitability to sustain populations of coldwater fish in Little Trout, Mukooda, and Locator lakes in VOYA and Richie Lake in ISRO. We used continuous water temperature data and both discrete and continuous DO concentration data to determine the following for each year: 1) the minimum volume of optimal habitat available; 2) the minimum volume of non-lethal habitat available; 3) the duration of exposure to sub-optimal habitat; and 4) the duration of exposure to lethal habitat for Lake Trout and Cisco. A secondary objective was to investigate the benefits of continuous DO monitoring in assessments of available coldwater fish habitat and oxythermal stress.

The information gained from these analyses can be used to estimate the risk of ongoing and predicted changes in oxythermal habitat and potential loss of coldwater fish habitat in VOYA and ISRO lakes. This study will contribute to the development of management strategies, including assessments of the oxythermal tolerance of native strains of fish and the potential to use more tolerant strains to restore populations. The results of this study may be applicable to lakes beyond those of VOYA and ISRO, including many lakes throughout the northern U.S. and southern Canada.

Methods

Volume and duration of both optimal and non-lethal oxythermal habitat available to Lake Trout and Cisco were estimated using temperature and DO data collected from the deepest area of each lake. To generate estimates, oxygen concentrations and temperatures were assumed to be consistent across the lake at each depth. Discrete DO data collected during routine water quality sampling trips and continuous temperature data recorded on vertical arrays of temperature loggers were used in this analysis.

Site Description

Little Trout, Mukooda, Locator Lakes in VOYA, and Richie Lake in IRSO were chosen for this study because, among VOYA and ISRO lakes with coldwater fish populations, they were the most at risk of losing coldwater fish species based on existing data. The deepest area in each lake was chosen for the monitoring location because it covers all depths.

Field Methods

Water quality monitoring sites are located in the deepest part of each of the study lakes as part of the Great Lakes Inventory and Monitoring Network's inland lake monitoring program (Elias et al. 2008). Discrete dissolved oxygen data were generally collected at each study lake on routine water quality monitoring trips in June, July, and late August/early September. Each visit took place at approximately the same time of day to minimize variation due to diel fluctuations. During sampling trips, a GPS and either a canoe or rowboat were used to locate the sampling site and an anchor was set. At the site, pre-calibrated Eureka, Hydrolab, or YSI multiparameter sondes were used to record profile readings of temperature, DO, pH and conductivity at every meter from the surface to the bottom.

Continuous temperature data were collected by deploying arrays of HOBO temperature (Model Pro V2) and temperature-pressure loggers (Model U-20) that collect data every hour year-round. These thermal arrays were deployed at the same locations as the water quality monitoring sampling sites. The thermal arrays consisted of data loggers strung at one-meter intervals on a line from the bottom of the lake to the surface, except during winter when the top logger was removed to prevent ice damage. They were held vertical by an anchor and a buoy. The data were offloaded, imported into Aquatic Informatics Aquarius Springboard, and then quality checks were conducted following the methods outlined in Damstra and VanderMeulen (2021).

Estimated Minimum Volumes of Optimal Habitat and Non-lethal Habitat for Lake Trout and Cisco

Dissolved oxygen data collected during routine water quality sampling events were used to calculate the minimum optimal habitat volume and minimum non-lethal habitat volume for Cisco and Lake Trout for all study years. Data for our analysis were accessed using a publicly available clearinghouse (National Water Quality Monitoring Council 2021). Temperature-DO profiles for each lake were generated so that the depths at which the optimal and non-lethal temperature and DO levels were located each year could be spatially defined.

To calculate the volume of optimal and non-lethal habitat for Lake Trout and Cisco in the four lakes, the Contour geoprocessing tool in ESRI ArcMap was used:

- Input: depth rasters available from the Minnesota Department of Natural Resources and NPS Great Lakes Inventory and Monitoring Network
- Contour interval: 1 meter
- Base contour: 0 meters
- Z-Factor: 0.3048 (because input raster data are in feet)
- Contour type: CONTOUR_SHELL

The output of this tool is a two-dimensional “slice” or “layer” at every meter below the lake surface. The volume between “slices” is calculated by:

$$\text{habitat volume} = [(slice\ area\ at\ 1\ meter + slice\ area\ at\ 2\ meters) \div 2] \times 1\ meter$$

In other words, it is the average volume of water between two contours. The tabulated result of volumes between all contours is commonly called a “stage storage table”, which indicates the total volume of water available at certain depths (Table 2). Subsequently, volumes of water at particular depths added together represent the estimated total volumes of optimal and non-lethal oxythermal habitat available to different fish species.

Table 2. Stage storage table for Little Trout Lake, Voyageurs National Park, Minnesota.

Depth (m)	Area (m ²)	Volume (m ³)	Storage Depth Interval (m)
0	1,098,725	1,040,366	0 to -1
-1	982,007	909,932	-1 to -2
-2	837,857	791,469	-2 to -3
-3	745,081	723,559	-3 to -4
-4	702,037	684,441	-4 to -5
-5	666,846	652,003	-5 to -6
-6	637,161	624,265	-6 to -7
-7	611,369	600,955	-7 to -8
-8	590,541	580,939	-8 to -9
-9	571,337	561,580	-9 to -10
-10	551,824	542,509	-10 to -11
-11	533,193	524,046	-11 to -12
-12	514,900	504,917	-12 to -13
-13	494,935	484,847	-13 to -14

Table 2 (continued). Stage storage table for Little Trout Lake, Voyageurs National Park, Minnesota.

Depth (m)	Area (m ²)	Volume (m ³)	Storage Depth Interval (m)
-14	474,760	464,675	-14 to -15
-15	454,590	443,541	-15 to -16
-16	432,492	422,040	-16 to -17
-17	411,587	401,057	-17 to -18
-18	390,526	377,074	-18 to -19
-19	363,622	349,654	-19 to -20
-20	335,685	322,543	-20 to -21
-21	309,401	286,079	-21 to -22
-22	262,757	235,076	-22 to -23
-23	207,395	196,352	-23 to -24
-24	185,310	178,492	-24 to -25
-25	171,674	165,943	-25 to -26
-26	160,213	154,365	-26 to -27
-27	148,518	131,691	-27 to -28
-28	114,865	–	–

Each depth of the stage storage table has a corresponding area and volume. From 6 to 9 meters, for example, the volumes for -6, -7, and -8 m were summed. To calculate the percentage of lake volume, the individually calculated volumes of minimum sub-optimal and non-lethal habitat were divided by the total lake volume.

Estimated Duration of Exposure to Sub-optimal Habitat and Non-lethal Habitat

Heat plots were created for each lake and year by importing continuous temperature data from the arrays into R Statistical Software (R Core Team 2019). The R package used to create the heat plots was “rLakeAnalyzer” (Winslow et al. 2019). The continuous temperature data were obtained from the NPS Aquarius WebPortal (NPS 2021).

