

Prediction of lake water temperature, dissolved oxygen, and fish habitat under changing climate

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Received: 22 July 2016 / Accepted: 28 January 2017 / Published online: 17 February 2017
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Abstract We applied a three-dimensional lake water quality model to investigate the influence of local meteorological conditions on fish habitat under one historical and two future climate change scenarios. Compared to the historical normal climate scenario, the averaged surface water temperature increases up to 4 °C and the dissolved oxygen concentration is 1 mgL⁻¹ less during the ice-free seasons under the future climate scenarios. The stratification periods expand up to 23% (46 days), thermocline depths increase 49%, and the onset of anoxia occurs 4 weeks earlier under the future climate scenarios. The dissolved oxygen concentrations and water temperatures are used as the key water quality parameters to investigate the temporal and spatial variabilities of fish habitat. The good growth, restricted growth, and lethal habitats for the coolwater fish change up to 14% of the total lake volume. Compared to the historical normal climate scenario, on average, the lake total volume for good growth, restricted growth, and lethal habitat of coolwater fish change +16, -18, and +85%, respectively. The most significant (70%) changes in lethal habitat for coolwater fish occurs in the upper 5 m of the water column. During summer, a modest increase of lethal habitat for coolwater fish (8% of total lake volume) has a pronounced impact on the good growth habitat. The prediction of spatial locations and time periods of potential fish habitats during stressed or lethal environmental conditions is becoming increasingly important for managing fish habitats under changing climate.

1 Introduction

Climate change impacts the physical, chemical, and biological processes of aquatic ecosystems (Hondzo and Stefan 1993; Whitehead et al. 2009; Kraemer et al. 2015). To predict the influence of climate change on the aquatic ecosystems, we need to understand the influence of climate change on the physical processes and the response of the biological and chemical processes to those changes

Electronic supplementary material The online version of this article (doi:10.1007/s10584-017-1916-1) contains supplementary material, which is available to authorized users.

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(Milly et al. 2008; Mooij et al. 2009; Fang and Stefan 2012). Furthermore, the interactions among aquatic physical, chemical, and biological processes in lakes are nonlinear and dynamic, and far from equilibrium. Therefore, understanding and evaluating potential climate change impacts on lake ecosystems require unsteady and multidimensional descriptors of water quality and biological habitat conditions (Missaghi et al. 2013). Computer models have been the primary tool for analysing the impact of climate change on lake ecosystems (Menshutkin et al. 2014; Moe et al. 2016). Three-dimensional (3D) computer models have the feature of reproducing the ecological processes in lakes at fine temporal and spatial (horizontal and vertical) scales that can enhance understanding of the interactive feedbacks among processes. We employed a 3D lake water quality model to evaluate the influence of local meteorological and global climate conditions on the main environmental parameters that ultimately determine fish habitat.

Much has been contributed to the prediction of the impact of climate change on freshwater lakes in the past four decades. Climate change is expected to alter lake water temperature (T), increase summer stratification, alter dissolved oxygen (DO) dynamics and expand anoxic (DO depleted) zones, and change aquatic fish habitats (Stefan et al. 2001; Kling et al. 2003). Fish habitat conditions are predicted to change their temporal and spatial distributions (Stasio et al. 1996; Mooij et al. 2009; Foley et al. 2012) driven partly by the mixing regime altered by a changing thermal structure. Climate change is also expected to increase streamflow fluctuations leading to lake water level changes and shifting ecosystem states (Coops et al. 2003) and alter streamflow water temperatures which can drastically change fish habitats in streams (Lynch et al. 2016).

Both T and DO are considered the most significant water quality parameters that influence freshwater fish habitat (Stefan et al. 2001) where T governs both the growth and the survival of fish, and future T changes will alter aquatic ecosystems and fish habitat (Sharma et al. 2007). Consequently, we selected T and DO as the key water quality parameters to evaluate and test them to explore their impact on fish habitat under different climatic scenarios. We investigated the temporal and spatial (vertical and horizontal) variability of fish habitat dynamics by integrating a 3D lake water quality model with fish habitat criteria under the past and changing climate. One measured historical scenario, and two predicted future climate change scenarios are implemented. We report the findings and analyses of historical and predicted climate change scenario impacts on T, DO, and fish habitat conditions.

