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Key Points:

- Lake bottom warming rates are dampened compared to surface warming rates
- Stratification responses to climate controlled by lake morphometry
- Tropical lake stratification is most sensitive to warming

Supporting Information:

- Figures S1 and S2 and Table S1

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Morphometry and average temperature affect lake stratification responses to climate change

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Abstract Climate change is affecting lake stratification with consequences for water quality and the benefits that lakes provide to society. Here we use long-term temperature data (1970–2010) from 26 lakes around the world to show that climate change has altered lake stratification globally and that the magnitudes of lake stratification changes are primarily controlled by lake morphometry (mean depth, surface area, and volume) and mean lake temperature. Deep lakes and lakes with high average temperatures have experienced the largest changes in lake stratification even though their surface temperatures tend to be warming more slowly. These results confirm that the nonlinear relationship between water density and water temperature and the strong dependence of lake stratification on lake morphometry makes lake temperature trends relatively poor predictors of lake stratification trends.

1. Introduction

Lake stratification responses to climate change affect people around the world through their impacts on water quality. Intensified thermal stratification of lakes can exacerbate lake anoxia [*Chapman et al.*, 1998; *Hecky et al.*, 2010; *Van Bocxlaer et al.*, 2012; *North et al.*, 2014; *Palmer et al.*, 2014], enhance the growth of planktonic, bloom-forming cyanobacteria [*Steinberg and Hartmann*, 1988; *Paerl and Huisman*, 2009; *Paerl and Paul*, 2012], and cause changes to internal nutrient loading with consequences for lake productivity [*O'Reilly et al.*, 2003; *Verburg et al.*, 2003; *Verburg and Hecky*, 2009]. Despite the recognition that climate change effects on lake stratification are ubiquitous [*Livingstone*, 2003; *Coats et al.*, 2006; *Saulnier-Talbot et al.*, 2014], global patterns in the impact of climate change on lake ecosystems including lake stratification remain uncertain [*Adrian et al.*, 2009; *Williamson et al.*, 2009].

Climate change has strongly influenced surface temperatures of lakes worldwide [*Schneider and Hook*, 2010]. The ecosystem consequences of climate change are often assumed to parallel warming rates [*Smol et al.*, 2005; *Solomon et al.*, 2007], but this is unlikely to be true of climate change effects on lake stratification. Due to the nonlinear relationship between water temperature and water density, the impact of temperature changes on lake stratification is highly dependent on average lake temperatures [*Lewis*, 1987, 1996]. Furthermore, lake stratification depends strongly on basin morphometric characteristics (mean depth, surface area, and volume) [*Lerman et al.*, 1995; *Butcher et al.*, 2015], which may constrain lake stratification responses to warming. For instance, the capacity for lake warming to lead to thermocline depth shifts may be dampened in large lakes where the depth of the thermocline is strongly constrained by a lake's fetch [*Gorham and Boyce*, 1989; *Mazumder and Taylor*, 1994; *Fee et al.*, 1996; *Boehrer and Schultze*, 2008; *MacIntyre and Melack*, 2010]. Thus, predicting lake stratification responses to climate change may depend on understanding how patterns in warming rates intersect with a lake's baseline temperature and morphometry to alter its stratification regime.

Given the importance of lake stratification for lake biota and water quality, we aim to determine which of the 26 lakes in our analysis are most susceptible to stratification changes in response to climate change. We compiled temperature profile data from lakes on five continents to test whether mean lake temperatures, lake warming rates, or lake morphometry can be used to predict the observed trends in lake stratification as indicated by the depth of the thermocline, the thermal stability of the water column (Schmidt stability), and the steepness of the thermocline (thermocline buoyancy frequency). Due to the extraordinary size and depth of some of the lakes in our analyses, they represent 3.0% of the cumulative lake surface area, and 44% of the cumulative liquid surface freshwater on Earth. The broad range of lake locations and characteristics represented in our analyses (Table S1 and Figure S2 in the supporting information) provides insights into controls on lake stratification trends and informs predictions of how the global population of lakes will respond to climate change.

