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LETTER

Winter inverse lake stratification under historic and future climate change

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Scientific Significance Statement

Much of the focus of climate change impacts on lakes has concentrated on the summer period with, for example, previous studies suggesting a lengthening of the summer stratified season. However, lakes are also exposed, and respond dramatically, to rapidly warming winters. Indeed, lake ecosystems and the organisms that live within them are influenced by physical and biogeochemical processes that occur during this comparatively understudied time of year. One of the most important physical processes that occurs in winter is inverse stratification. Here, we show that climate change leads to a shortening of the winter stratified period with some lakes no longer inversely stratifying by the end of this century. Changes in inverse stratification could trigger a chain of reactions in lakes, with implications for biodiversity.

Abstract

Millions of lakes inversely stratify during winter. Seemingly subtle variations in the duration of winter stratification can have major ecological effects by, for example, altering the vertical distribution of oxygen and nutrients in lakes. Yet, the influence of climate change on winter stratification has been largely unexplored. To fill this knowledge gap, here we used a lake-climate model ensemble to investigate changes in winter stratification from 1901 to 2099 across 12,242 representative lakes situated throughout the Northern Hemisphere. By the end of the 21st century, winter stratification duration is projected to shorten by an average of 18.5–53.9 d under Representative Concentration Pathways (RCPs) 2.6–8.5. Projected changes are faster in warmer geographical regions, in which 35–69% of lakes will no longer inversely stratify by 2070–2099 under RCPs 2.6–8.5. This shortening and loss of winter stratification will likely have numerous implications for lakes, including the misalignment of lifecycle events causing shifts in biodiversity.

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Author Contribution Statement: BD and RIW initiated the project with input from GAW and JJ. ZT provided the lake temperature projections. SLF contributed to data analysis. RIW led the design of visualizations, data analysis, and led the writing of the manuscript with input from all co-authors. All authors participated in discussions, revisions, and the final production of this manuscript.

Data Availability Statement: All raw model simulations are available at https://esg.pik-potsdam.de and the processed data are available at https://doi.org/10.5281/zenodo.5707929

Additional Supporting Information may be found in the online version of this article.

Stratification is a common and highly relevant phenomenon occurring in millions of lakes (Boehrer and Schultze 2008; Woolway et al. 2021). It is a strong driver for nutrient, energy, and oxygen availability, thereby being a key factor for the abundance and biomass of lake organisms. The seasonal cycle of stratification typically starts during the spring–summer period, where the stratifying effect of surface heat input out-competes vertical mixing, leading to a stratified regime developing in all but very shallow systems. This stable regime continues until the autumn period, when lakes start to lose heat to the atmosphere and both wind-stress and surface heat loss act to erode stratification and induce the autumnal overturn. Thereafter, a lake can either remain mixed until net surface heating resumes in the following spring or, if surface water temperatures cool below $\sim$4°C, the lake can become inversely stratified during winter. Inverse stratification (hereafter referred to as winter stratification) occurs as freshwater becomes less dense when temperatures cool below $\sim$4°C, which results in the vertical layering of the water column. This seasonal feature of stratification is common in over half of the world's lakes that experience ice cover (Hampton et al. 2017; Sharma 2019), but also in milder climatic regions where lakes do not freeze but surface temperatures cool below 4°C (Woolway et al. 2019).

The duration of winter stratification can have far reaching implications for lake ecosystems by, for example, altering the interactions between surface and bottom waters during winter and influencing the spatiotemporal (re)distribution of solutes (Jansen et al. 2021). A decoupling between surface and bottom waters in winter can alter dissolved oxygen concentrations at depth (Livingstone 1997; Rempfer et al. 2010) with implications for, among other things, internal phosphorus loading (Tammeorg et al. 2020) and the production and retention of potent greenhouse gases (Kortelainen et al. 2006; Bastviken et al. 2011). Importantly, a prolonged decoupling between lake ecosystem processes at the surface and at depth can influence temperature, light, and nutrient regimes, some of the key rules of life in lake ecosystems (Elser et al. 2020). Many lakes that are inversely stratified in winter are also ice covered, where ice further impacts stratification by reducing water mixing, atmospheric exchange, and light availability (Prowse et al. 2012). Understanding the thermal environment of lakes during the typically understudied winter season is therefore critical for anticipating the repercussions of climatic variations on lakes.