2 Materials and methods

2.1 Study site and field data

The computational domain of the study area was about 20% of Lake Minnetonka (60 km²; MN, US; 44° 54' N; 93° 41' W) including Halsted ($Z_{\max} = 10$ m), Cooks (8.5 m), Priest (8 m) and West Upper bays (24 m), and Six Mile and Langdon Lake creeks. Water samples were collected and analysed for a series of water quality parameters including T and DO. A more detailed description of the study area and a complete list of the observed meteorological data used in the study is described in the Online Resource 1.

2.2 Historical and future climate scenarios

Three different types of climate conditions of historical normal (HN), future normal (FN), and future extreme (FE) scenarios were selected for the study. Year 2000, with the similar values of

annual air temperature (T_a) and precipitation (P) averages to that of the 1981–2010 Climate Normals with annual average $T_a = 7.78$ °C and annual accumulated $P = 0.78$ myr⁻¹ (NOAA 2012), was designated as a surrogate for HN scenario. Year 2005, with the combined farthest values of annual averages of T_a (9.02 °C) and P (0.85 myr⁻¹) from the Climate Normals was designated as the historical extreme year. A set of monthly change fields (CF) (e.g. 2040–2069 output of the high-resolution Model for Interdisciplinary Research on Climate, MIROC3.2, minus 1961–1990 averages) for the grid point nearest (45° 42' N; 93° 38' W) to the study area was applied to develop the future climatic scenarios. The CFs were applied to the meteorological data of the HN scenario to generate the FN scenario and to the year 2005 to generate the FE scenario. A full description of the application of CFs and feasibility of the methods is provided in the Online Resource 2.

2.3 Model description

We employed the 3D lake hydrodynamic model ELCOM coupled to the ecological model CAEDYM. ELCOM uses hydrodynamic and thermodynamic models to simulate spatial and temporal variabilities of T and velocity distributions, and CAEDYM simulates biogeochemical and chemical water quality variables. Schematic representations of the model processes and descriptions of differential equations are provided by Hodges et al. (2000) for ELCOM and Romero and Imberger (2003) for CAEDYM. A detailed description of model evaluation and application of ELCOM-CAEDYM to the study area including model setup, configuration, parametrization, calibration, validation, performance, sensitivity, and model uncertainty analyses is provided by Missaghi and Hondzo (2010), and Missaghi et al. (2013) and additionally described in the Online Resource 3.

To simulate the FN scenario, the year 2000 in-lake water quality, initial conditions, and wind direction were all kept the same as in the HN scenario, except the metrological data were updated with the newly generated FN data and used the generated predicted stream inflows to the lake. The same procedure was then applied to create the FE scenario, using the year 2005 data as the base.

2.4 Fish habitat criteria

Suitable fish habitat is determined by a large number of environmental factors. However, T and DO are recognised as the two most significant water quality parameters that influence fish habitat (Cline et al. 2013). For this study, we adopted the mean coolwater fish thermal and DO criteria established by Stefan et al. (2001) which include fish species such as walleye and northern pike. The three types of coolwater fish habitats and their associated water temperature (T °C) and dissolved oxygen (DO mg L⁻¹) concentration criteria were designated as good growth (criteria = 16.3 °C < T < 28.2 °C) AND (DO > 3 mg L⁻¹), restricted growth (28.2 °C < T < 30.4 °C) OR (T < 16.3 °C AND DO > 3 mg L⁻¹), and lethal habitat (T > 30.4 °C) OR (DO < 3 mg L⁻¹). For comparison, the coldwater fish (such as brook trout, chinook salmon, and rainbow trout) and warmwater fish (such as bluegill, carp, channel catfish, largemouth bass) have lethal habitats with upper water temperature limits of 23.4 and 34.5 °C, respectively. The model was configured to generate the simulated T, DO, and other model output state variables in 27 depth layers at 1 m intervals. These outputs were then queried to evaluate each control volume (cell) for the three coolwater fish habitat types.