Lethal and sub-optimal temperature cutoffs were estimated based on the color variation scale in the heat plots (the reds and yellows in the heat plots represented warmer water, and the blues and purples represented colder water). Circles were inserted in the heat plot where sub-optimal and lethal DO started to occur for each fish species. The durations of exposure to sub-optimal and non-lethal habitat were estimated visually using these lines and the dates at the bottom of the heat plots.

Continuous Temperature and Dissolved Oxygen Arrays

National Park Service resource managers partnered with the U.S. Fish and Wildlife Service (USFWS) to deploy logger arrays that recorded both continuous temperature and oxygen data (miniDOT Loggers, Part Number 7392, Precision Measurement Engineering, Inc.). Arrays were deployed at ISRO in 2018 as part of a methods assessment (USFWS; unpublished data) and at both ISRO and VOYA in 2019 in support of this study. These new arrays were deployed near the temperature-only arrays that were already continuously recording in the deepest parts of Little Trout, Mukooda, and Richie lakes so that the two monitoring strategies could be compared based on 2019 data. In 2019 a temperature/DO array was also deployed for the first time in Locator Lake due to concerns about decreasing oxythermal habitat in that lake potentially affecting its native Cisco population.

Graphs were created using exploratory data (2019 only) from the new arrays to determine the usefulness of incorporating continuous DO readings into coldwater fish habitat monitoring programs at VOYA and ISRO. These data should be used with caution and are included here solely to provide an assessment of the benefits of continuous DO monitoring in support of coldwater fish habitat assessments. The continuous and discrete DO data matched well based on a visual assessment (See Results section, Figures 3–5: 2019 only, and Figure 6), but there are uncertainties about continuous DO data accuracy between discrete DO sampling events. Because water must diffuse across a sensor lens for oxygen to change the luminescence of a dye, fouling could impact the measurements. Continuous DO loggers with wipers are a new technology that has been developed to prevent biofouling and will be used moving forward.

Results

Estimated Minimum Volumes of Optimal Habitat and Non-lethal Habitat Using Discrete Dissolved Oxygen Data

Non-lethal and optimal Lake Trout and Cisco habitat were present during all open water seasons included in this study (2011–2019) in Little Trout Lake (Tables 3 and 4, Figure 3). For Lake Trout, estimates of the minimum volume of optimal habitat averaged $3,956,865 \text{ m}^3$ (sample standard deviation (sd)) = $566,834 \text{ m}^3$) or 30% (sd = 5%) of the lake volume, and estimates of the minimum volume of non-lethal habitat averaged $5,519,505 \text{ m}^3$ (sd = $558,117 \text{ m}^3$) or 41% (sd = 4%) of the lake volume. For Cisco, estimates of the minimum volume of optimal habitat averaged $5,233,435 \text{ m}^3$ (sd = $618,902 \text{ m}^3$) or 39% (sd = 5%) of the lake volume, and estimates of the minimum volume of non-lethal habitat averaged $7,185,309 \text{ m}^3$ (sd = $1,662,393 \text{ m}^3$) or 54% (sd = 13%) of the lake volume.

Non-lethal and optimal Lake Trout and Cisco habitat were present during all open water seasons included in this study (2015–2019) in Mukooda Lake (Tables 5 and 6, Figure 4). For Lake Trout, estimates of the minimum volume of optimal habitat averaged $5,712,540 \text{ m}^3$ (sd = $2,742,782 \text{ m}^3$) or 15% (sd = 7%) of the lake volume, and estimates of the minimum volume of non-lethal habitat averaged $11,388,196 \text{ m}^3$ (sd = $1,926,263 \text{ m}^3$) or 30% (sd = 5%) of the lake volume. For Cisco, estimates of the minimum volume of optimal habitat averaged $11,013,657 \text{ m}^3$ (sd = $1,701,871 \text{ m}^3$) or 29% (sd = 4%) of the lake volume, and estimates of the minimum volume of non-lethal habitat averaged $19,228,991 \text{ m}^3$ (sd = $8,431,832 \text{ m}^3$) or 51% (sd = 22%) of the lake volume.

Table 3. Estimates of the minimum volumes of optimal and non-lethal habitat, and whether Lake Trout were exposed to sub-optimal and lethal habitat in Little Trout Lake, Voyageurs National Park, Minnesota. Continuous temperature and discrete DO concentration data were used in this analysis. Optimal habitat is a subset of non-lethal habitat; thus, the percent lake volume for the two can total more than 100%.

Year	Min Optimal Habitat Range (meters)	Min Volume of Optimal Habitat (m ³)	% Lake Volume	Min Non-lethal Habitat Range (meters)	Min Volume of Non-lethal Habitat (m ³)	% Lake Volume	Exposure to Sub-optimal Habitat? (Y/N)	Exposure to Lethal Habitat? (Y/N)
2011	10 to 17	3,386,575	25	8 to 19	5,307,225	40	N	N
2012	10 to 17	3,386,575	25	8 to 19	5,307,225	40	N	N
2013	9 to 16	3,526,116	26	7 to 18	5,531,106	41	N	N
2014	8 to 18	4,930,151	37	7 to 20	6,257,833	47	N	N
2015	9 to 18	4,349,212	33	8 to 21	5,979,422	45	N	N
2016	9 to 17	3,948,156	30	8 to 19	5,307,225	40	N	N
2017	9 to 18	4,349,212	33	8 to 20	5,656,879	42	N	N
2018	9 to 18	4,349,212	33	8 to 21	5,979,422	45	N	N
2019	10 to 17	3,386,575	25	9 to 18	4,349,212	33	N	N

Table 4. Estimates of the minimum volumes of optimal and non-lethal habitat, and whether Cisco were exposed to sub-optimal and lethal habitat in Little Trout Lake, Voyageurs National Park, Minnesota. Continuous temperature and discrete DO concentration data were used in this analysis. Optimal habitat is a subset of non-lethal habitat; thus, the percent lake volume for the two can total more than 100%.

Year	Min Optimal Habitat Range (meters)	Min Volume of Optimal Habitat (m ³)	% Lake Volume	Min Non-lethal Habitat Range (meters)	Min Volume of Non-lethal Habitat (m ³)	% Lake Volume	Exposure to Sub-optimal Habitat? (Y/N)	Exposure to Lethal Habitat? (Y/N)
2011	9 to 20	5,075,940	38	7 to 20	6,257,833	47	N	N
2012	9 to 20	5,075,940	38	7 to 20	5,908,180	44	N	N
2013	9 to 19	4,726,286	35	6 to 19	6,532,444	49	N	N
2014	8 to 22	6,265,501	47	6 to 22	7,490,721	56	N	N
2015	9 to 21	5,398,483	40	7 to 21	6,580,377	49	N	N
2016	9 to 20	5,075,940	38	7 to 20	6,257,833	47	N	N
2017	9 to 21	5,398,483	40	7 to 21	6,580,377	49	N	N
2018	9 to 23	5,919,639	44	6 to 23	7,725,797	58	N	N
2019	10 to 19	4,164,706	31	0 to 19	11,334,215	85	N	N

