A Small Temperate Lake in the 21st Century: Dynamics of Water Temperature, Ice Phenology, Dissolved Oxygen, and Chlorophyll \(a\)

Zeli Tan\(^{1,2}\), Huaxia Yao\(^3\), and Qianlai Zhuang\(^{2,4}\)

\(^1\)Pacific Northwest National Laboratory, Richland, WA, USA, \(^2\)Department of Earth, Atmospheric, and Planetary Sciences, Purdue University, West Lafayette, IN, USA, \(^3\)Dorset Environmental Science Centre, Ontario Ministry of Environment and Climate Change, Dorset, Ontario, Canada, \(^4\)Department of Agronomy, Purdue University, West Lafayette, IN, USA

Abstract It is unclear how small temperate lakes will evolve physically and biologically in the whole water column under future climate because previous modeling studies usually focused on only one or two physical or biological state variables in the surface waters. Here we used a well-validated lake biogeochemistry model driven by different climate scenarios of the 21st century to predict the dynamics of ice phenology, water temperature, dissolved oxygen (DO), and chlorophyll \(a\) in a small Canadian temperate lake (0.714 km\(^2\)) that is oligotrophic and strongly stratified in summer, considering the influence of catchment hydrology. The ice season and thickness of the lake are projected to shrink substantially under warming, resulting in a positive energy feedback between climate and the lake. Due to the reduced heat diffusion and water mixing, the dynamics of water temperature in surface and deep waters of the lake are considerably different, with surface waters warmed dramatically but deep waters muted to warming. DO depletion is predicted to occur in the whole water column of the lake under warming, but the controlling processes are depth dependent. Unexpectedly, the predicted growth of the lake’s chlorophyll \(a\) is small under warming, due to the weakened convection and the mismatch of the timings of favorable solar radiation, thermal, and nutrient conditions. For the examined state variables, our prediction shows that only the dynamics of DO is significantly impacted by the changing catchment hydrology. This study suggests that similar temperate lakes will have diverse physical and biological responses to climate change.

Plain Language Summary Understanding the influence of climate change on the physical and biological states of small temperate lakes is important given their landscape’s abundance on the Earth surface. Using a well-validated lake biogeochemistry model, the dynamics of ice thickness, water temperature, dissolved oxygen, and chlorophyll \(a\) during the 21st century was simulated for a small temperate lake that is nutrient poor and seasonally ice-covered and experiences strong temperature stratification in summer. The model predicts that the lake would change dramatically under intense warming, including the occurrence of ice-free years and severe depletion of dissolved oxygen in the surface and deep waters. The model also predicts that chlorophyll \(a\) in the lake, a negative factor for water quality, would not increase rapidly under climate warming. This study highlights the importance to study small temperate lakes using complex lake biogeochemistry models that can simulate diverse lake processes and their interactions.

1. Introduction

Small lakes are prominent across the landscape in the temperate zone of the Northern Hemisphere, especially in North America and Europe (Verpoorter et al., 2014; Yamazaki et al., 2015). They play important roles in water resource, freshwater biodiversity, local climate, and carbon cycling (Brown & Duguay, 2010; Buffam et al., 2011; Cardille et al., 2007; MacKay et al., 2009; Tranvik et al., 2009). Although the rapid warming of land surface in the recent decades is well documented (Hartmann et al., 2013), it is not yet clear how water temperature of small temperate lakes will change in the future (Adrian et al., 2009; Gerten & Adrian, 2001; O’Reilly et al., 2015). First, the warming of surface waters in lakes is highly variable and region specific (O’Reilly et al., 2015). It is possible that small temperate lakes would experience a much stronger or weaker warming in the future when compared with other lakes worldwide. Second, the warming of lake waters can also be depth and season dependent. Studies found that small deep lakes may mute to the climate change signal in deep waters (Winslow et al., 2015) and respond differently to warming in summer and winter (Winslow et al., 2017).
In addition to water temperature, climate change also influences other important physical and biological state variables of temperate lakes, such as ice phenology, dissolved oxygen (DO), and chlorophyll a (Couture et al., 2015; Fang & Stefan, 1996; Kraemer et al., 2017). These variables regulate important biogeochemical processes (e.g., carbon burial and degradation) in both water and sediment columns (Evans et al., 2017; Ferland et al., 2014; Istvánovics & Honti, 2018; Müller et al., 2012; Obertegger et al., 2017) and are indicators of water quality (Dillon et al., 2003; Jiang et al., 2012). For instance, important cold-water fish such as salmon and brown trout thrive in a habitat of combining high DO concentrations and low water temperature (Dillon et al., 2003; Jiang et al., 2012), typical for the hypolimnion of natural temperate oligotrophic lakes. Importantly, climate change influences temperate lakes through both air-water interactions and terrestrial-aquatic interactions (Buffam et al., 2011; Cardille et al., 2007; Cole et al., 2007; Einarsdottir et al., 2017). For the latter, the transport of water, carbon, and nutrients from catchments to lakes could change considerably under future climate in temperate regions, which would inevitably affect the water and biogeochemical cycles in small temperate lakes (Anderson et al., 2014; Catalán et al., 2016; Couture et al., 2015; Tanentzap et al., 2017).

To date, our understanding of the future dynamics of these state variables in small temperate lakes is still limited (Couture et al., 2015; Fang & Stefan, 2009; Obertegger et al., 2017; Oliver et al., 2017; Yao et al., 2014). First, although the processes that control the dynamics of water temperature, ice phenology, DO, and chlorophyll a are closely interacted (Couture et al., 2015; Giling et al., 2017; Obertegger et al., 2017), the modeling studies for small temperate lakes usually only focused on one or two of these variables (Vincent et al., 2008; Yao et al., 2014) and few modeling studies have predicted the chlorophyll a dynamics (Fang & Stefan, 2009; Joehnk & Umlauf, 2001; Yao et al., 2014). Second, the difference of DO dynamics in surface and deep waters was less explored and the impacts of catchments on the future changes of lakes were sometimes ignored (Fang & Stefan, 2009). Third, although climate models have large uncertainties (Taylor et al., 2012), few modeling studies have considered their influences on predicting the dynamics of northern lakes. Lastly, it is rare that a lake model has been evaluated using long-term physical and biogeochemical observations before being used for future predictions.