3 Results

3.1 Model simulations for the past and future climate scenarios

The model outputs from the West Upper Bay, the largest and deepest of the four bays in the study area, were used for the analysis of the three climate scenarios of HN (year 2000), FN (year 2000 + CFs) and the FE (year 2005 + CFs). The results of each scenario presented hydrologically and climatically distinct seasonal outputs. Both T and DO emerged uniform throughout the water column after spring turnover, followed by epilimnion (surface water) T changes that reflected the seasonal pattern of T_a (Fig. 1a). In the case of FN scenario, a warmer T_a in March and stronger winds (not shown) in April caused an increased in hypolimnion T that made it warmer than the other two scenarios throughout the simulation periods (Fig. 1b). In all scenarios, T decreased rapidly starting November 1, followed by a uniform T throughout the water column caused by fall turnover. Under all scenarios, the simulated DO concentrations were at their seasonal maximum concentrations immediately after spring turnover (Fig. 1). A warmer hypolimnion in the FN scenario kept the DO concentrations less than the concentrations in the HN scenario. The warmer FN hypolimnion promoted the onset of anoxia as early as on April 15 which was a full month earlier than HN and 2 weeks sooner than the FE scenarios. Nonetheless, hypolimnion was mostly anoxic in all three scenarios by June 15 before the DO concentrations were restored to their maximum levels by fall turnover. The seasonally (Apr.15–Nov.1) averaged DO profiles of the FN, and FE scenarios mimicked each other and were 1 mgL^{-1} less than that of the HN. The seasonally averaged T in the future scenarios were 4°C in the surface and 2°C in the thermocline warmer than in the HN scenario, but the FE scenario had the coldest hypolimnion T (Fig. 1). In fact, the FE scenario had both the coolest T minimum and highest T maximum (Fig. 1), indicating an increased water column stability due to warmer surface water which minimises mixing. Thermocline (maximum change of T of at least 1°C per 1 m) began to form by April 25, in both the HN and FN scenarios. The averaged April and May monthly thermocline depth for HN (7.2 m) was 14% deeper than that of FN (6.2 m) whereas the FE thermocline formed 3 weeks earlier than both HN and FN and was an average of 49% deeper during the same period of April and May (10.5 m) (Fig. 1 and additional information in the Online Resource #4).

3.2 Fish habitat evaluation

Every control volume (cell) of model outputs of the entire study area was queried for coolwater fish T and DO criteria for good growth, restricted growth, and lethal habitats under the HN, FN, and FE scenarios. The number of cells of each type of habitat was computed and normalised by the total volume of the lake and reported as the percentage of the lake volume. The annual averages of good growth, restricted growth, and lethal habitats for fish were 33.3, 60.0, and 6.7% for HN, 42.4, 47.0, and 10.6% for FN, and 34.8, 51.2, and 14.0% for FE.

A vertical fish habitat distribution of the entire study area was made by computing the cumulative volume of all depth layers along with the percent of each type of fish habitat within every depth layer and plotting them over depth for all scenarios (Fig. 2). Almost all of the cells with lethal habitat in the HN scenario were located below the 10 m depth. Fish habitat changes in the future scenarios from the HN scenario were calculated (Fig. 2, inset) for each depth layers. Under future normal scenario (FN), the volume of the restricted growth habitat decreased 13 percentage points, whereas the good growth and lethal habitat increased 9 and