Due to its importance, winter stratification has been studied in individual lakes (Bruesewitz et al. 2015; Yang et al. 2020; Yang et al. 2021) but is unexplored across larger geographical regions. Furthermore, future projections of winter stratification have not yet been performed and evaluated. Indeed, our understanding of the influence of climate change on stratification during winter is considerably less than that of summer stratification (Magee and Wu 2017*a*; Shatwell et al. 2019; Ayala et al. 2020; Woolway et al. 2021) but having arguably similar ecological and biogeochemical importance. To bridge this knowledge gap, we here investigate the influence of climate change on winter stratification across the Northern Hemisphere. We analyzed daily simulations from a lake model, forced with climate data from an ensemble of 20th and 21st century climate projections, and investigated changes in the duration of winter stratification from 1901 to 2099.

Methods

Lake simulations

We evaluated the influence of climate change on winter stratification by investigating depth-resolved water temperature simulations from the ISIMIP2b (Inter-Sectoral Impact Model Intercomparison Project Phase 2b; https://www.isimip.org) Lake Sector. Most notably, we investigated lake temperature simulations generated by the 1D processed-based Arctic Lake Biogeochemistry Model (ALBM) (Tan et al. 2015, 2017, 2018; Guo et al. 2020, 2021). ALBM simulated vertical lake temperature profiles at a 0.5° × 0.5° grid resolution, based on the mean depth and surface area of all lakes within a given 0.5° grid. The dataset used to describe the size distribution of all lakes within each 0.5° grid has a horizontal resolution of 30 arc sec (Kourzeneva 2010; Choulga et al. 2014), and include all known lakes equal or greater than this size threshold. Our projections therefore represent a "typical lake" for each 0.5° pixel, notably simulating the average lake thermal environment in that location using the grid cell's climate forcing (Vanderkelen et al. 2020; Grant et al. 2021; Woolway et al. 2021)—for further details see Supporting Information Text S1. The number of "typical" lakes included in this study was 12,242. Historic (1901–2005) and future (2006–2099) climate model projections from GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-LR, and MIROC5 were used as input to ALBM. The future simulations include three climate change scenarios: Representative Concentration Pathway (RCP) 2.6 (low-emission scenario where emissions start declining at around 2020), 6.0 (medium-to-high-emission scenario where emissions peak at around 2080 and then decline), and 8.5 (high-emission scenario where emissions continue to rise throughout the 21st century). All processed data are openly available (Woolway 2021).

Definition of winter stratification and lake thermal regimes

The duration of winter stratification was calculated from the simulated lake temperatures. While there is no universal definition of stratification in lakes, water density thresholds are often used. In this study, a lake was considered stratified when a specific density difference threshold between surface and bottom waters was exceeded and, at the same time, the lake surface temperature (considered as the temperature of the first ice-free layer when ice is present) was colder than that at depth (i.e., the temperature at the deepest layer within the model). The duration of winter stratification was then calculated as the total number of days each year when inverse stratification exists. As there is little evidence to support the use of any single density threshold for defining a stratified day in lakes, in this study we use an ensemble of density thresholds (from 0.05 to 0.5 kg m^{-3} at 0.01 kg m^{-3} increments) for defining the presence of stratification (Woolway et al. 2017; Gray et al. 2020; Wilson et al. 2020). We use this ensemble to then calculate the average projected change in winter stratification across the studied sites.

To explore the main drivers of winter stratification and to identify lake types that are most susceptible to change, we separate our studied sites according to two categorization schemes defined in the literature. Firstly, we categorize our lakes according to the thermal categorization scheme of Yang et al., (2021), where ice-covered lakes are separated into cryomictic and cryostratified lakes. These winter mixing regimes are defined according to the water column average temperature at the time of ice formation (Yang et al. 2021). Cryostratified lakes exhibit winter stratification near the ice surface and have depth averaged temperatures between 2°C and 4°C, while cryomictic lakes have depth averaged temperatures between 0°C and 2°C at the time of ice formation (Yang et al. 2021). In interpreting some of our key findings, notably of future change, we also categorize our studied lakes according to the thermal regions in which they reside, following the definitions of Maberly et al. (2020). In the Northern Hemisphere, there are four primary lake thermal regions, which are referred to as Northern Frigid, Northern Cool, Northern Temperate, and Northern Warm.