To better understand the dynamics of small temperate lakes in the 21st century, we applied the process-based Arctic Lake Biogeochemistry Model (ALBM; Tan et al., 2015, 2017) to a small temperate lake in Canada. The ALBM simulates the temporal variability of water temperature, ice phenology, DO, and chlorophyll a in both surface waters and deep waters simultaneously. The influence of the lake catchment on the water and biogeochemical cycles of the lake was also explicitly evaluated. The lake model was calibrated using the first 7-year observations of the examined state variables and validated using the following 28-year observations. By using the ALBM and two Coupled Model Intercomparison Projection Phase 5 (CMIP5) climate scenarios, we aim to answer the following questions: (1) Will the water temperature and ice phenology of small temperate lakes change dramatically in the 21st century? (2) How will the thermal changes in these lakes affect the dynamics of DO and chlorophyll a? (3) How will catchment hydrology influence the dynamics of these state variables? (4) What are the effects of changing climate in surface and deep waters of small temperate lakes?

2. Methods

2.1. Site Description

Harp Lake (45°22′45″N, 79°8′8″W) is an inland headwater oligotrophic lake in Ontario, Canada (Yao et al., 2009, 2014) with a surface area of 0.714 km², maximum depth of 37.5 m, and mean depth of 13.3 m. Harp Lake and its catchment (4.7 km²) drain into the Muskoka River that ultimately flows into Lake Huron. It is located in the northern area of the humid continental climate zone which has very cold winter and mild summer. Similar to many lakes formed by glacial activities in the temperate region, Harp Lake is small, oligotrophic, seasonally ice-covered, and strongly stratified in summer (Messager et al., 2016; Wetzel, 2001; Winslow et al., 2015). Small glacial lakes with deep water are also common in the Canadian Shield: Six of the eight lakes (including Harp Lake) that are intensively monitored by the Dorset Environmental Science Centre have such shapes. Harp Lake is a popular site for lake model testing because of its continuous and intense monitoring since the 1970s (Hadley et al., 2014; Molot & Dillon, 2008; Yao et al., 2014). Each of the lake’s six inlets as well as its outlet was measured for flow discharge and sampled weekly or biweekly for
water temperature and chemistry. The weather station is located to the west of the lake (500 m from lake-shore), providing local daily climate data of air temperature, humidity, wind, solar radiation, and precipitation. Ice phenology (ice-on and ice-off dates) was recorded since 1975, and the thicknesses of ice and snow covers were measured in low frequency, roughly once a month during the period of January to April, covering 16 years from 1978 to 1993 (Yao et al., 2013, 2014). Field ice measurements include black ice from lake water and white or slush ice from melted snow. Lake water temperature and DO concentrations were recorded monthly, from 1 June 1978 to 31 December 2013 at the 25 fixed depths with the 1-m depth interval from 0 to 13 m and the 2-m depth interval from 13 to 35 m. Monthly chlorophyll a concentrations were recorded from 1 January 1980 to 31 December 2013 in the euphotic zone which approximately extends from surface to two times of the measured Secchi depth. For the days when Secchi depth was not measured (there were also no measurements of chlorophyll a in these days), the long-term average value of 4.21 m was used. Daily discharge of inlet and outlet streams and the weekly concentrations of dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), and total phosphorus (TP) in streams were also recorded. The measurements described above can be found in Data Set S1 in the supporting information.

2.2. Model Description

To simulate the dynamics of ice phenology, water temperature, and two water quality variables (i.e., DO and chlorophyll a) in Harp Lake, we used the one-dimensional process-based climate-sensitive ALBM (Tan et al., 2015, 2017). This model recently participated in a new-phase lake model comparison of short-term thermal and biogeochemical simulations on Harp Lake (Guseva et al., 2017). Because Harp Lake is located in the Great Lakes Region where winter snowfall can be particularly heavy, we included a new gray ice layer in the ALBM that accounts for the conversion from snow to white or slush ice when the weight of ice and newly fallen snow exceeds the buoyancy of the ice cover (Rogers et al., 1995; Vavrus et al., 1996). Under the heavy snow, the ice below the surface water level in the model would be depressed, resulting in the production of gray ice from the submerged snow layer. This equilibrium depth of snow supported by the ice cover was calculated according to the Archimedes’ theorem (Rogers et al., 1995):

\[ h_{\text{sm}} = \frac{h_i (\rho_w - \rho_i) + h_e (\rho_w - \rho_e)}{\rho_i}, \]

where \( h_i \) and \( h_e \) are the thickness (m) of ice and gray ice layers, respectively, and \( \rho_w, \rho_i, \rho_s \) and \( \rho_e \) are the density of water, ice, snow, and gray ice (\( \rho_w = 1,000 \text{ kg m}^{-3}, \rho_i = 917 \text{ kg m}^{-3}, \) and \( \rho_e = 890 \text{ kg m}^{-3} \)), respectively. The melting of gray ice was calculated according to the energy balance of the absorbed solar radiation, the net longwave radiation, and heat conduction or convection, similar to the snow layer (Fang & Stefan, 1994).

The light extinction coefficient, heat conductivity, and surface albedo used for gray ice in the model can be found in Rogers et al. (1995).

In addition to photosynthesis, respiration, and surface reaeration, the DO in Harp Lake is also supplied by stream inflows, which are assumed to be in equilibrium with atmospheric O2 concentrations (Couture et al., 2015). The specific parameters of photochemical degradation used for temperate lakes in the model were estimated from the work of Vachon et al. (2016) in Canada. According to Tan et al. (2017), photomineralization is not expected to have a major role in regulating DO concentrations in Harp Lake due to the lake’s deep depth.