2. Methods

2.1. Study Sites

We compiled temperature profiles for 26 lakes over the period from 1970 to 2010 from arctic, boreal, temperate, subtropical, and tropical regions. Temperature variations in these lakes have already been linked to climate change [*Ambrosetti and Barbanti*, 1999; *Quayle et al*., 2002; *Livingstone*, 2003; *Lorke et al*., 2004; *Coats et al*., 2006; *Dokulil et al*., 2006; *Hampton et al*., 2008; *Moore et al*., 2009; *Schneider and Hook*, 2010; *Hecky et al*., 2010; *Rimmer et al*., 2011; *Shimoda et al*., 2011; *Hsieh et al*., 2011; *Winslow et al*., 2014], but several of the temperature time series in our study have not been previously published in their full length (Atitlan, Moss, Sombre, Heywood, and Nkugute). The lakes included in our analysis represent a wide range of surface area (0.02 to 68,800 km^2), maximum depth (2.3 to 1642 m), and elevation (-212 to 1987 m above sea level) (Table S1). All are freshwater lakes except for Lake Kivu, which has a marked salinity gradient that affects its stratification. We analyzed the three basins of Lake Tanganyika independently as they span a significant latitudinal gradient, are separated by relatively shallow sills, and have divergent temperature and stratification trends. The temperature data for five lakes in our analysis did not span the entire range from 1970 to 2010, but all lakes had temperature data which started in 1976 or earlier and ended in 2004 or later. Some lakes had only one profile per year, while others had daily profiles from high-resolution data loggers. Several lakes had data gaps of more than 1 year. The mean data gaps (average time between temperature profile measurements) for Tanganyika, Kivu, Victoria, Nkugute, and Atitlan were 2, 3, 3, 7, and 10 years, respectively. Sensitivity analyses showed that data gaps of this size do not significantly bias our stratification trend estimates (Figure S1). The number of depths in each temperature profile varied across lakes from 8 to 16 depending on lake depth. We verified that the values for stability, thermocline depth, and thermocline strength that were calculated from temperature profiles with discrete depths closely matched those calculated based on high-resolution temperature profiles when they were available.

2.2. Temperature and Stratification Trend Estimation

The mean surface temperature, whole-lake temperature (volume-weighted), and bottom temperature were calculated from each temperature profile. From these profiles, we also calculated the Schmidt stability ($kJ\,m^{-2}$), thermocline depth (m), and Brunt-Väisälä buoyancy frequency (s^{-1}) at the thermocline using LakeAnalyzer [*Read et al*., 2011]. LakeAnalyzer used well-accepted methods of calculating lake stratification indices from in situ temperature profiles and hypsographic data. Schmidt stability (hereafter "stability") is the amount of energy required per unit area to mix a lake to homothermy without the exchange of heat [*Schmidt*, 1928; *Idso*, 1973]. Stability is a valuable metric because it is related to the potential for accumulation and depletion of deep water solutes in lakes [*Kling*, 1988]. The thermocline depth is the depth of the maximum density gradient in the water column and is a key variable controlling the depth niches of aquatic organisms [*Weyhenmeyer et al*., 2011]. The Brunt-Väisälä buoyancy frequency (hereafter "buoyancy frequency") is the angular frequency at which a parcel of water would oscillate if it was displaced from its location in the water column. We calculated the buoyancy frequency at the thermocline for each temperature profile to estimate the steepness of the thermocline—a key control on vertical mixing in aquatic systems [*Wüest and Lorke*, 2010]. A high buoyancy frequency signifies that the thermocline is steep and the resistance to vertical mixing at the thermocline is pronounced.