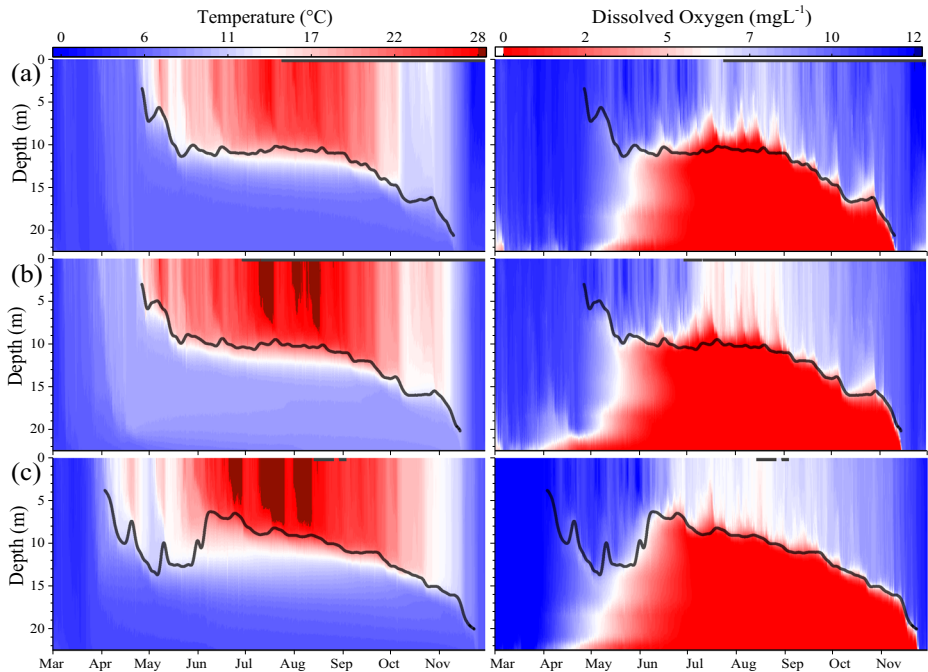


Fig. 1 Comparison of modelled water temperature ($^{\circ}\text{C}$) and dissolved oxygen (mgL^{-1}) in West Upper Bay under **a** historical normal, **b** future normal, and **c** future extreme climate scenarios. Horizontal and vertical axes of contour plots represent time and depth (m), respectively; with thermocline shown as dark lines. For full colour figures, please see the online manuscript

14 points, respectively. In the case of the future extreme (FE), good growth habitat changed little but restricted growth habitat decreased 8.8 percentage points, and lethal habitat expanded more than two times (increased from 6.7 to 14%) with 70% of those changes taking place in the top 5-m depth layers.

We next focused on the deepest depth of the study area, West Upper Bay, to investigate the fish habitat changes within the water column and throughout the simulation period. Contour plots of the three fish habitats simulated under the HN, FN, and FE scenarios (Fig. 3) clearly depicted the changes in fish habitat and correlated well with the findings of the whole lake volume analysis (Fig. 2). The period of restricted growth habitat from June 1 to the beginning of the simulation was shortened in both the FN and FE scenarios and replaced by an increase in good growth habitat which expanded earlier into the season by 2 and 3 weeks in the FE and FN, respectively. The lethal habitat started on May 12 in the HN, 2 weeks after (May 26) in the FE scenario, and in both cases quickly expanded from the bottom to 10 m depth by June 10. The lethal habitat started earliest in the FN scenario and was at 10 m depth 2 weeks earlier than both the FE and HN scenarios. Similar to the whole lake volume analysis (Fig. 2) and as depicted in the Fig. 4, the majority of changes took place in the upper 5 m of the water column.

We used the 3D feature of the model to investigate the spatial (horizontal) fish habitat heterogeneity in each of the three different climatic scenarios. We first depth-averaged the T and DO of the depth layers covering the entire study area in the top 5 m (depth with most fish