2.3. Simulation Protocols

For the projection period of 2015–2099, we used daily time series of climatic variables extracted from the CMIP5 Representative Concentration Pathways (RCP) 2.6 (low global warming) and RCP 8.5 (severe global warming) scenarios (Taylor et al., 2012). The sensitivity of the model simulations to climate drivers was tested by using an ensemble of simulations driven by seven different climate models in CMIP5 (i.e., CanESM2, CNRM-CM5, GFDL-CM3, HadGEM2-ES, IPSL-CM5A-MR, MIROC5, and MRI-CGCM3; https://esgf-node. lbl.gov/projects/esgf-lnl/). The delta-ratio bias correction method was applied to the CMIP5 data to preserve the consistency between the current and future boundary conditions (Tan & Zhuang, 2015a, 2015b). Specifically, after the correction, the monthly means of CMIP5 climatic variables during 2006–2014 were aligned with the observed monthly means at the same period. Under RCP2.6, the annual mean of surface air temperature, precipitation, and longwave radiation increase by 0.2–3.1°C, 91–314 mm, and 5.5–16.2 W m\(^{-2}\) during
Table 1
List of Parameters of the Arctic Lake Biogeochemistry Model for Sensitivity Analysis and Tuning

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Range</th>
<th>Final value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>k_{sed}</td>
<td>Thermal conductivity of sediment solid particles (W m⁻¹ K⁻¹)</td>
<td>[0.25, 2.9]</td>
<td>2.8</td>
<td>Tan et al. (2015)</td>
</tr>
<tr>
<td>c_{ps}</td>
<td>Heat capacity of sediment solid particles (J kg⁻¹ K⁻¹)</td>
<td>[750, 1930]</td>
<td>1770</td>
<td></td>
</tr>
<tr>
<td>ϕ</td>
<td>Sediment porosity (%)</td>
<td>[30, 60]</td>
<td>59</td>
<td></td>
</tr>
<tr>
<td>ρ_{sed}</td>
<td>Density of sediment solid particles (kg m⁻³)</td>
<td>[1500, 2700]</td>
<td>2240</td>
<td></td>
</tr>
<tr>
<td>OQ_{10}</td>
<td>Methane oxidation Q_{10} (unitless)</td>
<td>[1.4, 3.5]</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td>Q_{CH4}</td>
<td>Methane oxidation potential without substrate limitation (μmol m⁻³ s⁻¹)</td>
<td>[0.1, 100]</td>
<td>4.4</td>
<td></td>
</tr>
<tr>
<td>k_{MM,CH4}</td>
<td>CH₄ half-saturation of Michaelis-Menten kinetics (mmol m⁻³)</td>
<td>[1, 66.2]</td>
<td>18.6</td>
<td></td>
</tr>
<tr>
<td>k_{MM,CO₂}</td>
<td>O₂ half-saturation of Michaelis-Menten kinetics (mmol m⁻³)</td>
<td>[1, 200]</td>
<td>109</td>
<td></td>
</tr>
<tr>
<td>PQ_{10}</td>
<td>Methanogenesis Q_{10} for the ¹⁴C-enriched carbon pool (unitless)</td>
<td>[1.7, 16]</td>
<td>3.9</td>
<td></td>
</tr>
<tr>
<td>R_c</td>
<td>The fraction of the ¹⁴C-enriched carbon pool converted per year (yr⁻¹)</td>
<td>[0.002, 0.02]</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>α_H</td>
<td>The downward damping rate of the ¹⁴C-enriched carbon pool (m⁻¹)</td>
<td>[1.0, 10.0]</td>
<td>3.5</td>
<td></td>
</tr>
<tr>
<td>c_v</td>
<td>The velocity of bubble formation in lake sediments (d⁻¹)</td>
<td>[29.5, 407]</td>
<td>77.3</td>
<td></td>
</tr>
<tr>
<td>V_{m}</td>
<td>Maximum chlorophyll-specific photosynthetic rate (mg C [mg Chl]⁻¹ d⁻¹)</td>
<td>[18.36, 73.44]</td>
<td>73.2</td>
<td></td>
</tr>
<tr>
<td>V_{m}</td>
<td>Maximum chlorophyll-specific photosynthetic rate (mg C [mg Chl]⁻¹ d⁻¹)</td>
<td>[18.36, 73.44]</td>
<td>73.2</td>
<td></td>
</tr>
<tr>
<td>α_s</td>
<td>Initial slope of photosynthesis-irradiance curve of small algae (μmol photons)⁻¹ m² s⁻¹</td>
<td>[0.0015, 0.056]</td>
<td>0.0015</td>
<td>Makler-Pick et al. (2011)</td>
</tr>
<tr>
<td>α_l</td>
<td>Initial slope of photosynthesis-irradiance curve of large algae (μmol photons)⁻¹ m² s⁻¹</td>
<td>[0.002, 0.036]</td>
<td>0.036</td>
<td></td>
</tr>
<tr>
<td>β_s</td>
<td>Photo inhibition factor of small algae (μmol photons)⁻¹ m² s⁻¹</td>
<td>[0.0002, 0.002]</td>
<td>0.0017</td>
<td></td>
</tr>
<tr>
<td>β_l</td>
<td>Photo inhibition factor of large algae (μmol photons)⁻¹ m² s⁻¹</td>
<td>[0.0002, 0.002]</td>
<td>0.0004</td>
<td></td>
</tr>
<tr>
<td>k_{SRP, s}</td>
<td>Half-saturation for phosphorus uptake by small algae (mg P m⁻³)</td>
<td>[1, 150]</td>
<td>4.9</td>
<td></td>
</tr>
<tr>
<td>k_{SRP, l}</td>
<td>Half-saturation for phosphorus uptake by large algae (mg P m⁻³)</td>
<td>[1, 10]</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>ρ_s</td>
<td>Snow density (kg m⁻³)</td>
<td>[100, 300]</td>
<td>202</td>
<td>Rogers et al. (1995)</td>
</tr>
</tbody>
</table>

*Tuning parameters for the study of harp Lake are marked by an asterisk. The final values of other nontuning parameters are from Tan et al. (2017) for Toolik Lake.*

2015–2099, respectively (Table S1 in the supporting information). There are either no clear trends or very weak trends in wind speed, relative humidity, and solar radiation in this scenario (Table S1 and Figures S1–S5 in the supporting information). Under RCP8.5, the annual mean of surface air temperature and longwave radiation increase by 4.3–7.2°C and 28.4–44.4 W m⁻² during 2015–2099, respectively (Table S1). Precipitation increases in all the models (154–375 mm) but IPSL-CM5A-MR (Table S1). Similarly, there are either no clear trends or very weak trends in wind speed, relative humidity, and solar radiation under RCP8.5 (Table S1 and Figures S1–S3). Stream flows of the inlets and outlet of Harp Lake during 1978–2099 were simulated by the BROOK90 hydrological model (Figure S4), which has been widely used in North America (Federer et al., 2003; http://www.ecoshift.net/%E2%80%8Cbrook/%E2%80%8Cbrook90.htm). Minor parameter adjustments of the BROOK90 model were made for its application to the Harp Lake catchment, resulting in a Nash-Sutcliffe efficiency of 0.72 for monthly runoffs in the calibration period of 1978–2009 (Yao et al., 2014), as shown in Figure S5. For the loadings of carbon and nutrients during 2015–2099, we used the fitted concentration-discharge curves for DIC (mg L⁻¹), DOC (mg L⁻¹), and TP (μg L⁻¹) based on the measurements during 2010–2014 (Figure S6): DIC = 12.82 Q⁻⁰.¹⁷, DOC = 39.98 Q⁻₀.¹⁸, and TP = 199.83 Q⁻₀.₃⁴, where Q is discharge (m³ d⁻¹). Because the 1-D ALBM does not track the origins of either streamflows or the loadings of carbon and nutrients among different inlets (Tan et al., 2017), only the daily total amounts of these inputs from all of the six inlets were used.