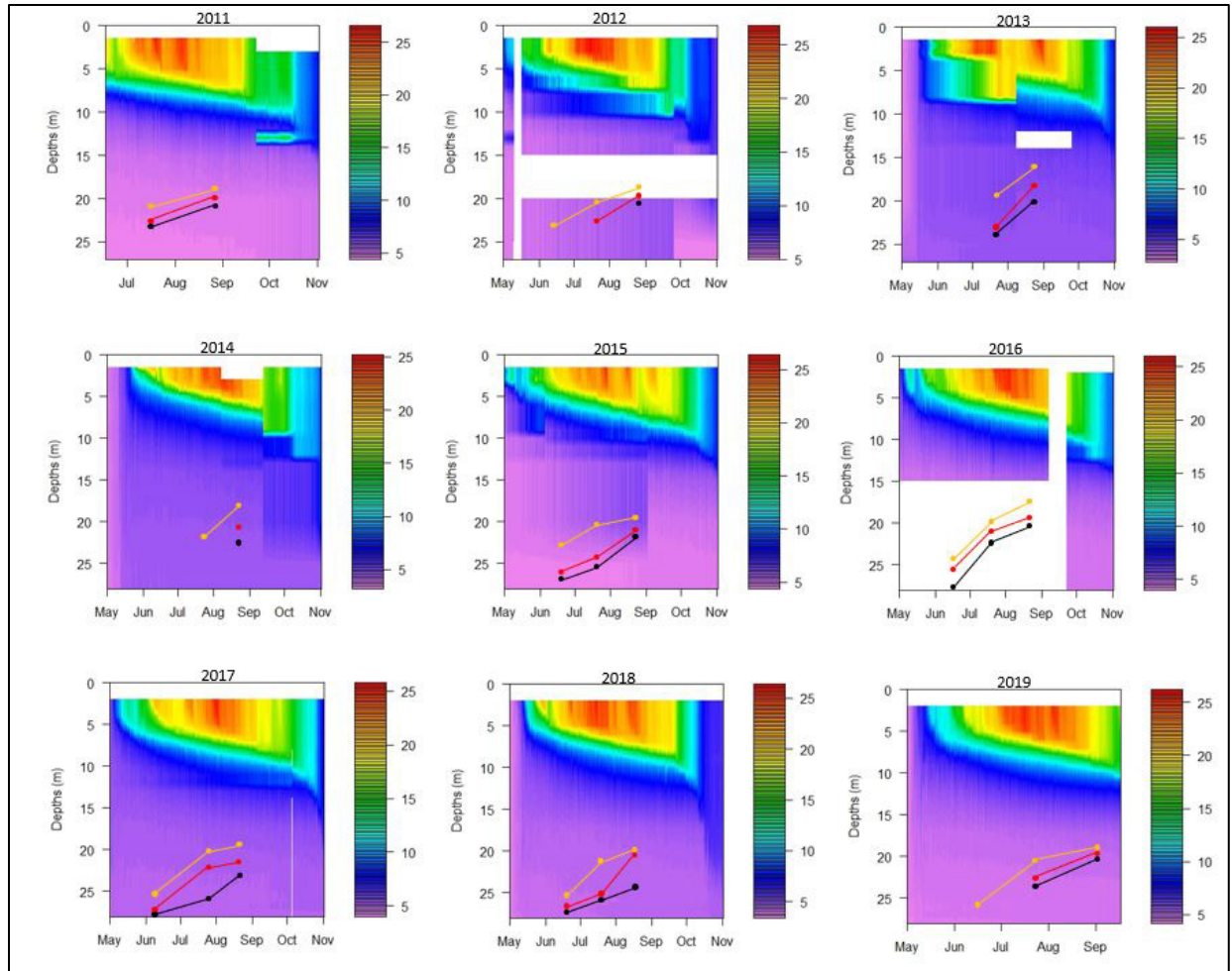


Figure 3. Heat plots showing oxythermal habitat in Little Trout Lake, Voyageurs National Park, for each open water season 2011–2019. Temperature loggers were deployed 1.5 m below the surface and then every 1 m to the lakebed. Temperature (°C) in the areas between loggers were estimated using linear interpolation. Dissolved oxygen (DO) measurements are represented by colored dots: black = 3 mg/L; red = 4 mg/L; and orange = 6 mg/L. The black, red, and orange lines represent linear interpolations of the depth at which DO was 3 mg/L, 4 mg/L, and 6 mg/L, respectively. The white areas represent areas where no data were collected. For Lake Trout, habitat warmer than 10°C or with less than 6 mg/L of DO is suboptimal, and habitat warmer than 15.5°C or with less than 4 mg/L of DO is lethal. For Cisco, habitat warmer than 20°C or with less than 3 mg/L of DO is lethal and water warmer than 11°C is suboptimal. This figure shows that optimal oxythermal habitat for Lake Trout and Cisco was available for the duration of DO monitoring in each year in Little Trout Lake; however, the continuous temperature data show that the volume of this habitat decreased toward the end of the open water season, including the period after the final DO measurement was made during each year. The color ramp to the right of each individual plot shows cooler temperatures (°C) on the bottom represented as purple and blues, moving towards warmer temperatures on the top represented as yellow and reds.

Table 5. Estimates of the minimum volumes of optimal and non-lethal habitat, and whether Lake Trout were exposed to sub-optimal and lethal habitat in Mukooda Lake, Voyageurs National Park, Minnesota. Continuous temperature and discrete DO concentration data were used in this analysis. Optimal habitat is a subset of non-lethal habitat; thus, the percent lake volume for the two can total more than 100%.

Year	Min Optimal Habitat Range (meters)	Min Volume of Optimal Habitat (m ³)	% Lake Volume	Min Non-lethal Habitat Range (meters)	Min Volume of Non-lethal Habitat (m ³)	% Lake Volume	Exposure to Sub-optimal Habitat? (Y/N)	Exposure to Lethal Habitat? (Y/N)
2015	10 to 12	3,692,640	10	8 to 14	11,018,531	29	N	N
2016	10 to 12	3,692,640	10	9 to 15	10,374,902	28	N	N
2017	10 to 13	5,401,259	14	9 to 15	10,374,902	28	N	N
2018	9 to 15	10,374,902	28	8 to 17	14,797,744	39	N	N
2019	10 to 13	5,401,259	14	9 to 15	10,374,902	28	N	N

Table 6. Estimates of the minimum volumes of optimal and non-lethal habitat, and whether Cisco were exposed to sub-optimal and lethal habitat in Mukooda Lake, Voyageurs National Park, Minnesota. Continuous temperature and discrete DO concentration data were used in this analysis. Optimal habitat is a subset of non-lethal habitat; thus, the percent lake volume for the two can total more than 100%.