Changes in the timing of stratification were not analyzed here as several lakes were stratified year round. However, we did determine the typical start and end dates of stratification in lakes that mix completely; only temperature profiles taken during the stratified period were used for trend estimation. We estimated the typical start and end dates of stratification by calculating the average day of the year over the entire observation period (1970–2010) on which the density stratification was sufficient to develop a persistent (lasting more than 5 days), midwater thermocline. Year-round data were used for lakes that are permanently stratified or partially stratified all year round.

To estimate trends in temperature and stratification indices during the stratified period, we removed the seasonal pattern from the temperature and stratification data and used Theil-Sen nonparametric regression for trend estimation [*Theil*, 1950; *Sen*, 1968]. We removed the seasonal pattern by first calculating a 30 day running mean over the course of a seasonal data curve made up of data pooled from all years for each lake. Then we calculated the difference between the 30 day running mean centered on each day of the year and the grand mean over the entire 40 year record. That difference was subtracted from raw measurements made on the same day of the year to remove variation in the data attributable to the time of year when the measurement was made. The seasonal detrending procedure was carried out independently for surface temperatures, whole-lake temperatures, bottom temperatures, and the three stratification indices. The nonparametric Mann-Kendall test was used to assess the significance of trends ($\alpha = 0.05$).

2.3. Predictors of Stratification Trends

Multiple linear regression models, hierarchical variance partitioning, and Akaike's information criterion (AIC) model selection were used to determine the best predictors of trends in lake stratification indices. One value (the trend over time) was calculated for each lake stratification index for each lake. The trends were then used as response variables in the models. We used multiple linear regression models designed to predict the magnitude of the stratification trends from nine variables that fell into one of three categories: lake morphometric predictors (average depth, surface area, and volume), average temperature predictors (surface temperature, whole-lake temperature, and the difference between surface and bottom temperatures), and temperature trend predictors (surface trend, whole-lake trend, and the difference between surface and bottom trends). Each lake was treated as a single observation of change through time. The response variables in each model (stability, thermocline depth, and buoyancy frequency trends) and the morphometric predictors were log transformed to attain normality in distributions, as confirmed by the Kolmogorov-Smirnov test. Published values were used for lake morphometric characteristics (maximum depth, mean depth, surface area, and volume).

We used Akaike's information criterion (AIC) [*Akaike*, 1981; *R Development Core Team*, 2013] forward and backward stepwise predictor selection to identify models that maximize explanatory power while minimizing the number of predictors (AIC selection criteria: $\delta\text{AIC} > 2$). The models for predicting stratification trends were refit using only the variables selected by the AIC. Using the most parsimonious model for trends in each stratification index, the significance of each predictor was assessed using the 95% confidence interval for its regression coefficient.

We also used hierarchical variance partitioning [*Mac Nally*, 1996; *R Development Core Team*, 2013] on each full model with all nine predictor variables to determine the independent contribution of each predictor variable to the total variance explained by the full multiple linear regression model. We compared across predictor variables and across categories of predictor variables (morphometric, average temperature, and temperature trends) to determine which variables had the most influence on the magnitude of stratification trends.

3. Results

3.1. Temperature and Stratification Trends

On average, lake surface temperatures, whole-lake temperatures, and bottom temperatures have warmed by 0.84°C, 0.43°C, and 0.05°C, respectively, over the period from 1970 to 2010 across the 26 lakes (Figure 1a). Significant increases in surface, whole-lake, and bottom temperatures were observed in 20, 14, and 9 lakes, respectively (Mann-Kendall $p < 0.05$). Significant decreases were only observed in the bottom temperatures of one lake (Lake Pielinen, Mann-Kendall $p < 0.05$). Lake surface temperature trends, whole-lake temperature trends, and bottom temperature trends were positively related to latitude (Pearson's correlation coefficient,

