CURRENT EVIDENCE

Hot tops, cold bottoms: Synergistic climate warming and shielding effects increase carbon burial in lakes

Maciej Bartosiewicz [1,2]*** *Anna Przytulska,*[1] *Jean-François Lapierre,*[2,3] *Isabelle Laurion,*[2,4] *Moritz F. Lehmann,*[1] *Roxane Maranger* [2,3]

[1]Department of Environmental Sciences, University of Basel, Basel, Switzerland; [2]Groupe de Recherche Interuniversitaire en Limnologie (GRIL), Basel; [3]Département des Sciences Biologiques, Université de Montréal, Montréal, Québec, Canada; [4]Centre Eau Terre Environnement, Institut National de la Recherche Scientifique, Québec, Québec, Canada

Scientific Significance Statement

Lakes play a significant role in the global carbon cycle where inputs from watersheds and primary production are either stored in sediments or lost to the atmosphere through respiration. Climate change is anticipated to increase atmospheric losses as water overlying sediments warms, thus reducing carbon storage. Lakes worldwide, however, are not only warming but are also losing transparency through eutrophication or browning. The synergistic result is that heat is trapped in the surface layers of more colored lakes, which in turn isolates colder bottom waters and sediments experience longer periods without oxygen. This bottom-water cooling increases overall carbon storage by reducing aerobic respiration, but stimulates methane production due to prolonged anoxia, thus potentially increasing the overall global warming potential of lakes.

Abstract

In this article, we challenge the notion that global warming stimulates organic matter mineralization and increases greenhouse gas emissions in lakes via direct temperature effects. We show that the interactive effects of warming and transparency loss due to eutrophication or browning overrides atmospheric warming alone. Thermal shielding enables a longer and more stable stratification that results in bottom-water cooling, prolonged anoxia, and enhanced carbon preservation in a large proportion of global lakes. These effects are strongest in shallow lakes where an additional burial of 4.5 Tg C yr^{-1} increases current global estimates by 9%. Despite more burial, the net global warming potential of lakes will increase via enhanced methane production, related to prolonged periods of anoxia, rather than warming. Our understanding of how whole-lake carbon cycling responds to climate change needs revision, as the synergistic influence of warming and transparency loss has much broader ecosystem level functional consequences.

*Correspondence: maciej.bartosiewicz@unibas.ch

Global climate and general circulation models predict an increase in air temperature by several degrees by the end of the 21st century, with consequences for terrestrial and aquatic environments. The warming of ecosystems can directly stimulate production and respiration, the latter being particularly sensitive to increasing temperatures (Shaver et al. 2000; Yvon-Durocher et al. 2010*a*). Direct warming effects are controlling the exchange of carbon between the terrestrial bio- and pedosphere, and the atmosphere, with either negative or positive feedbacks on climate through long-term burial of atmospheric carbon (Davidson and Janssens 2006), or the remineralization and evasion of old carbon stocks (Koven et al. 2011). However, warming can also indirectly affect production and respiration by modulating nutrient availability, moisture regime, species composition, and through changes in phenology (Shaver et al. 2000). These indirect effects on carbon processing can be even more pronounced than direct ones. For example, in terrestrial ecosystems, warming related increases in nutrient availability and vegetation coverage can result in accelerated organic matter (OM) turnover beyond the direct influence of temperature alone (Shaver and Jonasson 1999). Thus, a change in temperature must be considered within a broader context in order to account for ecosystem level outcomes, since competing or synergistic pathways will buffer, enhance, or even alter anticipated changes in processing.

Similar to terrestrial ecosystems, lakes are experiencing direct and indirect effects of global warming, and act as sentinels and regulators of climate change (Williamson et al. 2009). They play a crucial role in regional and global carbon budgets, with direct effects on climate (Tranvik et al. 2009). The rates of carbon processing, sequestration, and mineralization in lake waters and sediments depend on microbial activity, which is directly influenced by temperature (Gudasz et al. 2010). In agreement with the paradigm that temperature and metabolic activity are closely linked, warming of lakes is anticipated to increase the ratio of respiratory CO_2 release to photosynthetic CO_2 fixation (Yvon-Durocher et al. 2010*b*). Furthermore, methanogenesis is also anticipated to increase more rapidly than respiration to CO_2, due to its relatively higher activation energy (Yvon-Durocher et al. 2014), resulting in even greater feedbacks on climate. Since the current consensus seems to support that lakes globally are warming, carbon processing is anticipated to increase, resulting in a significant reduction in carbon burial and an increase in global warming potential (GWP) of gases emitted from lakes into the future (Moss et al. 2011).

Evidence that climate warming indeed results in increased carbon processing and gaseous carbon release from lakes, however, is weak. In fact, recent observations suggest that carbon burial in lakes and reservoirs may be increasing (Clow et al. 2015; Heathcote et al. 2015). One possible explanation for this mismatch is that most studies that have focused on the impact of atmospheric warming consider increased water temperature changes primarily in the upper, mixed, water column and extrapolate these potential effects on carbon processing to the whole lake. Yet most carbon processing likely occurs in the sediments and overlaying bottom waters (Tranvik et al. 2009). We argue that this oversimplification of surface warming does not consider differential temperature effects over the entire water column (i.e., effects on the overall density structure). Nor does it consider the potential for indirect, interactive effects of other climate-related, environmental changes (i.e., eutrophication/browning; Solomon et al. 2015; Rose et al. 2016) that may alter the way an entire lake responds to warming, and result in cascading effects on ecosystem functioning.

Warming-related eutrophication can seasonally override the direct temperature effect on metabolism, if increased biological production at the surface leads to a disproportionate summertime uptake of CO_2 (Finlay et al. 2015). Furthermore, the heat trapped in the surface of a more eutrophic or brown colored lake is not necessarily propagated toward the bottom waters and sediments. Therefore, current assumptions that general warming of lakes will result in enhanced sediment carbon turnover, decreased storage, and increased methanogenesis (e.g., Yvon-Durocher et al. 2014) do not necessarily apply. Indeed eutrophication-related reduction in lake-water transparency lowers vertical energy fluxes by creating a "shielding effect" that counteracts the effects of higher atmospheric temperatures on ecosystem metabolism. Recent work has shown that bottom waters in stratified lakes may actually be cooling in response to increasing atmospheric temperatures when considered together with transparency loss (Rose et al. 2016), but the biogeochemical implications of this phenomenon have not been elucidated. Neither have the anticipated synergistic and antagonistic effects on carbon cycling been considered in the broader context of global environmental change.

In this article, we argue that the thermal structure of lakes and thus whole-lake carbon processing is controlled by interactive effects of atmospheric warming and water transparency loss either through eutrophication or browning. In this context, the three resulting mechanisms regulating temperature and OM processing in lakes are: (1) enhanced surface warming that leads to a reduction in epilimnetic thickness, (2) reduction of heat transfer toward bottom waters, and (3) more extended periods of stronger water column stratification. We further argue that, together, these mechanisms act to decrease the overall sediment area that is exposed to warm waters and increase the duration and areal extent of sediment exposure to anoxia. Cooler bottom waters and prolonged anoxia would theoretically reduce carbon mineralization, but would respectively limit and enhance methanogenesis. But to what extent would these changes influence carbon processing in terms of mineralization and methanogenesis? To explore the synergistic influence of transparency loss and climate warming on the potential changes in carbon processing, we first summarized observational data on the changes in temperature and oxygen

stratification of lakes. In a second step, we ran a simple one-dimensional (1D) lake model (FLake) emulating the synergistic effects of climate change and transparency loss to provide realistic range of changes in bottom water temperature of lakes. Third, we applied observed and modeled temperature and stratification changes to currently accepted empirical equations describing effects of bottom temperature and oxygenation on the carbon mineralization and methane (CH_4) production. We then extrapolate how these potential changes in carbon processing would influence overall carbon burial and GWP in lakes of boreal and temperate regions.

Shielding of bottom waters

Eutrophication and browning are the two globally most important processes that cause rapid light attenuation in surface waters and may result in thermal shielding. Shielding effects occur when high phytoplankton biomass or colored dissolved organic matter (cDOM) increase the radiant heating of surface waters and water column stratification (Mazumder and Taylor 1994; Jones et al. 2005; Caplanne and Laurion 2008). Both ongoing eutrophication and browning have been reported to decrease transparency in 30–85% of all temperate and boreal lakes (Monteith et al. 2007; Dodds et al. 2009; Finstad et al. 2016). This shielding effect, trapping energy in surface waters, has essentially been ignored in studies that have evaluated the overall influence of climate change on lakes, and its potential synergistic impact on thermal structure and biological processing.

