Aquatic Sciences (2020) 82:6
https://doi.org/10.1007/s00027-019-0676-6

Aquatic Sciences

RESEARCH ARTICLE

Compound effects of water clarity, inflow, wind and climate warming on mountain lake thermal regimes

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Received: 8 April 2019 / Accepted: 7 October 2019
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Abstract

Many studies have examined the effects of climate warming on lake stability, but few have addressed environmental changes concomitant with climate change, such as alterations in water clarity and lake inflow. Although air temperature rise is a predominant factor linked to lake thermal characteristics, climate-driven changes at watershed scales can substantially alter lake clarity and inflow, exacerbating the effects of future air warming on lake thermal conditions. Without accounting for potential changes in clarity and inflow, future thermal predictions could be inaccurate. We employed the General Lake Model to simulate future thermal conditions (relative thermal resistance to mixing; RTRM) of small (< 12 ha) mountain lakes of the western United States by calibrating the model to a set of lakes in the Southern Rocky Mountains, USA. We found that after air temperature, alterations in inflow had the largest effect on lake thermal conditions, changes in wind had the least effect, and larger lakes experienced more than double the increase in lake stability than smaller lakes. Generally, clear, high inflow lakes had the lowest stability now, and in the future, while the largest overall increase in thermal stability occurred in larger lakes with low inflows and high turbidity. Assuming air temperature rise alone, summer stability of mountain lakes of the western United States was predicted to increase by 15–23% at + 2 °C air temperatures, and by 39–62% at + 5 °C air temperatures. When accounting for associated changes in clarity and inflow, lake stability was predicted to increase by 208% with + 2 °C air warming and 318% with at 5 °C air warming. Thus, ignoring the multivariate effects of climate change can substantially underestimate changes to mountain lake thermal and stratification regimes. Dimictic lakes may become more strongly stratified and polymictic lakes will experience more prolonged stratification. While predicted changes to lake temperatures may not be harmful to trout species that currently inhabit mountain lakes, longer and more intense stratification could cause indirect effects, such as hypoxia, that could reduce growth and survival of these organisms.

Keywords Climate change · Thermal stratification · General Lake Model · High elevation lakes

Introduction

Lakes are sensitive to climate (Adrian et al. 2009). One consequence of a warming climate is increased lake surface water temperatures (O'Reilly et al. 2015; Christianson et al. 2019), which can affect the resistance of the water column to mixing (lake stability) (Idso 1973). Indeed, climate change has already been shown to cause changes in stability (Shatwell et al. 2016; Woolway et al. 2017b) and mixing regime (Kirillin 2010; Michelutti et al. 2016; Ficker et al. 2017). These shifts can be ecologically significant because thermal stratification is one of the most prominent physical features of lakes (Dodds and Whiles 2010), and it drives a variety of processes including oxygen dynamics (Blottiere et al. 2017), and physiological rates of aquatic organisms (Brett 1971). Further, prolonged stratification can constrict

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Published online: 16 November 2019

coldwater habitat by increasing hypoxia in the hypolimnion (bottom layer) while warming and deepening the epilimnion (surface layer) (Stefan et al. 2001; Engelhardt and Kirillin 2014; Massaghi et al. 2017) resulting in a "temperature-oxygen squeeze" for coldwater organisms (Jacobson et al. 2008; Jiang et al. 2012). Even modest changes to stratification can cause major shifts in phytoplankton and zooplankton populations (Arvola et al. 2010) which are a basis of production in many lake food webs. Consequently, climate-induced changes to lake stratification can disrupt community composition and ecosystem properties (Woodward et al. 2010).

Although many studies have examined how climate change can alter lake stratification and thermal regimes (e.g., Butcher et al. 2015; Kraemer et al. 2015; Edlund et al. 2017), most have focused on the direct effects of air temperature change. This is likely due to the importance of air temperature as a driver, but also the ease of measurement and availability of long-term records of air temperature. However, lake stratification is also driven by other factors that can compound or mitigate the influence of a warming climate on lake thermal structure (Fee et al. 1996) and which have not received nearly as much attention in lake-climate change studies. Generally, these include (a) internal drivers like the surface energy balance and water clarity, (b) external drivers such as inflow and wind, and (c) morphometry. The surface energy balance is a complex process involving incoming and outgoing radiation, sensible and latent heat fluxes, and heat storage (Bonan 2016). Lake clarity can influence the surface energy balance by regulating the depth of light penetration (Hocking and Straskraba 1999; Houser 2006). Under low clarity conditions, incoming radiation is absorbed in a smaller volume of water, increasing surface temperature and stability (Read and Rose 2013). On the other hand, wind and inflow can reduce lake stability and promote mixing by disrupting temperature-driven water density gradients (Boehrer and Schultze 2008; Mi et al. 2018), and their importance is mediated by lake morphometry (Gorham and Boyce 1989; Read et al. 2012; Kraemer et al. 2015). It is unclear how these internal drivers, external drivers, and morphometry may act in concert with rising air temperatures to affect lake temperature and stability.

A few studies have incorporated some of these interdependencies by addressing how clarity (Gunn et al. 2001; Williamson et al. 2015; Rose et al. 2016; Strock et al. 2017), wind (von Einem and Graneli 2010; Woolway et al. 2017b), inflow (Rimmer et al. 2011), or lake size (Butcher et al. 2015; Winslow et al. 2015) can mediate effects of climate warming on lake stability. However, their relative importance and interactive effects are difficult to determine without considering them simultaneously. Further, climate change can also drive changes in water clarity, inflow, and wind, compounding effects of warming on lake stability (Adrian et al. 2009). For instance, climate change can be linked to global phenomena such as increasing forest fire frequency and intensity (Aponte et al. 2016). Forest fires can increase runoff, and sediment and nutrient delivery to lakes, which can directly and indirectly reduce water clarity (Bixby et al. 2015). Climate change is also altering precipitation patterns and affecting snowpack amount and melt timing in snowmelt-dominated regions, changing the volume and timing of spring runoff, and therefore, lake inflows (Barnett et al. 2005) and temperature (Sadro et al. 2018). Climate-induced depletion of perennial snowpack and glaciers, a worldwide concern (Hall and Fagre 2003; Radic et al. 2013), may exacerbate the effects of reduced annual runoff (Bliss et al. 2014; Huss and Hock 2018). Finally, atmospheric stilling has already occurred in many parts of the globe (Vautard et al. 2010), reducing surface wind energy inputs to lakes and prolonging stratification (Woolway et al. 2017b). Thus, climate change has multi-faceted effects on lake stability that should be considered together to better anticipate how lakes and their biota will respond to climatic and related environmental change.

Mountain lakes are particularly sensitive to climate change (Williamson et al. 2009; IPCC 2013) and climate-related environmental stressors like drought, forest fire, and perennial snow and ice retreat. But because they are usually remote, this class of lakes has been understudied (but see Moser et al. 2019). About 10% of the world's lakes lie above 2100 m in elevation (Verpoorter et al. 2014) and are widely distributed across the globe (Catalan and Donato-Rondón 2016), but relatively few studies have examined effects of climate change on mountain lake thermal conditions compared to their low elevation counterparts (Christianson et al. 2019). The remoteness of mountain lakes has also isolated them from many other anthropogenic environmental stressors such as land use change, development and invasive species. Thus, these lakes can be important refuge habitats for native aquatic species (Roberts et al. 2017). More information about how the thermal regime and stratification of mountain lakes may change in the future is needed to protect these relatively pristine ecosystems and the rare flora and fauna that inhabit them.

In this study we used contemporary field observations of weather and limnological characteristics to calibrate a lake hydrodynamic mechanistic model for a set of small (<12 ha) mountain lakes in the Southern Rocky Mountains, U.S. We then used model simulations to predict how future changes to air temperature would interact synergistically with other important drivers of lake stratification: inflow, water clarity, wind and lake size, to affect the thermal properties of small mountain lakes. The overall goal of our multivariate approach is to improve general understanding of how mountain lake summer stratification and thermal properties respond to an interacting complex of climate and climate-related stressors.

