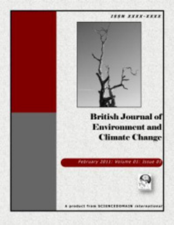

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Simulation and Validation of Cisco Habitat in Minnesota Lakes Using the Lethal-Niche-Boundary Curve

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Authors' contributions

This work was carried out in collaboration between all authors. Author XF designed the study, supervised the model runs and the data analyses and wrote and revised the manuscript. Author LJ provided valuable suggestions for the study design, ran the model for all cases, performed the data analyses, and reviewed the manuscript. Author PCJ developed the lethal-niche-boundary curve for adult cisco, provided temperature and DO profiles for 23 Minnesota lakes, and revised the manuscript. Author NZF interpreted the model results and revised the manuscript. All authors read and approved the final manuscript.

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ABSTRACT

Fish survival in lakes is strongly influenced by water temperature and dissolved oxygen (DO) concentration. A one-dimensional (vertical) lake water quality model MINLAKE 2012 was calibrated in 23 Minnesota lakes and used to simulate daily water temperature and DO concentrations in 36 representative lake types under past (1992–2008) climate conditions and a future climate scenario (MIROC 3.2). The 36 representative Minnesota lake types were developed based on three maximum depths (H_{max} = 4, 13, and 24 m), three surface areas (As = 0.2, 1.7, 10 km^2), and four Secchi depths (SD = 1.2, 2.5, 4.5, and 7 m, from eutrophic to oligotrophic lake). A fish habitat model using the lethal-niche-

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boundary curve of adult cisco (Coregnous artedi, a cold-water fish species) was then developed to evaluate cisco oxythermal habitat and survival in Minnesota lakes.The fish habitat model was validated in the 23 Minnesota lakes of which 18 had cisco mortality while 5 had no cisco mortality in the unusually warm summer of 2006. Cisco lethal and habitable conditions in the 23 lakes simulated by the model had anoverall good agreement with observations in 2006. After model validation, cisco lethal days in the 36 lake types were modeled using simulated daily temperature and DO profiles from MINLAKE2012. Polymictic shallow lakes with lake geometry ratio $A_s^{0.25}/H_{max} > 5.2\ m^{-0.5}$ were simulated to typically not support cisco oxythermal habitat under past climate conditions and the future climate scenario. Medium-depth lakes are projected to be most vulnerable to climate warming with most increase in the number of years with cisco kill (average increase 13 years out of 17 simulation years). Strongly stratified mesotrophic and oligotrophic deep lakes are possible to support cisco habitat under both past and future climate conditions, and these deep lakes are good candidates for cisco refuge lakes that should be protected against water quality deteriorations.

Keywords: Fish habitat model; cisco; lake water quality model; climate change.

1. INTRODUCTION

The increase of CO_2 and other greenhouse gases in the atmosphere is projected to cause climate warming, which will lead to increase in water temperature and hypolimnetic oxygen depletion during longer periods of summer stratification in lakes [1,2]. Fish habitat is constrained by water temperature, available dissolved oxygen (DO), food supply, human interference, and other environmental factors. In lakes, temperature and DO are the two most significant water quality parameters that affect survival and growth of cold-water fishes [3-5]. Therefore, projected changes in water temperature and DO concentrations are expected to have an effect on indigenous fish populations [6-8].

MINLAKE2012 used in the study was derived from a regional lake water quality model MINLAKE96, which was originally developed for Minnesota lakes and then applied to 27 lake types at 209 locations over the contiguous US in studying the response of temperature, DO, and fish habitat in the lakes to future climate changes. These lakes were simulated for a continuous 19-year period under past (1961-1979) climate and projected $2xCO_2$ climate scenarios [9]. Not all these lake types actually exist at all 209 locations investigated in the contiguous USA [8]. In many locations, they are hypothetical lakes. The generic approach, however, provides a good picture of how different lake types may behave in different parts of the country, especially under future climate scenarios for which there are no lake data.

Cisco *Coregonus artedi* is the most common cold-water stenothermal fish in Minnesota lakes. The Minnesota (MN) Department of Natural Resources (DNR) has sampled cisco from 648 lakes in netting assessments since 1946. These lakes are scattered throughout much of the central and northern portions of Minnesota. Cisco physiologically require cold, well-oxygenated water to survive, grow, and reproduce [10,11]. Cisco is a sensitive indicator of ecological stresses such as eutrophication and climate warming. For example, 18 lakes (Table 1) in north-central Minnesota experienced cisco mortality (Fig. 1) in the unusually hot summer of 2006 [12].

The physiological response of adult populations of different fish species to water temperature and DO levels has been the subject of numerous laboratory and field studies. Several fish habitat studies described, e.g., by Coutant [13], McCormick et al. [14], and Hokanson et al. [15], attempted to correlate fish survival, growth, and reproduction to chronic temperature and DO exposure. The oxythermal habitat approach commonly used lethal boundaries for temperature and DO in cold-water fish niche modeling [16]. Both upper (i.e. lethal) temperature and lower DO survival limits are constants and do not vary with time in those studies. These oxythermal habitat models determine the water volume or layer thickness in a stratified lake between the upper temperature and lower DO limits that represent either optimal thermal habitat [16] or non-lethal/useable habitat [8,17]. To study fish habitats in small lakes over the contiguous USA, the constant lethal temperature used for cold-water species was 23.4ºC and the constant DO limit was 3 mg/L [18]. Recently, Jiang et al. [19] used a single variable to quantify oxythermal habitat of cisco in Minnesota lakes, and the variable TDO3 was originally proposed by Jacobson et al. [20]. TDO3 is defined as the water temperature at 3 mg/L of DO, and the 3 mg/L was selected as a benchmark oxygen concentration that is probably lethal or nearly so for many cold-water species [11,17,21].

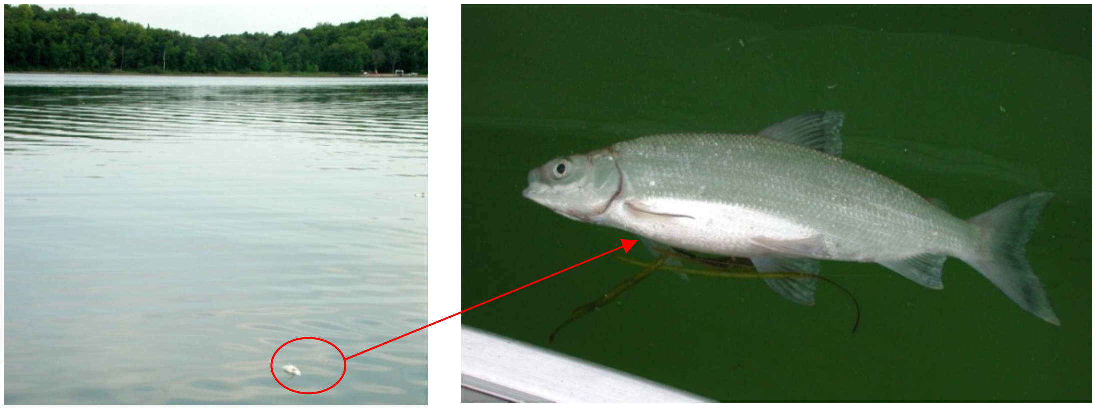

Fig. 1. Lake andrusia in minnesota had cisco mortality in July 2006 (photo: Peter C. Jacobson, minnesota department of natural resources)

In this study, the fish habitat model for cisco uses a fitted regression equation as the lethal niche boundary of adult cisco. The equation was developed by Jacobson et al. [12] in 2008. It mapped the temperatures and DO concentrations from the profiles measured in 16 Minnesota lakes that experienced cisco mortality in July and August 2006 (Table 1). First, the fish habitat model was validated in 23 Minnesota lakes and then used to project cisco lethal conditions in 36 representative lake types under past (1992–2008) climate conditions and a future climate scenario (MIROC 3.2). Based on the number of years with cisco kill and the number of annual cisco lethal days, lake types that most likely could not support cisco were identified, and lake types that can support cisco under both the past climate and the future climate scenario were identified as potential cisco refuge lakes.

2. MATERIALS AND METHODS

2.1 Simulation Models for Year-Round Water Quality

To make projections of water quality and fish habitat in small lakes under future climate scenarios, numerical simulation models of daily temperature and DO profiles are indispensable. The one-dimensional (vertical) year-round lake water quality model MINLAKE96 was developed to run continuously over many simulation years for both the open-water season and the ice-cover period [22]. The model uses a stacked layer system (Fig. 2); the layers consist of lake water and lake sediments during the open-water season and additional ice cover and snow cover during the winter ice-cover period [2]. It simulates daily water temperature profiles in a lake using daily weather data as input. (Fig. 2) is a schematic of a stratified lake including heat transfer components for the year-round water temperature model and typical temperature profiles in the summer and winter [23].

A lake is divided into a series of well-mixed horizontal water layers (Fig. 1) because the horizontal variations of water quality parameters are typically much smaller than the vertical variations in a small stratified lake. The one-dimensional, unsteady heat transfer equation in a lake was solved for daily vertical water temperature profiles [24]:

$$\frac{\partial T}{\partial t}=\frac{1}{A}\frac{\partial}{\partial z}\left(K_{zT}A\frac{\partial T}{\partial z}\right)+\frac{H_w}{\rho C_p} \qquad (1)$$

where $T(z, t)$ (°C) is the water temperature in a horizontal layer, t (day) is the time, $A(z)$ (m^2) is the horizontal area as a function of depth z (m) based on lake bathymetry input data, K_{zT} (m^2 day^{-1}) is the vertical turbulent heat diffusion coefficient, ρc_p (J m^{-3} $^oC^{-1}$) is the density of water (ρ) times heat capacity of water (c_p) and represents heat capacity per unit volume, and H_w (J m^{-3} day^{-1}) is the internal heat source strength per unit volume of water. Solar radiation absorption in the water column is the main contributor to the heat source term during the open-water season [25]. Heat exchange with the bottom sediment layer included in MINLAKE96 can be important in the shallow water layers and during the winter ice-cover periods [26].

Heat exchange between the lake and the atmosphere is treated as a source or sink term (Fig. 2) for the topmost water layer of a lake during the open-water season [$H_w(1)$ in Eq. (1) = $A_s/V(1)\times(H_{SN} + H_A - H_{BR} - H_E - H_C)$, where A_s is the lake surface area and $V(1)$ is the volume of the topmost/first water layer] due to the surface wind mixing. It includes surface heat fluxes *in* $J\ m^{-2}\ day^{-1}$ such as incoming heat from short-wave solar radiation (H_{SN}) and long-wave radiation (H_A) and outgoing heat from back radiation (H_{BR}), evaporation (H_E), and convection (H_C) related to wind speed (U). The computation of above surface heat fluxes and the internal heat source term (H_w) using daily weather input data has been discussed by Hondzo and Stefan [24] among others. During the ice-cover period [23], the model first simulates snow/ice thicknesses and sediment temperature profiles (heat conduction equation), then determines the heat source/sink terms, and finally solves the heat transfer equation to obtain water temperature profiles below the ice. The heat budget components through the water surface are directly linked to climate parameters that are related to future climate changes.