Widespread fertilizer use, population growth, and land use changes have resulted in increased eutrophication of surface waters globally. Climate change is known to further accelerate this process (Moss et al. 2011), either through the increased loading of allochthonous nutrients (Jensen and Andersen 1992) or through enhanced internal loading from more reduced sediments (Søndergaard et al. 2003; Brookshire et al. 2011). The rise in both temperature and nutrient availability through climate change, as well as anthropogenic activities, results in enhanced biological production (Michelutti et al. 2005), which may lead to the proliferation of surface blooms (Havens and Paerl 2015) and, in turn, associated thermal shielding of lower water column (Kumagai et al. 2000). Shielding as a consequence of eutrophication may be exacerbated by phytoplankton community shifts toward the dominance of smaller, pigment-rich phytoplankton species (Finkel 2001), which capture light more effectively (Descy et al. 1994). This effect may be amplified if phytoplankton blooms occur earlier and persist for longer during the year (Peeters et al. 2007). Population shifts and changes in phenology are projected to occur with increased warming and nutrient loading to lakes.

Increased browning of lakes is another widespread phenomenon, particularly in boreal latitudes (e.g., Monteith et al. 2007), caused by climate warming, changing hydrology,

and land use (Kritzberg 2017). Recent models predict a 30% increase in light absorption in boreal surface waters by 2030 as a function of higher cDOM concentrations (Weyhenmeyer et al. 2016), which influence key biological, chemical, and physical properties of lakes. The expected reduction in epilimnetic thickness as a function of increased DOM concentrations (Strock et al. 2017) will not only influence the overall thermal regime (Read and Rose 2013), but will also reduce the contact between sediments and warming waters. A recent analysis has demonstrated that the rate of transparency loss has increased by 12% in lakes and reservoirs in the continental U.S. from 2007 to 2012 (Leech et al. 2018), supporting that this issue is not only occurring, but at an unprecedented rate of change.

Given the intrinsic links between warming and reduced transparency in lakes, the direct and indirect effects of climate change cannot be considered separately. Counterintuitively, the intense surface warming of a brown or phytoplankton-rich lake may be associated with a weaker temperature increase, or even a relative cooling of bottom waters. In turn, stronger vertical temperature gradients foster prolonged stratification and extended periods of anoxia. Furthermore, small and shallow lakes (≤ 5 m deep) should be particularly prone to differential heat dissipation brought about by water column browning or eutrophication (Houser 2006; Bartosiewicz et al. 2015), since stratification in these systems may be more strongly influenced by transparency than by other factors (e.g., wind). Therefore, effects of both the size and depth of lakes must be taken into consideration.

Interactive effects of climate and shielding on lake thermal structure

Although many studies have suggested that surface waters of lakes and reservoirs are warming as a result of climate change (O'Reilly et al. 2015), reports about climate effects on bottom-water temperatures are rare. Simply assuming that hypolimnetic temperatures are increasing in parallel with warming of surface waters may be erroneous. In most lakes, heat exchange with the atmosphere can only directly influence surface temperatures. In contrast, temperature at depth is controlled primarily by the strength of thermal shielding and the redistribution of surface energy through mixing (Rose et al. 2016). Therefore, the link between atmospheric warming and increasing bottom water temperature is tenuous, particularly when the synergistic influence of browning and eutrophication on the thermal regime of lakes is considered.

Figure 1 provides a summary of the reported bottom-water temperature changes under climate warming and lake-water transparency effects. In the case of relatively deep (>20 m), transparent lakes, bottom temperatures show a general positive warming trend (Supporting Information Table S1). This follows the expected pattern based on the propagation of thermal energy in clear waters: atmospheric warming of
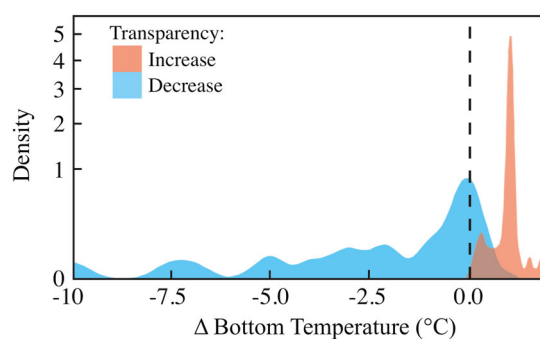
Fig. 1. Changes in bottom temperatures of lakes affected by climate warming and transparency loss. All data were taken from the literature; (*n* = 205, *see* Supporting Information Table S1 for details related to different lake depths, specific temperature changes in bottom waters, and associated references). Most cooling (72%) occurs in shallow (<5 m deep) lakes, and all of the reported warming was observed in deeper lakes (>5 m deep). Density represents the number of lakes within a temperature class bin corrected for the width of the temperature bin. Bins were set at 1.1°C in lakes with decreasing transparency and at 0.2°C in lakes with increasing transparency.

surface waters is efficiently transferred downward (Rose et al. 2016). However, during warming, temperatures in the bottom waters are increasing at a much slower rate than those at the surface (Kraemer et al. 2015), enhancing water column stability. This effect could be even more pronounced in warmer climates, since the warming of water by 1°C at an ambient temperature of 20°C results in a much greater increase in thermal stability than an equivalent change under colder conditions (e.g., <8°C). So, although the bottom waters of relatively deep clear lakes may indeed be gaining heat to some extent, the heating at depth is far less pronounced as compared to the surface, and the resulting temperature and density differentials strengthen stratification and stabilize the water column.

As opposed to lakes deeper than 20 m, bottom-water temperatures of lakes between 5 and 20 m depth do not systematically increase as a consequence of atmospheric warming (Supporting Information Table S1; Fig. 1). In fact, only under specific circumstances where transparency increases in parallel, either through effect of drought or deforestation, did downward propagation of the added heat result in warming of bottom waters. The majority of studies rather show that when transparency is decreasing and climate is warming, bottom waters are cooling. Surprisingly, there is mounting evidence that this is occurring in the bottom waters of many shallow lakes (<5 m) globally (Winslow et al. 2015; Supporting Information Table S1; Fig. 1). Given that surface waters of less transparent lakes gain heat more rapidly, they also tend to stratify earlier, for longer periods, and more strongly (Supporting Information Table S2), resulting in colder bottom waters throughout the growing season. Furthermore, earlier thermal isolation may result in more prolonged oxygen

depletion in the deeper water column, despite lower temperatures. As the cumulative areal coverage of small shallow lakes represents approximately half of the global lentic surface (Downing et al. 2006), their counterintuitive response to climate will influence our assessment of how global change affects carbon processing in lakes.

In summary, while current empirical evidence supports the notion that surface waters of lakes are warming, this is generally not the case for bottom waters (Fig. 1; Supporting Information Table S1). Observations point to contrasting responses with regards to bottom temperatures of deep vs. shallow lakes but warming over the entire water column only really occurred in deep clear systems, whereas the bottom waters of shallow turbid systems are typically cooling. Hence, warming and transparency loss must be considered in concert, as both are co-occurring worldwide. Our compilation in Fig. 1 and Supporting Information in Table S1 also suggests that lake depth needs to be taken into consideration since the relative changes in bottom water temperatures, which influence the overall carbon biogeochemistry, may be more pronounced in shallower systems than in deeper ones.

Modeling effects of climate change and transparency loss on bottom-water temperature and stratification

Although there is substantive evidence that the combined influence of transparency loss and climate warming results in bottom-water cooling, the magnitude of this change appears to vary considerably among lakes (Fig. 2; Supporting Information Table S1). This variability is likely a function of lake size, shape, depth, and initial temperature of the lake at the onset of stratification (where bottom waters will be relatively colder than the surface if onset is earlier and more rapid). Therefore, in order to provide a proof of concept and a plausible range of representative scenarios of changes in bottom water temperatures as a function of climate warming and transparency loss, we used the open-source 1D FLake-Global model (Mironov 2008; Kirillin et al. 2011; http://www.flake. igb-berlin.de) to emulate realistic warming scenarios in a climatic space for time substitution for both shallow (<5 m) and deeper (5–20 m) lakes of different transparency.