Statistical methods

To investigate the spatiotemporal variation in winter stratification across our studied sites during the historic period (1970–1999), we conducted Random Forests analysis. Predictor variables included the Northern Hemisphere cold season (November to April) air temperature and wind speed, lake depth and surface area. The climatic drivers were calculated as the average across the climate model ensemble (1970–1999), that is, resulting in an average for each lake. The *randomForest* function in R (Liaw and Wiener 2002; R Core Team 2019) was used for this analysis. Random forests are based on an ensemble of decision trees (Breiman 2001). We generated 1000 trees from which we calculated variable importance to generally identify how often a predictor variable was the most important predictor in a single decision tree. We used the mean decrease in accuracy, describing the prediction error calculated by the mean squared error (MSE) on the out-of-bag portion of the data (Liaw and Wiener 2002). We also used regression trees (De'ath and Fabricius 2000) to assess the main predictors of the across-lake variability in winter stratification across Northern Hemisphere lakes. The most parsimonious regression tree was selected by pruning the tree to the level where the complexity parameter minimized the cross-validation error. We calculated the percent variation explained by the regression tree (R^2) as: $R^2 = 1 -$ relative error (Sharma et al. 2012). Regression trees were developed in R using the *rpart* and *rpart.plot* functions (Therneau and Atkinson 2019; Milborrow 2020).

Results

Winter stratification in Northern Hemisphere lakes

Our long-term simulations of daily water temperatures suggest that the duration of winter stratification during the

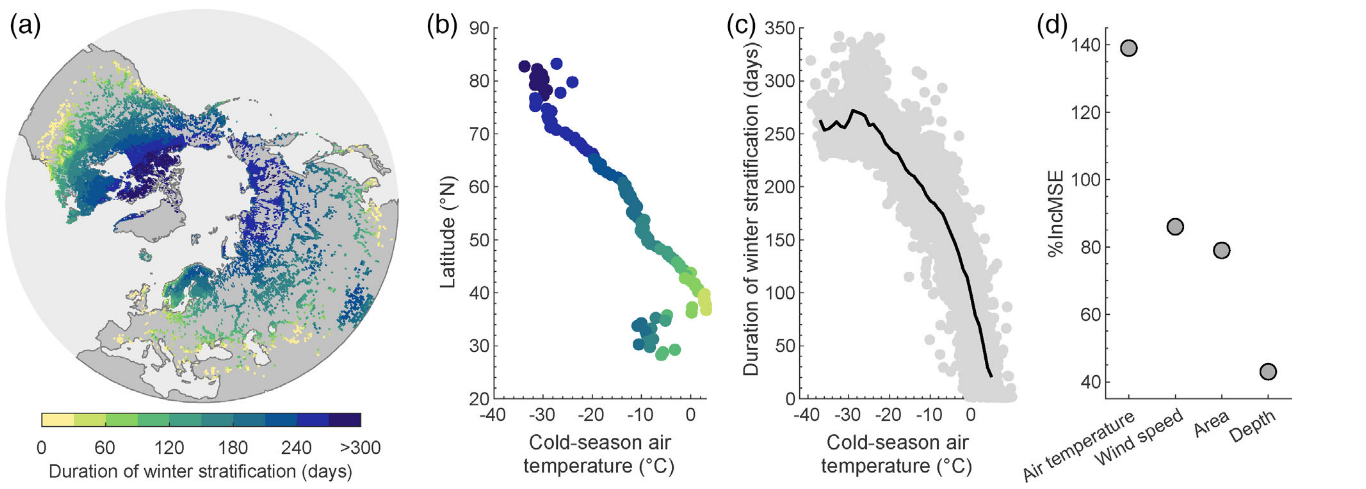

Fig. 1. Historic winter stratification duration in Northern Hemisphere lakes. Shown are the historic (1970–1999) spatial patterns in (**a**) the duration of winter stratification, and its relationship with latitude and the cold-season (November–April) average air temperature. In panel (**b**), cold-season air temperature and the duration of winter stratification (see panel (**a**) for scale) are averaged for each 0.5° latitude grid. In panel (**c**), the relationship between cold-season air temperature and the duration of winter stratification are shown for each year across the studied sites (gray points), and as averages for 1°C air temperature bins (black line). Also shown, in panel (**d**), are the results from the random forest analysis, illustrating the relative importance of the tested variables in predicting the duration of winter stratification across lakes. Variable importance is calculated as the percent increase in MSE (%IncMSE) of predictions estimated with an out-of-bag coefficient of variation as a result of variables being permuted. Higher values indicate greater importance of a predictor variable to the set of decision trees. All results are based on the average simulations across the model ensemble.