Dissolved oxygen concentration is viewed as one of the most important lake water quality parameters which indicate a lake's overall ecological health. The vertical DO profiles in the lake are computed from a balance between oxygen sources (surface reaeration and photosynthesis, Fig. 2) and oxygen sinks (sedimentary oxygen demand SOD, biochemical oxygen demand BOD, and plant respiration R). The numerical simulation model for daily DO profiles in a lake solves the one-dimensional, unsteady transport equation:

$$\frac{\partial C}{\partial t}=\frac{1}{A}\frac{\partial}{\partial A}\left(A\,K_Z\frac{\partial C}{\partial z}\right)-\frac{S_b}{A}\frac{\partial A}{\partial z}\theta_s^{T-20}+P_{MAX}\,\theta_p^{T-20}Min[L]\,Chla$$
$$-\frac{1}{YCHO2}k_r\theta_r^{\,T-20}Chla-k_b\theta_b^{\,T-20}BOD \qquad (2)$$

In Equation (2), $C(z, t)$ is the DO concentration in mg L^{-1} as a function of depth (z) and time (t), $K_z(z, t)$ is the DO vertical turbulent diffusion coefficient in m^2 day^{-1}, and S_b is the coefficient for SOD at 20℃ in mg O_2 m^{-2} day^{-1}. P_{MAX} is the maximum specific oxygen production rate by aquatic plants at 20°C under saturating light conditions in mg O_2 (mg *Chla*)$^{-1}$ day^{-1}. *Min[L]* is the light limitation determined by Haldane kinetics [27]. *Chla* is the chlorophyll-a concentration in mg L^{-1} to represent the biomass of aquatic plants in a lake. *YCHO2* is the yield coefficient, i.e., the ratio of mg chlorophyll-a to mg oxygen. The first-order decay rate coefficients are k_b and k_r for BOD and plant respiration (day^{-1}), respectively. The temperature adjustment coefficients for SOD, photosynthesis, BOD, and plant respiration are θ_s, θ_p, θ_b, and θ_r, respectively. BOD is in mg L^{-1}. Diffusive oxygen flux at the lake bottom is set equal to zero as a boundary condition.

Oxygen production is related to chlorophyll-a concentration and limitation of available light determined by Haldane kinetics. In the model, chlorophyll-a is specified by a mean annual value which depends on the specified trophic state of a lake and a function that calculates typical seasonal chlorophyll cycles [28] based on observational data from 56 lakes and reservoirs in Europe and North America [29]. In the model, the oxygen transfers through the water surface (reaeration) during the open-water season is used as an oxygen source or sink term in the topmost water (surface) layer of the lake after the reaeration is multiplied by the surface area and divided by the layer volume, and the surface oxygen transfer coefficient is calculated as a function of wind speed. SOD is treated as a sink term for each water layer because each water layer is in contact with sediments. BOD occurs in the water column along all water depths, and plant respiration for all water layers is a function of chlorophyll-a concentration.

For the DO simulations in a lake during the ice-cover period (Fig. 2), modifications must be made to account for the presence of an ice cover and low temperatures. For example, reaeration is zero because the lake ice cover prevents any significant gas exchange between the atmosphere and the water body. The water column oxygen demand (WOD in Fig. 2) is 0.01 g O^2 m^{-3} per day. DO concentrations were simulated after water temperature and snow/ice covers had been simulated. Equations (1) and (2) are solved numerically for time steps of one day and layer thicknesses from 0.02 m (near the water surface and the ice-water interface) to 1.0 m (when z >1.0 m) for small lakes using an implicit finite difference scheme and a Gaussian elimination method. Model parameters and detailed formulations of the year-round DO model (Equation 2) have been described elsewhere by Fang and Stefan [28,30].

Several modifications and refinements were made to develop MINLAKE2010 from MINLAKE96 for relative deep cisco lakes in Minnesota and have been reported elsewhere [31]. MINLAKE2012 used in this study is a spreadsheet model developed from MINLAKE2010 [31]. The most important upgrades of MINLAKE2012 compared to MINLAKE2010 are the conversion to a user-friendly Excel spreadsheet (for data input and displaying basic graphic results) and the introduction of variable temporal resolution, allowing the model to run at hourly and daily time step. The MINLAKE model was calibrated and validated against extensive Minnesota lake data: first using 5,378 water temperature and DO measurements for 48 lake years in 9 lakes for MINLAKE96 [23] and then using 7,384 water temperature and DO measurements for 439 lake years in 28 lakes for MINLAKE2010 [31].

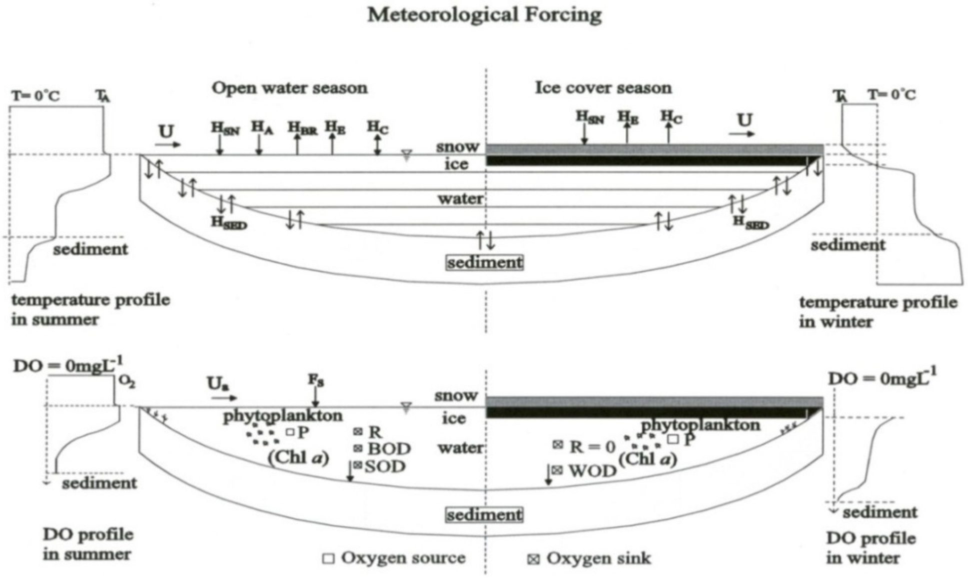

Fig. 2. Schematic of a stratified lake showing heat transfer components, oxygen sources and sinks for the year-round water temperature and DO model MINLAKE96/2010/2012, and typical temperature and DO profiles in summer (left) and winter (right)

2.2 Fish Habitat Projection Model

In lakes, water temperature and DO concentrations are two of the most important water quality parameters that affect the survival and growth of cold-water fishes [5]. In this study, the fish habitat model for cisco uses a fitted regression equation as the lethal-niche-boundary of adult cisco developed by Jacobson et al. [12] in 2008. The equation mapped the DO concentrations and water temperatures from the profiles measured in 16 Minnesota lakes that experienced cisco mortality in 2006 (Table 1). One profile was measured in each of the 16 lakes on the same day or a few days after reported mortality. The shifted exponential function given in Equation (3) is a fit of the 99th quartile nonparametric regression line bracketed the lethal combinations of observed oxygen and temperature in 16 lakes with midsummer (July 19 to August 6) mortality events in 2006 [12].

$$DO_{lethal} = 0.40 + 0.0000060\ e^{0.59 T_{lethal}} \qquad (3)$$

where DO_{lethal} and T_{lethal} are the DO concentrations (in mg/L) and the water temperatures (in ℃), respectively, which define the lethal niche boundary [12]. The computed DO_{lethal} is the required minimum DO concentration at a given water temperature T_{lethal} for cisco to survive. For the regression equation (3), the coefficients 0.40 and 0.0000060 are in mg/L and the coefficient 0.59 is in ℃$^{-1}$.

Equation (3) indicates the DO survival limit for adult cisco is not constant but depends on water temperature. The lethal-niche-boundary curve for cisco (Equation 3) was plotted in (Fig. 3) for three Minnesota lakes (Pine Mountain Lake, Itasca Lake, and Woman Lake). In comparison with the previous constant lethal temperature for cold-water fish species, i.e., 23.4℃ [18], the lethal temperature from Equation (3) is only 22.0℃ when 3.0 mg/L is used as the DO survival limit [12]. In this study, the required DO concentration DO_{lethal} was computed from the simulated water temperature in each water layer of a lake for each simulated day using Equation (3). The computed DO_{lethal} value was then compared with the simulated DO concentration in the same layer; lethal conditions for cisco were assumed to occur if the simulated DO was less than the DO_{lethal} value in all water layers (from the lake water surface to the lake bottom) on that day. In (Fig. 3), simulated DO was plotted against simulated temperature for three selected days in each of the three lakes. On July 28, 2006 in Pine Mountain Lake, all simulated temperature-DO data points (shown by the crosses) are located at the right side of or below the lethal-niche-boundary curve when simulated DO concentrations were below computed DO_{lethal} values at simulated temperatures at all water depths. The same situation of cisco lethal conditions was predicted to occur on July 31, 2006 in Itasca Lake and August 20, 2003 in Woman Lake.

If simulated DO concentrations are less than the DO_{lethal} values in only some of the water layers, lethal conditions for cisco are not assumed to occur on that day because cisco can swim to other water layers having suitable DO and temperature condition. These days with habitat at some depths are shown as filled triangles on (Fig. 3). When simulated DO concentrations are greater than the DO_{lethal} values in all water layers, fish can live in any depth of the lake, i.e., filled circles in (Fig. 3).

2.3 Representative Lake Types in Minnesota

It is infeasible to simulate more than 600 cisco lakes in Minnesota using MINLAKE2012. In this study, simulations of daily water temperature and DO profiles were made for 36 representative lake types in Minnesota before fish habitat was examined in these lakes. The 36 representative lake types was expanded from the 27 lake types used to study fish habitat in Minnesota [32] and in the contiguous USA [17]. Lakes were classified by lake geometry (surface area A_s and maximum depth H_{max}) and trophic state as related to Secchi depth (SD in Table 2). The representative surface areas chosen were 0.2, 1.7 and 10.0 km^2 for small, medium-size, and large lakes, respectively. The representative maximum depths chosen were 4, 13, and 24 m for shallow, medium-depth, and deep lakes, respectively. With these numbers, 9 lake types are obtained ranging from relatively large and shallow lakes to relatively small and deep lakes. More important than the geometric characteristics of each lake type is the likelihood of relating a strong or weak stratification in a lake to the lake's geometry ratio GR defined as $A_s^{0.25}/H_{max}$ [33], where A_s is in m^2 and H_{max} in m. The above 9 lake types cover geometry ratios from 0.88 to 14.06 m$^{-0.5}$ (Table 2). Polymictic lakes, i.e., large shallow lakes have the highest geometric ratio, while strongly stratified, i.e., small deep lakes have the lowest geometry ratio. The transition of stratification occurs when GR is between 3 and 5 m$^{-0.5}$ [32]. Hence, these nine lake types selected for the study include the full range of stratification behavior.