FLake is a 1D model that calculates the evolution of the horizontally averaged temperature profile in the water column of lakes. It does so by dividing the lake in different horizontal layers where the upper layer is treated as homogeneous and well mixed, whereas the thermocline is parameterized using a polynomial self-similar representation of the temperature profile, and the depth of the mixed layer is determined as a function of wind shear and heat exchange using a relaxation-type equation. In global configuration, it uses spatially explicit meteorological data (air temperature, wind speed, precipitation) for a perpetual 1-yr period (2005–2006). The meteorological data are uploaded into a gridded space for the purpose of weather forecasting to allow for the calculation of the
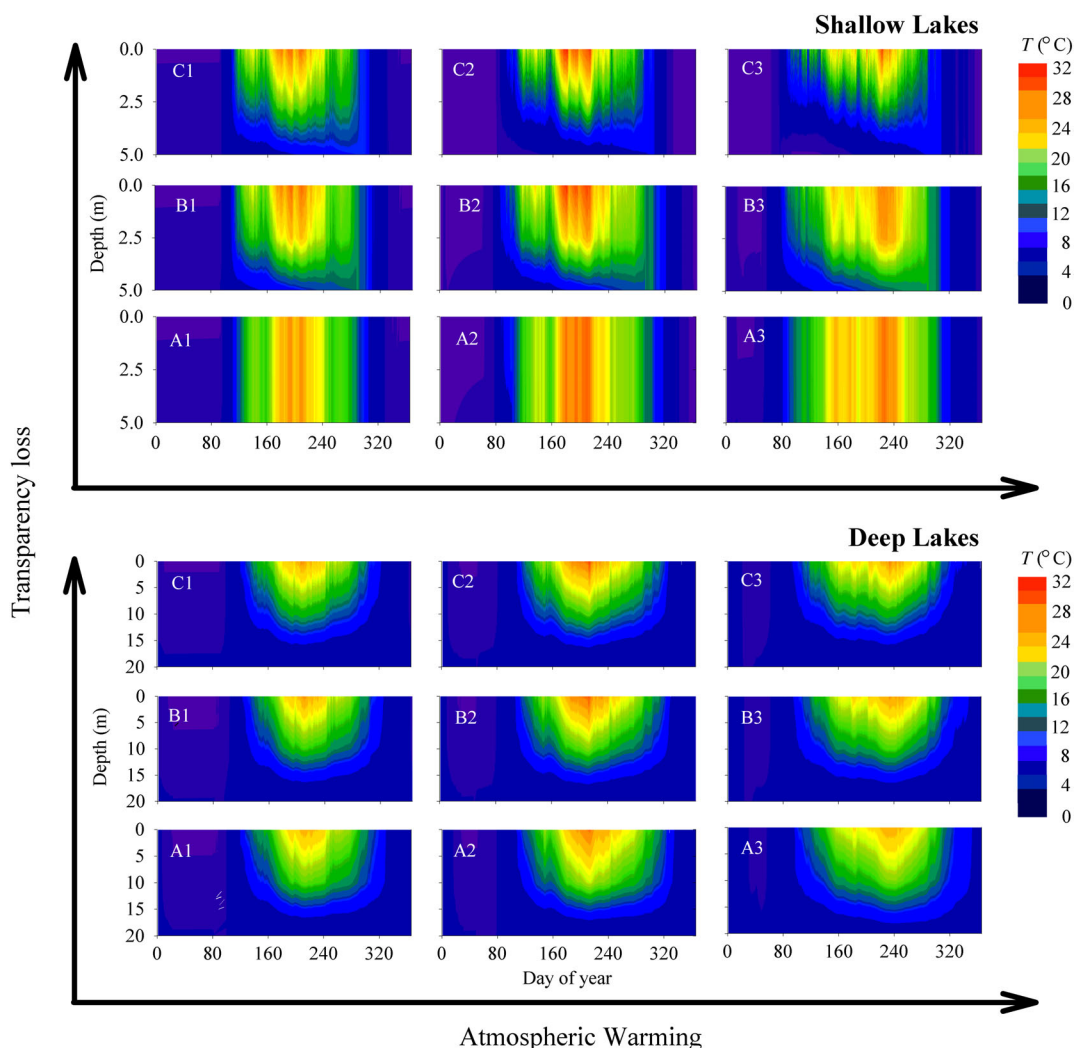
Fig. 2. Temperatures and stratification of shallow and deep lakes as a function of warming and transparency loss. Modeled temperature depth-profile results of an exemplary 5 and 20 m deep lake over an annual cycle using FLake. Letters represents changes in transparency from (**A**) "very clear" (Secchi depth, SD = 5 m) to (**B**) "clear" lake (SD = 2 m) to (**C**) "turbid" (SD = 1 m); numbers represent changes in average temperature: 1 is baseline temperature, 2 is baseline +2°C, and 3 is baseline +4°C.

approximate temperature and mixing patterns in freshwater lakes at specific locations around the world. A more comprehensive description and validation of model equations and parametrization are available in the original manual (Mironov 2008), and in Kirillin (2010). FLake is also being used to incorporate lakes within regional climate models (Shatwell et al. 2016; Thiery et al. 2016) and used by various meteorological agencies across Europe (Mironov et al. 2005). In the accessible online version, the input parameters include geographical coordinates, an average lake depth as well as an estimate of water clarity (i.e., imposed Secchi depth as a proxy for transparency loss through either browning or eutrophication). Differences in lake shape are not considered in the model and an average fetch of 3 km is assumed. Potential effects of in- and outflow are neglected. The purpose for creating the FLake

simulations under different climate, transparency, and interacting climate-transparency scenarios was in part to test our concept, but also to provide differential bottom water temperatures that could be applied to current empirical carbon processing models.

The simulations were based on mean annual atmospheric temperature trends representative for a north temperate region (baseline, Warsaw, 52.2297°N, 21.0122°E) as well as south temperate (Budapest, 47.4979°N, 19.0402°E) and Mediterranean (Ankara, 39.9334°N, 32.8597°E) regions. The latter two represent an annual average warming above baseline of +2°C and +4°C (Fig. 2, panels 1–3), respectively. Differences in annual precipitation may also influence stratification patterns (Rueda and MacIntyre 2010). Warsaw and Budapest had similar annual precipitation levels at 515 mm and 520 mm,

respectively (for the period between 2000 and 2008), and although Ankara's was somewhat lower at 420 mm, we considered any potential effects of differences in precipitation to be rather minor when compared to these of respective warming. For both shallow (< 5 m deep) and deeper lakes (5–20 m), we simulated reductions in water transparency (Secchi depth decrease from 5 to 2 to 1 m, Fig. 2, panels A–C), which could be ascribed either to browning or eutrophication, and compared the projected thermal dynamics (Fig. 2). We acknowledge that these are large changes in water transparency and would be associated to an increase in chlorophyll concentration of 5 μg L^{-1} to between 10 and 20 μg L^{-1} (Tilzer 1988) for greening or a change in water color of 5 μg L^{-1} to between 40 and 60 mg L^{-1} as Pt (Canfield and Hodgson 1983) for browning (*see* Kritzberg 2017). In the simulations below, the following scenarios were considered: (1) lakes under the influence of atmospheric warming but without change in transparency (Fig. 2, horizontal axes; 1–3), (2) lakes experiencing a reduction in transparency but without change in air temperature (vertical axes; A–C), and (3) lakes experiencing an increase in air temperature but also becoming less transparent (diagonal; Fig. 2A1, B2,C3).

First, when transparency was kept constant but atmospheric temperature increased (Fig. 2, same letter, different number), we observed an earlier onset of stratification in both shallow and deeper lakes, and either warming in surface and deep waters, or surface warming paired with negligible temperature change at the bottom, consistent with observational data (Fig. 1; Supporting Information Table S1). Temperature changes in bottom waters ranged between −0.3°C and 2.0°C in shallow lakes (Fig. 1 upper panel, C1 vs. C2 and A1 vs. A2, respectively), and between −0.02°C and 1.5°C in deeper lakes (Fig. 1 lower panel, C1 vs. C2 and A2 vs. A3). When temperature was kept constant, with decreasing transparency, the model predicts that the bottom waters are cooling, with temperature changes between −0.5°C and −5.8°C in shallow systems (Fig. 2 upper panel, C2 vs. B2 and B3 vs. A3), and between −0.02°C and −1.7°C in the deeper lakes (Fig. 2 lower panel, C1 vs. B1 and B3 vs. A3).