historic period (averaged here for all years from 1970 to 1999 from the lake-climate model ensemble as well as the ensemble of density thresholds) varies considerably across climatic regions (Fig. 1). We find that high latitude lakes, which are exposed to the coldest air temperatures, are inversely stratified for more than 200 d each year (Fig. 1). Our analysis also suggests that other climatic and lake morphological drivers influence the duration of winter stratification. These factors can explain some of the variability in its relationship with the cold season air temperature. For example, the cold season average wind speed plays a role in the duration of winter stratification, with lakes exposed to higher wind speeds typically experiencing a shorter winter stratified period. Also important, albeit having a relatively minimal influence across the studied sites compared to the above climatic drivers, are lake depth and surface area. When using all the predictor variables, the random forest analysis was able to explain as much as 93% of the across lake variation in the duration of stratification. The random forest analysis also described the most important predictor as the cold season air temperature, followed by the cold season wind speed, surface area, and depth, which are listed here from most to least important across our studied sites (Fig. 1d).

Among the studied sites that experience winter ice cover, our simulations indicate that 75% of lakes can be categorized as cryomictic, and the remainder as cryostratified (Fig. 2). A regression tree analysis (which explained 68% of the across lake variation) identifies average wind speed as the most important predictor of winter mixing regime (Fig. 2). Moreover, our simulations suggest that in regions with high near-surface wind speeds ($\geq$ 2.9 m s^{-1}), lakes are primarily cryomictic. Lakes in calmer regions can also be cryomictic if the lake surface area is relatively large ($\geq$ 2.9 km^2) and the average lake depth is relatively shallow (< 16 m). Cryostratified lakes are primarily situated in regions that experience low wind speeds (< 2.9 m s^{-1}) and have a relatively small surface