Methods

Study setting

Field observations were collected in the Rawah Wilderness Area (RWA) located in northern Colorado, USA (Fig. 1). The RWA covers 31,565 ha within the Roosevelt National Forest in the Medicine Bow Mountain Range and contains 25 named natural lakes ranging in size from 1 to 15 ha and with depths of 1–45 m. Elevations in the RWA ranges from 2560 to 3960 m above sea level. The RWA is in the Southern Rocky Mountains (SRM) which hosts about 2500 mountain lakes. Collectively, the western U.S. contains ~ 16,000 mountain lakes (Bahls 1992). The mountain lakes of the region share a number of characteristics that suggest that they may respond similarly to climate change. Most of these lakes are < 30 ha in surface area (Bahls 1992). Though latitude- and elevation-dependent, the growing season is short; in the SRM, lakes are typically ice-covered from October into June or July (Preston et al. 2016). Historically, the hydrology of the region and inflows to lakes have been driven by winter snow accumulation and summer runoff from snowmelt (Poff and Ward 1990; Sadro et al. 2018). Mountain lakes of the western U.S. are highly oligotrophic (Bahls 1992) but atmospheric deposition of anthropogenic nitrogen is increasing (Baron et al. 2012). Wildfire is another pervasive climate-related disturbance to mountain lakes throughout the western U.S.

Field observations

We gathered detailed measurements from six lakes in the RWA from June to September 2016 (Table 1). We chose lakes for our study that represented a relatively wide range of lake areas, depths and clarities present in the RWA. Five of the six RWA lakes remained stratified throughout the summer, but the shallowest lake (Big Rainbow) was polymictic (Fig. 2). Strong diel temperature fluctuations (< 2 to > 10 °C) occurred in all of the lakes, with cooling of the surface water at night. Temperature of the epilimnion (within 1 m of the surface) and hypolimnion (within 1 m of the bottom) were recorded hourly with Onset HOBO Pendant UA-002-08 data loggers placed in the middle, deepest part of each lake.

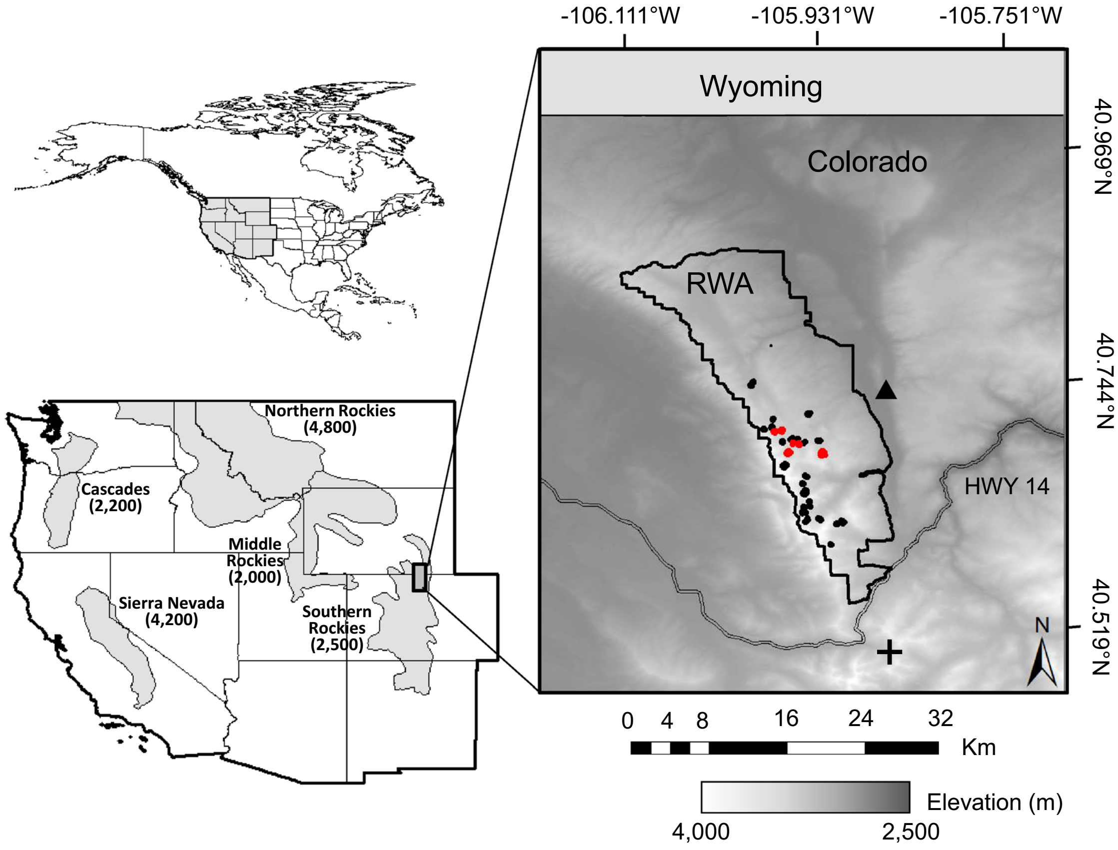

Fig. 1 Mountainous regions of the western U.S. with the approximate number of mountain lakes present in each, and location of the lakes (red) in the Rawah Wilderness Area where field sampling occurred. The location of the weather station used to gather climatological data (triangle) and site of the Michigan River stream gauge (cross) used for this study is also shown

Table 1 Physiographic and morphometric characteristics of six study lakes in the Rawah Wilderness Area, Colorado

Lake name	Latitude (°N)	Longitude (°E)	Elevation (m ASL)	Area (ha)	Maximum depth (m)	Secchi depth (m)
Big Rainbow	40.693	– 105.941	3275	2.4	4.3	0.8
Upper Sandbar	40.692	– 105.946	3263	3.3	7.4	3.2
McIntyre	40.704	– 105.961	3242	5.9	10.7	4.4
Sugarbowl	40.703	– 105.968	3288	3.1	15.2	3.6
Upper Camp	40.683	– 105.924	3270	15.4	23.5	3.1
Rawah #3	40.684	– 105.956	3316	8.5	35.1	2.7
Mean	40.696	– 105.947	3249	4.9	9.7	3.0

Secchi depth reported is the average value from at least two samples gathered from July 15–August 31, 2016

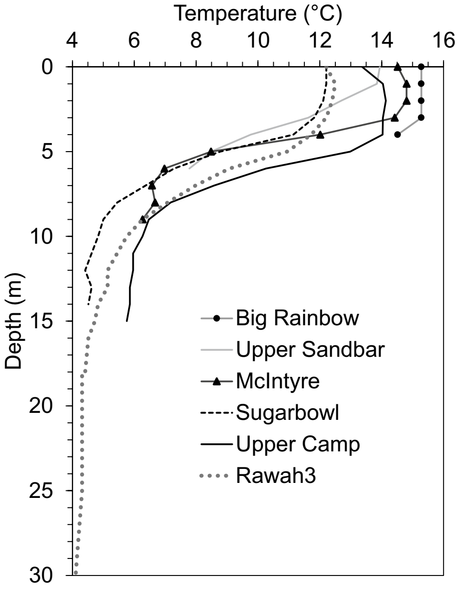

Fig. 2 Temperature profiles for six lakes in the Rawah Wilderness Area measured at 07:00 h on the day of maximum stratification (July 30, 2016)

Dissolved oxygen was measured once on August 17, 2016 at each lake using an Onset HOBO U26 dissolved oxygen sensor 1 m off the bottom at the deepest part of each lake. We measured water clarity at least monthly with a standard 20-cm diameter Secchi disk. Three of the six study lakes had observable surface inflows; an Onset HOBO Pendant UA-002-08 data logger was deployed in each to collect hourly inflow temperature.