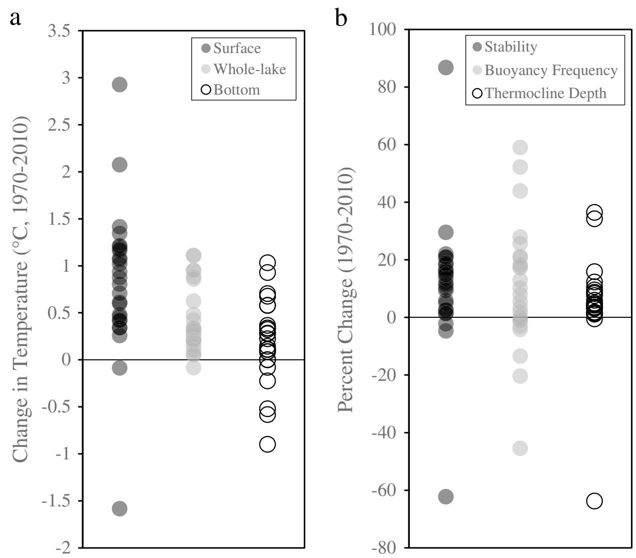

Figure 1. (a) Temperature change (Theil-Sen slope) for 26 globally distributed lakes (1970–2010). (b) The associated percent change in three lake stratification indices (1970–2010).

$r = 0.26$, 0.18, and 0.14, respectively) and negatively related to mean depth (Pearson's correlation coefficient, $r = -0.22$, -0.36, and -0.21, respectively).

Lake stratification is becoming more stable, with deeper and steeper thermoclines (Figure 1b). Of the 26 lakes, significant increases in buoyancy frequency, stability, and thermocline depth were observed in 17, 12, and 9 lakes, respectively (Mann-Kendall, $p < 0.05$). Only one lake had a significant decrease in buoyancy frequency (Mann-Kendall, $p < 0.05$), and no lakes had a significant decrease in Schmidt stability or thermocline depth (Mann-Kendall significance test, $p > 0.05$).

3.2. Predictors of Stratification Trends

Lake morphometric variables and the mean lake temperature are better predictors of lake stratification trends than lake warming rates. The morphometric predictors and average temperature predictors together explained a high percentage of the variance in stratification trends, while warming rates were comparatively unimportant. In sum, morphological variables and average temperature variables explained 94% of the explained variation in Schmidt stability trends, 81% of the explained variation in buoyancy frequency trends, and 83% of the explained variation in thermocline depth trends (Figure 2). Morphological variables were the best predictors of stability trends (70% of explained variance) and buoyancy frequency trends (64% of explained variance), while average temperatures were the best predictors of trends in thermocline depth (49% of explained variance). Mean depth explained the most variation in stratification trends across all three models (27%, on average, Figures 2 and 3a). Lakes with greater mean depths had larger changes in their stability but slightly smaller changes in buoyancy frequency (Figure 3a). Of the average temperature predictors, average surface temperature explained the most variation in stratification trends (12%, Figures 2 and 3b). Lakes with higher surface temperatures had larger changes in