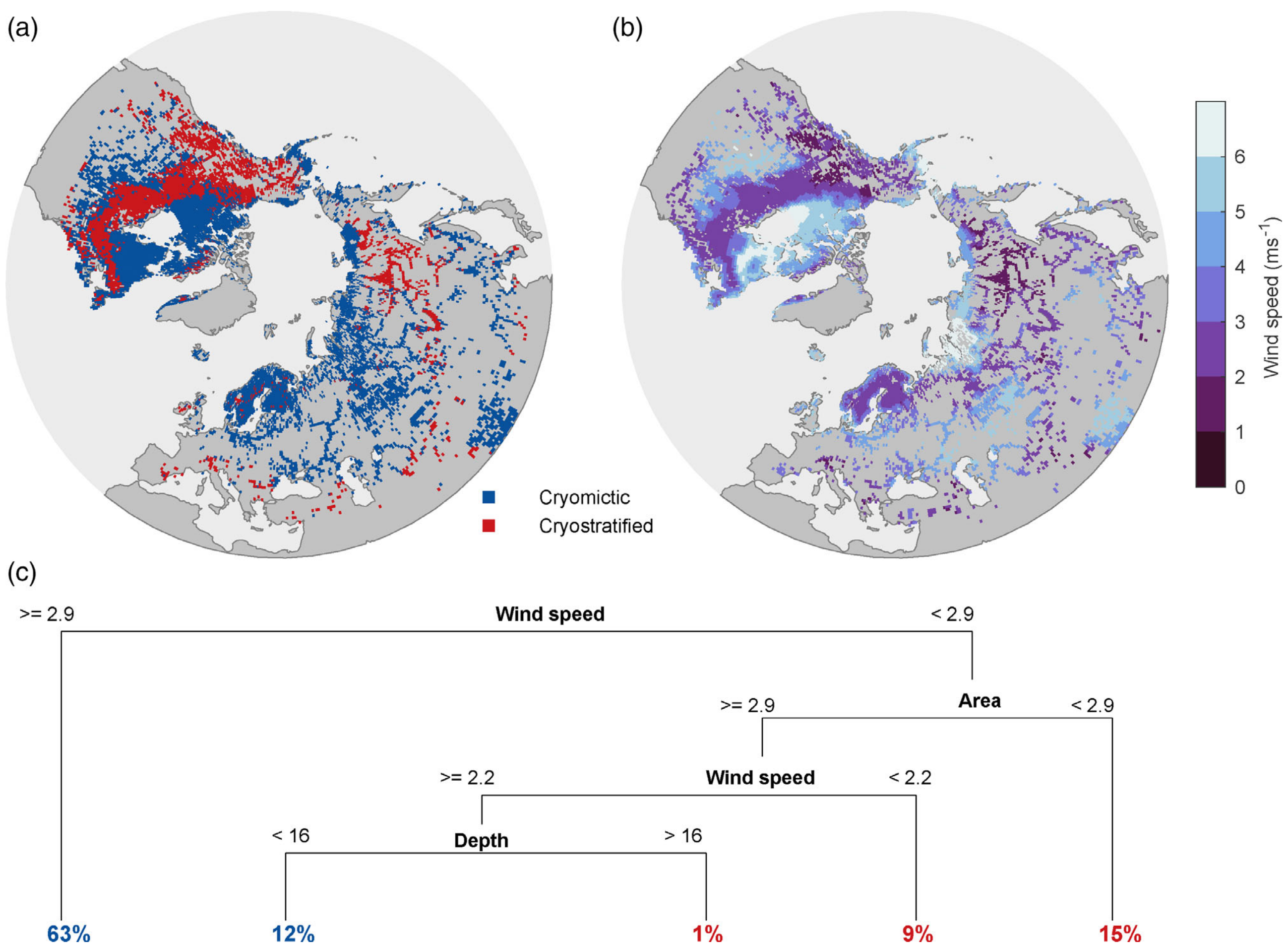

Fig. 2. Distribution of winter mixing regimes across Northern Hemisphere lakes. Shown for the historic period (1970–1999) are (**a**) the dominant winter mixing regime of the studied lakes, and (**b**) the cold season (November–April) average wind speed. Also shown, in panel (**c**), are the results from the regression tree analysis, which illustrates the main predictors of the across lake variability in winter mixing regime. The values below each of the leaves represent the percentage of the studied lakes that fall within each group.