Weather data were collected from a variety of sources or computed from established relationships. Because our study occurred in a Wilderness Area, the nearest existing weather stations were about 50 km away. At the beginning of our study we set up an Onset U30 remote weather station immediately adjacent to the RWA and < 10 km from the study lakes (Fig. 1). The weather station collected five weather metrics every hour: air temperature (°C), wind speed (m s^{-1}), relative humidity (%), precipitation (rain; mm), and solar radiation (W m^{-2}). We performed a quality check of the weather data by visually assessing the range of each metric for outliers and erroneous measurements and examining the persistence of each measurement temporally to monitor diel conditions, for example, and to detect missing values. To use accurate near-lake air temperatures for modeling we estimated the air temperature lapse rate to account for the 600 m elevation difference from the weather station and lakes. To do this, we deployed air temperature loggers near the study lakes at two sites. After accounting for the temperature lapse rate (3.7 °C), there was good agreement with the weather station and near lake air temperatures ($r = 0.90$, $p < 0.001$). Cloud fraction was calculated using the standardized ASCE Penman–Monteith method which uses the ratio of sampled solar radiation to calculate clear-sky radiation to estimate cloud fraction daily (ASCE-EWRI Task Committee Report 2005).

We evaluated if 2016 weather could represent nominal, contemporary conditions in the region by comparing our measurements to post-1980s regime shift (Reid et al. 2016) records from two nearby weather stations at similar elevations. One weather station was located about 50 km southeast of the RWA in Rocky Mountain National Park (“Loch Vale”; Baron and Mast 1992) and the other was located about 80 km northwest of the RWA at the Glacial Lakes Ecosystem Experiments Site (“GLEES”; Musselman 1994). The Loch Vale weather station provided daily air temperature and precipitation measurements during 1984–2016, while the GLEES station provided monthly air temperature, wind, solar radiation, and relative humidity measurements during 1989–2016.

Simulation modeling

We used the General Lake Model ver. 3.3.1 (GLM; Hipsey et al. 2012) in R ver. 3.3.2 (R Core Team 2016) to simulate the effects of climate and lake characteristics on lake stability and thermal regime. This model is a process-based, one-dimensional lake stratification model, which employs a vertically layered Lagrangian structure to simulate water temperature profiles while accounting for dynamic processes like mixing, inflows, outflows, and the surface energy balance. GLM has been used worldwide on a variety of lake types (Hipsey et al. 2012; Rose et al. 2016; Bruce et al. 2018). We used recommended parameter values (Hipsey et al. 2017) except for maximum layer thickness, which we estimated from lake size (Rose et al. 2016; Fenocchi et al. 2018; Hipsey et al. 2017). Inputs included a time series of meteorological data, and lake-specific data including physiography (surface area, maximum depth, elevation, latitude, and longitude), and water clarity [light attenuation coefficient, K_w, computed from Secchi depth (Z_{SD}) measurements as $K_w = 1.7\ Z_{SD}^{-1}$ (Idso and Gilbert 1974)].

We explored how climate and lake characteristics affect mountain lake stability and thermal regimes in three stages of increasing complexity. First, we calibrated GLM to the six study lakes in RWA and used the calibrated models to forecast the effects of increased air temperature alone on thermal properties of the RWA lakes. Then, to guide our evaluation of other climate-related factors, we explored the relative sensitivity of the RWA lakes to changes in air temperature, inflow, clarity, and wind. Finally, to predict more general mountain lake responses (a) within the RWA and (b) across the western United States, we used the calibrated model to simulate combinations of a range of air temperatures, inflows, and water clarities over a range of lake sizes. We dropped wind from consideration in the factorial experiments based on the results of the sensitivity analysis (explanation presented in "Results" section).

The model was calibrated to match the thermal and mixing regimes observed in each RWA lake during 2016. Although GLM allows for inflow, lake inflows can be difficult to quantify, so calibration of GLM is often accomplished by omitting inflow or treating inflow as a free parameter (Read et al. 2014; Bueche and Vetter 2015; Magee and Wu 2016; Fenocchi et al. 2018; Bruce et al. 2018). In our case, as in many mountain areas, established stream gauges were sparse, and installing stream gauges in a wilderness area was prohibited. Instead, we allowed inflow to vary during model calibration to maximize the fit between observed and predicted thermal conditions. Because warming of these lakes typically begins when spring snowmelt declines (Sadro et al. 2018), we modeled thermal regimes during the post-runoff, open water period. We validated predicted low flow conditions by comparing them to (1) summer stream flows measured from a nearby site at a similar elevation (Michigan River near Cameron Pass, CO; 3168 m ASL), (2) stream flows at similar elevations across the SRM (NHD dataset described below), and (3) in situ inflow estimates from four lakes in the RWA with surface inflow measured using the float method (Hauer and Lamberti 1996) on August 17, 2016. Outflows were set to equal inflows because water level in the lakes did not change during our study.

Simulations began on June 18, close to the average ice-off date for nearby mountain lakes at the same elevation (Preston et al. 2016), but we analyzed output starting on July 15. We eliminated this initial simulation period from analysis to allow for an ample 'spin up period' (as in Bruce et al. 2018) and account for uncertainty in initial conditions, which were near isothermal for each lake. Also, by including results starting on July 15 we: (1) eliminated the influence of a large inflow pulse during the runoff period, which could confound our effect of inflow and (2) standardized the window in which we simulated each lake to account for different ice-off dates among lakes. Simulations ended on August 31, encompassing the period of maximum thermal stability for this region (Christianson et al. 2019). Many mountain lakes in the region enter fall mixis shortly after this date. Goodness of fit of the model's predicted temperatures for each lake was assessed using root mean square error (RMSE):

$$\mathrm{RMSE} = \sqrt{\frac{\sum_{i=1}^{N}\left(Pred_i - Obs_i\right)^2}{N}}, \tag{1}$$

where N is the number of observations, Pred_i is the predicted daily minimum temperature, and Obs_i is the observed daily minimum temperature. We used daily minimum temperatures to account for nocturnal cooling, which is substantial in montane environments (Christianson et al. 2019) and it can disrupt stratification (Barbosa and Padisak 2002). The daily minima were also used to determine if the lake remained stratified during each 24-h period, or if each lake mixed (equal surface and bottom temperatures).

To evaluate the effect of increased air temperatures alone on lake thermal properties we compared effects of nominal air temperatures to changes predicted from two future (2081–2100 relative to a 1986–2005 base period; IPCC 2013) air temperature scenarios for the region: representative concentration pathway (RCP) 4.5 and RCP 8.5. These scenarios represent the current most probable and extreme projections of climate change (IPCC 2013). For the SRM, RCP 4.5 projects a 2 °C increase in air temperature, and RCP 8.5 projects a 5 °C air temperature increase (IPCC 2013). We increased nominal daily air temperatures by these amounts and predicted the effects on RWA lake temperatures and water column stability with GLM. Lake stability was expressed as the relative thermal resistance to mixing (RTRM; Birge 1916), and calculated as:

$$\mathrm{RTRM} = \frac{\left[\left(1 - 6.63\times10^{-6}\left(BT-4\right)^2\right) - \left(1 - 6.63\times10^{-6}\left(ST-4\right)^2\right)\right]\times10^{6}}{8}, \tag{2}$$

where BT is bottom temperature, and ST is surface temperature. A benefit of using RTRM as a stability metric is that it considers the non-linearity of the water density:temperature relationship, and therefore, better reflects lake stability than a simple surface-bottom temperature difference which is sometimes used as an index of stability. For this study we assessed lake stability by computing the average daily RTRM (aveRTRM) over the 6-week simulation period, and minimum RTRM (minRTRM) which is the minimum RTRM experienced over the simulation period.