Secchi (disk) depth is a common limnological parameter to measure transparency of a lake [34,35]. It was used in previous fish habitat studies [17,32] to represent both trophic state (primary productivity of biomass or photosynthesis of plants) and radiation attenuation in a lake, which is used to quantify how much solar energy reaching the water surface can penetrate through a water column to heat water and to support photosynthesis of aquatic plants. The representative Secchi depths of 1.2, 2.5, and 4.5 m were previously selected for eutrophic, mesotrophic, and oligotrophic Minnesota lakes [32], respectively, using Carlson's trophic state index [36]. Minnesota cisco lakes are generally deeper, more transparent, and less trophic than other lakes in Minnesota [37]. For example, 10% of 620 cisco lakes have mean Secchi depths of 5.0–9.5 m. Therefore, the fourth Secchi depth of 7.0 m was added creating 9 new representative lake types for the study. A set of virtual cisco lakes with SD = 7.0 m was used before to study cisco refuge lakes in Minnesota [19]. Therefore, the 36 representative lake types (Table 2) were characterized by a 3×3×4 matrix consisting of (a) three different lake surface areas, (b) three lake maximum depths, and (c) four Secchi depths. These representative values for each parameter (Table 2) were selected from the data analysis of these parameters in the Minnesota Lakes Fisheries Database containing lake survey data for 3002 lakes [38] and 620 cisco lakes [37].

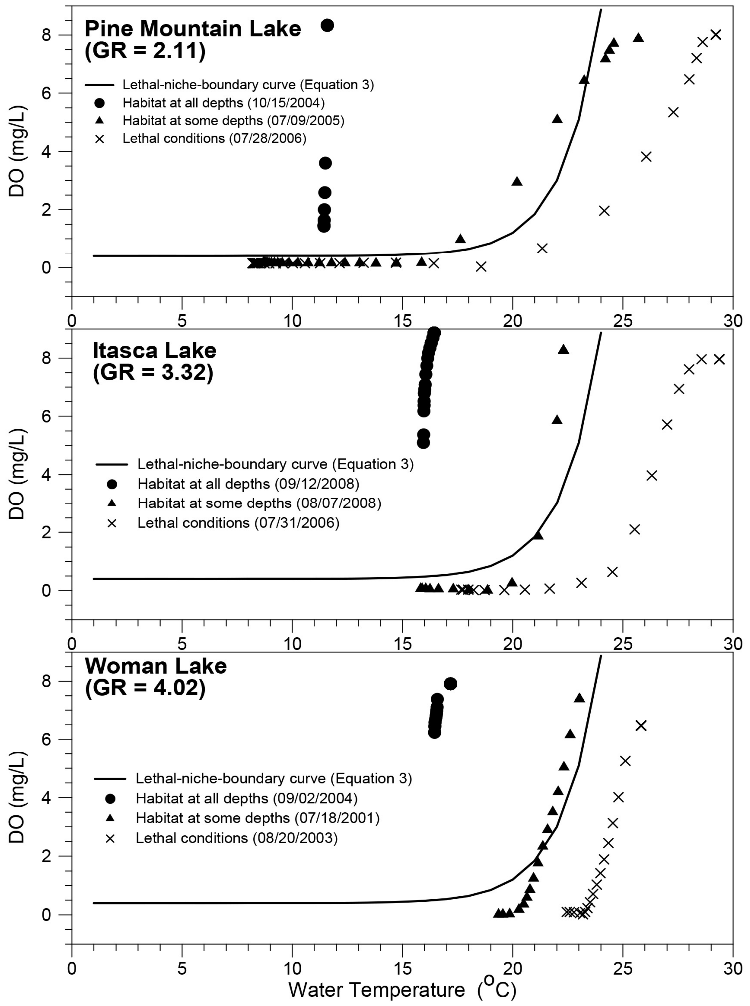

Fig. 3. Simulated DO versus simulated temperature for three selected days to show three different types of fish habitat in Pine Mountain Lake, Itasca Lake, and Woman Lake (Table 1) and the lethal-niche-boundary curve of adult cisco (Equation 3). The geometry ratio GR in $m^{-0.5}$ is defined as $A_s^{0.25}/H_{max}$ (surface area A_s is in m^2 and maximum depth H_{max} in m)

Table 1. Maximum depth (H_{max}), lake geometry ratio (*GR*), and fish habitat validation results for 23 Minnesota lakes. Simulated and observed days with lethal conditions for cisco are given as julian days

Lake name (H_{max} in m, *GR*)	**Lethal conditions**			**Simulated lethal days in 2006**	**Observed mortality day in 2006**	**Model agreement**
	First day	**Last day**	**No. of days**			
Little Turtle (8.8, 4.21)	181	222	38	182(4)[1], 187(4), 193(30)	200 (7/19) [2]	Yes (Yes) [3]
Andrusia (18.3, 2.75)	192	234	39	192(37), 233(2)	202 (7/21)	Yes (Yes)
Little Pine (Otter Tail) (19.2, 2.77)	199	216	17	199(1), 201(16)	203 (7/22)	Yes (Yes)
Cotton (8.5, 6.07)	188	225	36	188(1), 190(1), 192(34)	205 (7/24)	Yes (Yes)
Pine Mountain (23.8, 2.11)	192	241	49	192(45), 238(4)	207 (7/26)	Yes (Yes)
Leech (13.0, 10.91)	189	217	22	189(1), 195(6), 203(15)	211 (7/30)	Yes (Yes)
Itasca (13.7, 3.32)	189	222	31	189(1), 193(30)	209 (7/28)	Yes (Yes)
Gull (24.4, 3.26)	209	227	19	209(19)	210 (7/29)	Yes (Yes)
Woman (16.5, 4.02)	183	224	36	183(2), 187(1), 190(1), 193(32)	210 (7/29)	Yes (Yes)
Little Pine (Crow Wing) (11.0, 2.90)	183	240	48	183(5), 190(39), 233(3), 240(1)	214 (8/2)	Yes (Yes)
Eighth Crow Wing (9.1, 4.11)	195	222	28	195(28)	216 (8/4)	Yes (Yes)
Bemidji (23.2, 3.13)	212	217	6	212(6)	208 (7/27)	Yes (No)
Mille Lacs (12.8, 11.89)	216	241	26	216(26)	204 (7/23)	Yes (No)
Star (28.7, 2.26)	212	216	5	212(5)	200 (7/19)	Yes (No)
Seventh Crow Wing (12.8, 2.49)	196	215	20	196(20)	216 (8/4)	Yes (No)
Long (39.6, 1.22)	216	216	1	216(1)	218 (8/6)	Yes (No)
Carlos (49.7, 1.15)			0	No kill	239 (8/27)	No
Straight (19.2, 1.94)			0	No kill	213 (8/1)	No
Reference lakes without cisco kill in 2006						
Big Trout (39.0, 1.24)			0	No kill	No kill	Yes
Kabekona (40.5, 1.38)			0	No kill	No kill	Yes
Scalp (27.4, 1.15)			0	No kill	No kill	Yes
Ten Mile (63.4, 1.06)			0	No kill	No kill	Yes
Rose (41.8, 1.12)			0	No kill	No kill	Yes

Note: [1] stands for a Julian Day in 2006 and the number of continuous cisco lethal days from the lethal day predicted by the fish habitat model. [2] Julian Day followed by month and date in 2006 inside brackets, [3] the first Yes/No gives the agreement of cisco lethal prediction and reported cisco mortality in 2006 and Yes/No inside brackets gives the agreement whether or not cisco lethal days from the model include reported the date with cisco mortality

2.4 Past Climate and Future Climate Scenario

Climate conditions control water temperature and DO distribution in a lake. Climate scenarios are model inputs of MINLAKE 2012 for producing water temperature and DO concentration scenarios for the study lakes (23 lakes in Table 1 and 36 representative lake types in Table 2), which are used to assess potential changes in cisco habitats in the lakes. Forty-eight years (1961–2008) of recorded daily weather data, which were obtained from the Solar and Meteorological Surface Observation Network (SAMSON) and Midwestern Regional Climate Center, were used to describe past climate conditions for the study lakes. Weather data used for lake modeling consist of daily air temperature, dew point temperature, wind speed, solar radiation, percent sunshine, and precipitation (both rainfall and snowfall).

Projected changes in climate conditions were obtained from the output of the Model for Interdisciplinary Research on Climate, MIROC 3.2 [39], which was developed by University of Tokyo's Center for Climate System Research, the National Institute for Environmental Studies; and the Frontier Research Center for Global Change of the Japan Agency for Marine-Earth Science and Technology. The output from the MIROC 3.2 model with high spatial resolution used in the study has a surface grid whose spatial resolution is roughly 1.12 degrees latitude and longitude, which has 17 grid center points in Minnesota. Some global circulation models (GCMs) used before have only one or two grid points in Minnesota [8]. For all GCM grid center points, the differences or ratios known as "change fields" were produced and reported at a monthly interval. The 2070–2099 change field data, 30 year averages compatible with the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) [40], were downloaded from the IPCC's website to use in the study. These monthly climate parameter differences or ratios predicted by MIROC 3.2 were then applied to measured daily climate conditions (1961–2008) month by month to produce the projected daily future climate scenario. Monthly differences (or ratios) from the MIROC 3.2 grid center point closest to a weather station were used for the station. The average monthly increases in air temperature range from 3.6℃ to 4.7℃ (3.6–3.8℃ from July–September) in Bemidji, Minnesota.