Year	Min Optimal Habitat Range (meters)	Min Volume of Optimal Habitat (m ³)	% Lake Volume	Min Non-lethal Habitat Range (meters)	Min Volume of Non-lethal Habitat (m ³)	% Lake Volume	Exposure to Sub-optimal Habitat? (Y/N)	Exposure to Lethal Habitat? (Y/N)
2015	9 to 15	10,374,902	28	7 to 15	14,612,987	39	N	N
2016	10 to 16	9,662,638	26	7 to 16	15,873,794	42	N	N
2017	10 to 18	11,697,517	31	8 to 16	13,703,495	36	N	N
2018	9 to 18	13,670,588	36	7 to 18	17,908,673	47	N	N
2019	10 to 16	9,662,638	26	0 to 16	34,046,008	90	N	N

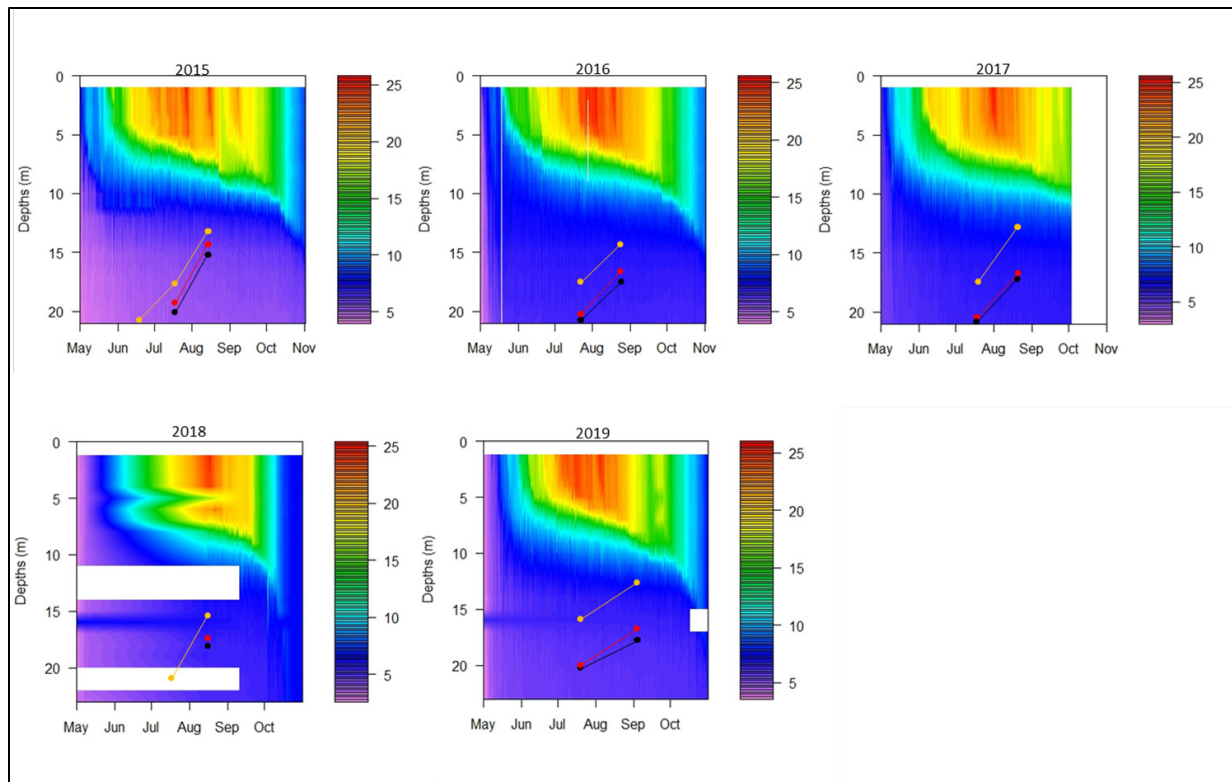


Figure 4. Heat plots showing oxythermal habitat in Mukooda Lake, Voyageurs National Park, for each open water season 2015–2019. Temperature loggers were deployed 1.5 m below the surface and then every 1 m to the lakebed. Temperature ($^{\circ}\text{C}$) in the areas between loggers were estimated using linear interpolation. Dissolved oxygen (DO) measurements are represented by colored dots: black = 3 mg/L; red = 4 mg/L; and orange = 6 mg/L. The black, red, and orange lines represent linear interpolations of the depth at which DO was 3 mg/L, 4 mg/L, and 6 mg/L, respectively. The white areas represent areas where no data were collected. For Lake Trout, habitat warmer than 10°C or with less than 6 mg/L of DO is suboptimal and habitat warmer than 15.5°C or with less than 4 mg / L of DO is lethal. For Cisco, habitat warmer than 20°C or with less than 3 mg/L of DO is lethal and water warmer than 11°C is suboptimal. This figure shows that optimal oxythermal habitat for Lake Trout and Cisco was available for the duration of DO monitoring in each year in Mukooda Lake; however, the continuous temperature data show that the volume of this habitat decreased toward the end of the open water season, including the period after the final DO measurement was made during each year. The color ramp to the right of each individual plot shows cooler temperatures ($^{\circ}\text{C}$) on the bottom represented as purple and blues, moving towards warmer temperatures on the top represented as yellow and reds.

Non-lethal and optimal conditions for Cisco were present in Locator Lake in 2019 (Table 7). Discrete water quality data were collected prior to 2019 in Locator lake, but because 2019 was the first year during which continuous temperature data were collected there, previous years were not included in this analysis. For Cisco, the minimum volume of optimal habitat was estimated at $347,603 \text{ m}^3$ or 25% of the lake volume, and the minimum volume of non-lethal habitat was $433,508 \text{ m}^3$ or 31% of the lake volume in 2019.

Based on temperature and DO data used in this analysis, if Cisco were present in Richie Lake, they would have been exposed to lethal habitat during every open water season from 2010 through 2013

and from 2015 through 2019 (Table 8, Figure 5). The estimated duration Cisco would have been exposed to sub-optimal habitat each study year ranged from 62 to 136 days, and the duration they would have been exposed to lethal habitat ranged from 31 to 57 days (Table 8).

Table 7. Estimates of the minimum volumes of optimal and non-lethal habitat, and whether Cisco were exposed to sub-optimal and lethal habitat in Locator Lake, Voyageurs National Park, Minnesota. Continuous temperature and discrete DO concentration data were used in this analysis. Optimal habitat is a subset of non-lethal habitat; thus, the percent lake volume for the two can total more than 100%.

Year	Min Optimal Habitat Range (meters)	Min Volume of Optimal Habitat (m ³)	% Lake Volume	Min Non-lethal Habitat Range (meters)	Min Volume of Non-lethal Habitat (m ³)	% Lake Volume	Exposure to Sub-optimal Habitat? (Y/N)	Exposure to Lethal Habitat? (Y/N)
2019	6 to 12	347,603	25	5 to 12	433,508	31	N	N

Table 8. Estimates of the minimum volumes of optimal and non-lethal habitat, and the duration of exposure to sub-optimal and lethal habitat for Cisco in Richie Lake, Isle Royale National Park, Michigan. Continuous temperature and discrete DO concentration data were used in this analysis.