We examined the sensitivity of thermal conditions in our RWA study lakes to changes in air temperature, summer inflow, clarity, and wind by varying each separately by 20% above and below nominal conditions (as in Bruce et al. 2018). The percent change in surface and bottom temperatures and lake stability were computed for each variation. To investigate how the response of lake stability to air temperature rise is modified by individual lake characteristics, we modeled the range of lake surface areas (2.4–15.4 ha), maximum depths (4.3–35.1 m), Secchi depths (0.8–4.4 m) and inflows (0.04–0.30 $m^3\ s^{-1}$) observed across all lakes in the RWA at nominal air temperatures and at + 2 °C and + 5 °C scenarios. We performed simulations that represented all combinations of the range of these lake characteristics. Then, to infer the relative importance of each factor for lake stability (aveRTRM), we analyzed output from these simulations using multiple regression. The primary predictors were air temperature, surface area, maximum depth, Secchi depth, and inflow. Data were log-transformed to account for non-normality, and AIC model selection was employed using the 'dredge' function of the 'MuMin' package in R. Residual diagnostic plots were examined to assess normality and variance of the errors, and we checked for covariance using the 'vcov' function in R.

The final set of simulations addressed how air temperature rise interacts with the broader range of mountain lake characteristics found across the western U.S. Summer inflow data were obtained from the National Hydrography Dataset (NHD) gathered from the Western U.S. Stream Flow Metrics website (RMRS 2019). We used stream flow data for stream segments located at elevations above 2100 m for the four major river basins of the SRM (Upper Colorado, Rio Grande, Arkansas, and Lower Missouri) to represent the regional range of inflow. Lake clarity, area and depth data were obtained for almost 3300 mountain lakes in the western U.S. from the EPA National Lakes Assessment datasets for years 1985, 2007, and 2012 (USEPA 2019), and from a database of natural lakes in Colorado (Colorado Parks and Wildlife, unpublished). The 10th, 50th, and 90th percentiles for each characteristic were used to represent low/small, medium and high/large levels of inflow, water clarity, and lake size (Table 3). Lake size categories were defined by the percentiles for both area and depth, except that we used 3.9 m as the shallowest depth because GLM was difficult to calibrate at shallower depths. Thus, small lakes were characterized as 3.9 m in depth and 0.81 ha in area, medium lakes were defined as 5.8 m in depth and 2.99 ha in area, and large lakes were defined as 20 m in depth and 11.98 ha in area. We use these terms subjectively and in the context of mountain lakes which, as a whole, are generally considered small (Bahls 1992). These sizes represent the range of lakes from the gathered datasets, not necessarily the entire size range of mountain lakes present. Each combination of characteristics and levels was simulated at nominal air temperatures, and at + 2 °C and + 5 °C warming scenarios.

For each simulation we computed two stability metrics (aveRTRM, percent change in aveRTRM) and two temperature metrics (percent change in surface and bottom temperature). We also gathered an ecologically relevant measure of surface and bottom temperatures. The warmest 30-day running mean of daily mean water temperature (M30AT; Roberts et al. 2013) was calculated for both the surface and bottom of each lake scenario. M30AT has been used to determine suitable thermal habitat for Cutthroat Trout *Oncorhynchus clarkii*, which are common in mountain lakes across the western U.S. Briefly, thermal thresholds were defined as follows: M30AT < 8.0 °C is too cold for growth and survival of young trout, while 8.0–9.0 °C can restrict growth in trout up to age-1. An M30AT from 9.1 to 18 °C is considered optimal for growth and recruitment of trout, while 18.1–19.9 °C can reduce growth, and M30AT > 20.0 may limit or prevent the growth of trout (Roberts et al. 2013).

Results

Field observations

Regional climate data showed that the weather during 2016 was not anomalous. All weather variables used as inputs to GLM were within one standard deviation of the most recent tri-decadal mean and outliers, missing data, and persistence errors were not detected. Thus, 2016 represented a reasonable baseline for current climate conditions of north-central Colorado mountain lakes, and these data were used as the nominal conditions in climate change scenarios. Oxygen concentrations from 1 m above the substrate showed that the RWA lakes that stratify for most of the summer have oxygen concentrations of < 2.5 mg L^{-1}, limiting habitat for coldwater fish (Saari et al. 2018).

Simulation modeling

There was good correspondence between observed temperatures and temperatures predicted by GLM for all six lakes. The average RMSE across lakes was ≤ 1.26 °C (Table 2).

Table 2 Results of GLM calibration for the six Rawah Lakes, including inflow, and root mean square error (RMSE) for fitted surface temperature, bottom temperature, and the difference between surface and bottom temperature

Lake name	Inflow (m^3 s^{-1})	RMSE (°C)		
		Surface	Bottom	Difference
Big Rainbow	0.15	1.06	0.88	1.03
Upper Sandbar	0.08	1.11	1.48	1.89
McIntyre	0.04	1.86	1.48	1.34
Sugarbowl	0.06	1.38	1.30	1.33
Upper Camp	0.30	1.22	0.36	1.26
Rawah #3	0.30	0.90	0.51	0.72
Average	0.16	1.26	1.00	1.26

Generally, RMSE was lower for bottom temperatures than surface temperatures, but only by ~ 0.3 °C on average. Results for the clearest lake (McIntyre) showed the largest surface RMSE (1.86 °C) and bottom RMSE (1.48 °C), while results for the largest and deepest lake (Rawah #3) had the smallest surface temperature RMSE (0.90 °C), and second smallest for bottom temperature RMSE (0.51 °C). The RMSE of surface-bottom temperature difference was also low, and similar to RMSE of surface temperatures across lakes. Inflows estimated during calibration ranged 0.04–0.30 m^3 s^{-1} (Table 2), which falls within the range of the 10th and 90th percentile of stream flows in the NHD within the elevation range of the SRM (Table 3). Also, a nearby stream gauge in the Michigan River had a similar average flow (0.05 m^3 s^{-1}) over the time period of this study. Further, the difference between the average calibrated inflows of the study lakes and the average measured inflows of four RWA lakes was only 0.03 m^3 s^{-1}.

Air temperature rise alone caused a substantial increase in water column stability (Fig. 3). On average, across all six RWA lakes, a 2 °C increase in air temperature resulted in a 34% increase in stability, while a 5 °C increase in air temperature increased stability by 81%. Stability increases were greater in the largest lakes. The relative increase in stability in the + 2 °C scenario in the deepest lake (Rawah #3) was similar to the relative increase in stability in the

Table 3 Some characteristics of mountain lakes in the western U.S

Characteristic	Number of waters	10th percentile	Median	90th percentile	Source
Surface area (ha)	1909	0.81	2.99	11.98	USEPA (2019); CPW
Maximum depth (m)	1712	1.5	5.8	20.0	USEPA (2019); CPW
Secchi depth (m)	472	1.96	5.00	10.74	USEPA (2019)
Inflow (m^3 s^{-1})	56,829	0.001	0.015	0.593	RMRS (2019)

Described inflows are from stream segments within the four major river basins of the Southern Rocky Mountains. The CPW source denotes unpublished data used by permission from Colorado Parks and Wildlife