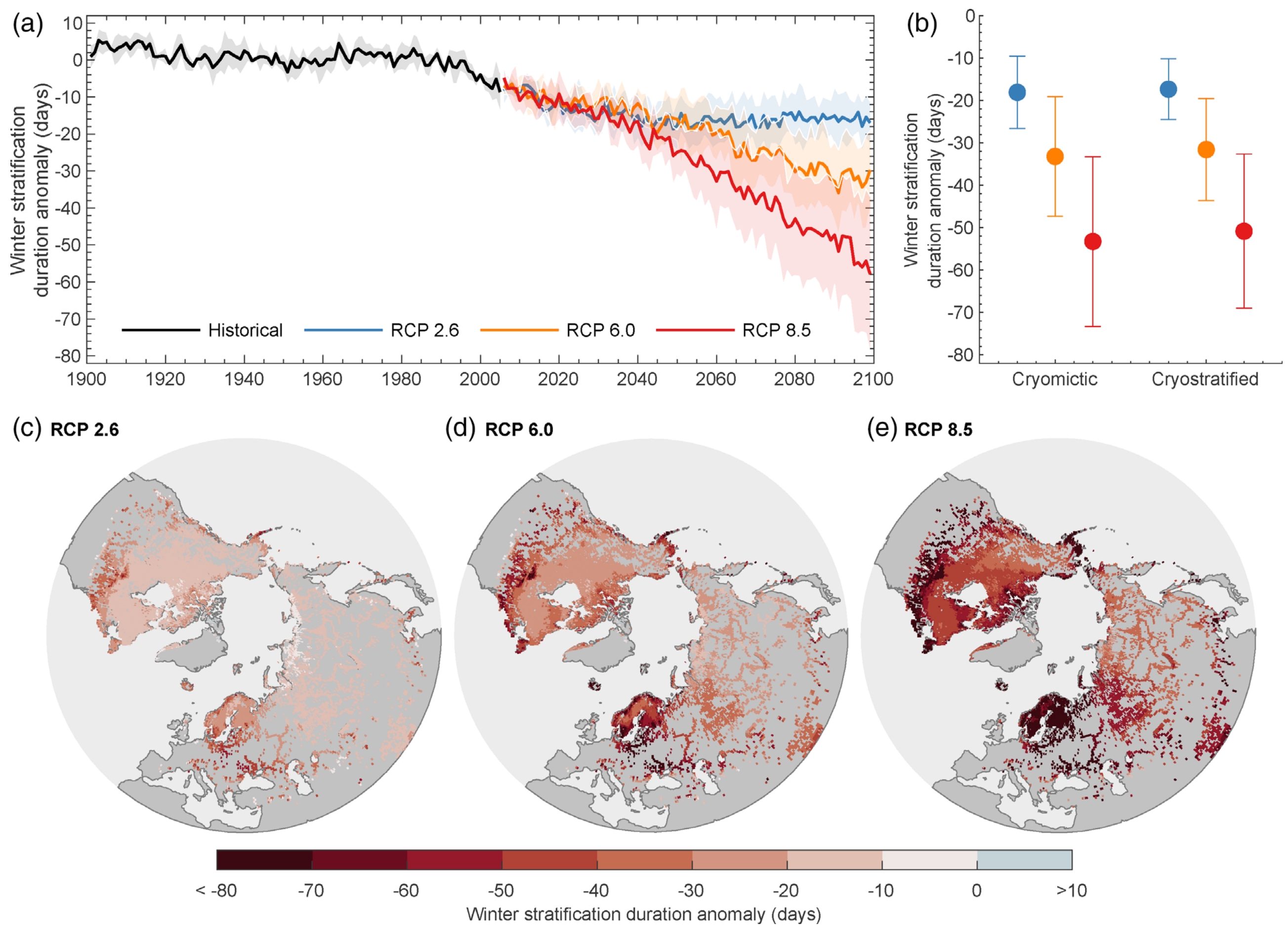

Fig. 3. Historic and future projections of winter lake stratification duration. Temporal and spatial variations in the duration of winter stratification. The temporal changes in winter stratification are shown (**a**) from 1901 to 2099 under historic (1901–2005) and future (2006–2099) climate change scenarios (RCP 2.6, 6.0, 8.5). The thick lines show the average across all lake-climate models, and the shaded regions represent the standard deviation across the ensemble. Panel (**b**) shows the average change (and standard deviation) in winter stratification duration by 2070–2099, separated by lake mixing regimes (i.e., cryomictic and cryostratified). Panels (**c**–**e**) show the spatial patterns in winter stratification duration anomalies by the end of the 21st century (2070–2099) under (**c**) RCP 2.6, (**d**) RCP 6.0, and (**e**) RCP 8.5. Anomalies are quoted relative to the 1970–1999 average. All results are based on the average simulations across the model ensemble.

area (<2.9 km^2). Our projections also suggest that a cryostratified mixing regime can occur in larger and deeper lakes situated in regions with low wind speed (Fig. 2).

Winter stratification under climate change

Our projections suggest that the duration of winter stratification will shorten during the 21st century. Under RCP 2.6, the average duration of winter stratification will be 18.5 ± 8.8 d (quoted uncertainties represent the standard deviation from the model ensemble and the ensemble of density thresholds used) shorter by the end of the 21st century (2070–2099) compared to the historic period (1970–1999), although minimal change is projected after ~ 2020, following a decline in greenhouse gas emissions. Under RCP 6.0 and 8.5, the average duration of winter stratification will be 33.3 ± 14.1 and 53.9 ± 19.9 d shorter, respectively. Our projections suggest some differences between winter stratification anomalies in cryomictic and cryostratified lakes under RCP 6.0 and 8.5, but no major differences are suggested under RCP 2.6 (Fig. 3b). We also calculate that only a relatively small number of lakes will transition to a different winter mixing regime this century. For example, under RCP 2.6–8.5, only 0.1–1% of the studied lakes will transition from cryomictic to cryostratified, and only 1–3% of lakes will transition from cryostratified to cryomictic by the end of the century (2070–2099), with all other studied lakes being categorized by their historic mixing regime.

The greatest projected change in the duration of winter stratification occurs in the warmest climatic regions. By calculating the percent change in winter stratification by 2070–2099, our simulations suggest that the relative change is greatest in the warmest lake regions (Fig. 4). Within the four