Most strikingly, however, when lakes warm and simultaneously become less transparent, the transparency effect apparently overrides the effect of warming, resulting in net hypolimnetic cooling. In shallow lakes, bottom temperatures decreased by between 0.6°C and 4.8°C from the initial temperature of 8.8°C (*see* DeStasio et al. 1996 for expected range of initial temperatures and Supporting Information S2 for details). Furthermore, the combined influence of surface-water warming and shielding resulted in an extension of the stratification period by 21–161 d (defined as the period when the difference between bottom and surface *T* is >7°C or $N \approx 0.2$ s^{-1}, and indicative of a very stable stratification even in shallow lakes; Pernica and Wells 2012). These effects were also observed for deeper lakes, yet were much less pronounced, with hypolimnetic cooling between 0.01°C and

0.3°C (Fig. 1; lower panel B2 vs. A1 and C3), and a stratification lengthening by 29–38 d. Indeed, the predicted changes in the thermal structure of the model lakes stand in good agreement with literature reports (Supporting Information - Tables S1, S2). The FLake model thus offers some general and validated parameterization for testing the impacts of climate and transparency changes on hypolimnetic temperature and the timing of stratification, which we can use, in turn, to evaluate changes in ecosystem carbon metabolism.

Effects of climate warming and transparency loss on lake carbon processing

In the following sections, we explore the potential interactive effects of transparency loss and climate warming on whole-lake carbon processing in lakes for boreal and temperate regions. We specifically assess carbon burial efficiency as a function of changes in carbon mineralization, and CH$_4$ production as a function of (1) hypolimnetic temperature changes, and (2) spatiotemporally expanded anoxia. Bottom cooling and prolonged anoxia was observed in both shallow (<5 m) and deeper lakes (5–20 m), but changes in temperature as a function of thermal shielding were much stronger in shallow lakes (Fig. 1 and Supporting Information Table S1). Therefore, for the purposes of this exercise, we describe potential changes in the carbon dynamics of shallow lakes with more detail throughout the text and report results for deeper lakes by largely referencing Fig. 3. We apply the bottom water temperature range predicted by the FLake model determined from the combined influence of surface warming and transparency loss, estimated at −0.6°C and −4.8°C for shallow lakes (Fig. 2, upper panel) and −0.01°C and −0.3°C for deeper lakes (Fig. 2,
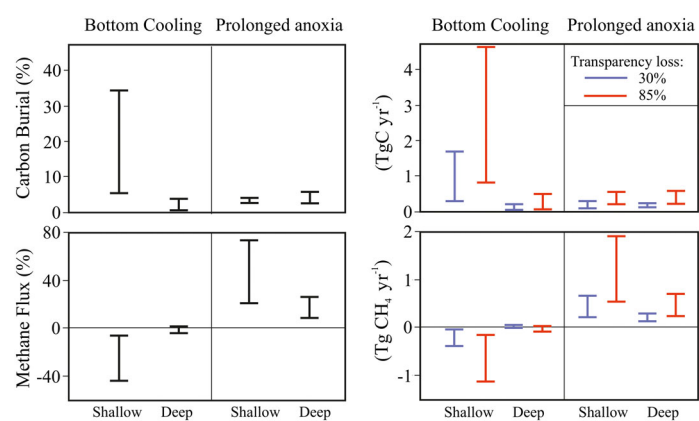

Fig. 3. Range in proportional changes (%) in carbon burial and methane flux as a function of bottom cooling or prolonged anoxia (left panels); values derived using modeled and measured estimates applied to well-known metabolic equations. Proportions upscaled to changes (Tg yr^{-1}) in processing for shallow (0–5 m) and deeper (5–20 m) lakes in boreal and temperate regions anticipated to be undergoing a range (30–85%) of transparency loss (right panels). Summary of ranges and values is provided in Supporting Information Table S3.

lower panel). In order to provide an estimate of prolonged anoxia, we assume that the amount of time for bottom waters to achieve anoxia remains the same under climate warming and transparency loss, so that changes in oxygen exposure time (OET) of sediments will be a direct function of the increased stratification period (Williamson et al. 2015).

Climate warming together with eutrophication or browning result in an earlier onset and more prolonged stratification by 10–30% annually (Supporting Information Table S2), a range also confirmed using FLake. Our assumption that prolonged stratification is directly proportional to duration of bottom water anoxia can be considered conservative, as it accounts only for a decrease in the O_2 flux toward bottom waters and not for any enhanced microbial consumption due to higher OM loadings, which will further reduce the OET of sediments (Nürnberg 1995). Differential changes in carbon processing, both in terms of mineralization and methanogenesis, as a function of temperature and prolonged anoxia were assessed using empirically accepted relationships from the literature as well as an empirically derived equation from literature data compilation. We then assess the implication for relative carbon storage and GWP in lakes across boreal and temperate regions (*see* Supporting Information S1).

Influence of bottom cooling on carbon burial and methanogenesis

Change in the rate of carbon processing as a function of bottom water cooling was estimated using a well-supported empirical relationship ($R^2 = 0.43$, $n = 574$) that predicts changes in carbon mineralization (in $mg\,C\,m^{-2}\,d^{-1}$) with ambient sediment temperature (Gudasz et al. 2010; T in $°C$):

$$Carbon\ mineralization = 10^{(0.036 \times T + 1.64)}$$

Key assumptions for our estimations of carbon burial are that (1) a change in the amount of carbon mineralization corresponds to a change in the fraction of carbon buried (%), (2) bottom-water temperature is a good predictor of sediment temperature (e.g., Cyr 2012), and (3) although the equation is nonlinear, the temperature differential used in this case was in the linear portion of the curve. For the scenario of a bottom water-cooling by $4.8°C$ in shallow lakes, carbon burial increases by 34%. Alternatively, a cooling by $0.6°C$ results in a relative increase of around 5% (*see* Supporting Information S2). Burial also increased in deeper lakes, but this effect was less striking than in shallow ones (Fig. 3).

Elevated temperatures accelerate carbon mineralization in general, but methanogenesis is particularly sensitive to warming. Higher sediment temperatures typically result in a relative increase in the benthic production of CH_4 vs. CO_2, given the higher activation energy of methanogenesis. As a consequence, bottom water-cooling should downregulate methanogenesis in sediments and result in decreasing benthic CH_4 fluxes. This effect can be quantified using the empirical

relationship between benthic diffusive CH_4 fluxes (FCH$_4$ in $\mu mol\,m^{-2}\,h^{-1}$) in lakes and the temperature at the sediment-water interface (Yvon-Durocher et al. 2011):

$$\ln(FCH_4) = -0.85 \times 1/(k \times T) + 36.5$$

where k is Boltzmann's constant and T is temperature (in K). Applying this equation ($R^2 = 0.43$, $n = 131$) and integrating the predicted range of bottom water temperature reduction for shallow (0.6–$4.8°C$) lakes results in a relative decrease of the net CH_4 efflux from sediments by 7–45% whereas the influence for deeper lakes was negligible (Fig. 3; *see* Supporting Information S2). Assuming that CH_4 oxidation would remove a fixed proportion of the produced CH_4 in any given lake, the temperature-change related shifts in benthic CH_4 production can be directly translated into changes in lake CH_4 emissions. It is important to note that our estimates consider diffusive fluxes only, and we do not consider the large portion of CH_4 emitted through ebullition. Moreover, any possible effects of temperature changes on the proportion of CH_4 oxidized in the water column have not been taken into consideration.

Influence of prolonged anoxia on carbon burial and methanogenesis

The earlier onset and prolonged stratification period predicted as a function of climate warming and transparency loss is assumed to translate into the proportional extension of the anoxic period. More reduced conditions are known to lower the overall carbon mineralization. Thus, carbon burial in lakes depends on the bottom redox conditions, and can be parameterized as function of the OET (the period of time sediments is exposed to oxygenated pore water; OET given in years; Hartnett et al. 1998; Sobek et al. 2009; *see* Supporting Information S3):

$$Carbon\ burial = a - (b \times \log OET)$$

where a and b are experimental constants for sediments dominated by either allochthonous (more refractory) or autochthonous (more labile) OM, respectively. We estimate that for shallow lakes, OET would change from 1 yr (taken as a baseline; Sobek et al. 2009) to 0.9 yr (if hypolimnetic anoxia is extend by 10%), and from 1 to 0.7 yr (if extended by 30%). Using these assumptions, model results suggest that mineralization would decrease by 1.1–3.7% in shallow ecosystems. This effect was less pronounced in deeper lakes (Fig. 3).