Table 2. Morphometric characteristics and 'names' of the 36 representative lake types simulated with the MINLAKE 2012 model

Maximum depth (m)	**Surface area A_S (km^2)**	**Secchi depth, *SD* (m)**				**Geometry ratio (GR)**
		1.2	**2.5**	**4.5**	**7.0**	**$A_s^{0.25}/H_{max}$**
H_{max}=4	0.2	LakeR01	LakeR02	LakeR03	LakeR28	5.29 $m^{-0.5}$
	1.7	LakeR04	LakeR05	LakeR06	LakeR29	9.03 $m^{-0.5}$
	10	LakeR07	LakeR08	LakeR09	LakeR30	14.06 $m^{-0.5}$
H_{max}=13	0.2	LakeR10	LakeR11	LakeR12	LakeR31	1.63 $m^{-0.5}$
	1.7	LakeR13	LakeR14	LakeR15	LakeR32	2.78 $m^{-0.5}$
	10	LakeR16	LakeR17	LakeR18	LakeR33	4.33 $m^{-0.5}$
H_{max}= 24	0.2	LakeR19	**LakeR20**[1]	**LakeR21**	**LakeR34**	0.88 $m^{-0.5}$
	1.7	LakeR22	**LakeR23**	**LakeR24**	**LakeR35**	1.50 $m^{-0.5}$
	10	LakeR25	**LakeR26**	**LakeR27**	**LakeR36**	2.34 $m^{-0.5}$

Note: [1] These highlighted lakes are strongly stratified mesotrophic and oligotrophic deep lakes

3. RESULTS AND DISCUSSION

3.1 Simulated Water Temperature and DO under Past and Future Climate

MINLAKE2012 configured for each of the 23 lakes (Table 1) was first calibrated using available measured temperature and DO profiles by adjusting calibration parameters to obtain the best match with measured profiles. Model calibration parameters include the wind-sheltering coefficient, the sedimentary oxygen demand coefficient, the multiplier of the diffusion coefficient in metalimnion, and the multiplier for chlorophyll-a concentration below the mixed layer. These parameters were well studied for many other Minnesota lakes with necessary guidance for model calibration [31]. Weather data from the closest station were used as model input for calibration. Five weather stations (Bemidji, Brainerd, Grand Rapids, and St. Clouds in Minnesota and Fargo in North Dakota) were used in the study, and weather data at Bemidji were used for 9 of 23 study lakes. (Fig. 4) shows time-series of measured and simulated water temperatures in Woman Lake from 2000 to 2006 and projected temperatures under MIROC 3.2 future climate scenario at three depths (1.0, 7.5, and 15.0 m below the surface). Average standard error (root mean square error) between simulated and measured water temperatures from 18-day profiles (362 data pairs) from 2000 to 2006 was 2.05℃. Average standard error between simulated and measured DO concentrations was 1.93 mg/L. Simulated water temperatures matched well with measured temperatures at three different depths except one simulated temperature at 15.0 m in 2006 (Fig. 4). The measured and simulated water temperatures at all three depths responded to the weather variations of each season every year. Surface temperatures ranged from 0.0 to 28.7℃ in 2000–2006 and are projected to range from 0.2 to 31.6℃ under the future climate scenario. Projected increases of surface temperatures during the open-water seasons range from 0.3 to 10.2℃ with a mean increase of 3.6℃ and standard deviation of 1.1℃ for six years. Water temperatures at all three depths are projected to increase under the future climate scenario (Fig. 4).

Woman Lake located in Cass County, Minnesota has a maximum depth of 16.5 m and a surface area of 19.2 km^2. Woman Lake is oligotrophic due to its mean Secchi depth 4.2 m and mean chlorophyll-a concentration 2.6 µg/L and has relatively weak stratification because its geometry ratio 4.02 $m^{-0.5}$ is larger than 3.0 $m^{-0.5}$. The weak stratification in Woman Lake is indicated by mean temperature difference 2.1℃ (standard deviation 2.3℃) between surface and bottom layers during the open-water seasons under both past and future climates (Fig. 4). Attenuation of solar radiation with water depth and vertical mixing are major factors that control the formation of temperature stratifications in a lake during the summer months. Projected increases of bottom temperatures during the open-water seasons are up to 6.8℃ with mean increase 2.2℃ (standard deviation 2.3℃) in Woman Lake (Fig. 4).

Simulated DO matched well with measured DO during summer periods at three different depths except one simulated DO at 15.0 m in 2003 (Fig. 5). Measured and simulated DO near the lake bottom reached anoxic conditions in every late summer in Woman Lake, but anoxic conditions only lasted a short duration (Fig. 5). DO stratification between surface and bottom layers ranged from 0 to 12.3 mg/L with mean stratification 3.0 mg/L and standard deviation 3.1 mg/L during the open-water seasons in 2000–2006. DO stratification (Fig. 5) was stronger than temperature stratification (Fig. 4) in Woman Lake because various chemical and biological oxygen demands and weaker vertical mixing resulted in lower DO in hypolimnion (deep depths). DO during winter ice-cover periods under the future climate scenario is projected to be higher than DO under past climate conditions because of reduction in snow and ice thicknesses and shorter ice-cover period, which were reported before in other northern lakes by Fang and Stefan [2]. DO during the open-water seasons is projected to be slightly lower than DO under past climate conditions. Projected differences of surface DO between the future and past climates are up to -1.9 mg/L with mean decrease -0.6 mg/L in Woman Lake during the summer months.

(Figs. 4 and 5) are examples to show temperature and DO variations in Woman Lake under past climate conditions and the future climate scenario, and similar variations over seasons and similar changes due to climate warming are projected to occur in other study lakes. These changes in water temperature and DO concentration in lakes are eventually projected to affect cisco habitat, which will be discussed below.

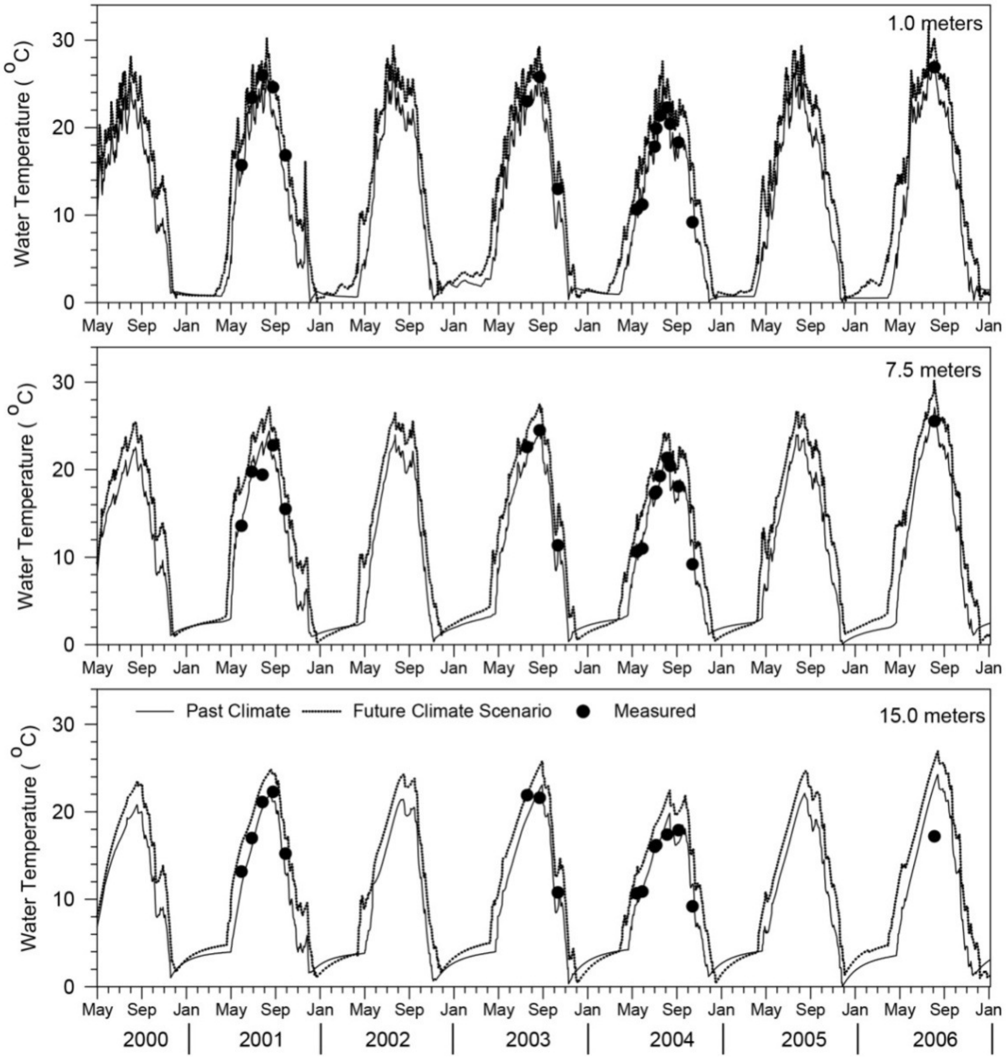

Fig. 4. Time-series plots (2000–2006) of simulated and measured water temperatures at 1.0, 7.5, and 15.0 m depths for Woman Lake in Minnesota under past climate conditions and the future climate scenario (MIROC 3.2)

Average standard errors between measured and simulated temperatures and DO concentrations were 1.57°C and 1.72 mg/L, respectively, for all 23 Minnesota lakes (Table 1). There were six study lakes with only one profile in 2006 for model calibration. The Nash-Sutcliffe efficiency (NSE) model coefficient [41] is typically used to assess the predictive power of numerical simulation models. It is defined as:

$$NSE = 1 - \frac{\sum_{n=1}^{N} (O^n - P^n)^2}{\sum_{n=1}^{N} (O^n - \overline{O})^2} \tag{4}$$

Where N is the number of observation and predication data pairs, O^n is the value of the n^{th} observed data, P^n is the n^{th} predicted value from the model, and $\overline{O}$ is the average value of all observed data. The *NSE* can range from -∞ to 1. An efficiency of 1 (*NSE* = 1) corresponds to a perfect match between modeled values and observed data. An efficiency of 0 (*NSE* = 0) indicates that the model predictions are as accurate as the mean of the observed data, whereas as efficiency less than zero (NSE <0) occurs when the observed mean is a better predictor than the model. The closer the model efficiency is to 1, the more accurate the model is. Average *NSE* for temperature simulations in the 23 lakes is 0.86 and for DO simulations is 0.66. Therefore, MINLAKE2012 was well calibrated for the 23 lakes.

3.2 Validation of Fish Habitat Model

The fish habitat model uses simulated daily temperature and DO profiles in a lake to check day by day whether cisco habitable or lethal conditions occur. (Fig. 3) shows three types of cisco habitat in three different Minnesota lakes. The first case is when cisco habitat exists at all water depths, i.e., simulated DO concentrations are greater than DO_{lethal} values calculated using simulated temperatures and Equation (3), in which all DO-temperature data points (filled circles in Fig. 3) are located to the left side of or above the lethal-niche-boundary curve. The three example days 10/15/2004 in Pine Mountain Lake, 9/12/2008 in Itasca Lake, and 9/2/2004 in Woman Lake, are the first cases of survivable cisco habitat at all water depths. The second case is when cisco habitat exists at some depths, i.e., simulated DO concentrations are less than calculated DO_{lethal} values in only some of the water layers. Cisco lethal conditions were not assumed to occur because cisco could swim to other water layers with suitable DO and temperature conditions. For example, Pine Mountain Lake on 7/9/2005 (filled triangles in Fig. 3) had lower DO at higher temperatures near the surface and near anoxic DO (0.2 mg/L) in the hypolimnion. Therefore, layers near the surface and in the hypolimnion could not support cisco habitat, but some intermediate layers had high enough DO at simulated temperatures to support cisco habitat. Itasca Lake on 8/7/2008 and Woman Lake on 7/18/2001 had suitable cisco habitat in the surface layers and no cisco habitat in the bottom layers (Fig. 3). Itasca Lake located in Clearwater County, Minnesota has a maximum depth of 13.7 m and a surface area of 4.3 km^2. Itasca Lake is mesotrophic due to its mean Secchi depth 2.8 m and mean chlorophyll-a concentration 10.4 µg/L and has relatively weak stratifications because of its GR = 3.32 [32,33].