Year	Min Optimal Habitat Range (meters)	Min Volume of Optimal Habitat (m ³)	% Lake Volume	Min Non-lethal Habitat Range (meters)	Min Volume of Non-lethal Habitat (m ³)	% Lake Volume	Exposure to Sub-optimal Habitat	Exposure to Lethal Habitat
2010	None	0	0	None	0	0	15 June–15 Oct (122 days)	17 July–18 Aug (32 days)
2011	None	0	0	None	0	0	1 June–15 October (136 days)	15 July–10 Sept (57 days)
2012	None	0	0	None	0	0	25 May–5 Oct (134 days)	5 July–10 Aug (37 days)
2013	None	0	0	None	0	0	20 Aug–20 Oct (62 days)	15 Aug–15 Sept (32 days)
2015	None	0	0	None	0	0	25 June–20 Oct (118 days)	20 July–20 Aug (32 days)
2016	None	0	0	None	0	0	20 June–25 Oct (128 days)	10 Aug–15 Sept (36 days)
2017	None	0	0	None	0	0	25 July–25 Oct (93 days)	10 Aug–10 Sept (31 days)
2018	None	0	0	None	0	0	15 June–10 Oct (117 days)	5 Aug–10 Sept (36 days)
2019	None	0	0	None	0	0	15 June–10 Oct (117 days)	15 July–1 Sept (48 days)

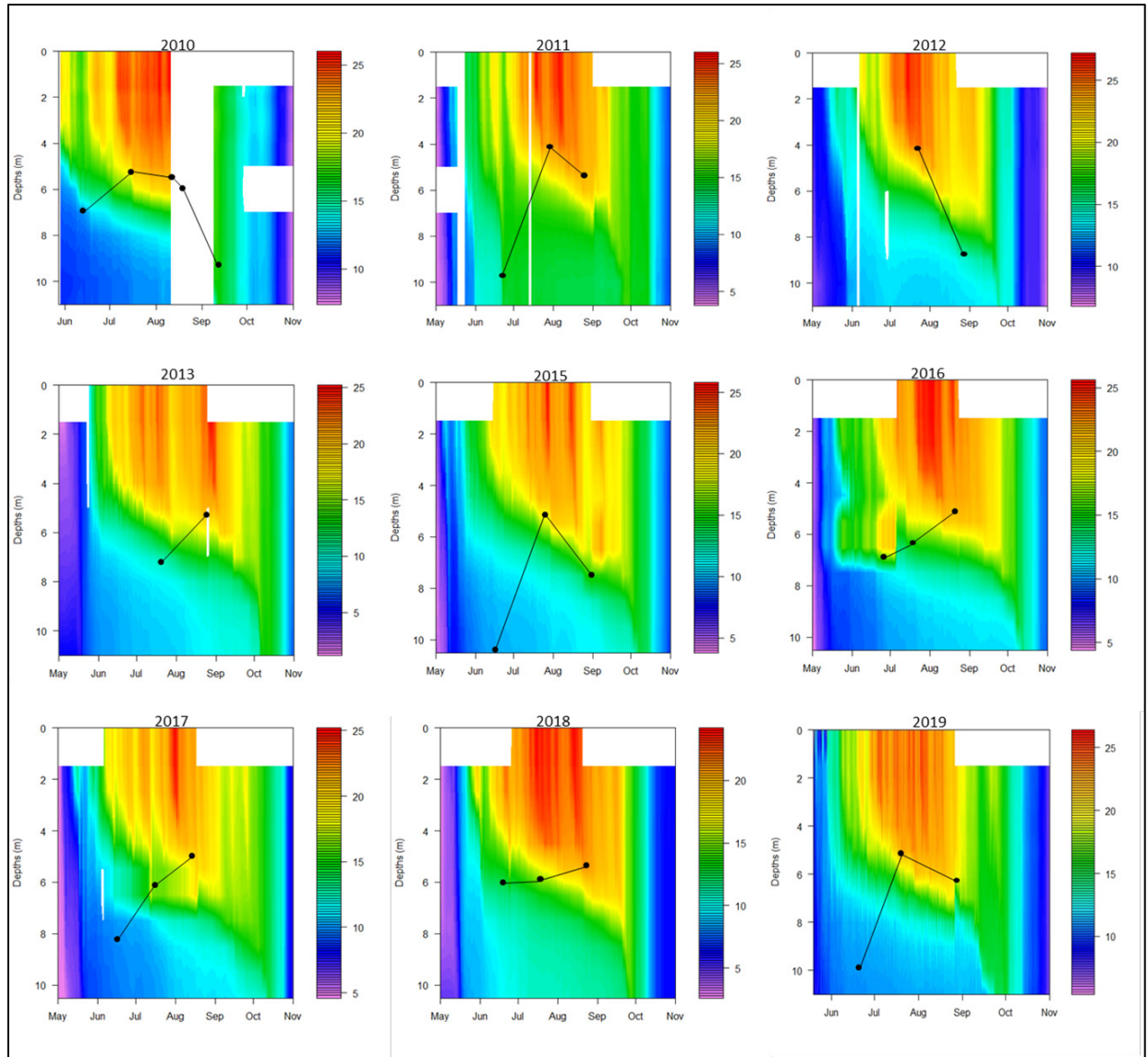


Figure 5. Heat plots showing oxythermal habitat for Cisco in Richie Lake, Isle Royale National Park, for each open water season 2010–2013 and 2015–2019. Temperature loggers were deployed 1.5 m below the surface and then every 1 m to the lakebed. Temperature (°C) in the areas between loggers were estimated using linear interpolation. Dissolved oxygen (DO) measurements at 3 mg/L are represented by black dots. The black lines represent linear interpolations of the depth at which DO was 3 mg/L. The white areas represent areas where no data were collected. For Cisco, habitat warmer than 20°C or with less than 3 mg/L of DO is lethal, and water warmer than 11°C is suboptimal. The color ramp to the right of each individual plot shows cooler temperatures (°C) on the bottom represented as purple and blues, moving towards warmer temperatures on the top represented as yellow and reds.

Assessment of Optimal Habitat and Non-lethal Habitat Using Continuous Dissolved Oxygen Data

Continuous temperature and DO data from 2019 were available for Little Trout, Mukooda, Locator, and Richie lakes via U.S. Fish and Wildlife Service arrays. Due to biofouling, the data were used with caution and solely for an exploratory assessment. In addition to showing DO levels throughout the open water period, the data show the late season contraction in optimal and non-lethal habitat for Lake Trout and Cisco in Little Trout, Mukooda, and Locator lakes (Figure 6). There is a pronounced contraction in optimal and non-lethal oxythermal habitat for Lake Trout and Cisco, especially in Locator Lake where Cisco may have been restricted to a 1–2-m stratum in fall, after the final discrete DO measurements were made during routine water quality monitoring. The data also show that if Cisco were present in Richie Lake, they would have been exposed to sub-optimal and potentially lethal oxythermal conditions for more than a month in 2019.