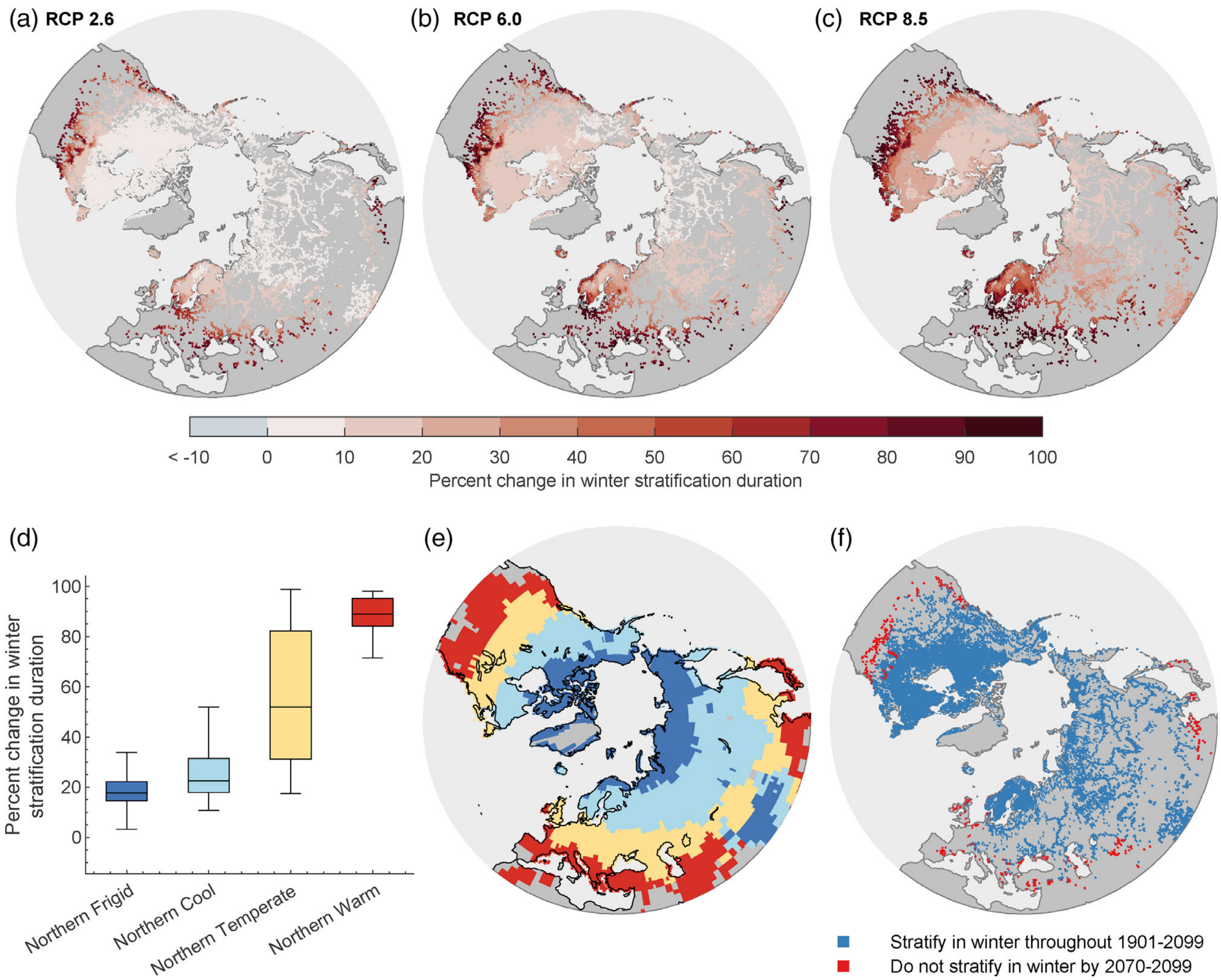

Fig. 4. Percent change in the duration of winter stratification by 2070–2099. Shown in panels (**a–c**) are the spatial patterns in the percent change in the duration of winter stratification by the end of the 21st century (2070–2099), relative to the historic period (1970–1999), under (**a**) RCP 2.6, (**b**) RCP 6.0, and (**c**) RCP 8.5. Positive values indicate a shortening of the winter stratified season. Shown in panel (**d**), are the percentage change in winter stratification averaged across the four dominant lake thermal regions in the Northern Hemisphere (the location of which are shown in (**e**) under RCP 8.5). Also shown, in panel (**f**), are the lakes which are projected to not inversely stratify by the end of this century (red), and those that are projected to experience some winter stratification throughout the study period (blue). Results in panel (**f**) are shown from the model simulations under RCP 8.5. All simulations are based on the average across the lake-climate model ensemble.

lake thermal regions that describe the climatic conditions of our studied sites, we calculate that the average percent change under RCP 2.6–8.5 will be greatest in Northern Warm lakes (63.8–88.6%), followed by Northern Temperate lakes (27.7–56.3%), and the relative change will be considerably less in the Northern Cool (9.7–28.5%) and Northern Frigid (6.5–20.4%) lakes. Furthermore, some of the largest percent changes in winter stratification occur in lakes that are projected to no longer experience winter stratification by the end of this century, that is, where their surface temperatures will not cool below 4°C. Many Northern Warm lakes will experience this transition, and no longer inversely stratify by 2070–2099. Our simulations suggest that 35%, 45%, and 69% of Northern Warm lakes that currently experience winter stratification, will no longer inversely stratify by the end of the century under RCP 2.6, 6.0, and 8.5, respectively.