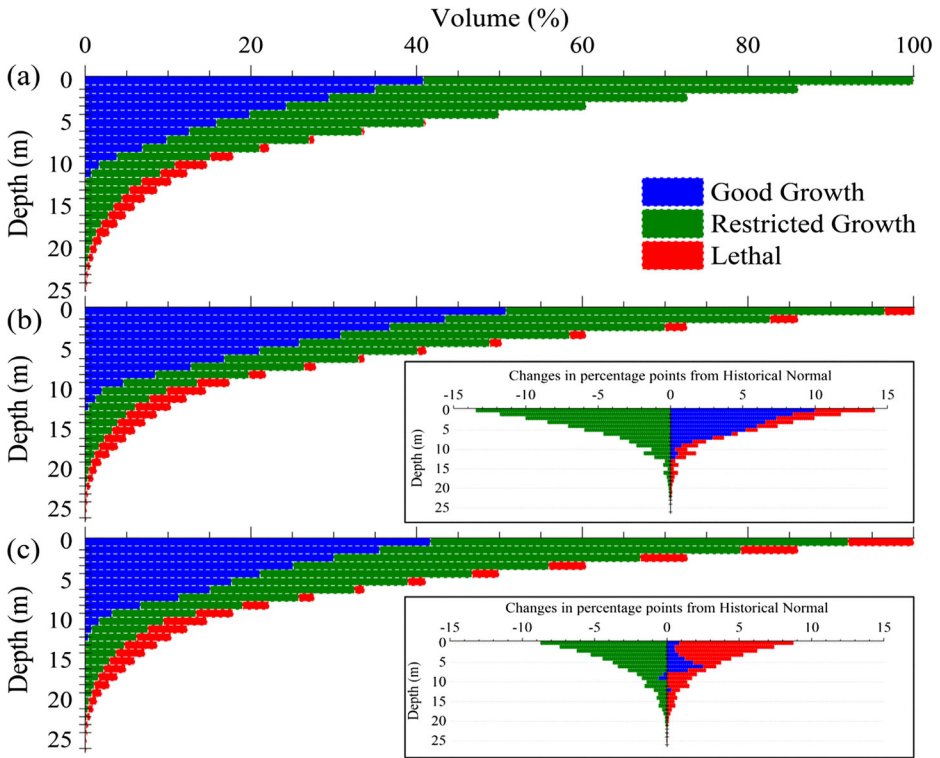


Fig. 2 Hypsographic curves, showing the percentage of total lake volume of the entire study area (*x*-axis) over depth (*y*-axis) for the averaged good growth, restricted growth, and lethal habitats for fish under simulated **a** historical normal, **b** future normal, and **c** future extreme climate scenarios, with the *insets* showing the changes in percentage points from the historical normal. For full colour figures, please see the online manuscript

habitat changes). The T and DO of each of the cells of this averaged thickness layer were then averaged weekly over the entire simulation period and finally evaluated accordingly for the three fish habitat types. The impact of undesirable habitat for fish depends on its severity and the duration that fish are exposed to it. Fish may find temporary refuge, an area free from disturbances, predation, or competition or survive the stress during the very short and sudden habitat changes. For our purposes, we used a 7-day long (weekly) averaged fish habitat criteria to evaluate the changes in fish habitat. A week long exposure to restricted growth or lethal habitat was deemed sufficient time to use as a metric for our evaluations and to show stress or harm to fish, as employed in studies in the USA (Fang and Stefan 2012) and the UK (Elliott and Bell 2011). The comparison of the surface areas for each of the selected five periods under the simulated HN, FN, and FE scenarios depicted the expansion of lethal habitat on July 7–14 and development of good growth habitat earlier in the season in both the FN and FE scenarios (Fig. 3). Under the HN scenario, the entire surface area (of the top 5 m) of the study area was evaluated as restricted growth habitat on June 2–7, where average T was less than 16 °C but then entirely changed to good growth habitat under the FN and FE scenarios. The lethal habitat expanded in the FE scenario from the month of July into earlier in the season (through June 23–30) and peaked later in the season (August 3) (Fig. 4).