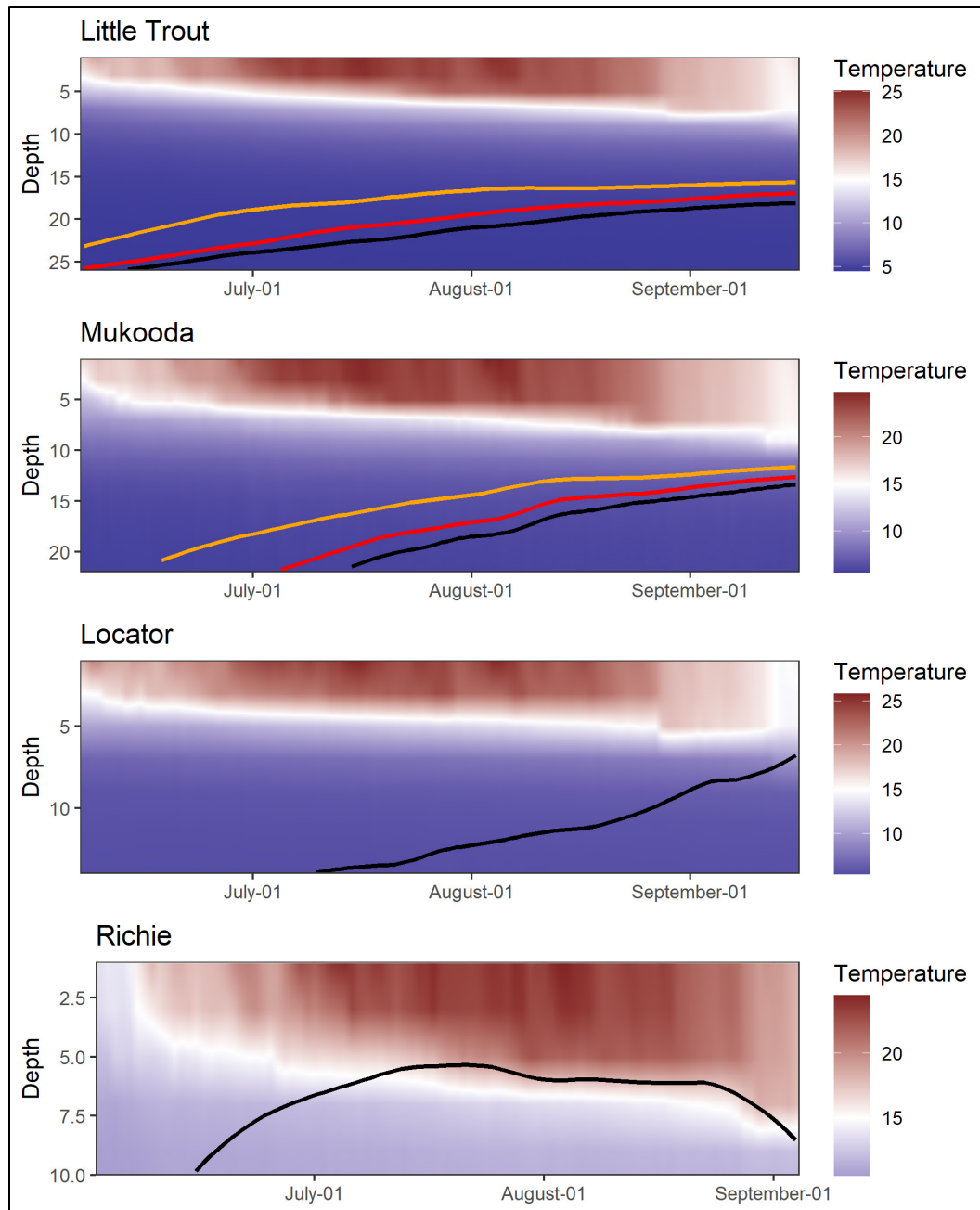


Figure 6. Heat plots based on continuous temperature and dissolved oxygen data collected in Little Trout, Mukooda, Locator, and Richie lakes in 2019. Data loggers were deployed 1 m below the surface and then every 2 m to the lakebed. The areas between loggers were estimated using linear interpolation. The black, red, and orange lines represent the estimated depths at which DO was 3 mg/L, 4 mg/L, and 6 mg/L, respectively. Red and orange lines are included for lakes with Lake Trout populations only as these are habitat thresholds for Lake Trout. The continuous DO data elucidate the late season contraction in suitable coldwater fish habitat in Mukooda, Little Trout, and Locator lakes and the lack of non-lethal habitat for Cisco in Richie Lake. The color ramp to the right of each individual plot shows cooler temperatures (°C) on the bottom represented as blues, moving towards warmer temperatures near the surface represented as reds.

Discussion

Coldwater fish exposed to changing oxythermal regimes may decrease in abundance, experience range contractions, or be extirpated. Voyageurs and Isle Royale National Parks are located near the southern extent of the geographical distribution of coldwater fish. The changing climate, the high conservation value of native coldwater fish species (Gorman et al. 2014; MN DNR 2018, 2019), and the variability among lakes and annual weather conditions emphasize the need for coldwater fish habitat monitoring programs in VOYA and ISRO.

Using continuous temperature data and discrete oxygen measurements collected during routine water quality monitoring trips, oxythermal habitat available to populations of native coldwater fish was assessed in Little Trout, Mukooda, and Locator lakes in Voyageurs National Park and in Richie Lake in Isle Royale National Park. The resulting estimates show that non-lethal and optimal Lake Trout and Cisco habitat existed for the duration of DO monitoring during all open water seasons in Little Trout Lake (2011–2019; Tables 3 and 4), Mukooda Lake (2013–2019; Tables 5 and 6), and Locator Lake (2019; Table 7). Any Cisco present in Richie Lake would have been exposed to lethal oxythermal conditions in all study years (2010–2013 and 2015–2019; Table 8). The band of suitable habitat was narrower in Mukooda Lake (Figure 4) than in Little Trout Lake, but because Mukooda has a greater area than Little Trout (approx. 300 ha vs. approx. 100 ha), the volume of suitable habitat in Mukooda was larger than in Little Trout (Tables 3–6). Ice-out was later than average at VOYA in 2018 and the volume of coldwater fish habitat was estimated to be as high or higher than during other years in the VOYA study lakes, which may be due to the later ice out and associated colder temperatures. This was especially pronounced in Mukooda due to its larger area. The larger habitat volume may be one reason that the Lake Trout in Mukooda appear to be more abundant than in Little Trout (MN DNR 2018, 2019). The band of suitable habitat in Locator Lake appeared to be very narrow at the end of the season (see Figure 6). Although the limited dataset for Locator Lake provided only a small record for analysis, the fact that the DO in the hypolimnion appeared to be lost at an accelerated rate in early fall suggests that the Cisco in this lake may experience stress related to available habitat. The Richie Lake results corroborated earlier analyses that indicated that Cisco would be unlikely to persist there (Gorman et al. 2014).

Although recent surveys show that the Lake Trout populations in Little Trout and Mukooda lakes have likely declined, the declines may be due to factors other than oxythermal stress such as predation and competition with other species (MN DNR 2018, 2019). Still, temperature increases from climate change could exacerbate the negative effects of interspecific competition on Lake Trout. For example, Rahel and Olden (2008) predicted that there would be a to six-fold increase in per capita consumption of salmonids by Smallmouth Bass (*Micropterus dolomieu*) and Walleye (*Stizostedion vitreum*) for every 1.8°F increase of annual river temperature on the Columbia River. In Little Trout Lake, Walleye, Smallmouth Bass, and Northern Pike (*Esox lucius*) were not detected in the earliest surveys, suggesting that these species have since been introduced (MN DNR 2019). Recent fisheries surveys in Little Trout Lake show that these three species have increased in abundance and may have affected the Lake Trout population (MN DNR 2019).