Extended periods of anoxia will potentially stimulate methanogenesis and enhance benthic CH_4 fluxes and its evasion to the atmosphere. Using data from a series of boreal and temperate lakes, we developed an equation for quantifying CH_4 flux (FCH$_4$) at the sediment-water interface as a function of oxygen penetration depth (L in mm, *see* Supporting Information Fig. S1, $R^2 = 0.4$, $p < 0.001$):

$$\log\,(FCH_4) = -0.158 \times L + 1.89$$

Given the equation above and assuming typical values for *L* in shallow lakes (*see* Supporting Information S4), the projected decrease in L can result in a relative increase of the benthic CH_4 flux by 20–73% in shallow lakes, when *L* decreases by 10–30%, that is, proportionally to the extended period of time a lake remains stratified. Benthic fluxes also increased in deeper lakes (Fig. 3), highlighting the importance of prolonged anoxia in favoring methanogenesis.

Implications for lake carbon budgets

In order to consider how climate warming and transparency loss is influencing global carbon cycling in lakes, we upscaled the relative percent changes in carbon burial and methane production estimated here (summarized in Fig. 3; Supporting Information Table S3) as a function of the total amount buried or emitted from lakes across boreal and temperate regions. Shallow lakes from these regions are estimated to bury 15.75 Tg C yr^{-1} and emit 3.06 Tg CH_4 yr^{-1} in total (*see* Supporting Information S1, S2). If 30–85% of these systems are losing transparency (*see* "Shielding of bottom waters" section) and warming, estimates from this study suggest that overall shallow lakes are burying more carbon primarily as a function of cooler bottom water temperatures and emitting more CH_4 due to prolonged anoxia (Figs. 3–4). The most intriguing and counterintuitive aspect of our analysis is that this synergistic effect of thermal shielding results in *an overall net carbon burial increase* (Fig. 4), which is contrary to general assumptions of increasing carbon loss as a function of enhanced mineralization under climate warming (Gudasz et al. 2010). Globally lakes are estimated to bury 50 Tg C yr^{-1} ($\pm$ 20 Tg C yr^{-1} or $\pm$ 40%; Cole et al. 2007). When we sum the most extreme bottom-cooling and prolonged anoxia scenario and correct for loss due to methanogenesis (Fig. 3, Supporting Information Table S3), we estimate an additional net burial of 4.5 Tg C yr^{-1}, or 9% of global total as an upper bound, and this from shallow lakes in the boreal and temperate regions only. Of course, our lower-bound estimate of 0.22 Tg C yr^{-1} would suggest a rather minor effect, thus we acknowledge that there is still a great degree of uncertainty around our estimates, all of which are based on metabolic equations that themselves have modest predictability (Gudasz et al. 2010; Yvon-Durocher et al. 2011). Regardless, we argue that our first-order estimates suggest a clear direction and a plausible range of effects for the importance of thermal shielding on lake carbon dynamics that should tested more carefully.

It should be noted that our calculations of the synergistic effects of warming and transparency loss focused on the changes in bottom water temperature and oxygen alone. Other factors that will result as a function of these effects not addressed in this analysis may additionally alter carbon dynamics. For example, climate warming will also affect water
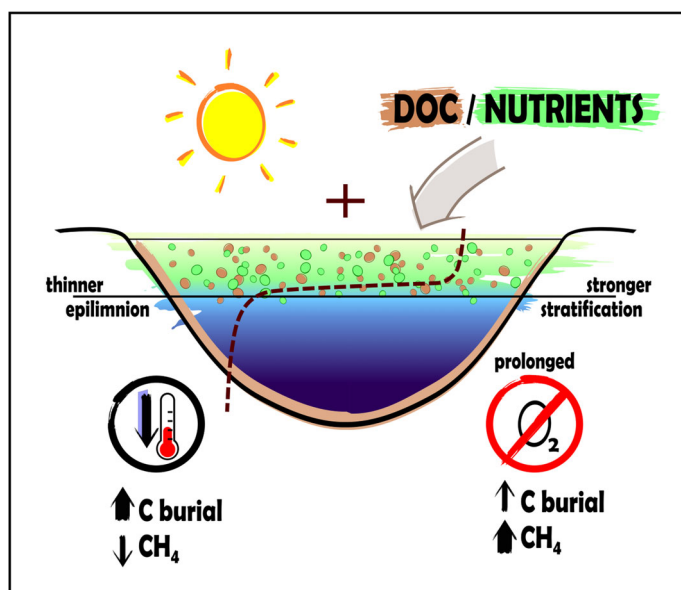

Fig. 4. Effects of climate change on temperature and oxygen stratification in lakes losing and retaining water transparency. In contrast to clear water lakes, green or brown lakes may develop a "thermal shield" that reduces epilimnion thickness and leads to a relative cooling, as well as deoxygenation of bottom waters that influence overall carbon transformation.

residence time by changing lake-mixing regimes. A recent study suggests an overall reduction in lake mixing, where polymictic systems would become dimictic, even monomictic with climate change (Woolway and Merchant 2019), thus increasing the water residence time of the hypolimnion, which would further enhance carbon burial to the sediments (Catalan et al. 2016). The combined effect of climate warming and transparency loss would in fact exacerbate this issue. Another element we did not consider is the potential increase in OM delivery to sediments anticipated in lakes that are either browning or becoming more eutrophic (Heathcote and Downing 2012; Anderson et al. 2014; Isidorova et al. 2016). Therefore, our estimates should be considered conservative. Furthermore, feedbacks through prolonged anoxia, where nutrient rich anoxic bottom waters would stimulate phytoplankton growth (Bartosiewicz et al. 2016; Creed et al. 2018; Deng et al. 2018), may result in sequestering even more carbon to the sediments then is currently being suggested.

It is difficult to disentangle the full nature of the effects of a thinner epilimnion, the increased stability of the water column, and prolonged anoxia as a function of thermal shielding and climate warming, as there will be multiple cascading effects on nutrient availability and food web structure that will alter ecosystem functioning (Molot et al. 2014; Urrutia-Cordero et al. 2016). Even in our own analysis, we fully recognize that cooling temperatures and longer periods of anoxia are co-occurring in the bottom-waters; however, our estimates do not correct for how carbon processing is influenced via

these interacting changes. Thus, our values must not be taken as absolute but as first-order estimates.

The notion that climate change can result in increasing carbon burial has been suggested by others (Clow et al. 2015; Heathcote et al. 2015), challenging the previously held assumption that lakes were losing more carbon due to warming (Gudasz et al. 2010). This study, however, provides a mechanistic explanation as to how anthropogenic factors synergistically affect differential carbon processing rates, that results in this observed overall enhanced burial (Fig. 2). Our work not only supports recent broad scale findings, but reconciles that losses may not be occurring since most lakes that show hot tops may, in fact, hide a cold bottom. Indeed, if we upscale the $1 \, \text{g C m}^{-2} \, \text{yr}^{-1}$ per 1°C reported for carbon burial in Heathcote et al. (2015) to the total surface area of temperate and boreal lakes (75% of global total), and assume a warming of 4°C, this would result in an increased carbon burial by $11.45 \, \text{Tg C yr}^{-1}$ for all lakes in those regions, or $3.7 \, \text{Tg C yr}^{-1}$ for shallow lakes only. This value is close to the one derived here using first principles (i.e., $4.5 \, \text{Tg C yr}^{-1}$). As described above, both numbers may still be underestimates as effects of land use change and increasing OM deposition to sediments of lakes in temperate regions will likely exacerbate burial even further.

Increased CH_4 production from lakes as a function of climate warming (Marotta et al. 2014) and eutrophication (Del Sontro et al. 2018; Sepulveda-Jauregui et al. 2018) has also been previously reported. However, our results suggest that this will be more a function of prolonged anoxia (and potentially an increase in OM deposition) rather than system warming. In fact, our approach supported that bottom cooling reduced methanogenesis. However, the net effect in shallow lakes was higher overall CH_4 production due to changes in redox conditions. Enhanced methanogenesis as a function of prolonged anoxia reduced overall net carbon burial, but increased the estimated net GWP (*see* Supporting Information S5 for details) from diffuse methane emissions. Part of this additional CH_4 will be oxidized before reaching the surface (Bastviken et al. 2008); therefore, it is unclear what proportion of this production will actually reach the atmosphere. However, at least in shallow lakes, enhanced evasion is probable.