When simulated DO concentrations are less than the DO_{lethal} values in all water layers, fish can't live in any depth of the lake, therefore, lethal conditions for cisco occur on that day. (Fig. 6) shows simulated DO versus simulated temperature during two periods (7/11/2006–8/24/2006 and 8/26/2006–8/29/2006) in Pine Mountain Lake when cisco lethal conditions were predicted by the fish habitat model using the cisco lethal-niche-boundary curve. Pine

Mountain Lake located in Cass County, Minnesota has a maximum depth of 23.8 m (deep lake) and a surface area of 6.36 km^2. Pine Mountain Lake is a mesotrophic stratified lake because of its mean Secchi depth 2.4 m, mean chlorophyll-a concentration 6.5 µg/L, and GR = 2.11. Surface water temperatures in Pine Mountain Lake reached 29.4℃ on July 31, 2006.

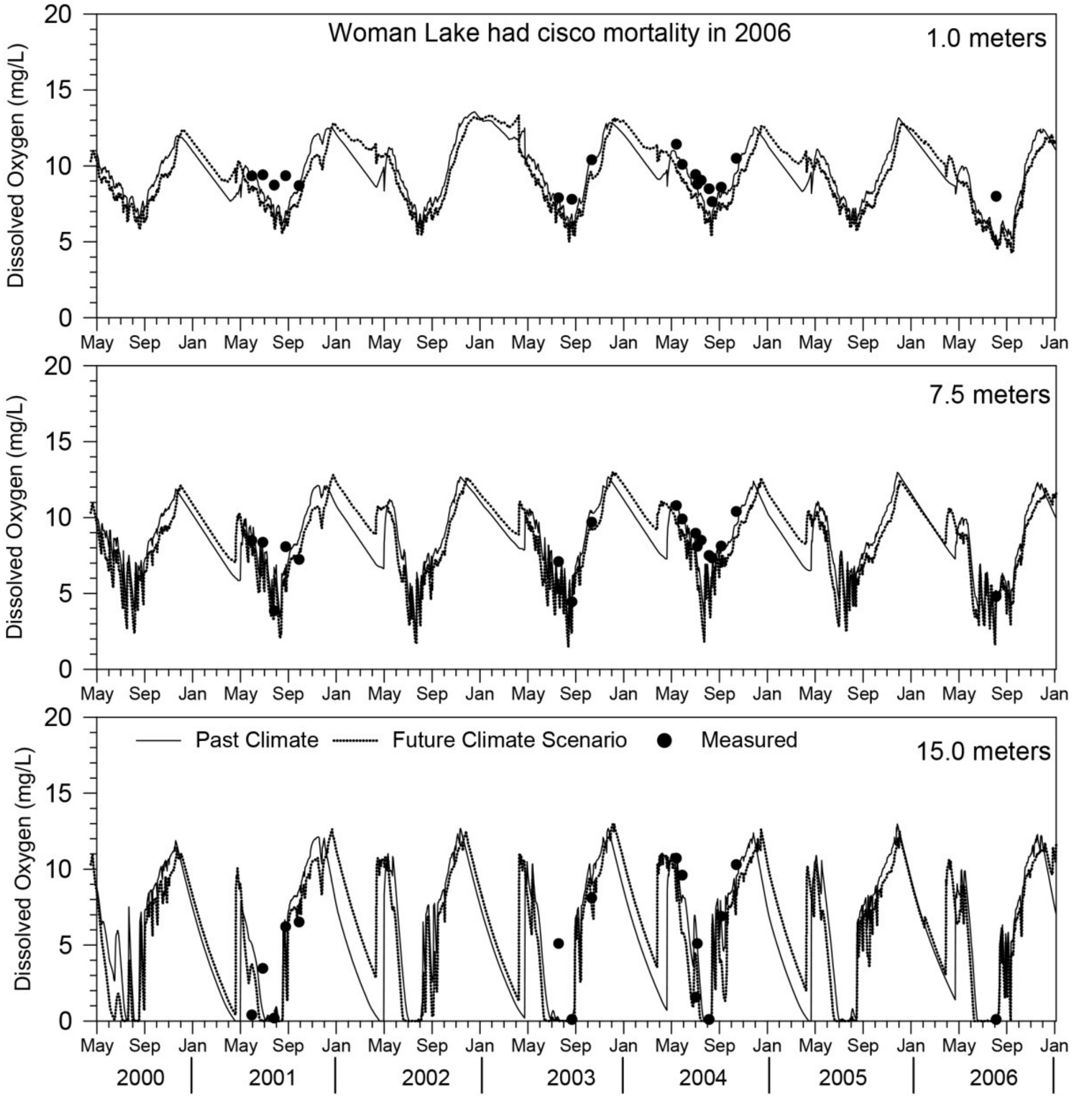

Fig. 5. Time-series plots (2000–2006) of simulated and measured DO concentrations at 1.0, 7.5, and 15.0 m depths for Woman Lake in Minnesota under past climate conditions and the future climate scenario (MIROC 3.2)

Another study [42] concluded that lethal temperature for adult cisco is about 22.1℃. In the 49 days in Pine Mountain Lake (Fig. 6), 43% of water depths had temperatures greater than 22.1ºC, and 58% of water depths had DO < 3 mg/L. Therefore, cisco mortality in Pine Mountain Lake was reported on July 26, 2006 [12] when the fish habitat model predicted continuous 16 days of lethal conditions starting from July 11, 2006.

The fish habitat modeling using the cisco lethal-niche boundary curve was validated in the 23 study lakes. Validation results are summarized in (Table 1) for each lake, which lists the first Julian Day, the last Julian Day, and the total number of days with cisco lethal conditions predicted by the model in 2006 (hindcast or backtesting). It also lists the first Julian Day and the number of continuous days with cisco lethal conditions predicted in 2006. For example, Little Turtle has "182(4)" under "simulated lethal days in 2006" in (Table 1) that means lethal conditions were simulated on Julian Day 182 (July 1, 2006) and the number of continuous cisco lethal days is four (Julian Days 182–185). The Julian Day and month/day in 2006 inside brackets when cisco mortality was reported in each lake is listed under "Observed mortality day in 2006" in (Table 1) and used to examine model agreement. In the last column of Table 1, the first Yes/No gives the agreement of cisco lethal prediction and reported cisco mortality in 2006, and the second Yes/No inside brackets gives the agreement whether or not cisco lethal days from the model includes reported date with cisco mortality. For example, in Pine Mountain Lake the fish habitat model predicted a total of 49 days from July 11 (Julian Day 192) to August 29 (Julian Day 241) having cisco lethal conditions, which agree with reported cisco mortality in 2006; and the period of predicted cisco lethal conditions includes the reported day with cisco mortality, i.e., July 26 or Julian Day 207. Therefore, the model agreement with mortality observation is Yes (Yes) as listed in Table 1. The fish habitat model predicted the Yes (Yes) agreement in 11 of the 18 lakes that experienced cisco mortality in 2006.

For five lakes (Bemidji, Mille Lacs, Star, Seventh Crow Wing, and Long), the model predicted cisco lethal conditions, but the predicted lethal periods did not include corresponding reported cisco mortality days in 2006; these lakes have the Yes (No) agreement (Table 1). For three lakes (Bemidji, Mille Lacs, and Star), cisco lethal conditions were predicted to occur after the reported cisco mortality days in 2006. In the Seventh Crow Wing Lake, cisco lethal conditions were predicted to occur from Julian Day 196 to 215 (August 3) in 2006, and the cisco mortality was reported on August 4. This case can be considered as Yes (Yes) agreement because cisco mortality might be reported one or a few days after cisco mortality occurred when study lakes were not constantly monitored and observed. Long Lake was predicted with only one day of lethal conditions. Long Lake located in Otter Tail County, Minnesota has a maximum depth of 39.0 m (deep lake) and a surface area of 5.1 km^2. Long Lake is a mesotrophic strongly stratified lake because of its mean Secchi depth 3.0 m, mean chlorophyll-a concentration 7.2 μg/L, and GR = 1.22. There was only one day in 2006 with observed temperature and DO profiles in Long Lake for model calibration.

There are two lakes (Straight Lake and Lake Carlos) that the model did not predict cisco lethal conditions, but they had cisco mortality in 2006; the model has the No agreement with mortality observation (Table 1). Lake Carlos located in Douglas County, Minnesota has a maximum depth of 49.7 m and a surface area of 10.5 km^2. Lake Carlos is a mesotrophic strongly stratified lake because of its mean Secchi depth 3.0 m, mean chlorophyll-a concentration 5.0 μg/L, and GR = 1.15. The late summer cisco mortality event that occurred on August 27 in Lake Carlos did not fit the lethal-niche-boundary curve developed from the midsummer events in 16 lakes [12]. Based on the lethal-niche-boundary curve and measured profiles on September 1, 2006 [12], cisco could exist in some surface layers with low temperatures and high DO, but could not exist in the hypolimnion with anoxic conditions. Jacobson et al. [12] also studied the 5 reference lakes that did not experience cisco mortality in 2006. These five reference lakes are all deep strongly stratified lakes (GR < 1.4 in Table 1). The fish habitat model using simulated temperature and DO profiles predicted no lethal conditions for cisco in all five references lakes (Table 1). Therefore, the fish habitat model has overall good agreement in the 23 study lakes with and without cisco mortality reported in 2006.

3.3 Fish Habitat Simulations in 36 Representative Lake Types

To understand cisco habitat and to determine cisco kill in different lake types, daily water temperature and DO profiles were simulated using MINLAKE2012 under past (1991–2008) climate conditions from Bemidji weather station and the corresponding future climate scenario (MIROC 3.2). Bemidji weather station is close to most of the 23 study lakes (Table 1) and has 18 years of weather data. In previous regional fish habitat projections [43], water temperature and DO profiles were averaged over the entire simulation period before the fish habitat model was applied. In this study, the fish habitat model for cisco was applied every day year by year from 1992 to 2008 using simulated daily water temperature and DO profiles. Results for the first simulation year (1991) were not used for cisco modeling in order to remove the possible effect of initial conditions.