Although continuous temperature data were available for multiple years for most of the study lakes, DO data were limited to one-to-three discrete data points per open water season from existing monitoring programs at VOYA and ISRO. Thus, it is possible that the existing dataset missed events in which oxygen and temperature conditions were not optimal for coldwater fish. Continuous oxygen monitoring, while more equipment- and resource-intensive, offers several advantages over discrete oxygen measurements. In addition to ensuring that short-term oxythermal habitat changes were detected, continuous DO data collected by the USFWS in 2019 allowed inspection of the late season constriction in oxythermal habitat that took place after the final discrete DO data profiles were collected in August each summer (Figure 6). The continuous DO dataset showed that Cisco oxythermal habitat in Locator decreased markedly after the final discrete data collection and approached zero in mid-September. This indicates that the linear interpolation of discrete DO data had not provided an accurate estimate of this constriction in habitat (see Figure 6). Incorporating continuous DO monitoring into the coldwater fish habitat monitoring programs at VOYA and ISRO would provide more comprehensive information on the timing and duration of oxythermal constrictions. This would allow resource managers to more accurately assess the likelihood of impacts to coldwater fish populations in lakes over time.

If resources are limited to the extent that continuous oxygen monitoring is not possible, continuous temperature monitoring with more frequent discrete DO monitoring is an alternative that can provide valuable information. For example, biweekly monitoring from May through September from 1997 to 1999 on Locator and Mukooda lakes provided a description of oxythermal conditions throughout the summer and early fall. Temperature/oxygen profiles from September showed that the thermoclines were still present and that oxythermal constrictions on coldwater habitat did occur (Whitman et al. 2002, VOYA/USGS unpublished data).

The results of this assessment are consistent with Gorman et al.'s (2014) assessment of the potential impact of 21st century climate change on the inland lakes at VOYA and ISRO. Coldwater fish may thermoregulate behaviorally by selecting thermally heterogeneous microhabitats (Brett 1971), but they are constrained by the range of temperatures and DO available in the environment. In Richie Lake, Cisco would have been exposed to lethal habitat during every open water season from 2010 through 2013 and from 2015 through 2019 (see Table 8); they would have been exposed to lethal habitat from 31 to 57 days per year during this period. Given these findings and noting that recent Richie Lake fisheries surveys have yielded no Cisco, it is very likely that Cisco have been extirpated from Richie Lake due to changes in oxythermal habitat driven by climate change. This is also supported by evidence of additional climate-driven biological changes in Richie Lake. Specifically, recent sediment samples taken from cores showed an increase in abundance of certain diatom species in Richie Lake (Edlund et al. 2017). Such species shifts are indicative of changing patterns in lake temperature and mixing, which have appeared to push Richie Lake over a threshold to a condition in which periodic harmful algal blooms have become a regular part of the lake's ecology (Edlund et al. 2011).

Conclusions

Coldwater fish habitat conditions varied greatly among the four study lakes, ranging from excellent coldwater habitat in two lakes to none in one lake. Continuous oxythermal habitat monitoring is recommended in all VOYA and ISRO lakes with populations of coldwater fish. This monitoring could complement management strategies such as controlling or reducing harvest, preventing nutrient enrichment, and stopping the establishment of aquatic invasive and introduced fish species. These management strategies decrease stress on coldwater fish species and may increase their chance of survival, despite reductions in oxythermal habitat. The importance of oxythermal habitat monitoring is underscored by projected climate warming, the variability in habitat conditions among lakes and among years, and the high conservation value of native populations of coldwater fish. The information gained through this study and future oxythermal habitat monitoring may be valuable not only to VOYA and ISRO, but also to those managing lakes throughout the northern United States and southern Canada.

Literature Cited

- Blanchfield, P. J., L. S. Tate, J. M. Plumb, M. L. Acolas, and K. G. Beaty. 2009. Seasonal habitat selection by lake trout (*Salvelinus namaycush*) in a small Canadian shield lake: Constraints imposed by winter conditions. *Aquatic Ecology* 43(3):777-787.
- Breneman, D., and M. Seeley. 2011. *Voyageur Skies: Weather and Wilderness in Minnesota's National Park*. Afton Historical Press, Afton, Minnesota.
- Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *American Zoology* 11:99–113.
- Damstra, R., and D. D. VanderMeulen. 2021. Standard operating procedure #14: Moored temperature arrays, version 1.0. *In* J. Elias, R. Axler, E. Ruzycki, and D. VanderMeulen. 2022. Water quality monitoring protocol for inland lakes: Great Lakes Inventory and Monitoring Network, version 1.2. Natural Resource Report. NPS/GLKN/NRR—2022/2349. National Park Service, Fort Collins, Colorado.
- Damstra, R., D. VanderMeulen, and J. Elias. 2014. Monitoring water quality of inland lakes, Great Lakes Network, 2012: Data summary report. Natural Resource Data Series NPS/GLKN/NRDS—2014/629. National Park Service, Fort Collins, Colorado.
- Dillon, P. J., B. J. Clark, L. A. Molot, and H. E. Evans. 2003. Predicting the location of optimal habitat boundaries for lake trout (*Salvelinus namaycush*) in Canadian Shield lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 60(8):959–970.
- Eby, L. A., O. Helmy, L. M. Holsinger, and M. K. Young. 2014. Evidence of climate-induced range contractions in bull trout *Salvelinus confluentus* in a Rocky Mountain watershed, USA. *PLoS One* 9(6):e98812.
- Edlund, M. B., J. E. Almendinger, X. Fang, J. M. R. Hobbs, D. D. VanderMeulen, R. L. Key, and D. R. Engstrom. 2017. Effects of climate change on lake thermal structure and biotic response in northern wilderness lakes. *Water* 9(9):678.
- Edlund, M. B., J. M. Ramstack, D. R. Engstrom, J. E. Elias, and B. Moraska Lafrancois. 2011. Biomonitoring using diatoms and paleolimnology in the western Great Lakes national parks. Natural Resource Technical Report NPS/GLKN/NRTR—2011/447. National Park Service, Fort Collins, Colorado.
- Elias, J. E., R. Axler, and E. Ruzycki. 2008. Water quality monitoring protocol for inland lakes: Great Lakes Inventory and Monitoring Network. Version 1.0. Natural Resources Technical Report NPS/GLKN/NRTR—2008/109. National Park Service, Fort Collins, Colorado.