We performed the sensitivity analysis of the ALBM parameters using the approach described in Tan et al. (2017). First, we conducted a screening test over all of the parameters listed in Table 1 to identify the most influential parameters. The screening test is based on the Morris elementary effects method for global sensitivity analysis that perturbs only one input parameter in each model run (Morris, 1991). Then, we did a quantitative, explicit evaluation of the relative importance and interactions among the influential parameters.

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using the variance-based Sobol’s sensitivity index analysis (Saltelli et al., 2010). The influential parameters identified by the screening test were calibrated against the observations of the examined state variables (ice-on and ice-off dates, ice and snow thickness, water temperature and DO at different depths, and chlorophyll $a$) during 1979–1985 using a Monte Carlo-based Bayesian recursive parameter estimation method (Tan & Zhuang, 2015a; Thiemann et al., 2001). The calibrated model was then evaluated against the observations during 1986–2013 using the root mean square error (RMSE) and the normalized RMSE (the RMSE divided by the range of observations) metrics. The RMSEs of different state variables have the same weights in the model calibration. To estimate the dynamics of Harp Lake in the 21st century, we ran an ensemble of projections that include 14 separate simulations, which are for two climate scenarios and seven climate models. For each projection, we ran the model from 1978 to 2099 with the period of 1978–2014 driven by the measured climate and the period of 2015–2099 driven by the CMIP5 future climate. For reference projections, we assume that the discharge and carbon and nutrient loads from the Harp Lake catchment have no interannual variations during 2015–2099 and are equal to the measured mean values during 2006–2013. To evaluate the influence of catchment hydrology, we ran another ensemble of 12 projections with the future discharge simulated by the BROOK90 model under the CMIP5 climate scenarios (Figure S4). The future discharge projection for GFDL-CM3 has not been included because the climate model does not output some variables that the BROOK90 model needs.

The dynamics of Harp Lake in the 21st century were evaluated for the following variables: (1) annual peak thickness of ice and snow cover, (2) day of year of ice-on and ice-off dates, (3) mean water temperature in the five depth zones (0–2 m, 2–5 m, 5–10 m, 10–15 m, and 15–35 m) during 15 May to 15 November (hereafter “the M2N period”), (4) mean DO concentrations during the M2N period in the five depth zones as same as water temperature, and (5) the mean chlorophyll $a$ concentration in the euphotic zone during the M2N period. To better understand the causes for the dynamics of the above state variables, we also calculated the mean mixing layer thickness ($H_{mix}$) during the M2N period, the mean total heat diffusivity during the M2N period in the five depth zones as same as water temperature, and two energy fluxes ($Q_{sw}$ and $Q_{air}$) important for the lake’s energy balance. $Q_{sw}$ is the annual mean flux of solar radiation absorbed by Harp Lake, and $Q_{air}$ is the annual mean net upward energy flux from the lake to the air, including net thermal radiation, sensible heat, and latent heat. To evaluate the impact of catchment hydrology on Harp Lake, we also calculated the mean vertical profiles of water temperature, DO concentrations, and total heat diffusivity in the late 21st century, which are defined as the temporal average of these variables for the all M2N periods during 2095–2099.

3. Results

Based on the screening sensitivity test (Figure 1), we selected 12 parameters ($p_r$, $R_c$, $a_{sh}$, $R_{gw}$, $V^0_m$, $V_b$, $V_f$, $DOC_{gw}$, $\alpha_0$, $a_b$, $\beta_b$, and $k_{SRP}$, ) from Table 1 that significantly affect the simulation of the examined state variables in Harp Lake. For these key parameters, their relative importance and interactions are shown in the Sobol sensitivity index analysis (Figure 2). The screening test indicated that for the oligotrophic Harp Lake, the simulation of water temperature in both surface and deep waters is not sensitive to the model parameters listed in Table 1 that relate the light attenuation coefficient to the levels of chromophoric dissolved organic matter and chlorophyll $a$ (Tan et al., 2017). The simulation of the ice-on and ice-off dates is the most sensitive to snow density $p_s$ (Figures 1 and 2) which affects the dynamics of the heat-insulation snow cover. Although the simulation of water temperature is very robust in the sensitivity tests, its minor changes caused by the perturbation of the chromophoric dissolved organic matter level ($DOC_{gw}$) can significantly affect the simulation of the ice-on date (Figure 2). As indicated by the tests, the simulation of DO in the lake is sensitive to $DOC_{gw}$ and $V^0_m$ that are related to heterotrophic respiration. Unsurprisingly, the dynamics of the chlorophyll $a$ in the euphotic zone is sensitive to the parameters that are related to photosynthesis ($V^0_m$, $\alpha_0$, and $k_{SRP}$, ), autotrophic respiration ($V_b$), and nutrients ($V_f$ and $DOC_{gw}$).

The ALBM can reproduce the seasonal variability of ice and snow covers during 1978–1993 and the interannual variability of ice-on and ice-off dates during 1979–2013 in Harp Lake (Figures S7 and S8). The model can also reproduce the seasonal and interannual variabilities of water temperature and DO concentrations at different depth zones during 1978–2013 (Figures S9 and S10). For chlorophyll $a$ in the euphotic zone, the model can well simulate the seasonal variability of the mean concentration during 1980–2013 (Figure S11). Further,
the decline of the chlorophyll $a$ concentration after 1991 is clearly reproduced (Figure S11). RMSEs and normalized RMSEs (in brackets) of these simulated variables during the validation period are listed in Table 2. Relatively, the model has better performance in simulating water temperature and DO in surface waters than in deep waters. It is consistent with the claim that 1-D lake models may not well represent near-bottom turbulence caused by seiching and wind-driven currents (Wüest et al., 2000). Similar to other lake models (Saloranta & Andersen, 2007; Yao et al., 2014), the simulated ice and snow thickness and chlorophyll $a$ concentrations in the ALBM are less accurate.