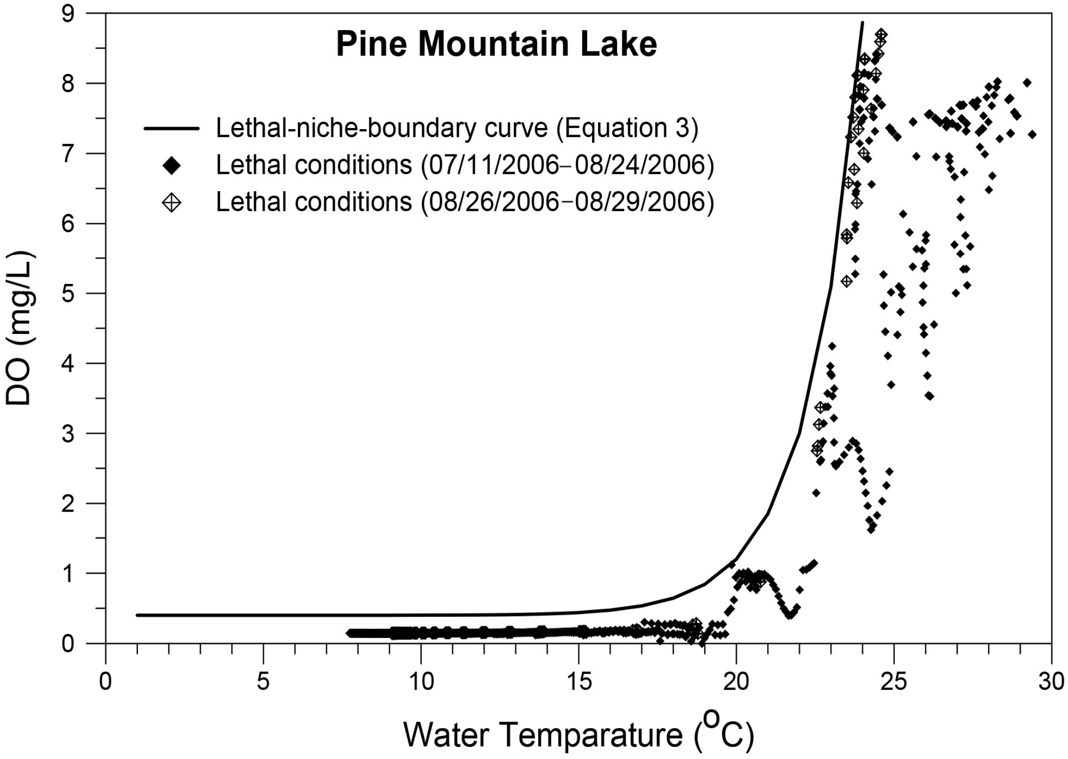

Fig. 6. Simulated DO versus simulated temperature in 49 cisco lethal days in Pine Mountain Lake and the lethal-niche-boundary curve of cisco

3.3.1 Total days of cisco lethal conditions in each year

Total days of lethal conditions for cisco in each year over 17 simulation years were used to create box plots (Fig. 7) showing the maximum, minimum; and 25%, 50%, and 75% quartile values simulated for each of the 36 representative lake types in Minnesota under past climate conditions (bottom) and MIROC 3.2 future climate scenario (top). Different scales for *y* axis were used for results under past climate conditions (maximum 50 days) and the future climate scenario (maximum 100 days) in (Fig. 7). The bottom graph of (Fig. 7) has *x* axis showing lake name and the top graph has *x* axis showing corresponding GR ($m^{-0.5}$) value and SD (m) in brackets. Lethal conditions may be continuous for many days or discontinuous for some days (Table 1). For the 12 shallow lakes with GR ≥ 5.29 $m^{-0.5}$, median annual days of cisco lethal conditions ranged from 13 to 22 days under past climate conditions and are projected to range from 47 to 55 days under the future climate scenario (Fig. 7). These results indicate that shallow lakes typically cannot support cisco habitat. In the MNDNR cisco lake database there are total 620 cisco lakes, of which 37 lakes have GR ≥ 5.29 $m^{-0.5}$ and maximum depths less than 11.0 m. There are 14 lakes with H_{max}< 5.0 m that are classified as shallow lakes in Minnesota [32], of which 13 lakes have GR > 5.29 $m^{-0.5}$ and one lake has GR = 4.4 $m^{-0.5}$. These lakes had cisco observed in the past but most likely, they cannot sustain cisco habitat.

For the 12 medium-depth lakes with H_{max} = 13.0 m (LakeR10–LakeR18 and LakeR31–LakeR33), GR values are 1.63, 2.78, and 4.33 $m^{-0.5}$ (Table 2). Median annual days of cisco lethal conditions ranged from 0 to 1 day under past climate conditions and are projected to range from 19 to 49 days under the future climate scenario (Fig. 7). Under past climate conditions, cisco lethal conditions reached a maximum of 30 days for medium-depth lakes during the unusual hot summer in 2006. These lakes are vulnerable to climate warming because lethal conditions are projected up to 80 days.

For the 12 deep lakes with H_{max} = 24 m (LakeR19–LakeR27 and LakeR34–LakeR36), eutrophic deep lakes (LakeR19, R22, and R25) and mesotrophic large deep lake (LakeR26 with GR = 2.34 $m^{-0.5}$) are projected to have some cisco lethal days under the future climate scenario (Fig. 7). Cisco lethal conditions, however, were not simulated to occur under past climate conditions (1992–2008). Large deep lakes with GR = 2.34 $m^{-0.5}$ seem require Secchi depth more than 2.5 m to have non-lethal conditions under the future climate scenario. Other strongly stratified mesotrophic and oligotrophic deep lakes (LakeR20, R21, and R34 with GR = 0.88; LakeR23, R24, and R35 with GR = 1.50, and LakeR27 and R36 with GR = 2.34 in Table 2) are possible to support cisco habitat under both past and future climate conditions (Fig. 7). These deep lakes are good candidates of cisco refuge lakes[19,44].

The results for deep lakes under past climate conditions seem to have certain disagreement with cisco mortality observations (Table 1). Minnesota lakes with H_{max}< 20.0 m were classified as deep lakes [32], and 7 of the 18 study lakes with cisco mortality in 2006 are deep lakes with GR ranging from 1.15 to 3.26 $m^{-0.5}$. Generalized model parameters [45] were used for simulations in the 36 representative lake types, but for the 23 lakes (Table 1), model parameters were first calibrated against measured profiles before the cisco habitat model was applied. Differences in model parameters is one of the major reasons for disagreement in habitat projections and suggest that other oxythermal habitat parameters, e.g., TDO3 [20], should be used for studying cisco fish habitat in relatively deep lakes. TDO3 computed in the fixed and variable benchmark periods were successfully used to classify Minnesota cisco lakes into tier 1 to tier 3 refuge lakes [19,44].

(Fig. 7) shows annual cisco lethal days are strongly dependent on lake stratification characteristics (i.e., GR) but vary relatively weakly with trophic status (i.e., SD). The four lakes with the same GR but different Secchi depths were grouped together to compute mean and standard deviation of annual cisco lethal days under past climate conditions and the future climate scenario (Fig. 8). There are consistent patterns of average annual lethal days for each group of lakes with the same maximum depth (shallow, medium-depth, and deep).

Shallow lakes (GR > 5.2 $m^{-0.5}$) have large numbers of cisco lethal days, medium-depth lakes (GR = 1.63, 2.78, and 4.33 $m^{-0.5}$) have cisco lethal days increasing with geometry ratio (Fig. 8), and deep lakes (GR = 0.88, 1.50, and 2.34 $m^{-0.5}$) have little or no cisco lethal days.

The four lakes with GR = 1.63 $m^{-0.5}$ (LakeR10–R12 and LakeR31) are small medium-depth lakes (A_s = 0.2 km^2 and H_{max} = 13.0 m). Cisco lethal days projected for these four lakes (especially under the future climate scenario) are different from deep lakes with GR less or greater than 1.63 $m^{-0.5}$ (Fig. 8). These results may indicate that fish habitat modeling for deep lakes should be separated from the modeling for medium-depth lakes. To further prove the point, four deep lakes (LakeR41–R44) having GR = 1.63 $m^{-0.5}$ (A_s = 2.32 km^2 and H_{max} = 24.0 m) were created, and daily temperature and DO profiles were simulated using MINLAKE2012 under past climate conditions and the future climate scenario. The simulated number of annual cisco lethal days in these four deep lakes is zero for all years (1992–2008) under past climate conditions and is projected to be zero under the future climate scenario except for LakeR41, an eutrophic deep lake having one year with 4 days of cisco lethal projection. Therefore, simulations of cisco lethal days in these deep lakes (LakeR41–R44) are consistent with other deep lakes but different from medium-depth lakes with the same geometry ratio. Other fish habitat parameters, e.g., good-growth period for cold-water fish in 27 Minnesota lake types, had similar discontinuous patterns in some medium-depth and deep lakes in a previous study [17]. In the MNDNR cisco lake database, there are 385 medium-depth lakes with 5 m ≤ H_{max}< 20 m and 221 deep lakes with H_{max}≥ 20 m. Therefore, it is recommended to model cisco habitat and survival separately for medium-depth lakes and deep lakes in the future.

3.3.2 Number of years with cisco kill

It is still uncertain how many days that violate the non-survival or lethal-niche limits are necessary to result fish mortality. In previous regional fish habitat projections [32] when daily water temperature and DO concentration profiles used for fish habitat simulations were long-term (30-year) averages, fish kill was assumed to occur when the number of non-survival days (either consecutive or discontinuous) totaled at least seven. In this study, a sensitivity analysis on the number of continuous lethal days for determining cisco kill was performed when daily profiles were not averaged over 17 years (1992–2008), but cisco lethal conditions were checked in each day year by year. A cisco kill was assumed to occur if the number of continuous lethal days was greater than 3, 7, and 14 days for the sensitivity analysis. The 3 days are the half of 7 days used before, and 14 days are double of 7 days. For the 11 study lakes (Table 1) in which the simulated lethal days included the reported cisco mortality days in 2006, the number of continuous lethal days to the mortality day was calculated and ranged from 2 (Gull Lake) to 25 (Little Pine Lake in Crow Wing County) days. Median value of the number of continuous lethal days to the mortality day was 14 days (mean value 13 days with a standard deviation 7 days). This result is another reason to use 14 days for the sensitivity analysis.