- Elias, J. E., and R. A. Damstra. 2011. Monitoring water quality of inland lakes, Great Lakes Network, 2009 and 2010: Data summary report. Natural Resource Data Series NPS/GLKN/NRDS—2011/163. National Park Service, Fort Collins, Colorado.
- Elias, J., and D. VanderMeulen. 2008. Monitoring water quality of inland lakes, 2007: Annual summary report. Great Lakes Inventory and Monitoring Network Report GLKN/2008/05. National Park Service, Ashland, Wisconsin.
- Evans, D. O., J. M. Casselman, and C. C. Willox. 1991. Effects of exploitation, loss of nursery habitat and stocking on the dynamics and productivity of lake trout populations in Ontario lakes. Lake Trout Synthesis. Ontario Ministry of Natural Resources, Toronto, Ontario.
- Fang, X., L. Jiang, P. C. Jacobson, H. G. Stefan, S. R. Alam, and D. L. Pereira. 2012. Identifying cisco refuge lakes in Minnesota under future climate scenarios. Transactions of the American Fisheries Society 141(6):1608–1621.
- Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17:581–613.
- Fuller, L. M., A. K. Brennan, L. R. Fogarty, K. A. Loftin, H. E. Johnson, D. D. VanderMeulen, and B. M. Lafrancois. 2017. Detection of microcystin and other cyanotoxins in lakes at Isle Royale National Park, Pictured Rocks National Lakeshore, and Sleeping Bear Dunes National Lakeshore, northern Michigan, 2012–13. U.S. Geological Survey Scientific Investigations Report 2017–5122. U.S. Geological Survey, Reston, Virginia. Available at: <https://dx.doi.org/10.3133/sir20175122>.
- Gorman, O. T., L. Kallemeyn, and R. Maki. 2014. Biogeographic patterns of inland lake fish communities at Isle Royale, Voyageurs, and Sleeping Bear Dunes national park units. Natural Resource Technical Report NPS/GLKN/NRTR—2014/893. National Park Service, Fort Collins, Colorado.
- Hubbs, C. L., and K. F. Lagler. 1949. Fishes of Isle Royale, Lake Superior, Michigan. Papers of the Michigan Academy of Sciences, Art, and Letters 33:73–133.
- Jacobson, P. C., H. G. Stefan, and D. L. Pereira. 2010. Coldwater fish oxythermal habitat in Minnesota lakes: Influence of total phosphorus, July air temperature, and relative depth. Canadian Journal of Fisheries and Aquatic Sciences 67(12):2002–2013.
- Jacobson, P. C., T. S. Jones, P. Rivers, and D. L. Pereira. 2008. Field estimation of a lethal oxythermal niche boundary for adult ciscoes in Minnesota lakes. Transactions of the American Fisheries Society 137(5):1464–1474.
- Jacobson, P. C., X. Fang, H. G. Stefan, and D. L. Pereira. 2013. Protecting cisco (*Coregonus artedii* Lesueur) oxythermal habitat from climate change: Building resilience in deep lakes using a landscape approach. Advances in Limnology 64:323–333.

- Jiang, L., X. Fang, H. G. Stefan, P. C. Jacobson, and D. L. Pereira. 2012. Oxythermal habitat parameters and identifying cisco refuge lakes in Minnesota under future climate scenarios using variable benchmark periods. *Ecological Modelling* 232:14–27.
- Kallemeyn, L. W. 2000. A comparison of fish communities from 32 inland lakes in Isle Royale National Park, 1929 and 1995–1997. U. S. Geological Survey Report USGS/BRD/BSR2000-0004. U. S. Geological Survey, Columbia Environmental Research Center, Columbia, Missouri.
- Kallemeyn, L. W., K. L. Holmberg, J. A. Perry, and B. Y. Odde. 2003. Aquatic synthesis for Voyageurs National Park. U. S. Geological Survey Report USGS/BRD/ITR2003-0001. U. S. Geological Survey, Columbia Environmental Research Center, Columbia, Missouri.
- Koelz, W. 1931. The Coregonid fishes of northeastern America. *Papers of the Michigan Academy of Sciences, Art, and Letters* 13:303–432.
- Martin, N. V., and C. H. Olver. 1976. The distribution and characteristics of Ontario lake trout lakes. Ontario Ministry of Natural Resources. Fish and Wildlife Research Branch. Research Report 97.
- Mechenich, C., J. A. VanDeHey, J. E. Cook, D. J. Mechenich, J. L. McNelly, and G. J. Kraft. 2015. Natural resource condition assessment: Voyageurs National Park. Natural Resource Report NPS/VOYA/NRR—2015/1007. National Park Service, Fort Collins, Colorado.
- MN DNR (Minnesota Department of Natural Resources). 2012. Locator Lake management plan. Minnesota Department of Natural Resources, International Falls, Minnesota.
- MN DNR (Minnesota Department of Natural Resources). 2018. Mukooda Lake management plan. Minnesota Department of Natural Resources, International Falls, Minnesota.
- MN DNR (Minnesota Department of Natural Resources). 2019. Little Trout Lake management plan. Minnesota Department of Natural Resources, International Falls, Minnesota.
- NPS (National Park Service). 2021. Aquarius WebPortal website. Internal database available to NPS employees at <https://irma.nps.gov/AQWebPortal>.
- National Water Quality Monitoring Council. 2021. Water Quality Portal website. Available at: www.waterqualitydata.us/portal/#mimeType=csv.
- O'Reilly, C. M., S. Sharma, D. K. Gray, S. E. Hampton, J. S. Read, R. J. Rowley, P. Schneider, J. D. Lenters, P. B. McIntyre, B. M. Kraemer, and G. A. Weyhenmeyer. 2015. Rapid and highly variable warming of lake surface waters around the globe. *Geophysical Research Letters* 42(24):10–773.
- Plumb, J. M., and P. J. Blanchfield. 2009. Performance of temperature and dissolved oxygen criteria to predict habitat use by lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences* 66:2011–2023.

- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: [r-project.org](https://www.R-project.org).
- Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22(3):521–533.
- Wetzel, R. G. 1983. *Limnology*, 2nd edition. Saunders College Publishing, New York.
- Winslow, L., J. Read, R. Woolway, J. Brentrup, T. Leach, J. Zwart, S. Albers, and D. Collinge. 2019. rLakeAnalyzer: Lake physics tools. R package version 1.11.4.1. CRAN - Package rLakeAnalyzer. Available at: [r-project.org](https://www.R-project.org).
- Whitman, R., M. Nevers, L. Last, T. Horvath, T. Goodrich, S. Mahoney, and J. Nefczyk. 2002. Status and trends of selected inland lakes of the Great Lakes cluster national parks. Report to the NPS Midwest Region and Great Lakes Cluster National Parks. Interagency Agreement #1443IA603097017, U. S. Geological Survey-GLSC-Lake Michigan Ecological Research Station, Porter, Indiana.

The Department of the Interior protects and manages the nation's natural resources and cultural heritage; provides scientific and other information about those resources; and honors its special responsibilities to American Indians, Alaska Natives, and affiliated Island Communities.

NPS 139/186267, 172/186267, September 2022

National Park Service
U.S. Department of the Interior



[Natural Resource Stewardship and Science](#)

1201 Oakridge Drive, Suite 150
Fort Collins, CO 80525

EXPERIENCE YOUR AMERICA™