The additional CH_4 diffusion from shallow lakes estimated here ($0.75 \, \text{Tg CH}_4 \, \text{yr}^{-1}$) would increase the current global lake emissions of $9.7 \, \text{Tg CH}_4 \, \text{yr}^{-1}$ (CV = 210% (CV is coefficient of variation); Bastviken et al. 2011) by 8%, and generate an additional $25 \, \text{Tg CO}_2$ equivalents yr^{-1} in terms of GWP. However, when we considered the additional carbon burial in sediments which would reduce overall GWP, the net effect is offset to $8 \, \text{Tg CO}_2$ equivalents yr^{-1}. When we repeated the same calculations for deeper lakes (5–20 m; Fig. 3), we found the net effect of prolonged anoxia on GWP to be more pronounced. The additional amount of CH_4 produced as a function of prolonged anoxia would be about $0.55 \, \text{Tg CH}_4 \, \text{yr}^{-1}$,

but since cooling effects on carbon burial are less pronounced, the net increase in GWP would be stronger, at $15 \, \text{Tg CO}_2$ equivalents yr^{-1}.

Summary and knowledge gaps

In this study, we developed a process-based understanding and provided first-order estimates of different carbon transformations in shallow lakes that are both warming and losing transparency across boreal and temperate biomes. These changes result in the earlier onset and prolonged stratification leading to colder lake bottoms and an extended period of anoxia, which in turn influences carbon cycling (Fig. 4). Our findings provide a mechanistic explanation for the observed increase in carbon burial in lakes, through a reduction in processing associated to bottom cooling and prolonged anoxia. While our results support the predicted increase in CH_4 emissions and a higher GWP of gases emitted from lakes in the future, they also underscore that enhanced benthic CH_4 production should be attributed to prolonged anoxia rather than to direct warming effects. Our first-order estimates, however, suggest that this production in terms of GWP is apparently considerably offset by enhanced burial, particularly in shallow lakes.

Although this study provides a first attempt to understand and quantify the interacting effects of climate change and transparency loss on carbon processing in lakes, many gaps remain. First, there is a considerable amount of variability as to the extent in which bottom waters are cooling due to thermal shielding among lakes (Fig. 1). Identifying the relative importance of how different morphometric, land use and landscape features influence water column stability, sediment exposure, and nutrient exchange between strata, among lake types, and across different regions would enable a better understanding of how broadly lakes are responding to the synergistic effects of transparency loss and climate change. In this context, lake size and shape will influence stratification, water residence time, and mixing regimes, and as a consequence the amount of sediment exposed to colder hypolimnia. Indeed, smaller systems and artificially created ones particularly in agricultural regions are known to play a disproportionately important role in both carbon burial and greenhouse gas production (Downing et al. 2008; Ollivier et al. 2018), likely due to their higher sediment to volume ratios, as well as their relatively higher lake productivity as a function of land cover change (Anderson et al. 2013). While our results support that small, shallow lakes may respond more to shielding effects than deeper systems, the exact strength of the synergetic effects of atmospheric warming and anthropogenic eutrophication or browning on carbon burial and methane fluxes as a function of broader morphometric features across climatic regions remains to be determined.

The magnitude and pathways of carbon transformation and sequestration between lakes that are browning vs. those

that are greening will also likely differ given differences in DOM origin and composition (Wachenfeldt and Tranvik 2008). However, our understanding of how differences in OM quality influence carbon transformations with regards to the synergistic effects of transparency loss and climate is poor. Stronger summertime stratification and prolonged anoxia will lead to higher production and proliferation of blooms due to enhanced P, Fe, and ammonium inputs from sediment stores (Molot et al. 2010; Bartosiewicz et al. 2016) and increase the availability of contaminants to the food web (MacMillan et al. 2015). Furthermore, lakes that are browning tend to become more eutrophic as nutrients, entering concomitantly with cDOM, stimulate primary production (Creed et al. 2018). This stimulation, however, will work only to a certain point, since reduced light conditions will quickly limit phytoplankton growth in brown lakes (Seekell et al. 2015). In green lakes, phytoplankton can also become light-limited, but in this case via self-shading at very high biomass concentrations. Thus, biomass production may result in a higher net overall burial in eutrophic systems compared to ones that are browning, but methane production may also increase at a higher rate (Del Sontro et al. 2018). The full extent of how OM quantity and quality influence the relative carbon dynamics and GWP in green vs. brown lakes experiencing thermal shielding remains to be fully explored.

Exciting future research directions should include a more comprehensive evaluation of interacting anthropogenic effects on the biophysical structuring of lakes that ultimately influences their ecosystem functioning. In the case of transparency loss and climate warming, particular attention should be given to evaluate direct effects of increasing OM deposition and its quality on benthic carbon burial as a function of cooling temperatures, and CH_4 production as a function of more reduced conditions in the sediments. Feedbacks of nutrient resuspension on carbon dynamics between lakes that are browning vs. those that are becoming more eutrophic may be of considerable interest since they are likely to respond differently due to changing light conditions and differences in carbon quality. Given the crucial role of lakes in the global carbon and greenhouse gas cycles, our study provides some new considerations for future research that should validate potential synergistic effects of transparency loss and climate change in waters that are greening and browning around the globe.

References

Anderson, N. J., R. D. Dietz, and D. R. Engstrom. 2013. Land-use change, not climate, controls organic carbon burial in lakes. Proc. R. Soc. B Biol. Sci. **280**: 20131278. doi:10.1098/rspb.2013.1278

Anderson, N. J., H. Bennion, and A. F. Lotter. 2014. Lake eutrophication and its implications for organic carbon sequestration in Europe. Glob. Chang. Biol. **20**: 2741–2751. doi:10.1111/gcb.12584

Bartosiewicz, M., I. Laurion, and S. MacIntyre. 2015. Greenhouse gas emission and storage in a small shallow lake. Hydrobiologia **757**: 101–115. doi:10.1007/s10750-015-2240-2

Bartosiewicz, M., I. Laurion, F. Clayer, and R. Maranger. 2016. Heat-wave effects on oxygen, nutrients, and phytoplankton can alter global warming potential of gases emitted from a small shallow lake. Environ. Sci. Technol. **50**: 6267–6275. doi:10.1021/acs.est.5b06312

Bastviken, D., J. J. Cole, M. L. Pace, and M. C. Van de Bogert. 2008. Fates of methane from different lake habitats: Connecting whole-lake budgets and CH_4 emissions. J. Geophys. Res. Biogeosci. **113**: 1–13. doi:10.1029/2007JG000608

Bastviken, D., L. J. Tranvik, J. A. Downing, P. M. Crill, and A. Enrich-Prast. 2011. Freshwater methane emissions offset the continental carbon sink. Science **331**: 50. doi:10.1126/science.1196808

Brookshire, J. E. N., S. Gerber, J. R. Webster, J. M. Vose, and W. T. Swank. 2011. Direct effects of temperature on forest nitrogen cycling revealed through analysis of long-term watershed records. Glob. Chang. Biol. **17**: 297–308. doi:10.1111/j.1365-2486.2010.02245.x

Canfield, D. E., and L. M. Hodgson. 1983. Prediction of Secchi disc depths in Florida lakes: Impact of algal biomass and organic color. Hydrobiologia **99**: 51–60. doi:10.1007/BF00013717

Caplanne, S., and I. Laurion. 2008. Effect of chromophoric dissolved organic matter on epilimnetic stratification in lakes. Aquat. Sci. **70**: 123–133. doi:10.1007/s00027-007-7006-0

Catalán, N., R. Marcé, D. N. Kothawala, and L. J. Tranvik. 2016. Organic carbon decomposition rates controlled by water retention time across inland waters. Nat. Geosci. **9**: 501–504. doi:10.1038/ngeo2720

Clow, D. W., S. M. Stackpoole, K. L. Verdin, D. E. Butman, Z. Zhu, D. P. Krabbenhoft, and R. G. Striegl. 2015. Organic carbon burial in lakes and reservoirs of the conterminous United States. Environ. Sci. Technol. **49**: 7614–7622. doi:10.1021/acs.est.5b00373

Cole, J., and others. 2007. Plumbing the global carbon cycle: Integrating inlands waters into the terrestrial carbon budget. Ecosystems **10**: 172–185. doi:10.1007/s10021-006-9013

Creed, I. F., and others. 2018. Global change-driven effects on dissolved organic matter composition: Implications for food webs of northern lakes. Glob. Chang. Biol. **24**: 3692–3714. doi:10.1111/gcb.14129