Using 3, 7, and 14 continuous lethal days for determining cisco kill, (Fig. 9) shows the numbers of years with cisco kill simulated for the 36 representative lake types in Minnesota for 17 simulation years under past (1992–2008) climate conditions (blue triangles) and the future climate scenario (black circles). The *x* axis gives lake's geometry ratio, and the four lake types with the same geometry ratio (Table 2) were grouped together to compute mean and standard deviation of the number of years with cisco kill. Under past climate conditions, the 12 shallow lakes (LakeR01–LakeR09, LakeR28–LakeR30, GR = 5.29, 9.03, and 14.06 $m^{-0.5}$) were simulated to have cisco kills on average in 14 to 15 years when 3 continuous lethal days was used to determine whether cisco kill happens or not. Under the future climate scenario (MIROC 3.2), the 12 shallow lakes are projected to have cisco kills in all 17 simulation years. These results provide strong evidence to indicate that shallow lakes cannot support cisco habitat. In the MNDNR cisco lake database, there are only 14 lakes that are classified as shallow lakes with H_{max}< 5 m [32]. These shallow lakes are weakly stratified or polymictic with relatively high temperatures from surface to bottom during the summer which caused summer cisco kill almost every year from 1992–2008. Although cisco was observed in these 14 lakes in the past, whether cisco still exists in them is unknown. The projection under the future climate scenario shows they are not favorable to support cisco habitat every year.

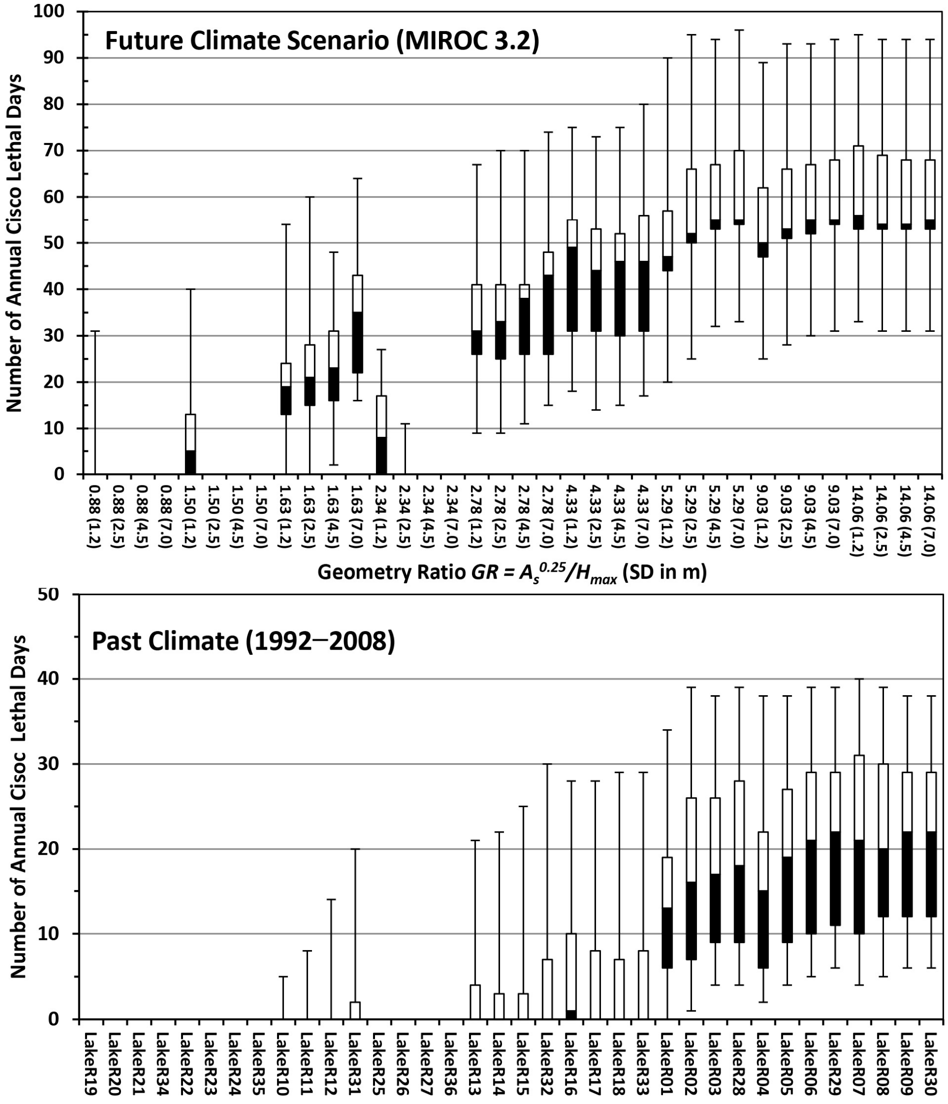

Fig. 7. Box plots of number of annual cisco lethal days simulated for the 36 representative lake types in Minnesota under past climate conditions (bottom) and the future climate scenario (top)

When 7 continuous lethal days were used to determine whether cisco kill happens, the 12 shallow lakes were simulated to have cisco kills on average in 11 to 12 years (range from 9 to 13 years) under past climate conditions and are projected to have 17 years of cisco kills under the future climate scenario. When 14 continuous lethal days were used to determine whether cisco kill happens, the 12 shallow lakes were simulated to have only 1 year (2006) with cisco kill under past climate conditions and are projected to have 11 to 12 years of cisco kills under the future climate scenario. It projects there are more years with cisco kills in some medium-depth lakes than in the 12 shallow lakes under the future climate scenario (Fig. 9). This finding may indicate that 14 continuous lethal days for determining cisco kill may be longer than how many lethal days would be needed for cisco mortality to occur because it gives inconsistent results on fish habitat projections. Therefore, the 14 continuous lethal days for determining cisco kill is not recommended for further fish habitat study.

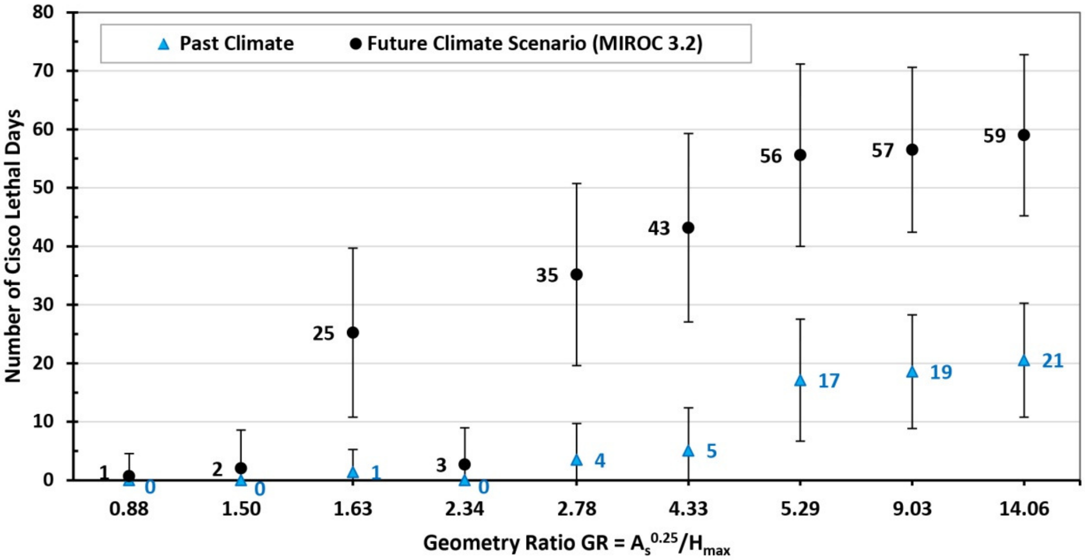

Fig. 8. Number of annual cisco lethal days (mean ± standard deviation) simulated for the 36 representative lake types with 9 GR values under past climate conditions and the future climate scenario

Using 3 continuous lethal days for determining cisco kill, the 12 medium-depth lakes were simulated to have cisco kills on average in 2 to 7 years (range from 1 to 8 years) under past climate conditions and are projected to have 16 to 17 years of cisco kills under the future climate scenario. Using 7 continuous days for determining cisco kill, the 12 medium-depth lakes were simulated to have cisco kills on average in 1 to 5 years (range from 0 to 6 years) under past climate conditions and are projected to have 15 to 17 years (range from 13 to 17 years) of cisco kills under the future climate scenario. (Fig. 9) shows medium-depth lakes are most vulnerable to climate warming with average increase of 13 years with cisco kill (range from 9 to 15 years).

The 12 deep lakes were simulated to have no cisco kill under past climate conditions using either 3 or 7 continuous lethal days for determining cisco kill. The 12 deep lakes are projected to have on average 1 to 4 years (range from 0 to 9 years) or 0 to 2 years (range from 0 to 6 years) of cisco kills under the future climate scenario when 3 and 7 continuous lethal days were used for determining cisco kill, respectively. Only eutrophic deep lakes (*SD* = 1.2 m, LakeR19, LakeR22 and LakeR25) and large mesotrophic deep lake (A_s = 10 km^2, *SD* = 2.5 m, LakeR26) are projected to have a few years with cisco kill under the future climate scenario. (Fig. 9) shows most mesotrophic and oligotrophic deep lakes can support cisco habitat under both past climate conditions and the future climate scenario and are good candidates for cisco refuge lakes, as supported by previous studies [19,44]. It seems that 3 or 7 continuous lethal days for determining cisco kill provide quite reasonable results for cisco kill simulations in shallow, medium-depth, and deep lakes in Minnesota.