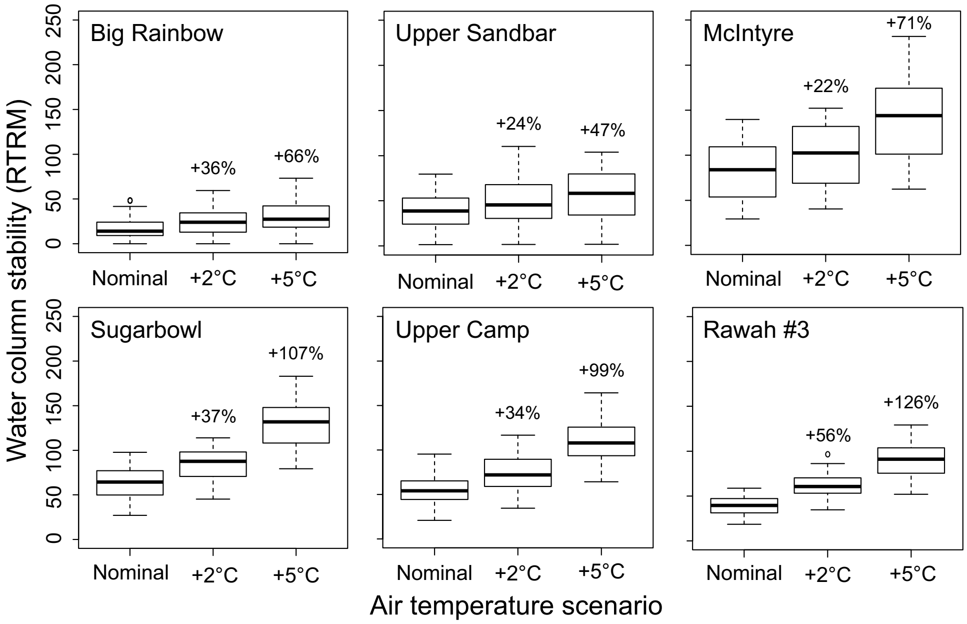

Fig. 3 Boxplots showing predicted water column stability (aveRTRM) of the six study lakes under nominal, + 2 °C, and + 5 °C air temperature scenarios. Percentages show the change in stability relative to nominal conditions

two smallest lakes in the + 5 °C scenario. We also noted that the most turbid, but shallowest lake (Big Rainbow), had a larger relative increase in stability in the + 2 °C scenario than in 3 out of 5 deeper, clearer lakes. The highest nominal stability, and lowest relative increase in stability occurred in the clearest lake which also had the lowest calibrated inflow (McIntyre). Thus, results from simulations in the six RWA lakes suggest that the response in lake stability to climate warming depends on lake size, clarity, and inflow.

The sensitivity analysis confirmed that water temperatures and stability of the RWA lakes were most responsive to air temperature change (Fig. 4). The effect of air temperature was positive and higher air temperatures increased stability and water temperatures more than the same proportional reduction in air temperatures reduced stability and water temperatures. Stability and surface temperatures were negatively related to inflow, and the changes were larger for reduced inflow than for increased inflow. Bottom temperatures were positively related to inflow. Thus, warmer and drier conditions will have compound effects on water column stability and water temperatures in the RWA lakes. Changes in lake clarity and wind speed produced smaller effects. The effect of changes to water clarity were variable and lake-specific, but changes were generally < 10% of the nominal value. In general, stability and water temperatures were negatively related to changes in wind speed, and < 10% of the nominal value. Because of the low sensitivity of lake thermal structure to wind relative to other factors, we did not include wind in further analyses.

We performed 3888 simulations representing all combinations of RWA lake areas, depths, clarity and inflow under nominal, + 2 °C, and + 5 °C air temperature scenarios. In general, lake stability increased with lake area and depth and decreased with Secchi depth and inflow, and the relationships appeared to be asymptotic (Fig. 5). Under nominal air temperatures, inflow produced the greatest variation in aveRTRM (74%). Variations in aveRTRM due to depth (67%) and area (63%) were similar, and greater than the variation due to water clarity (44%). These patterns were similar in the increased air temperature scenarios. Across the range of lake characteristics average stability increased by 24% and minimum stability increased by 57% on average with a + 2 °C change in air temperature and increased by an average of 71% and 173% respectively with a + 5 °C change in air temperature. Depth produced the greatest relative increase in minRTRM (> 1000%), and clarity produced the lowest relative increase (22%). The effect of depth on aveRTRM and minRTRM was greatest for depths < 20 m; increases in depth above about 20 m had almost no effect on lake stability metrics.

Across the range of RWA lake characteristics, the multiple regression analysis showed that air temperature, area, depth, clarity, and inflow were all significant predictors of lake stability (AICc = – 4790.46, AIC weight = 1, $R^2 = 0.91$, $p < 0.001$) (Table 4). Residual diagnostics also supported the

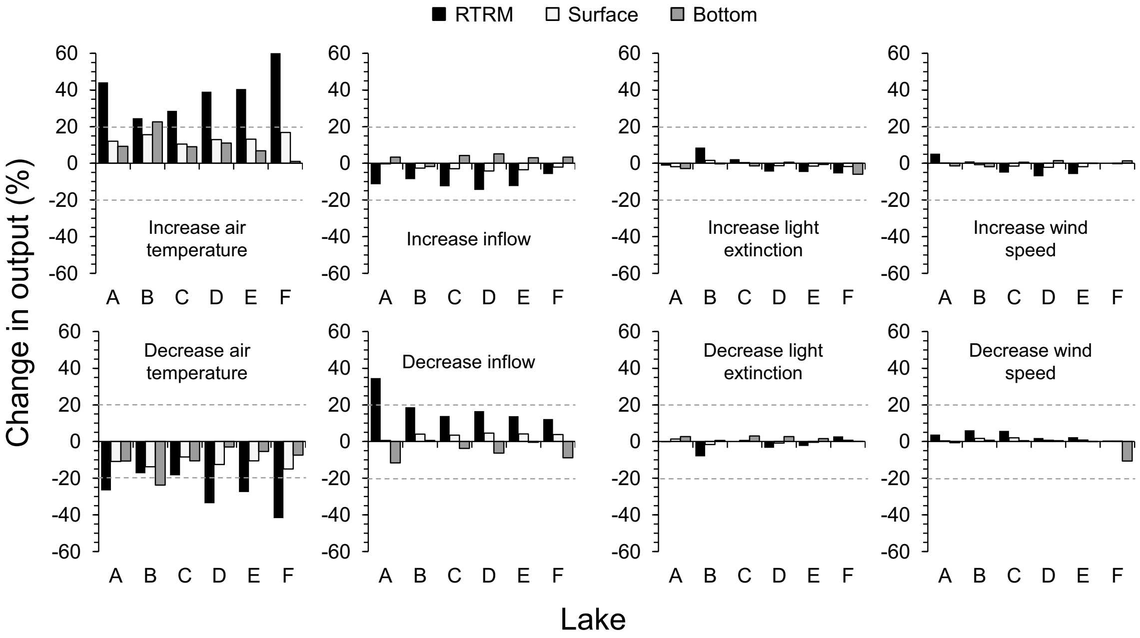

Fig. 4 Results of a sensitivity analysis assessing the effects of a ± 20% change in air temperature, inflow volume, clarity, and wind speed on predicted surface temperature, bottom temperature and stability (aveRTRM) for the six study lakes: Big Rainbow (A), Upper Sandbar (B), McIntyre (C), Sugarbowl (D), Upper Camp (E), and Rawah #3 (F)

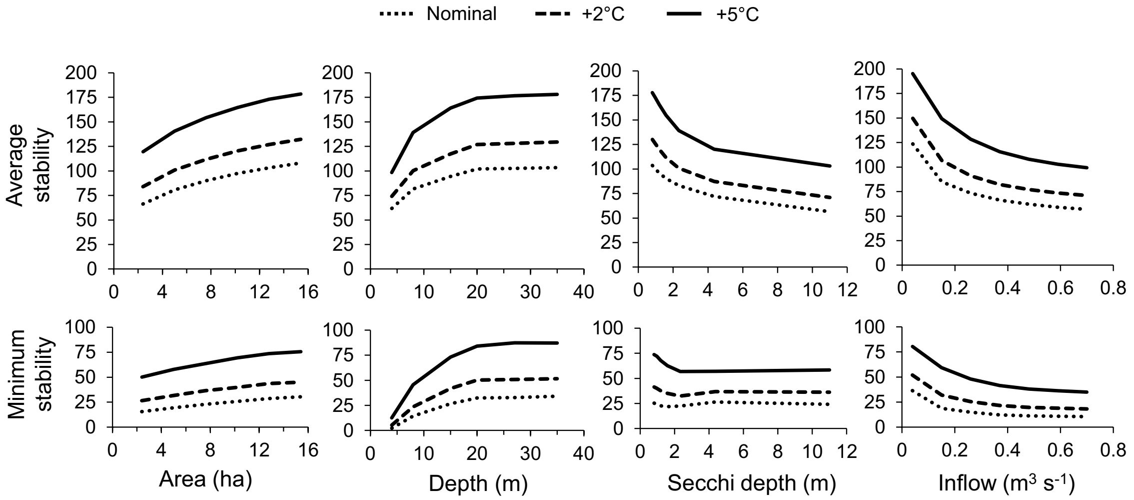

Fig. 5 Predicted effects of lake area, depth, Secchi depth, and inflow on average (aveRTRM) and minimum (minRTRM) water column stability under three air temperature scenarios. Ranges of the independent variables correspond to the ranges found in the RWA lakes and the western United States