Cyr, H. 2012. Temperature variability in shallow littoral sediments of Lake Opeongo (Canada). Freshw. Sci. **31**: 895–907. doi:10.1899/11-099.1

Davidson, E. A., and I. A. Janssens. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature **440**: 165–173. doi:10.1038/nature04514

Del Sontro, T., J. J. Beaulieu, and J. A. Downing. 2018. Greenhouse gas emissions from lakes and impoundments: Upscaling in the face of global change. Limnol. Oceanogr.: Lett. **3**: 64–75. doi:10.1002/lol2.10073

Deng, J., H. W. Paerl, B. Qin, Y. Zhang, G. Zhu, E. Jeppesen, Y. Cai, and H. Xu. 2018. Climatically-modulated decline in wind speed may strongly affect eutrophication in shallow lakes. Sci. Total Environ. **645**: 1361–1370. doi:10.1016/j.scitotenv.2018.07.208

Descy, J. P., C. S. Reynolds, and J. Padisak [eds.]. 1994, *Phytoplankton in turbid environments: Rivers and shallow lakes. Developments in hydrobiology*. (Reprinted from Hydrobiologia), v. **100**. Kluwer Academic Publishers. doi:10.1007/978-94-017-2670-2

DeStasio, and others. 1996. Potential effects of global climate change on small north-temperate lakes: Physics, fish, and plankton. Limnol. Oceanogr. **41**: 1136–1149. doi:10.4319/lo.1996.41.5.1136

Dodds, W. K., W. W. Bouska, J. L. Eitzmann, T. J. Pilger, K. L. Pitts, A. J. Riley, J. T. Schloesser, and D. J. Thornbrugh. 2009. Eutrophication of US freshwaters: Analysis of potential economic damages. Environ. Sci. Technol. **43**: 12–19. doi:10.1021/es801217q

Downing, J. A., and others. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnol. Oceanogr. **51**: 2388–2397. doi:10.4319/lo.2006.51.5.2388

Downing, J. A., J. J. Cole, J. J. Middelburg, R. G. Striegl, C. M. Duarte, P. Kortelainen, Y. T. Prairie, and K. A. Laube. 2008. Sediment organic carbon burial in agriculturally eutrophic impoundments over the last century. Global Biogeochem. Cycles **22**: 1–10. doi:10.1029/2006GB002854

Finkel, Z. V. 2001. Light absorption and size scaling of light-limited metabolism in marine diatoms. Limnol. Oceanogr. **46**: 86–94. doi:10.4319/lo.2001.46.1.0086

Finlay, K., R. J. Vogt, M. J. Bogard, B. Wissel, B. M. Tutolo, G. L. Simpson, and P. R. Leavitt. 2015. Decrease in CO_2 efflux from northern hard-water lakes with increasing atmospheric warming. Nature **519**: 215–218. doi:10.1038/nature14172

Finstad, A. G., T. Andersen, S. Larsen, K. Tominaga, S. Blumentrath, H. A. de Wit, H. Tømmervik, and D. O. Hessen. 2016. From greening to browning: Catchment vegetation development and reduced S-deposition promote organic carbon load on decadal time scales in Nordic lakes. Sci. Rep. **6**: 1–8. doi:10.1038/srep31944

Gudasz, C., D. Bastviken, K. Steger, K. Premke, S. Sobek, and L. J. Tranvik. 2010. Temperature-controlled organic carbon mineralization in lake sediments. Nature **466**: 478–483. doi:10.1038/nature09186

Hartnett, H. E., R. G. Keil, J. I. Hedges, and A. H. Devol. 1998. Influence of oxygen exposure time on organic carbon preservation in continental margin sediments. Nature **391**: 572–575. doi:10.1038/35351

Havens, K. E., and H. W. Paerl. 2015. Climate change at a crossroad for control of harmful algal blooms. Environ. Sci. Technol. **49**: 12605–12606. doi:10.1021/acs.est.5b03990

Heathcote, A. J., and J. A. Downing. 2012. Impacts of eutrophication on carbon burial in freshwater lakes in an intensively agricultural landscape. Ecosystems **15**: 60–70. doi:10.1007/s10021-011-9488-9

Heathcote, A. J., N. J. Anderson, Y. T. Prairie, D. R. Engstrom, and P. A. Del Giorgio. 2015. Large increases in carbon burial in northern lakes during the Anthropocene. Nat. Commun. **6**: 10016. doi:10.1038/ncomms10016

Houser, N. J. 2006. Water color affects the stratification, surface temperature, heat content, and mean epilimnetic irradiance of small lakes. Can. J. Fish. Aquat. Sci. **63**: 2447–2455. doi:10.1007/s10021-015-9848-y

Isidorova, A., A. G. Bravo, G. Riise, S. Bouchet, E. Björn, and S. Sobek. 2016. The effect of lake browning and respiration mode on the burial and fate of carbon and mercury in the sediment of two boreal lakes. J. Geophys. Res. Biogeosci. **121**: 233–245. doi:10.1002/2015JG003086

Jensen, S. H., and F. O. Andersen. 1992. Importance of temperature, nitrate, and pH for phosphate release from aerobic sediments of four shallow, eutrophic lakes. Limnol. Oceanogr. **37**: 577–589. doi:10.4319/lo.1992.37.3.0577

Jones, I., G. George, and C. Reynolds. 2005. Quantifying effects of phytoplankton on the heat budgets of two large limnetic enclosures. Freshw. Biol. **50**: 1239–1247. doi:10.1111/j.1365-2427.2005.01397.x

Kirillin, G. 2010. Modeling the impact of global warming on water temperature and seasonal mixing regimes in small temperate lakes. Boreal Environ. Res. **15**: 279–293.

Kirillin, G., J. Hochschild, D. Mironov, A. Terzhevik, S. Golosov, and G. Nützmann. 2011. FLake-Global: Online lake model with worldwide coverage. Environ. Model. Softw. **26**: 683–684. doi:10.1016/j.envsoft.2010.12.004

Koven, C. D., B. Ringeval, P. Friedlingstein, P. Ciais, P. Cadule, D. Khvorostyanov, G. Krinner, and C. Tarnocai. 2011. Permafrost carbon-climate feedbacks accelerate global warming. Proc. Natl. Acad. Sci. USA **108**: 14769–14774. doi:10.1073/pnas.1103910108

Kraemer, B. M., and others. 2015. Morphometry and average temperature affect lake stratification responses to climate change. Geophys. Res. Lett. **42**: 4981–4988. doi:10.1002/2015GL064097

Kritzberg, E. S. 2017. Centennial-long trends of lake browning show major effect of afforestation. Limnol. Oceanogr.: Lett. **2**: 105–112. doi:10.1002/lol2.10041

Kumagai, M., and others. 2000. Effect of cyanobacterial blooms on thermal stratification. Limnology **1**: 191–195. doi:10.1007/s102010070006

Leech, D. M., A. I. Pollard, S. G. Labou, and S. E. Hampton. 2018. Fewer blue lakes and more murky lakes across the continental US: Implications for planktonic food webs. Limnol. Oceanogr. **63**: 2661–2680. doi:10.1002/lno.10967

MacMillan, G. A., C. Girard, J. Chételat, I. Laurion, and M. Amyot. 2015. High methylmercury in Arctic and subarctic ponds is related to nutrient levels in the warming eastern Canadian Arctic. Environ. Sci. Technol. **49**: 7743–7753. doi:10.1021/acs.est.5b00763

Marotta, H., L. Pinho, C. Gudasz, D. Bastviken, L. J. Tranvik, and A. Enrich-Prast. 2014. Greenhouse gas production in low-latitude lake sediments responds strongly to warming. Nat. Clim. Change **4**: 467–470. doi:10.1038/nclimate2222

Mazumder, A., and W. D. Taylor. 1994. Thermal structure of lakes varying in size and water clarity. Limnol. Oceanogr. **39**: 968–976. doi:10.4319/lo.1994.39.4.0968

Michelutti, N., and others. 2005. Recent primary production increases in arctic lakes. Geophys. Res. Lett. **32**: L19715. doi:10.1029/2005GL023693

Mironov, D., N. Schneider, B. Ritter, and E. Heise. 2005. Implementation of a Lake Model FLake into the Limited-Area NWP System LM of the German Weather Service: Preliminary results, p. 4–15. Research activities in atmospheric and oceanic modelling. Report no. 35.

Mironov, D. V. 2008. Parameterization of lakes in numerical weather prediction. Description of a lake model, p. 41. COSMO Technical Report no. 11, Deutscher Wetterdienst.