Figure 1. Screening sensitivity tests ($u^*$ is the ratio of model output variance to parameter variance) of model parameters (Table 1) for the simulated ice-on and ice-off dates, mean temperature of surface (0–5 m) and bottom (10–35 m) waters, mean DO of surface (0–5 m) and bottom (10–35 m) waters, and mean chlorophyll $a$ concentration in the euphotic zone.
The ALBM predicts that Harp Lake is to experience diverse changes in the 21st century under the severe warming RCP8.5 scenario (Figures 3–6 and Table 3). For ice phenology, the peak thickness of ice and snow covers are projected to decrease dramatically during 2015–2099 under RCP8.5 (Figure 3), with the reduction of 40 ± 8 cm and 14 ± 2 cm, respectively (Table 3). Under RCP8.5, the length of ice season in Harp Lake is projected to shrink considerably during 2015–2099 (Figure 3), with the ice-on date delayed by 44 ± 17 days and the ice-off date advanced by 44 ± 16 days, respectively (Table 3). For both ice and snow covers, the largest changes occur in the HadGEM2-ES simulation which is driven by higher climate warming (Table S1). Under the RCP8.5 scenarios of HadGEM2-ES and CanESM2, Harp Lake is predicted to even experience totally ice-free years in the late 21st century (Figure 3). For water temperature, surface waters are projected to undergo much more intense warming than deep waters under RCP8.5 (Figure 4). The increase of water temperature at the surface zone (0–5 m) is 5.2 ± 1.1°C during 2015–2099 (Table 3). In contrast, the increase of water temperature at the bottom zone (15–35 m) is negligible (0.1 ± 0.1°C) during the same period (Table 3). Under RCP8.5, the GFDL-CM3 simulation predicts the largest warming (6.9°C) in surface waters but the smallest
During 1986–2015, the GFDL-CM3 RCP8.5 and the CNRM-CM5 RCP8.5 predict the largest and smallest warming in surface waters, respectively. The trends of ice phenology, water temperature, and DO concentrations are reversed in the 2060s or 2070s (Figures 3–5). Under both scenarios, the DO concentrations in deepwater layers (10–35 m) are more noticeable under RCP2.6 than that under RCP8.5 (Figure 6), which corresponds to higher wind speed in the late 21st century (Table S1). For DO, although the concentrations are predicted to decrease in both surface and deep waters under RCP8.5 (Figure 5), the relative decrease rate is much larger in deep waters (Table 3). The relative decrease rates of DO at the five depth zones from surface to bottom are 9.7 ± 2.2%, 15.1 ± 2.2%, 28.8 ± 3.8%, 36.7 ± 5%, and 41.2 ± 11.8%, respectively, during 2015–2099. As described above, the RCP8.5 simulations of GFDL-CM3 and CNRM-CM5 predict the largest and smallest warming in surface waters, respectively. The results show that they also predict the largest and smallest decrease of DO in surface waters during 2015–2099, with the decrease of 1.2 mg L⁻¹ in the GFDL-CM3 simulation and of 0.7 mg L⁻¹ in the CNRM-CM5 simulation. In deep waters, the largest DO decrease (2.0 mg L⁻¹) is driven by the IPSL-CM5A-MR RCP8.5 and the smallest DO decrease (0.9 mg L⁻¹) is driven by the CanESM2 RCP8.5. For chlorophyll a, the concentration in the euphotic zone increases slightly (Figure 6) by 0.3 ± 0.2 μg L⁻¹ during 2015–2099 under RCP8.5 (Table 3). And the predicted increase of the chlorophyll a concentration is even close to zero under the IPSL-CM5A-MR RCP8.5, which has low wind speed in the late 21st century (Table S1).

The lake dynamics under the weak warming RCP2.6 are much different from the described under RCP8.5 (Figures 3–6 and Table 3). As warming peaks in the middle of the century under RCP2.6 (Figure S1), the trends of ice phenology, water temperature, and DO concentrations are reversed in the 2060s or 2070s (Figures 3–5). For example, 6 years after the ensemble-mean air temperature passes its peak in 2067 (Figure S1), the ensemble-mean air temperature at the top three depth zones starts to decline (Figure 4). As a result, the changes of these state variables are less substantial in the late 21st century (Table 3). Under RCP2.6, the peak thickness of ice and snow covers are projected to decrease only by 9 ± 7 and 4 ± 3 cm, respectively, during 2015–2099 (Table 3). And during 2015–2099, the ice-on date will only be delayed by 8 ± 3 days and the ice-off date will move forward by 20 ± 7 days (Table 3). Under RCP2.6, water temperature in surface waters increased by less than 2°C (Table 3), much smaller than the increase under RCP8.5. However, the negligible increase of water temperature in deep waters is projected by both scenarios (Figure 4). In the water column, the DO concentrations in the late 21st century are higher than the DO minima simulated in the 2070s under RCP2.6 (Figure 5). But the recovery is much faster in surface waters than in deep waters (Figure 5 and Table 3). For chlorophyll a, the increase of its concentration (0.6 ± 0.2 μg L⁻¹) in the euphotic zone during 2015–2099 is more noticeable under RCP2.6 than that under RCP8.5 (Figure 6), which corresponds to higher wind speed in the late 21st century under RCP2.6 (Figure 3 and Table S1).

The energy exchange between Harp Lake and the atmosphere is projected to increase in the 21st century under climate warming (Figure S12). The solar radiation absorbed by Harp Lake, $Q_{sw}$, is projected to increase by 10.6 ± 2.4 W m⁻² under RCP8.5 and by 4.6 ± 3.1 W m⁻² under RCP2.6 during 2015–2099 (Table S2). The larger increase of $Q_{sw}$ under RCP8.5 corresponds to the faster shrinking of the ice-cover season (Figure 3). Under climate warming, Harp Lake is projected to transport more energy to the air (Figure S12) and become more stable (Figures S12 and S13). Under RCP8.5, $Q_{sw}$, $H_{mix}$, and the total heat diffusivity at 5–10 m (thermocline) are projected to increase by 6.8 ± 3.1 W m⁻², 0.7 ± 0.2 m, and (1.2 ± 1.2) × 10⁻⁶ m s⁻², respectively, during 2015–2099 (Table S2). Under RCP2.6, Harp Lake is projected to become less stable in the late 21st century, with an increase of the total heat diffusivity at 5–10 m (thermocline; Table S2).