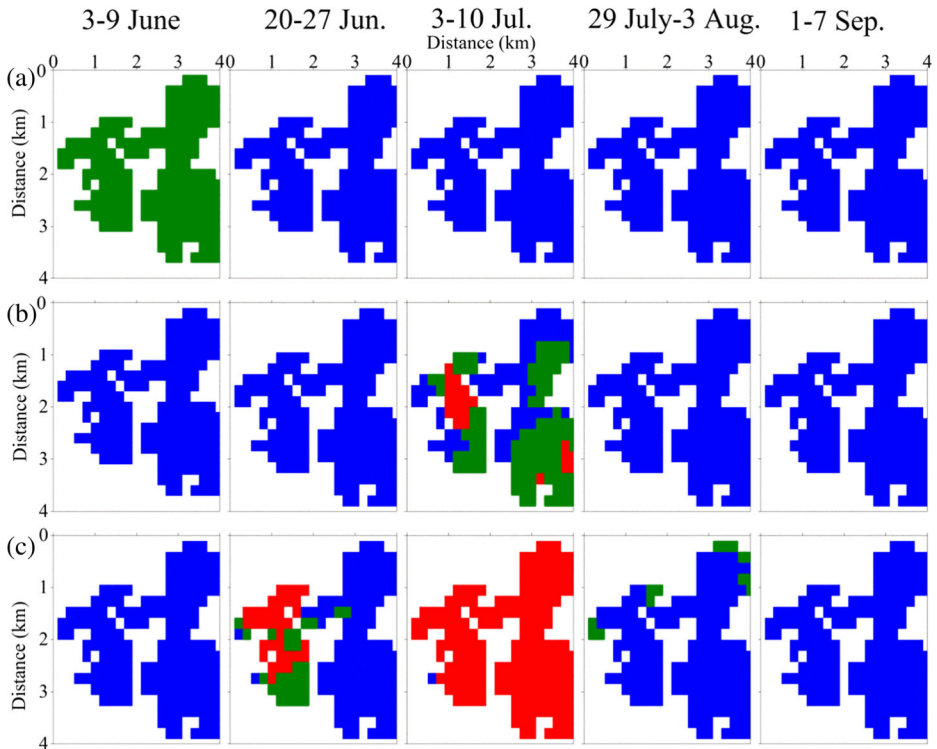


Fig. 3 Comparison of the entire study area with good growth habitat (*black/blue*), restricted growth habitat (*grey/green*), and lethal habitat (*light grey/red*) for coolwater fish habitats based on the predicted model variables averaged weekly for the top 5 m of water column under simulated **a** historical normal, **b** future normal, and **c** future extreme scenarios covering the entire study area with all *horizontal* and *vertical* axes as distance in kilometer. For full colour figures, please see the online manuscript

4 Discussion

4.1 Model simulations for the past and future climate scenarios

With the benefit of the spring turnover (uniform density and entire mixing of water column), at the beginning of simulation period, the simulated T were imposed throughout the water column by the meteorological conditions and therefore provided similar boundary conditions before the onset of stratification in the lake. The water column in the FN scenario began warming up the earliest in the season (March 20) followed by the FE scenario (April 1) with the HN scenario at last on April 15. At the end of the season, the stratification periods ended on November 7 for the HN scenario (199 days), lasted to November 12 for the FN scenario (206 days), and ended on Nov. 22 for the FE scenario with 46 days (23% increase) longer than the HN stratification period. In both future scenarios, the surface water T mimicked the predicted warmer air temperature, T_a , and followed the T_a seasonal changes whereas the hypolimnion T changes were less responsive to T_a . The warmer surface water T increases the water column stability which resists mixing and can create cooling of hypolimnion (Hondzo and Stefan 1993; Livingstone 2003; Butcher et al. 2015) as observed in the FE scenario which had the warmest surface water T and the coolest hypolimnion T . The combined