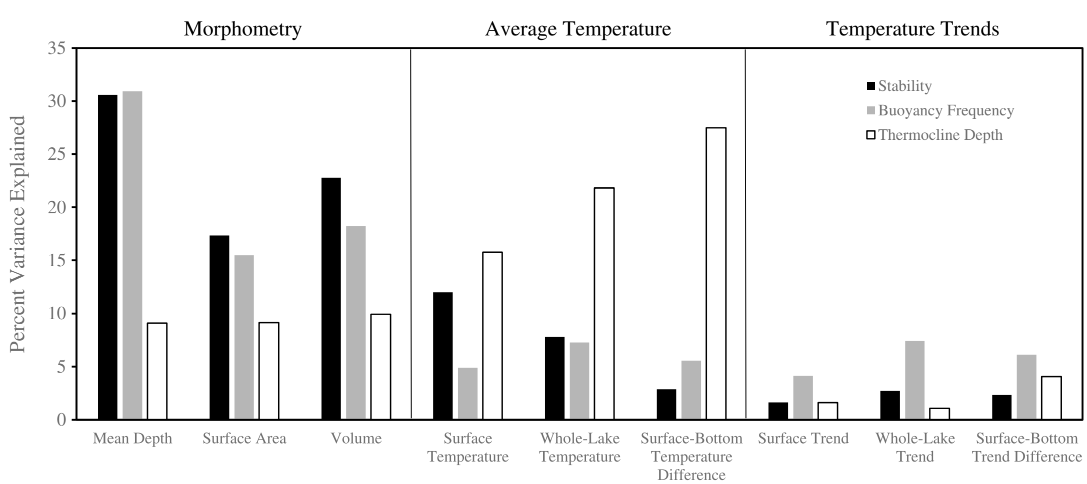

Figure 2. The variance in long-term (1970–2010) trends in lake stratification indices explained by nine predictor variables as a percentage of variance explained by the full model. Predictor variables for each stratification index are grouped by morphometry, baseline temperature, and warming rate. All bars of a given shade sum to 100%.

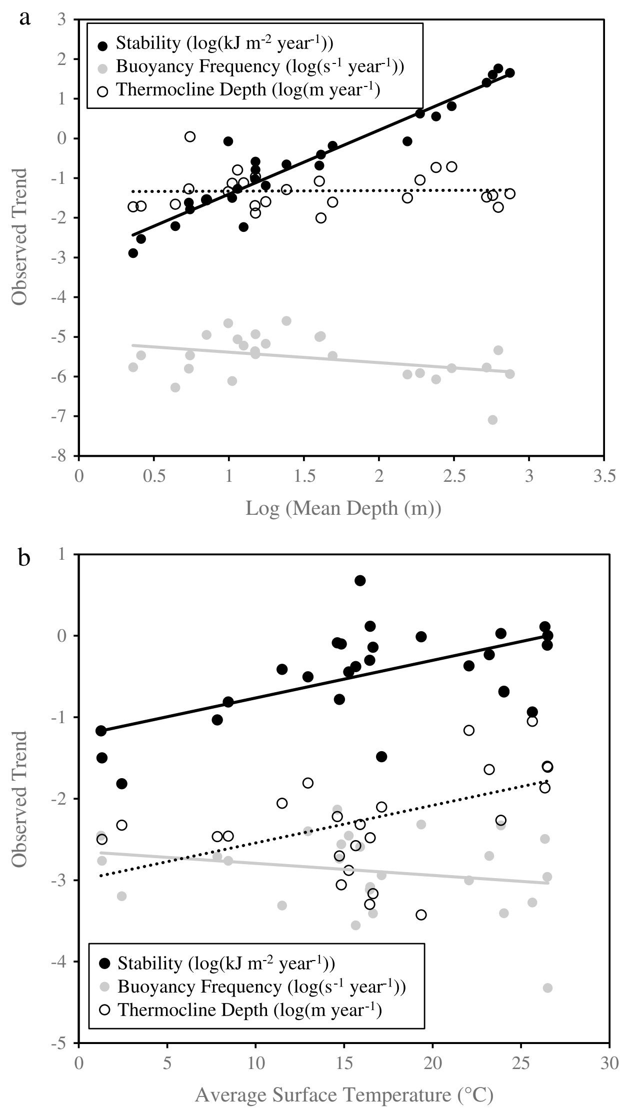

Figure 3. (a) Long-term (1970–2010) trends in lake stratification indices as a function of mean depth. Variance in trends explained by baseline temperature has been removed. (b) Long-term (1970–2010) trends in lake stratification indices as a function of the average surface temperature across the entire time series. Variance in trends explained by lake morphometry has been removed.

stability and thermocline depth but small buoyancy frequency trends (Figure 3b). Temperature trends explained little of the variation in stability (4%), thermocline depth (4%), and buoyancy frequency (6%) trends, respectively. Thus, multiple linear regression models of stratification index trends are largely unaffected by removing warming rates from the model (Figure 4).