Our simulations show that the change of catchment hydrology has significant effects on the dynamics of DO (Figure 7) but negligible effects on the dynamics of water temperature, ice phenology, and chlorophyll a (Figures S14–S19). Under both scenarios, the DO concentrations in deepwater layers (10–35 m) are
projected to become severely depleted in the late 21st century. For the water layer of 10–15 m, the lake model predicts that the DO concentration can be as low as 3.0 ± 0.6 mg L\(^{-1}\) under RCP8.5 and 4.5 ± 0.7 mg L\(^{-1}\) under RCP2.6, respectively, during 2095–2099. For the water layer of 15–35 m, the model predicts that the DO concentration can be as low as 1.5 ± 0.3 mg L\(^{-1}\) under RCP8.5 and 2.1 ± 0.6 mg L\(^{-1}\) under RCP2.6, respectively, during 2095–2099. But the change of water diffusivity and convective mixing is unlikely the cause for the negative effect of catchment hydrology on the DO concentrations because the dynamics of energy fluxes, heat diffusivity, and convective mixing change little in the simulations (Figures S20–S23).

Figure 3. Time series of the simulated ice-on and ice-off day of year (DOY) and the simulated annual peak snow and ice thickness at Harp Lake during 1979–2014 under the measured climate (black) and during 2015–2099 under the RCP2.6 and RCP8.5 climate scenarios (blue). The blue lines are the mean values, the dark shaded areas are the standard deviations, and the light shaded areas are all runs. For ice-on DOY under RCP8.5, the gaps represent ice-free years (presented in the plot) simulated by HadGEM2-ES and CanESM2.
4. Discussion

4.1. Impacts of Climate Change on Heat Budget

As identified by previous studies (Fang & Stefan, 1996; Fang & Stefan, 2009; O’Reilly et al., 2015; Vavrus et al., 1996; Yao et al., 2014), the ice phenology and surface water temperature of small temperate lakes are

![Figure 4](image-url)
sensitive to climate change. If severe climate warming continues in this century, it is possible that snow and ice covers of many small temperate lakes in warmer or similar climate conditions to that of Harp Lake will totally disappear. The simulated reduction (88 ± 33 days) of the ice season at Harp Lake under RCP8.5 is much larger than that (on average of 48 days) of Yao et al. (2014) which involved four lake models but only under a

**Figure 5.** Time series of the simulated mean dissolved oxygen in the five depth zones of Harp Lake during 1979–2014 under the measured climate (black) and during 2015–2099 under the RCP2.6 and RCP8.5 climate scenarios (blue). (left column) RCP2.6 simulations and (right column) RCP8.5 simulations. The blue lines are the mean values, the dark shaded areas are the standard deviations, and the light shaded areas are all runs.
single climate scenario (with air temperature increasing by 4.85°C over the century, weaker than the RCP8.5 used in our simulations). But the simulation is close to the predicted reduction (more than 70 days) of Fang and Stefan (2009) which involved the MINLAKE96 model and a 2 × CO2 climate scenario. This difference implies that for the projection of ice phenology the uncertainty caused by climate scenarios and models could be much larger than that caused by lake models (the predicted changes in ice season were 43, 40, and 30 days for Minlake, Hostetler, and GLM lake models, respectively, in Yao et al., 2014 trials). Thus, it is important to study the dynamics of temperate lakes using an ensemble of climate models. Some previous studies suggested that in temperate lakes the ice-off date would show a stronger sensitivity to climate warming than the ice-on date (Vavrus et al., 1996). This sensitivity difference is not supported by our simulations. Possibly, this sensitivity difference only occurs in much shallower temperate lakes, such as the three Wisconsin lakes of Vavrus et al. (1996), under some specific climate scenarios (Vavrus et al., 1996). Our study indicates that there will be a positive energy feedback between climate and seasonally ice-covered temperate lakes under intense warming. In the future, climate warming may reduce the ice season of the seasonally ice-covered lakes and cause them to absorb more solar radiation in the early spring and early winter. In the end, a large fraction of the absorbed radiation is returned to the air in the

![Figure 6](https://example.com/figure6.png)

**Figure 6.** Time series of the simulated mean chlorophyll a in the euphotic zone of Harp Lake during 1979–2014 under the measured climate (black) and during 2015–2099 under the RCP2.6 and RCP8.5 climate scenarios (blue). The blue lines are the mean values, the dark shaded areas are the standard deviations, and the light shaded areas are all runs.

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### Table 3

Summary of the Simulated Mean Ice Phenology, Water Temperature, Dissolved Oxygen (DO), and Chlorophyll a During 2010–2014 Under the Measured Climate and During 2095–2099 Under the RCP2.6 and RCP8.5 Scenarios (std: Standard Deviation)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Units</th>
<th>2010–2014</th>
<th>2095–2099 (RCP2.6)</th>
<th>2095–2099 (RCP8.5)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean ± std</td>
<td>Max</td>
<td>Min</td>
</tr>
<tr>
<td>Peak ice thickness</td>
<td>cm</td>
<td>59</td>
<td>50 ± 7</td>
<td>58</td>
</tr>
<tr>
<td>Peak snow thickness</td>
<td>cm</td>
<td>22</td>
<td>18 ± 3</td>
<td>22</td>
</tr>
<tr>
<td>Ice-on day of year (DOY)</td>
<td>day</td>
<td>344</td>
<td>352 ± 3</td>
<td>357</td>
</tr>
<tr>
<td>Ice-off DOY</td>
<td>day</td>
<td>112</td>
<td>102 ± 7</td>
<td>110</td>
</tr>
<tr>
<td>Temperature</td>
<td>°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–2 m</td>
<td></td>
<td>18.1</td>
<td>19.7 ± 0.5</td>
<td>20.4</td>
</tr>
<tr>
<td>2–5 m</td>
<td></td>
<td>16.3</td>
<td>17.8 ± 0.5</td>
<td>18.6</td>
</tr>
<tr>
<td>5–10 m</td>
<td></td>
<td>8.6</td>
<td>9.5 ± 0.8</td>
<td>10.4</td>
</tr>
<tr>
<td>10–15 m</td>
<td></td>
<td>4.9</td>
<td>5.4 ± 0.4</td>
<td>6.0</td>
</tr>
<tr>
<td>15–35 m</td>
<td>°C</td>
<td>4.1</td>
<td>4.2 ± 0.2</td>
<td>4.5</td>
</tr>
<tr>
<td>DO</td>
<td>mg L⁻¹</td>
<td>9.3</td>
<td>9.0 ± 0.1</td>
<td>9.2</td>
</tr>
<tr>
<td>0–2 m</td>
<td></td>
<td>9.3</td>
<td>8.9 ± 0.1</td>
<td>9.1</td>
</tr>
<tr>
<td>2–5 m</td>
<td></td>
<td>8.0</td>
<td>7.3 ± 0.3</td>
<td>7.8</td>
</tr>
<tr>
<td>5–10 m</td>
<td></td>
<td>6.0</td>
<td>5.2 ± 0.6</td>
<td>6.1</td>
</tr>
<tr>
<td>10–15 m</td>
<td></td>
<td>3.4</td>
<td>2.6 ± 0.6</td>
<td>3.7</td>
</tr>
<tr>
<td>Chlorophyll a</td>
<td>μg L⁻¹</td>
<td>1.9</td>
<td>2.5 ± 0.2</td>
<td>3.0</td>
</tr>
</tbody>
</table>
form of thermal radiation, sensible heat, and latent heat. Under warming conditions, the summertime surface water temperature of small temperate lakes could increase substantially in the 21st century, which is consistent with the prediction of Fang and Stefan (2009) and the observations of O’Reilly et al. (2015).