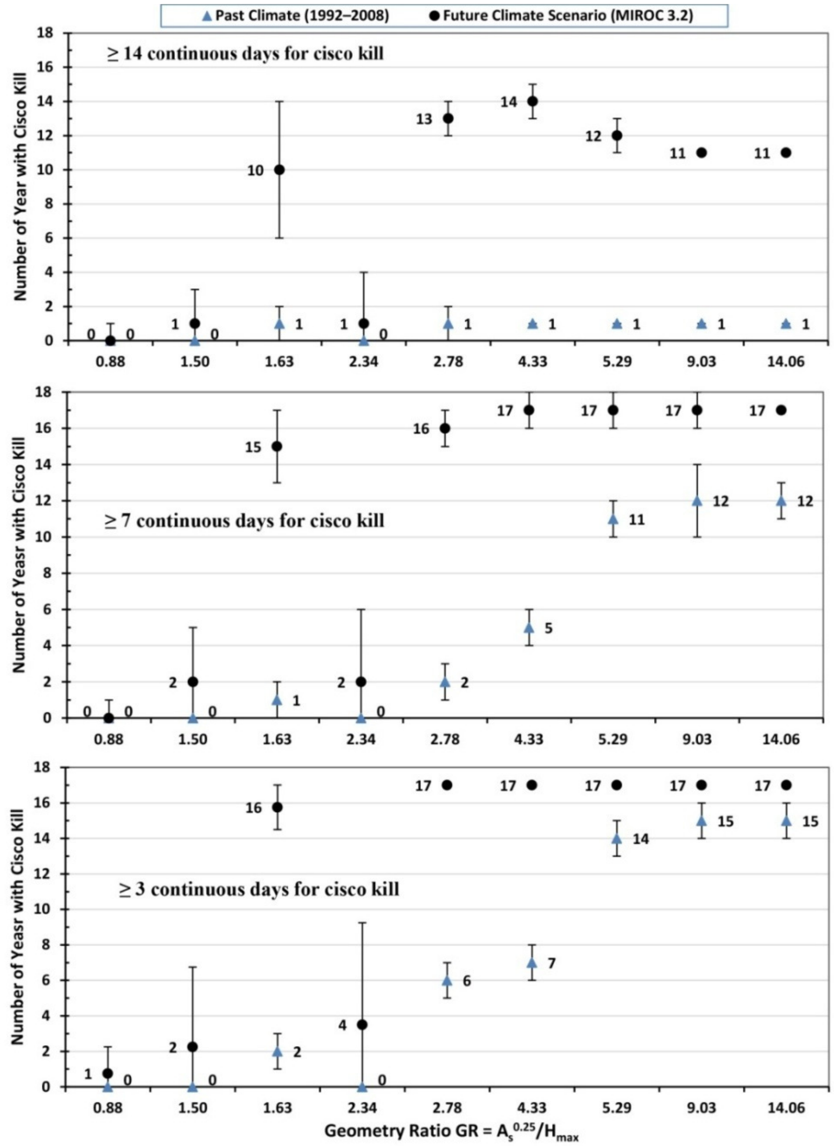

Fig. 9. Numbers of years with cisco kill simulated for the 36 representative lake types in Minnesota under past climate conditions (triangles) and the future climate scenario (circles) using 3, 7, and 14 continuous lethal days for determining cisco kill

The box plots of the numbers of annual continuous lethal days greater than or equal to 3 and 7 days simulated for the 36 lake types in Minnesota under past climate conditions (1992–2008) and the future climate scenario (MIROC 3.2) are presented in (Fig. 10). Those lethal days that are not continuous for 3 or 7 days were excluded, therefore, the number of annual continuous lethal days in any lake presented in (Fig. 10) is less than or equal to the number of annual lethal days reported in (Fig. 7) for the corresponding lake. Under past climate conditions, one to a few years with cooler summers did not result in cisco kills in the 12 shallow lakes, but most other years had cisco kills with annual continuous lethal days up to 36 days (Fig. 10). Under the future climate scenario, projected annual continuous lethal days are up to 94 days and 40 days in shallow lakes and eutrophic deep lakes, respectively. Medium-depth lakes are projected to have relatively large change in annual continuous lethal days (Fig. 10, different scales on *y* axis). As explained before, the four medium-depth lakes with GR = 1.63 $m^{-0.5}$ seem to behave different from other deep lakes with similar geometry ratio (Fig. 10), which means they should be studied separately from deep lakes.

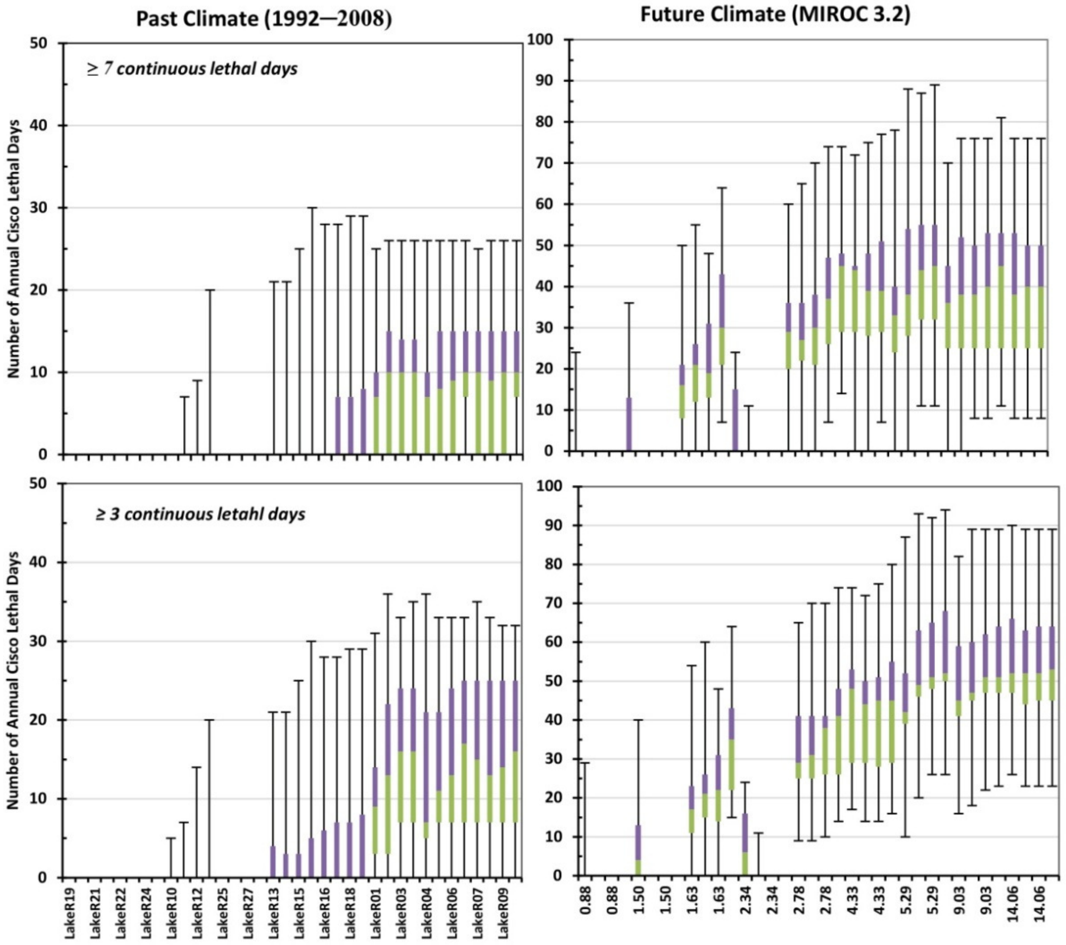

Fig. 10. Numbers of annual continuous lethal days greater than or equal to 3 and 7 continuous days simulated for the 36 lake types in Minnesota under past climate conditions (1992–2008 Bemidji weather data) and the future climate scenario (MIROC 3.2)

3.4 Limitation

Frey [11] postulated that young ciscoes are more tolerant of high temperatures and low DO concentrations than the larger and older ciscoes; they can survive through hot summers in a thin stratum above the thermocline in stratified deep lakes. Therefore, summer mortality events primarily affect adult cisco. Cisco populations can persist in lakes with multiple years of mortality as long as some juveniles remain in the lakes. Recruitment of juveniles is therefore as important to cisco's survival as the duration of exposure to lethal conditions, but recruitment is not included in current simulations and projections. At the same time, the shallow lakes that are projected to have cisco kill every year with continuous lethal conditions up to 94 days (Fig. 10) under the future climate scenario are most likely not able to sustain cisco habitat at any life stage.

The increase in the number of annual lethal days in different lake types (Table 2) are projected under one future climate scenario (MIROC 3.2) in this study. Many hydrologic studies conducted on the impacts of climate warming or climate change on watersheds and aquatic systems used an assemblage of GCMs. Future studies on cisco habitat projections should include more GCM future climate scenarios, e.g. the Canadian Climate Centre (CCC) GCM 2.0 and CCC Coupled GCM 3.1. Overall, the projection of fish kill and fish growth in lakes is still a challenging and growing research area and needs further model validation with more field observations of fish species in different lakes.

4. CONCLUSION

Both water temperature and DO in lakes are projected to change due to future climatic warming. The one-dimensional lake water quality model MINLAKE2012 was used to simulate daily water temperatures and DO concentrations under past climate conditions (1992–2008) and MIROC 3.2 future climate scenario in the 36 representative lake types in Minnesota. A fish habitat model using the lethal niche-boundary curve proposed by Jacobson et al. [12] was developed to evaluate cisco lethal conditions and survival in Minnesota lakes. The fish habitat model uses simulated temperatures to compute required minimum DO concentrations for adult cisco to survive. When simulated DO is less than the minimum required DO based on the lethal-niche-boundary curve at all water depths or layers, lethal conditions for cisco were assumed to occur. Using the fish habitat model, we have obtained the following conclusions:

(1). MINLAKE2012 was calibrated against measured profiles in 23 Minnesota lakes (Table 1) with average standard error of 1.57℃ for temperature and 1.72 mg/L for DO. The fish habitat model using the lethal-niche-boundary curve was applied to the 23 lakes and successfully simulated lethal conditions in 16 of the 18 lakes that experienced adult cisco mortality in 2006 and habitable conditions in five references lakes that experienced no adult cisco mortality in 2006. Projections from the fish habitat model had an overall good agreement with cisco mortality and survival in 2006.

(2). The 12 shallow lake types with lake geometry ratio greater than 5.2 $m^{-0.5}$ had 10 to 16 years with many continuous lethal days during 17 simulation years under past climate conditions and are projected to have 16 to 17 years with cisco kill (Fig. 8) under the future climate scenario. Those shallow lakes projected to have continuous lethal conditions up to 94 days (Fig. 10) are most likely not able to sustain cisco habitat. This finding supports that there are only 14 shallow lakes out of the 620 cisco lakes (MNDNR database).

(3). The 12 medium-depth lakes (H_{max} = 13 m) were simulated to have lethal conditions under both past climate conditions and the future climate scenario. It is projected that medium-depth lakes have the largest increase in the number of years with cisco kill (average increase 13 years ranging from 9 to 15 years out of 17 simulation years) due to climate warming. Therefore, cisco in the medium-depth lakes are most vulnerable to climate change.

(3). The four medium-depth lakes with GR = 1.63 $m^{-0.5}$ seem to behave differently in fish habitat projections than deep lakes with similar geometry ratio (Figs. 7–10). In the future, fish habitat projections in medium-depth lakes should be studied separately from deep lakes.

(4). Most mesotrophic and oligotrophic deep lakes are good candidates for cisco refuge lakes that can support cisco habitat under both past climate conditions and the future climate scenario. Eutrophic deep lakes and large (surface area) mesotrophic deep lakes are projected to have cisco kills when continuous lethal days are greater than 3 or 7 days. The 3 or 7 continuous lethal days for determining cisco kill give quite reasonable results for cisco kill simulations in all lake types in Minnesota and are recommended for future fish habitat study. Using 14 continuous lethal days for determining cisco kill may be longer than how many lethal days would be needed for cisco mortality to occur and is not recommended for further fish habitat study.

CONSENT

Not applicable.

ETHICAL APPROVAL

Not applicable.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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