Discussion

In this study, we provide the first assessment of changes in the duration of winter stratification across Northern Hemisphere lakes under future climate change. Our projections suggest that the duration of winter stratification is influenced primarily by the average air temperature during the cold season. Air temperature can influence winter stratification by (i) altering the duration of ice cover in lakes that freeze annually (Weyhenmeyer et al. 2011; Sharma 2019), and (ii) in lakes that do not freeze, it can influence the minimum surface water temperature that is reached (Woolway et al. 2019). Our analysis also suggested that wind speed, which is typically greater over larger lakes (Woolway et al. 2018) due to, among other factors, the comparatively smaller wind shielding effects (Read and others 2012), was an important predictor of winter stratification duration. Notably, lakes exposed to higher wind speeds experienced shorter stratified periods. Near-surface wind speed can influence winter stratification by either delaying ice formation and/or leading to an earlier ice break-up in lakes that freeze (Kirillin et al. 2012; Magee and Wu 2017*b*), or mixing vertical density gradients that form in ice-free lakes. Moreover, higher wind speeds can mix the water column following ice break-up, which otherwise would be driven primarily by convective mixing, with a knock-on effect on the duration of winter stratification. Our analysis also identified an influence of lake depth, with deeper lakes experiencing longer stratification, due primarily to the longer period of convective mixing that occurs in deep lakes prior to surface waters reaching 4°C in spring (Austin 2019; Cannon et al. 2019; Cortés and MacIntyre 2020; Yang et al. 2021). In agreement with Yang et al. (2021), our study also suggested that wind speed and lake morphometry are the most important predictors explaining the across lake variation in the winter mixing regimes in lakes (Fig. 2). As suggested by Yang et al. (2021), lakes subjected to more intense wind mixing during autumn/winter will often experience lower water column temperatures, and thus influence early winter temperature profiles and, subsequently, the mixing regime.

Our projections suggest that the duration of winter stratification will shorten considerably this century, which we expect will have substantial effects on lake ecosystems (Jansen et al. 2021). A shorter period of winter stratification can have consequences for biogeochemistry by altering the interactions between surface and bottom waters. Most notably, as the vertical mixing of oxygenated surface waters is limited during winter stratification, and oxygen is consumed at the sediment–water interface (Mathias and Barica 1980; Hondzo 1998), lakes can consequently often experience oxygen depletion at depth (Deshpande et al. 2016; Deshpande et al. 2017; Jansen et al. 2019; Jane et al. 2021). A shorter winter stratified period may, in turn, lead to more oxygenated bottom waters (Flaim et al. 2020), which will alter fish habitat (Magnuson et al. 1985; Hasler et al. 2009), limit the buildup and emissions of greenhouse gases when mixed conditions resume (Denfeld et al. 2018; Jansen et al. 2019; Zimmermann et al. 2021), and alter the quantity of nutrients available to fuel primary production in the growing season (Hampton et al. 2017). The ecological consequences of a shorter winter stratification period will, however, depend on timing (mis) matches with other important events, such as precipitation, snowmelt, ice-off and the onset of summer stratification (Dugan 2021; Woolway et al. 2021).

Although we consider our results robust, and believe that they fill an important knowledge gap, there are some limitations to consider when interpreting our key findings. Firstly, in this study, we estimated the duration of winter stratification based on water temperature projections. While the use of water temperature to estimate the density difference between surface and bottom waters, and likewise the duration of stratification, is widely used, most studies have focused on the summer period where vertical temperature differences are relatively large. As we focused on the winter period, where temperature differences between surface and bottom water are quite small in comparison, other processes could also have an important effect. For example, under ice cover, chemical stratification (e.g., where solutes contribute to the density of freshwater) can be a key driver of hydrodynamic processes in some lakes (Malm et al. 1998; MacIntyre et al. 2018; Cortés and MacIntyre 2020), and salinization can delay or prevent turnover in spring (Ladwig et al. 2021). In lakes with short residence times, chemical and thermal stratification can also be influenced by river and groundwater inflows (Pasche et al. 2019; Cortés and MacIntyre 2020), which are not considered in our simulations. Also, as our projections are generated with a 1D process-based lake model, horizontal features in lakes are not considered. This limitation means that the within-lake variations in temperature and stratification are not captured (Woolway and Merchant 2018) and that horizontal transport does not influence winter stratification. Density-driven currents could transport warm, dense water from the littoral zone downslope to greater depth, which would likely have the greatest effect on the density gradient in small to medium-sized lakes (MacIntyre et al. 2018). Despite these limitations, our results provide an important step forward in understanding lake responses to a warming world.

Code availability

The code used to produce the figures in this paper is available from the corresponding author upon request.

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