Our results also suggest that, for small temperate lakes with deep water, the bottom proportion of lake water could be almost muted to climate warming. This result is consistent with some observations on small lakes (Winslow et al., 2015) but not widely emphasized by previous numerical projections (Fang & Stefan, 2009). As the warming of surface waters is prominent and there is negligible solar radiation in deep waters, this stability of deepwater temperature is likely caused by the weakened heat exchange between surface and deep waters. As shown in Figures S12 and S13, climate warming dampens water mixing in summer and reduces total heat diffusivity in the thermocline. The relative stability of deep waters suggests that if only temperature is considered, those cold water fishes can survive under climate warming by migrating downward. Another finding of this study is that in regard to water temperature, many small temperate lakes can respond very quickly to the reverse of the warming trend (RCP2.6), as shown for the deep Harp Lake (Figure 4).

### 4.2. Impacts of Climate Change on Water Quality and Carbon Budget

Our simulations suggest that the dynamics of ice phenology and water temperature under climate warming are not perfect indicators of the dynamics of water quality in temperate lakes of similar sizes. First, unlike water temperature, DO in deep waters is sensitive to climate change (Figure 5). In fact, as presented in section 3, summer DO can decrease at a much larger degree in deep waters than in surface waters.
because of the weaker vertical exchange of lake water in warming climate. Second, climate warming may only drive minor changes of chlorophyll $a$ in the euphotic zone (Figure 6). Third, in deep waters the recovery of DO would be much slower than the recovery of water temperature if climate warming were reversed, such as under RCP2.6 (Figures 4 and 5).

There are mainly four processes controlling the long-term variability of DO concentrations in oligotrophic lakes (Fang & Stefan, 2009; Stefan & Fang, 1994): net primary production, heterotrophic respiration, surface reaeration, and gaseous oxygen dissolution. In surface waters of Harp Lake, because gas diffusivity, water mixing, and net primary production are predicted to change mildly (Figures 6, S12, and S13), the simulated increase of DO deficit is mainly caused by the increase of heterotrophic respiration (mainly through aerobic organic carbon degradation) and the decrease of oxygen solubility, both of which are driven by water warming (Fang & Stefan, 2009; Stefan & Fang, 1994). In deep waters of Harp Lake, because water temperature is predicted to be stable and net primary production is negligible (Figures 4 and 6), the simulated increase of DO depletion is mainly caused by the decline of water diffusivity and mixing and the earlier occurrence of water overturning. The slow recovery of deepwater DO in Harp Lake under RCP2.6 can be explained by the weak mass exchange between surface and deep waters in this deep stratified lake, as well as the increase of heterotrophic respiration due to thermocline deepening (Giling et al., 2017). Importantly, under climate warming, the processes described above are expected to drive the similar dynamics of DO in other oligotrophic temperate lakes with strong summer stratification because rapid surface water warming, increased ecosystem respiration, and weakened water convection may also occur there (Fang & Stefan, 2009; Yankova et al., 2017; Zwart et al., 2016). To restore the ecological functions of deep stratified temperate lakes, more investment on oxygenation or artificial mixing will be needed. The results also imply that the cold fish species that are adapted to rich DO will not be able to migrate downward to escape the effect of climate warming in similar lakes (Stefan et al., 1996).

The negligibly small growth of chlorophyll $a$ in Harp Lake is not expected given that phytoplankton of cold lakes grows faster under higher light availability and warmer water (Tan et al., 2017). But at least one study observed the occurrence of the similar stasis of chlorophyll $a$ in the lakes of the northeast U.S. despite large environmental changes (Oliver et al., 2017). Also, the similar weak coherence between climate drivers and ecosystem metabolism is widely recognized in river ecosystems (Bernhardt et al., 2018). It was argued that the main reason for this incoherence is the mismatch of the timings of optimum radiation, thermal, and nutrient conditions (Bernhardt et al., 2018). A similar argument may be also valid here. As shown in Figure 8, although climate warming produces favorable thermal conditions for phytoplankton in the early spring and early winter, the timings of favorable solar radiation and nutrient conditions are still lagged far behind. The combined effect is the limited growth of phytoplankton in Harp Lake under climate warming. In addition, two other factors could also partly contribute to the unexpected chlorophyll $a$ stasis: (1) Stronger water stratification under warming reduces nutrient exchange between surface and deep waters of Harp Lake in summer, and (2) autotrophic respiration is more sensitive to water warming than photosynthesis (Kraemer et al., 2017; Yvon-Durocher et al., 2010). Because most of small temperate lakes have shorter ice seasons than Harp Lake (Fang & Stefan, 2009) and many of them, such as cold dimictic lakes, have weak water convection (Fang & Stefan, 1996; Yankova et al., 2017), the little growth of chlorophyll $a$ predicted here may be not rare.