According to AIC, the best predictors of stability trends were mean depth, average whole-lake temperature, and the average difference between surface and bottom temperatures. All three variables were significant predictors of stability trends (multiple linear regression, $R^2 = 0.91$, $p < 0.05$). The best predictors of thermocline depth trends were lake volume, average whole-lake temperature, and average difference between surface temperature and bottom temperature. All three were significant predictors, but the resulting model explained considerably less of the variation in thermocline depth trends (multiple linear regression, $R^2 = 0.60$, $p < 0.05$). The best predictors of buoyancy frequency were mean depth, volume, and whole-lake warming rate. Mean depth and volume were significant predictors of trends in buoyancy frequency (multiple linear regression, $p < 0.05$) while whole-lake warming rate was not (multiple linear regression, $p = 0.11$). The resulting model explained a relatively small proportion of the variance ($R^2 = 0.40$, $p < 0.05$). Moderate nonrandom patterning in the residuals of models for thermocline depth and buoyancy frequency suggested that the models overestimated trends when the observed change was small and underestimated trends when the observed change was large.

4. Discussion

Lake stratification in the 26 lakes in our analysis has become more stable with deeper and steeper thermoclines. The consistency of the trends across lakes suggests a global driver of these changes over the last 40 years. Of the predictor variables that we investigated, lake morphometric variables and mean lake temperature explain the most variation in the magnitude of stratification trends across lakes. Knowing a lake's surface temperature trend, its whole-lake temperature trend, and the difference between its surface and bottom temperature trends does not considerably increase our ability to predict its stratification responses to climate change.

Changes in lake stability increase as a function of lake depth, as has been shown previously at the regional scale [*Butcher et al.*, 2015]. This finding suggests that the extension of the stratified season in lakes that fully mix or the reduction in the spatial extent of mixing in lakes that partially mix will be most common in deep lakes. In contrast to lake stability, the magnitude of shifts in buoyancy frequency was negatively correlated to

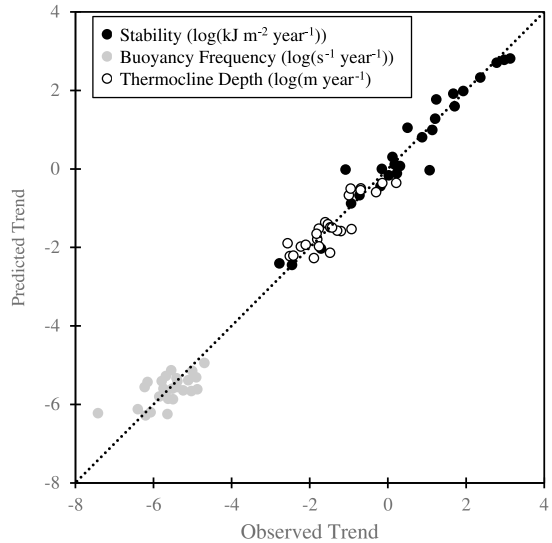

Figure 4. Predicted stratification trends versus observed stratification trends. Statistical models were fit to lake stratification data and used to predict the magnitude of long-term (1970–2010) stratification trends in each lake. Predicted trends here use models without warming rates as predictors. Predictors in the model included morphometric variables (mean depth, surface area, and volume) and average lake temperature variables (surface temperature, whole-lake temperature, and the difference between surface and bottom temperature). We compare predicted trends from statistical model output to the actual long-term trend based on in situ temperature data from each lake.

lake depth. Thus, higher turbulent energy in large lakes [*Gorham and Boyce*, 1989] may make the depth of the thermocline more resistant to change even as the surface warms. Thus, global patterns in the responses of lake stability to climate change will, in part, depend on global patterns of lake depth. Regions with many large, deep lakes may be most susceptible to ecosystem changes associated with increases in lake stability, while regions with many small lakes may be most susceptible to ecosystem changes associated with the strength of the thermocline.