Table 4 Results of multiple regression analysis to investigate relationships among lake stability (aveRTRM), air temperature and lake characteristics

	Candidate models	AICc	ΔAICc	w_i
1	Area + depth + flow + clarity + temp	− 4790.46	0.00	1
2	Area + depth + flow + temp	− 1561.64	3228.82	0
3	Depth + flow + clarity + temp	− 1474.17	3316.29	0
4	Area + depth + clarity + temp	− 851.06	3939.40	0
5	Area + flow + clarity + temp	126.04	4916.51	0
6	Depth + flow + temp	232.32	5022.78	0
7	Area + depth + flow + clarity	417.73	5208.20	0
8	Area + depth + temp	645.11	5435.57	0
9	Depth + clarity + temp	694.91	5485.38	0
10	Area + flow + temp	1335.62	6126.09	0
	…			
30	Area	3919.19	8709.65	0
31	Clarity	3940.70	8731.17	0

ΔAICc is difference between the Akaike information criterion of the given model and the model with the lowest AICc; AICc weight (w_i) indicates the probability of the particular model being the best in the candidate set

full model, with no non-normality or residual dependence. Of the climate-related factors, air temperature had the largest effect, followed by clarity and then inflow. With other parameters held constant a 20% change in air temperature resulted in an average 32.42% change in aveRTRM. A 20% change in clarity or inflow resulted in a 4.62% and 4.46% change in aveRTRM, respectively. Although actual changes in these factors would be region- and time- specific, their cumulative effects are important. For example, change in lake stability was predicted to be 28% higher with reductions in clarity and inflow coupled with air temperature increase (41.50%), compared to effects of a 20% increase in air temperature alone. Lake area and depth were also important. A 20% change in depth or area resulted in a 5.24% and 4.47% change in aveRTRM, on average, indicating that the response of lake stability to climate-related factors will be mediated by lake morphometry.

Expanding our inference to the range of characteristics of small mountain lakes in the western U.S., generally, larger lakes had higher stability under all air temperature scenarios, water clarities and inflows than smaller lakes (Fig. 6). On average, the stability of the large size class of lakes in our study was predicted to increase more under + 2 °C (23%) and + 5 °C (62%) air temperatures scenarios than the stability of our small lakes that was predicted to increase by 15% at + 2 °C and 39% at + 5 °C, on average. Lakes with the lowest inflow were predicted to increase in stability by 20% at + 2 °C and 59% at + 5 °C, on average, while the lakes with the highest inflow were predicted to increase in stability by 19% at + 2 °C and 40% at + 5 °C. Air temperature rise had a similar relative effect on stability of clear and turbid lakes. The clearest lakes were predicted to increase by 21% at + 2 °C and 53% at + 5 °C compared to the most turbid lakes that were predicted to increase by 17% at + 2 °C and 49% at +5 °C, on average. Overall, the largest relative change in stability from air temperature rise occurred in large, clear lakes with high inflows (112% at + 5 °C), demonstrating the influence that clarity and inflow can have on lake stability.

Changes to lake stability resulting from air temperature rise were compounded by concurrent reductions to water clarity or inflow. In fact, step changes in inflow or clarity from high to moderate or moderate to low had larger effects on stability than the effect of air temperature rise predicted

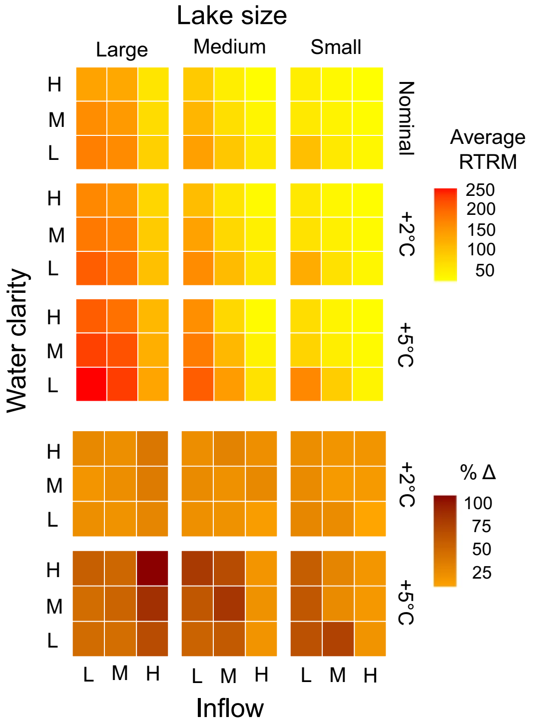

Fig. 6 Predicted cumulative effects of air temperature, lake size, clarity and inflow on lake stability (aveRTRM). Categories for lake characteristics were defined as the 10th, median, and 90th percentiles for mountain lakes in the western U.S. Top panel compares stability under nominal, + 2 °C and + 5 °C air temperature scenarios, and the bottom panel shows the relative change (%) in stability resulting from air temperature rise

in climate change scenarios (Fig. 6). For example, if clarity declined from high to moderate at + 2 °C then aveRTRM was predicted to increase by 53%, and by 92% at + 5 °C, on average, and a shift from moderate to low clarity at + 2 °C increased aveRTRM by 66% and 113% at + 5 °C, on average. If inflow decreased from high to moderate then aveRTRM was predicted to increase by 130% at + 2 °C, on average, and 201% on average at + 5 °C. A change in inflow from moderate to low was predicted to increase aveRTRM by 88% at + 2 °C and 151% at + 5 °C, on average. The greatest change to stability occurred when clarity and inflow declined simultaneously, as might be expected to accompany climate change. For example, if clarity changed from moderate to low and inflow changed from high to moderate then stability was predicted to more than double (208%) at + 2 °C air temperatures and triple (318%) at + 5 °C air temperatures.

Lake size had a similar effect on lake surface and bottom temperatures (Fig. 7), where generally, larger lakes in our simulation set had higher surface temperatures than small lakes. However, surface temperatures of small lakes increased more with air temperature rise than in large lakes. On average, the surface temperatures of small lakes were predicted to increase by 12% at + 2 °C and 16% at + 5 °C, whereas large lake surface temperatures were predicted to increase at only 9% at + 2 °C and 12% at + 5 °C. Thus, lake surface temperatures may become more homogenous across lake sizes as air temperatures rise. Under nominal air temperatures, the range of lake surface temperature spanned 7.3 °C, while at + 2 °C it spanned 6.8 °C and at + 5 °C the span in surface temperatures declined to 5.8 °C. Bottom temperatures in small lakes were also more responsive to air temperature rise than in large lakes. On average, bottom temperatures of small lakes were predicted to increase by 12% at + 2 °C and 16% at + 5 °C, while only 2% at + 2 °C and 1% at + 5 °C in large lakes; however, unlike surface temperatures, some scenarios resulted in decreased bottom temperatures. Generally, high turbidity and low inflow resulted in lower bottom temperatures. Larger lakes also had decreasing bottom temperatures under air warming predominantly more than small lakes. Large lakes of all clarities at low and moderate inflows had slightly decreasing bottom temperatures with rising air temperatures, whereas only low inflow, low clarity small lakes had decreasing bottom temperatures at + 5 °C.