The concentrations of DO and chlorophyll $a$ strongly regulate the carbon dynamics of small temperate lakes (Couture et al., 2015; Evans et al., 2017). Especially, as lake water becomes anoxic, the substantial shift in the pathways of carbon cycling would occur. For example, anoxic conditions in deep waters would favor methane (CH$_4$) production over carbon dioxide (CO$_2$) production (Tan et al., 2015). Anoxic conditions would also favor carbon burial over carbon degradation (Evans et al., 2017) and result in a loss of bioavailable nitrogen (Fennel, 2017). These effects, as well as the impacts of water temperature and ice phenology on carbon cycling (MacIntyre et al., 2010; Sepulveda-Jauregui et al., 2015), indicate that our model framework can be used to evaluate the carbon dynamics under changing climate conditions in the future.

### 4.3. Influence of Catchment Hydrology

For the examined state variables, only the dynamics of DO is found to be influenced considerably by the change of catchment hydrology of Harp Lake. It is not surprising that the effects of catchment hydrology on ice phenology and water temperature are limited because on the daily basis the energy exchange between lake waters and stream discharge is usually small. But this negligible effect is not expected for
the dynamics of chlorophyll a because warmer climate is predicted to increase nutrient loading from the catchment (Figure 8). Similar to the discussion in section 4.2, this negligible effect should be mainly explained by the mismatch of the timings of nutrient loading and other growth conditions of phytoplankton (i.e., solar radiation). As shown in Figure 8, the increase of stream discharge mainly occurs in the winter when solar radiation is limited and the growing season is yet to come. In addition, nutrient loading is also limited by the negative discharge-concentration curves used in the study (Figure S6). For the DO dynamics, the influence of catchment hydrology is substantial. It seems that because the organic carbon transported from the catchment in winter can be degraded in the water column later in summer, the mismatch of the

Figure 8. Mean monthly solar radiation, air temperature, inlet discharge, inlet dissolved inorganic carbon loading, inlet dissolved organic carbon loading, and inlet total phosphorus loading at Harp Lake during 2010–2014 (black) and during 2095–2099 (colored).
timings of the carbon supply and the favorable degradation conditions does not limit the increase of DO consumption. In all, we argued that for small temperate lakes that are oligotrophic and seasonally ice covered, catchment hydrology would have substantial impacts on the dynamics of DO but limited impacts on the dynamics of chlorophyll $a$ under climate warming unless stream discharge in summer or nutrient loading from municipal and/or industrial sectors increases.

4.4. Uncertainty of Climate Drivers

As presented in this study and other publications (Huber & Zanna, 2017), the prediction of aquatic systems is sensitive to the uncertainty of climate drivers. For example, there are large differences of the simulated ice-on and ice-off dates between different climate models. And because deepwater DO and surface water nutrient concentrations are controlled by water mixing and diffusion, the dynamics of DO and chlorophyll $a$ are especially sensitive to the future changes of wind field (Figures 5 and 6). Many studies also indicated that the understanding of the future wind is important for correctly estimating greenhouse gas emissions from aquatic ecosystems (Holgerson et al., 2016; MacIntyre et al., 2010). The trends of climate drivers (e.g., wind) simulated by climate models are with large uncertainties; for example, the climate models shown in Table S1 and Figure S3 do not capture the “global stilling” effect, the observed decadal decline of near-surface wind speed between $-0.004$ and $-0.017$ m $s^{-1}$ $yr^{-1}$ for midlatitude regions including North America (McVicar et al., 2008; Vautard et al., 2010). These uncertainties may have biased our site-level simulations. As small lakes are overwhelmingly abundant, regional extrapolation with our model considering the uncertain climates is therefore a challenge.

4.5. Uncertainty of Model Parameters

Our sensitivity analysis implies that the ALBM can make robust simulations of water temperature for small temperate lakes that have similar trophic status to Harp Lake even without calibration. The analysis also indicates that to better model the ice-on and ice-off dates for small temperate lakes, it is necessary to use refined parameterization methods of snow density in ALBM (Bartelt & Lehning, 2002; Rogers et al., 1995). Similar to other publications (Couture et al., 2015; Schladow & Hamilton, 1997), the simulation uncertainties related to model parameters are large for biological lake state variables (DO and chlorophyll $a$). As the sensitive parameters for the simulation of DO and chlorophyll $a$ are related to water convection, groundwater hydrology, and phytoplankton and microbial metabolism, it would be necessary to improve the parameterization of these processes in the ALBM.

5. Conclusions

We applied a process-based lake biogeochemistry model (ALBM) in a small temperate lake in Canada to evaluate the dynamics of ice phenology, water temperature, DO, and chlorophyll $a$ of similar temperate lakes (small, oligotrophic, seasonally ice-covered and strongly stratified in summer) under different climate change scenarios. It was found that for these lakes the dynamics of these state variables at different depth zones can be substantially different under climate change. The model prediction suggested that the ice season and ice thickness of small temperate lakes in warmer or similar climate conditions to that of Harp Lake would shrink considerably under severe climate warming. The prediction also suggested that for small temperate lakes with strong summer stratification, although their surface waters may be warmed substantially, their deep waters would be somewhat muted to climate change. There would be a positive energy feedback between climate and small temperate lakes with seasonal ice cover. With the shrinking of the ice season, both the lakes and air gain energy directly or indirectly from more available solar radiation. For small temperate lakes that strongly stratify in summer, their DO concentrations may decrease in summer in both surface and deep waters under climate warming. But the causes of their decreases are different, with the decrease in surface waters mainly caused by water warming and the decrease in deep waters mainly caused by weakened water vertical exchange. For oligotrophic temperate lakes with weak water convection, the chlorophyll $a$ concentration in the euphotic zone would be stable under climate warming. This chlorophyll $a$ stasis is likely caused by the weakened convection and the mismatch of the timings of favorable environmental conditions (i.e., solar radiation, temperature, and nutrients) for the metabolism of phytoplankton. Our analysis further indicated that for small temperate lakes that are oligotrophic and seasonally ice covered, the shift of catchment hydrology under a changing climate would only affect the dynamics of DO significantly in all of the examined state variables. The recovery of deep waters to oxygenated conditions would be slow even if severe warming were
reversed. Biologically, because cold temperature would be preserved but DO deficit would increase in deep waters, only cold fishes that are adaptive to low oxygen conditions can survive under intense warming. Our results also implied that critical changes in carbon cycling could occur in small temperate lakes in the future.

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