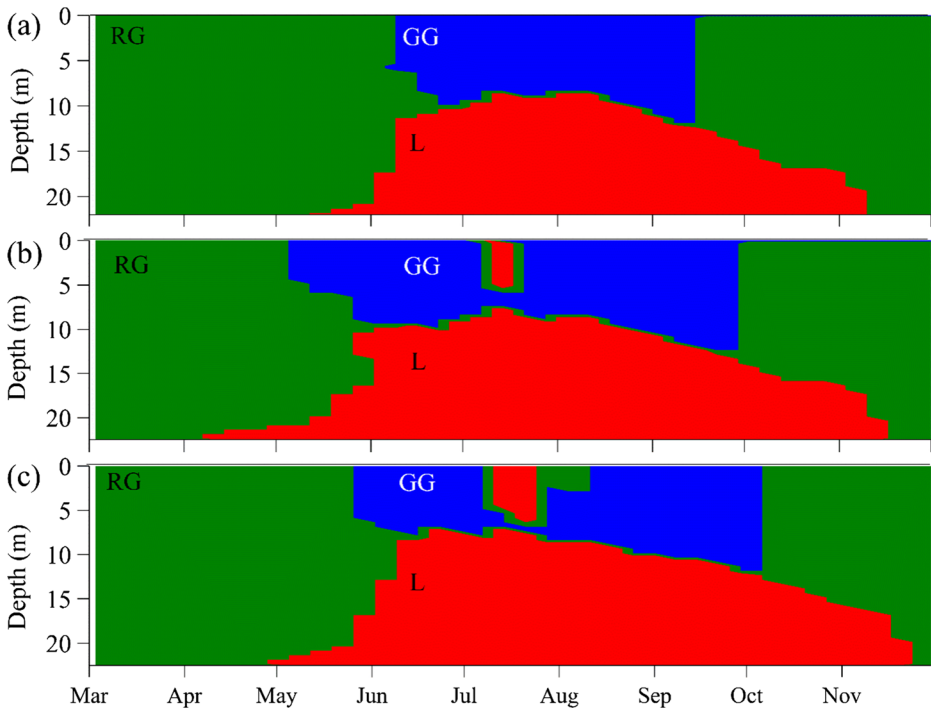


Fig. 4 Contour plots of good growth (*GG*), restricted growth (*RG*), and lethal (*L*) habitats for fish based on the predicted model variables averaged weekly under simulated **a** historical normal, **b** future normal, and **c** future extreme climate scenarios at the deepest point (West Upper Bay) of the study area. For full colour figures, please see the online manuscript

influence of higher wind speed (ave. $WS > 4.5 \text{ ms}^{-1}$) and rising T in the FE scenario early in the year forced the thermocline deeper than in HN and FN conditions (Fig. 1). The thermocline depth rapidly decreased after June where a warmer surface had stabilised the water column (less mixing) followed by persistent low wind conditions (ave. $WS < 4 \text{ ms}^{-1}$). Except with a few deviations, the DO depletion areas (anoxic zone) also closely followed the mixing boundaries delineated by thermocline (Fig. 1).

The surface water DO concentrations were episodic and mostly reflected the influence of wind speed. For example, a 48% increase in wind speed (3.5 ms^{-1} – 5.23 ms^{-1}) on June 24 caused a sudden deepening of DO rich epilimnion and a decrease in low DO concentrations in the hypolimnion (Fig. 1b). Furthermore, the wind induced mixing in combination with the stream inflow caused mixing of the anoxic bottom layers and therefore can produce low column-averaged DO concentrations which can have major consequences on fish habitats (Jeppesen et al. 2010). The thermal structure also plays a major role in the plankton community by shaping plankton species succession dynamics, algae biomass, fish habitat (Elliott and Bell 2011), and ultimately the aquatic food web (Wetzel 2001; Sastri et al. 2014). The predicted extended and stronger stratification has significant implications as it can influence the timing of fish spawning, reduce the exchange of nutrients between the stratum and interrupt the transfer of energy and food supply to fish, control DO concentration dynamics, and alter fish habitats.

4.2 Fish habitat evaluation

We used T values and DO concentrations to delineate and evaluate coolwater fish habitats as previously established by Stefan et al. 2001 and used by others (e.g. Fang et al. 2012) to analyse and report significant temporal and spatial shift and displacement of fish habitats under future climate change scenarios. Under the HN scenario, the fish habitat ratio of good growth:restricted growth:lethal changed from 5:9:1, to 4:4:1 in FN scenario, and to 2:4:1 in the FE scenario. Clearly, the lethal habitat grew to a larger fraction of the total available fish habitat under the FN and FE scenarios. Most of fish habitat shifts and changes (70%) were concentrated in the top 5 m of the water column (Fig. 2) with 5–15% of the fish habitats changing within each depth layer. Only 5 and 1% of fish habitats changed in each depth layer below 5 and 10 m depth, respectively.