As with stability, including effects of changing clarity and inflow produced greater change in surface and bottom temperatures than under air warming alone. If clarity decreased from high to moderate then surface temperatures increased by 15% at + 2 °C and 32% at + 5 °C, on average, while a shift from moderate to low clarity resulted in surface temperature increases of 14% at + 2 °C and 30% at + 5 °C (Fig. 7). Decreasing inflow from high to moderate resulted in surface temperature increases of 35% at + 2 °C and 53% at + 5 °C, on average, and a decrease in inflow from moderate to low was predicted to increase surface temperatures by 20% at + 2 °C and 34% at + 5 °C. The largest increase in surface temperature was predicted when clarity and inflow both changed from high to moderate, resulting in an increase of 43% at + 2 °C and 61% at + 5 °C. Bottom temperature changes were more complex and demonstrated the collective influences of lake size, clarity, and inflow. Generally, bottom temperatures in our large lakes changed very little (< 2% on average), compared to medium and small lakes where changes were larger and could be positive or negative. For example, in our medium sized lakes, clarity changes combined with air increases led to decreased bottom temperatures at low inflow (− 31% on average) and increased bottom temperatures at high inflow (35% on average). But at moderate inflows, bottom temperatures in medium sized lakes increased when clarity decreased from high to moderate, and bottom temperatures decreased when clarity shifted from moderate to low. The only reduction in bottom temperatures of small lakes occurred at low inflow with a clarity change of moderate to low (− 36% on average). The largest overall change occurred in small lakes where reducing clarity and

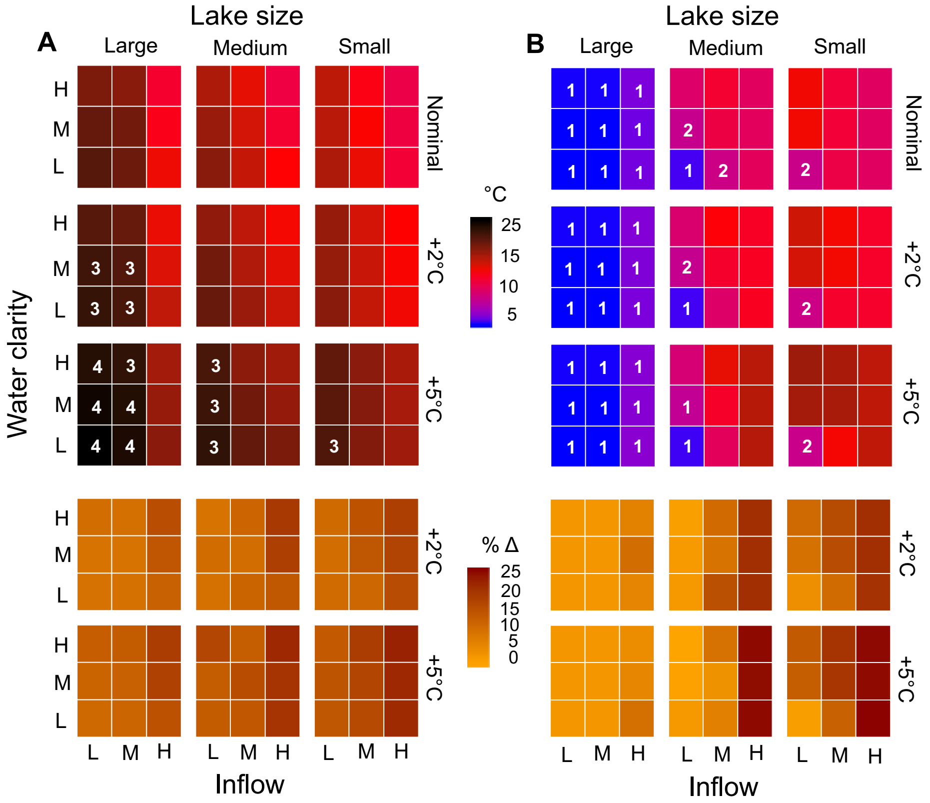

Fig. 7 Predicted cumulative effects of air temperature, lake size, clarity and inflow on lake surface (**a**) and bottom (**b**) temperatures (M30AT). Categories for lake characteristics were defined as the 10th, median, and 90th percentiles for mountain lakes in the western U.S. Top panel compares lake temperatures under nominal, +2 °C and +5 °C air temperature scenarios, and the bottom panel shows the relative change (%) in lake temperatures resulting from air temperature rise. Combinations of lake conditions with predicted temperatures harmful for Cutthroat Trout (trout) are indicated as follows: (1) too cold for growth and survival of young trout, (2) restricted growth for trout up to age-1, (3) reduced growth for adult trout, and (4) limited to no growth of adult trout

inflow from high to moderate led to a 32% increase in bottom temperatures at +2 °C and 56% increase at +5 °C.

Even when accounting for the combined effects of air temperature change and changes to water clarity and inflow, our simulations suggest that declines in thermal habitat for trout in mountain lakes will be limited. Reductions in the quality of thermal habitat for trout were greatest in large lakes, where optimal habitat in the epilimnion was restricted to conditions of high inflow or high water clarity at +2 °C and high inflow only at +5 °C, but the hypolimnion of all large lake scenarios suggested that temperatures were too cold for growth and survival of young trout. In medium sized lakes detrimental thermal effects in the epilimnion and hypolimnion only occurred under low inflow conditions. Impairments to thermal habitat for trout in small lakes were only predicted at +5 °C in lakes with lowest water clarity and inflow conditions.

Discussion

We found that air temperature rise is the dominant force driving changes to the thermal regimes of mountain lakes, but other environmental stressors associated with climate change can compound air temperature effects. We showed that habitat conditions in mountain lakes are vulnerable to environmental stressors associated with climate change that alter lake inflows and water clarity. These factors can have greater effects on lake stability and temperature regime than higher air temperatures. Predictions of the effects of air temperature rise alone could underestimate effects on lake stability by > 100% when coupled with extreme environmental events such as severe drought and wildfire. These events can be episodic, but when combined with climate warming will increase the mean and variability of lake stability and temperatures. We also found that sensitivity of mountain lake thermal conditions to climate-related stressors was highly variable over the small size range of mountain lakes present in the western U.S. (Bahls 1992). Thus, effects of climate change on mountain lake thermal properties depend on lake size, and predictions could greatly underestimate effects without accounting for linked environmental stressors that compound the effects of air temperature rise.

Because lake surface temperatures are closely linked to atmospheric conditions (Adrian et al. 2009), it is reasonable that air temperature rise is predicted to play a major role in future lake thermal conditions (Schneider and Hook 2010; O'Reilly et al. 2015; Woolway et al. 2017a). Air temperature rise has already increased surface temperatures of mountain lakes in the region (Sadro et al. 2018; Christianson et al. 2019). The nonlinear relationship between temperature and water density indicates that climate warming will have a larger effect on lake stability than cooling (Kraemer et al. 2015), especially at the relatively low temperatures typical of mountain lakes. We predicted that future warming could more than double the stability of the RWA lakes. However, climate warming also has indirect effects on lake stability and thermal conditions.

Rising air temperatures hasten snowmelt and warm the resulting streamflow (Musselman et al. 2017; Isaak et al. 2012), and these changes to timing and temperature of lake inflows compound the effects of warmer air on lake stability. Recession of perennial snowpack and glaciers is a global phenomenon (Fountain et al. 2012) and this loss may reduce summer inflows to lakes (Hoffman et al. 2007; Clow 2010), especially during droughts which are typically moderated by glacial melt (Fountain and Tangborn 1985). Rising temperatures coupled with current trends in nutrient enrichment of mountain lakes may increase algal production (Nanus et al. 2012; Roberts et al. 2017) and reduce water clarity. Warming is also increasing the frequency and intensity of forest fires in the region (Westerling et al. 2006: Riley and Loehman 2016), which could contribute to further reductions in lake clarity with implications for lake stability and surface warming. Finally, atmospheric stilling has been demonstrated in mountainous regions elsewhere (You et al. 2010; Michelutti et al. 2016), highlighting the potential importance of understanding the effects of reduced wind stress on mountain lake stability and thermal regimes. Further, some lakes larger than those presented here have been shown to be more sensitive to wind than was found in our study (Von Einem and Graneli 2010).