Stability and thermocline depth trends were positively related to lake surface temperature with warmer lakes having larger changes in stability and thermocline depth. This suggests that lake stratification patterns may be more sensitive to climate change in the tropics than in temperate and arctic regions, because lake temperature during the stratified period in each lake was strongly correlated to lake latitude. This observed pattern echoes previous work which used numerical simulations to show that lake stratification in warm, tropical lakes is more sensitive to changing surface temperatures [*Lewis*, 1996]. This latitudinal gradient in lake stratification sensitivity arises from the nonlinear relationship between water temperature and water density. The magnitude of thermocline shifts was also dampened in lakes with large temperature differences between the surface and bottom temperatures. Surface-bottom temperature differences tend to be greatest at midlatitudes, thus reducing thermocline shifts there.

Long-term temperature monitoring is carried out in only a small fraction of the world's lakes, which limits the predictive capacity of our statistical models. For instance, climate-change-mediated shifts in water clarity [*Gaiser et al*., 2009], lake level [*Coops et al*., 2003], and wind speed [*Young et al*., 2011] may explain a large portion of the variation left unexplained by our lake stratification models. Our predictions of global lake stratification responses to climate change could be improved considerably by accounting for regional and lake-specific changes in these variables. Future work with more lakes will be less encumbered by the risk of model overfitting and will be free to incorporate these variables as predictors.

We urge caution in the use of our models to predict lake stratification responses to climate change for certain lake types that are not well represented in our analyses. While the lakes in our analyses represent 44% of the global liquid surface freshwater, they represent only 2.2×10^{-5}% of all lakes on Earth [*Verpoorter* et al., 2014]. The lakes with the most consistent, data-rich, in situ temperature profile records are almost all from temperate, subarctic, and arctic regions; relatively few are from tropical and subtropical regions. Of the tropical lakes included in our analyses, rift lakes and crater lakes are overrepresented. In reality, most tropical lakes may be fluvial in origin [*Lewis*, 1996], but to our knowledge there are no fluvial lakes with long-term temperature profile data sets. Most long-term lake temperature monitoring programs initiated during the last few decades still focus on middle- and high-latitude lakes, so this bias is unlikely to be remedied in the near future (but see *Saulnier-Talbot et al*. [2014]). Remote sensing has circumvented this bias for surface temperatures, but our results show that surface temperature trends have little association with shifts in stratification. Unfortunately, understanding lake stratification requires temperature profile data, which are challenging to collect on a regular basis. Given the significant increases in stratification observed in most of the lakes analyzed in this study, it is clear that understanding the effects of climate change on the world's lakes will require a much broader monitoring network for temperature profiles.

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While we did not include ecological data in our analyses, the stratification trends analyzed here have direct implications for lake ecosystem dynamics. The shifts in lake stratification will intensify the confinement of dissolved oxygen, nutrients, particles, and nonmotile organisms to specific lake strata with profound effects on lake ecosystems [*O'Reilly et al.*, 2003; *Adrian et al.*, 2009; *Shimoda et al.*, 2011; *North et al.*, 2014]. Our results indicate that while stratification changes are likely to be felt across latitude, deep tropical lakes like the African rift lakes, the ancient lakes of Indonesia, and the crater lakes of Central America may be most susceptible to shifts in lake stratification. The resulting ecological shifts that may result are particularly hazardous, because tropical lakes provide critical sources of nutrition to adjacent human populations and tend to be hotspots of freshwater biodiversity [*Vadeboncoeur et al.*, 2011; *Brawand et al.*, 2014].

5. Conclusion

In situ temperature profile observations from 26 globally distributed lakes were used to study how lake warming rates intersect with a lake's baseline temperature and morphometry to alter its stratification. Calculations of lake mixing indices over time from 1970 to 2010 showed that, on average, lake stratification is becoming more stable with deeper and steeper thermoclines. The magnitude of stratification responses to climate change across lakes was associated with lake average temperature and morphometry, but not with warming rates. These results suggest that the influence of climate change on lake temperature and stratification is ubiquitous but may be felt most strongly in large tropical lakes.

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