The 3D feature of our model allowed us to analyse the spatial (horizontal) expansion of lethal habitat of coolwater fish habitats starting from the mid-season and the contracting of the good growth habitat from the edges (Fig. 3). Other studies have also shown that under a warming climate change scenario, a reduction of favourable lake fish habitat takes place in edges and nearshore habitat (Cline et al. 2013). Areas of the lake with depths shallower than the mixing depth (thermocline) were susceptible to an increase in T and a shift from good growth to restricted growth and lethal habitat (Fig. 2).

The combination of the lethal habitat increasing in one period and the good growth habitat for fish receding earlier in the year separated the good growth habitat period for over 3 weeks in July (Fig. 4). With good growth habitat for fish contracted and separated, the coolwater fish had no potential refuge during the 3 weeks of lethal habitat conditions in July (Fig. 4). Fish are living organism with an array of behavioural dynamics that may manifest many unknown attributes and establish their own ecological consequences and assemblages when faced with ecological stresses (Britton et al. 2010), such as developing foraging forays into anoxic zones (Roberts et al. 2012). However, a complete separation of good growth habitat with no refuge for coolwater fish (Fig. 4) will lead to summer fish kill.

In our analysis, we did not consider fish migration out of the study area and assumed that our study area was physically enclosed similar to an entire lake basin. In the case of an enclosed basin with the lack of a refuge during the good growth habitat separation, fish cannot physiologically change quickly enough to adapt to the shifting and changing of their habitats. If fish cannot adopt new territory by moving outside of their stressed basin, then they may become locally extinct, and their population may shift to other area lakes or towards higher latitude and altitudes (Jeppesen et al. 2010). The shift and changes of coolwater fish habitat will influence species competition and prey interactions (Al-Chokhachy et al. 2013; Cline et al. 2013), affecting the existing stress of competition or the stress of a newly introduced and better-suited species to the new habitat (Britton et al. 2010). Therefore, providing permanent or temporary refuge during good growth habitat separation becomes an important consideration for lake managers. Consequently, the ability to forecast the spatial and temporal locations of fish refuge during stressed or lethal habitat conditions becomes essential for conservation planning (Isaak et al. 2015).

5 Conclusion

We used a 3D coupled hydrodynamic, water quality, and ecological model to simulate one historical and two future climate change scenarios. The historical normal, future normal, and future extreme climate model scenarios provided boundary conditions to predict T and DO concentrations in the

lake. Each modelling scenario generated unique thermal structure and DO concentration pattern that ultimately defined fish habitats. The 3D modelling analysis revealed both the influence of the specific and combined changes of the meteorological forcing data on T and DO and their influences on the temporal, horizontal, and vertical coolwater fish habitat distribution.

Under the extreme future climate change scenario, the results suggest an increase in surface water temperature up to 4 °C and decrease in DO concentration by 1 mgL⁻¹ during the ice-free season. The onset of stratification increases up to 46 days, and thermocline depth increases as much as 64% in 1 week (April 27–May 4). The thermocline depth increases on average 32% from April to May. Under the future normal climate change scenario, the onset of anoxia occurs 4 weeks earlier. The findings are in general accordance with the reported T and DO changes in Minnesota lakes under the past and future climate change scenarios. For the first time, we report the 3D changes of T and DO that define the spatial and temporal habitats of fish in the lake. Under the extreme future and future normal climate scenarios, on average, the lake total volume of good growth, restricted growth, and lethal habitat for coolwater fish changed +16, -18, and +85%, respectively. The most significant changes of lethal fish habitat (70%) occurred in the upper 5 m of the water column. The good growth habitat was separated for 3 weeks due to the modest increase of lethal fish habitat (8% of lake total volume) in the summer. We demonstrate that temporal and 3D heterogeneities of T and DO are important drivers which describe the potential changes of fish habitats under changing climate. The ability to predict the fish habitat with fine spatial and temporal resolutions could facilitate innovatively and targeted fish management strategies which potentially can reduce the impact of climate change on fish habitat in lakes.

Acknowledgements The ELCOM-CAEDYM software was provided by Center for Water Research at the University of Western Australia. The Minnesota Supercomputer Institute provided the use of their computing services with Dr. Ravi Chityala providing invaluable technical assistance. The authors would like to thank the anonymous reviewers for their valuable comments and suggestions.

Compliance with ethical standards

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

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