Molot, L. A., G. Li, D. L. Findlay, and S. B. Watson. 2010. Iron-mediated suppression of bloom-forming cyanobacteria by oxine in a eutrophic lake. Freshw. Biol. **55**: 1102–1117. doi:10.1111/j.1365-2427.2009.02384.x

Molot, L. A., and others. 2014. A novel model for cyanobacteria bloom formation: The critical role of anoxia and ferrous iron. Freshw. Biol. **59**: 1323–1340. doi:10.1111/fwb.12334

Monteith, D. T., and others. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature **450**: 537–540. doi:10.1038/nature06316

Moss, B., and others. 2011. Allied attack: Climate change and eutrophication. Inland Waters **1**: 101–105. doi:10.5268/IW-1.2.359

Nürnberg, G. K. 1995. Quantifying anoxia in lakes. Limnol. Oceanogr. **40**: 1100–1111. doi:10.4319/lo.1995.40.6.1100

O'Reilly, C. M., and others. 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophys. Res. Lett. **42**: 773–781. doi:10.1002/2015GL066235

Ollivier, Q. R., D. T. Maher, C. Pitfield, and P. I. Macreadie. 2018. Punching above their weight: Large release of greenhouse gases from small agricultural dams. Glob. Chang. Biol. **25**: 721–732. doi:10.1111/gcb.14477

Peeters, F., D. Straile, A. Lorke, and D. M. Livingstone. 2007. Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. Glob. Chang. Biol. **13**: 1898–1909. doi:10.1111/j.1365-2486.2007.01412.x

Pernica, P., and M. Wells. 2012. Frequency of episodic stratification in the near surface of Lake Opeongo and other small lakes. Water Qual. Res. J. **47**: 227–237. doi:10.2166/wqrjc.2012.001

Read, J., and K. C. Rose. 2013. Physical responses of small temperate lakes to variation in dissolved organic carbon concentrations. Limnol. Oceanogr. **58**: 921–931. doi:10.4319/lo.2013.58.3.0921

Rose, K. C., L. A. Winslow, J. S. Read, and G. J. A. Hansen. 2016. Climate induced warming of lakes can be either amplified or suppressed by trends in water clarity. Limnol. Oceanogr.: Lett. **1**: 44–53. doi:10.1002/lol2.10027

Rueda, F. J., and S. MacIntyre. 2010. Modelling the fate and transport of negatively buoyant storm–river water in small multi-basin lakes. Environ. Model. Softw. **25**: 146–157. doi:10.1016/j.envsoft.2009.07.002

Seekell, D. A., J. F. Lapierre, and J. Karlsson. 2015. Trade-offs between light and nutrient availability across gradients of dissolved organic carbon concentration in Swedish lakes: Implications for patterns in primary production. Can. J. Fish. Aquat. Sci. **72**: 1663–1671. doi:10.1139/cjfas-2015-0187

Sepulveda-Jauregui, A., J. Hoyos-Santillan, K. Martinez-Cruz, K. M. Walter Anthony, P. Casper, Y. Belmonte-Izquierdo, and F. Thalasso. 2018. Eutrophication exacerbates the impact of climate warming on lake methane emission. Sci. Total Environ. **636**: 411–419. doi:10.1016/j.scitotenv.2018.04.283

Shatwell, T., R. Adrian, and G. Kirillin. 2016. Planktonic events may cause polymictic-dimictic regime shifts in temperate lakes. Sci. Rep. **6**: 24361. doi:10.1038/srep24361

Shaver, G. R., and S. Jonasson. 1999. Response of arctic ecosystems to climate change: Result of long-term field experiments in Sweden and Alaska. Polar Res. **18**: 245–256. doi:10.1111/j.1751-8369.1999.tb00300.x

Shaver, G. R., and others. 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis. Bioscience **50**: 871–882. doi:10.1641/0006-3568

Sobek, S., E. Durisch-Kaiser, R. Zurbrügg, N. Wongfun, M. Wessels, N. Pasche, and B. Wehrli. 2009. Organic carbon burial efficiency in lake sediments controlled by oxygen exposure time and sediment source. Limnol. Oceanogr. **54**: 2243–2254. doi:10.4319/lo.2009.54.6.2243

Solomon, C. T., and others. 2015. Ecosystem consequences of changing inputs of terrestrial dissolved organic matter to lakes: Current knowledge and future challenges. Ecosystems **18**: 376–389. doi:10.1007/s10021-015-9848-y

Søndergaard, M., J. P. Jensen, and E. Jeppesen. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. Hydrobiologia **506**: 135–145. doi:10.1023/B:HYDR.0000008611.12704.dd

Strock, K. E., N. Theodore, W. G. Gawley, A. C. Ellsworth, and J. E. Saros. 2017. Increasing dissolved organic carbon concentrations in northern boreal lakes: Implications for lake water transparency and thermal structure. J. Geophys. Res. Biogeosci. **122**: 1022–1035. doi:10.1002/2017JG003767

Thiery, W., E. L. Davin, S. I. Seneviratne, K. Bedka, S. Lhermitte, and N. P. van Lipzig. 2016. Hazardous thunderstorm intensification over Lake Victoria. Nat. Commun. **7**: 12786. doi:10.1038/ncomms12786

Tilzer, M. M. 1988. Secchi disk—chlorophyll relationships in a lake with highly variable phytoplankton biomass. Hydrobiologia **162**: 163–171. doi:10.1007/BF00014539

Tranvik, L. J., and others. 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnol. Oceanogr. **54**: 2298–2314. doi:10.4319/lo.2009.54.6_part_2.2298

Urrutia-Cordero, P., M. K. Ekvall, and L. A. Hansson. 2016. Local food web management increases resilience and buffers against global change effects on freshwaters. Sci. Rep. **6**: 29542. doi:10.1038/srep29542

Wachenfeldt, E., and L. J. Tranvik. 2008. Sedimentation in boreal lakes—the role of flocculation of allochthonous dissolved organic matter in the water column. Ecosystems **11**: 803–814. doi:10.1007/s10021-008-9162-z

Weyhenmeyer, G. A., R. A. Muller, M. Norman, and L. J. Tranvik. 2016. Sensitivity of freshwaters to browning in response to future climate change. Clim. Change **134**: 225–239. doi:10.1007/s10584-015-1514-z

Williamson, C. E., and others. 2009. Lakes and reservoirs as sentinels, integrators, and regulators of climate change. Limnol. Oceanogr. **54**: 2273–2282. doi:10.4319/lo.2009.54.6_part_2.2273

Williamson, C. E., E. P. Overholt, R. M. Pilla, T. H. Leach, J. A. Brentrup, L. B. Knoll, E. M. Mette, and R. E. Moeller. 2015. Ecological consequences of long-term browning in lakes. Sci. Rep. **5**: 18666. doi:10.1038/srep18666

Winslow, L. A., J. S. Read, G. J. A. Hansen, and P. C. Hanson. 2015. Small lakes show muted climate change signal in deepwater temperatures. Geophys. Res. Lett. **42**: 355–361. doi:10.1002/2014GL062325

Woolway, R. I., and C. J. Merchant. 2019. Worldwide alteration of lake mixing regimes in response to climate change. Nat. Geosci. **12**: 271–276. doi:10.1038/s41561-019-0322-x

Yvon-Durocher, G., A. P. Allen, J. M. Montoya, M. Trimmer, and G. Woodward. 2010*a*. The temperature dependence of the carbon cycle in aquatic ecosystems. Adv. Ecol. Res. **43**: 267–313. doi:10.1016/B978-0-12-385005-8.00007-1

Yvon-Durocher, G., J. I. Jones, M. Trimmer, G. Woodward, and J. M. Montoya. 2010*b*. Warming alters the metabolic balance of ecosystems. Philos. Trans. R. Soc. B **365**: 2117–2126. doi:10.1098/rstb.2010.0038

Yvon-Durocher, G., J. M. Montoya, M. Trimmer, and G. Woodward. 2011. Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. Glob. Chang. Biol. **17**: 1681–1694. doi:10.1111/j.1365-2486.2010.02321.x

Yvon-Durocher, G., A. P. Allen, D. Bastviken, R. Conrad, C. Gudasz, A. St-Pierre, N. Thanh-Duc, and P. A. del Giorgio. 2014. Methane fluxes show consistent temperature dependence across microbial to ecosystem scales. Nature **507**: 488–491. doi:10.1038/nature13164