When climate and associated environmental factors are considered independently, we found that air temperature increases had the largest effect on lake stability and water temperatures. However, our sensitivity analysis demonstrated that these other environmental factors can also alter lake thermal conditions substantially. Air temperature changes are probably more predictable and will likely continue to increase into the future (IPCC 2013). Changes to environmental factors such as inflows and water clarity are less predictable and will likely occur more sporadically in the future because they are associated with periodic extreme events like forest fires and drought (Schindler 2009; Miller and Piechota 2011). However, it is reasonable to expect that the frequency and intensity of these factors may increase in the western U.S. as the climate warms. In combination, climate and associated environmental factors can cause dramatic changes in lake thermal conditions compared to effects of air temperature rise alone.

Traditional sensitivity analyses, such as the one presented in our study, allow scientists to understand individual effects of changing climate and environmental conditions on lakes, but realistically these changes do not occur alone and they can interact. These interactions can compound the effects of each factor individually, intensifying effects of climate change on lakes. For example, air temperature rise increases evaporation rates and can allow the atmosphere to retain more moisture (Bonan 2016). This can result in decreased precipitation and drier conditions in the watershed. Drier terrestrial conditions can increase forest fire activity, and therefore, increase suspended sediment and nutrient inputs to lakes, which can increase primary production and decrease water clarity (Schindler 2009). This could amplify lake heterotrophic processes that contribute to a climate feedback loop by supplying additional greenhouse gases to the atmosphere that further increase air temperatures (Huttunen et al. 2003).

Climate change can increase lake stability and that is important because a lake's mixing regime can affect its thermal response to temperature change (Butcher et al. 2015; Kraemer et al. 2015). For example, dimictic lakes differ from polymictic lakes in the distribution of heat in the water column (Hondzo and Stefan 1993; Kirillin 2010). Effects of warming are concentrated in the epilimnion of dimictic lakes and hypolimnetic temperatures can be constant or decrease slightly. Polymictic lakes typically show nearly uniform warming across the water column. These patterns were present in our simulations. Hypolimnetic temperatures in large lakes changed little, while in small lakes bottom temperatures increased. Surface temperature changes were also greater in small lakes. Persistent stratification in large, deep lakes restricts warming to the epilimnion, compared to smaller, polymictic lakes, but the shallower depth and volume of small lakes result in higher temperatures throughout the water column. Thus, lake morphometry is a determinant of mixing regime and temperature profiles. Worldwide, stability is increasing the most in deeper lakes (Kraemer et al. 2015) but hypolimnion temperatures have been relatively unaffected (Butcher et al. 2015). As environmental conditions change, more small, shallow lakes could exceed a stability tipping point and become dimictic, resulting in warmer surface water and a cooler hypolimnion.

In the RWA lakes, it appeared that such a tipping point is reached at a daily minimum RTRM of ~ 30. This corresponded to a daily minimum surface-bottom temperature difference of only about 2 °C. When stability was below this threshold stratification was brief and intermittent and the lakes continued to mix periodically throughout the summer. Lakes that sustained a ≥ 2 °C difference in surface and bottom temperatures during diurnal cooling stayed stratified for longer periods throughout the summer. Others have found that this RTRM value corresponds to the development of a metalimnion and limited mixing of the water column (Kortmann et al. 1982; Barbiero et al. 1997). In our nominal scenario, the minRTRM of 30 was reached at a maximum depth of about 20 m, on average across all lake types and conditions. This means that under current conditions, lakes that were at least 20 m deep remained stratified throughout the summer. However, under certain conditions, such as high turbidity and low inflow, much smaller lakes can reach this stability threshold. On average, across the > 3500 possible combinations of turbidities, water clarities, inflows, and lakes sizes present in the RWA, our simulations showed that the maximum depth associated with a minRTRM of 30 drops from 20 m to about 8 m under a + 5 °C air warming scenario. Based on the range of maximum depths in our regional dataset, this implies that climate change could cause an additional 26% of mountain lakes to develop prolonged stratification. Also, our simulations show that, generally, minRTRM is changing much more than averageRTRM under climate and environmental change.

Many investigators have used temperature difference between surface and bottom layers to define the likelihood of prolonged stratification. However, RTRM is a more appropriate method for evaluating lake stability because RTRM considers water density differences rather than an absolute temperature difference between surface and bottom (Kortmann et al. 1982). Because water density changes nonlinearly with temperature stability, metrics that explicitly incorporate temperature effects on density will become more useful as lakes become warmer in the future. Rising temperatures can increase lake stability even when temperature differences between surface and bottom layers do not change. For example, when lake surface temperature is 13 °C, a 2 °C surface-bottom temperature difference results in RTRM < 30, while the same surface-bottom temperature difference results in RTRM > 30 at a surface temperature of 15 °C. The particular RTRM threshold for stratification is site-specific. For example, lakes in areas with strong winds, and lakes with high surface area to depth ratio or high inflows may require larger RTRM values to experience persistent stratification. However, because even small changes in temperatures can lead to considerable changes in RTRM, especially at higher temperatures, air temperature rise will likely shift the mixing regimes of some mountain lakes. These changes to stability could be intensified by concomitant decreases in lake clarity and/or inflows.

A few other studies have also shown that decreased clarity can increase surface temperatures, while increased clarity, depending on maximum depth, can decrease surface temperatures and increase bottom temperatures (Butcher et al. 2015; Rose et al. 2016). In lakes where changes to water clarity will co-occur with climate warming the effects of climate change on lakes can be underestimated unless water clarity is included in models. Further, climate-related changes in water clarity could be much greater than the 20% perturbations in our simulations (McEachern et al. 2000; Rose et al. 2016).While some have demonstrated how lake inflow can influence lake stability (Carmack 1978; Rimmer et al. 2011), inflow is frequently unknown or neglected in lake thermal analyses (e.g.: Read et al. 2014; Winslow et al. 2017). In our study, the importance of including inflow as a driver of lake stability and thermal conditions is supported by the fact that under all conditions and climate scenarios the lakes with the lowest stability and coolest surface temperatures were those with high inflows. Inflow can also have a large effect on small and medium lake bottom temperatures. High inflows in small to medium lakes maintained low stability despite air temperature warming. These lakes remain polymictic and heat is contributed to bottom waters during periods of mixing. The complex effects of inflow on lake thermal properties make it important to include in predictions of lake climate responses, especially in regions with hydrographs driven by snowmelt, such as in high elevation areas of the western U.S.

High elevation areas are important for conservation of coldwater species. Although mountain lakes are warming and becoming more stable, our simulations and another recent study in the region (Roberts et al. 2013) showed that most of these generally cool systems will maintain suitable habitat for Cutthroat Trout. However, if air temperatures increase by 5 °C, we predict that surface temperatures in the largest lakes may become too warm for trout growth and hypolimnetic temperatures will become too low to support young trout. Further, earlier and more prolonged stratification could result in decreased hypolimnetic oxygen concentrations (Massaghi et al. 2017) making the hypolimnion even less suitable for trout. On the other hand, climate change may make temperatures in small to medium sized lakes more favorable for trout growth, as long as food availability is adequate.

This study has some potential limitations. First, we calibrated our model to a relatively limited set of mountain lakes in the Southern Rocky Mountains over a short time period. Mountain lakes across the western U.S. share some basic characteristics (e.g., morphometry, trophic state, hydrology), so our primary conclusions should be applicable to many small lakes outside the SRM. However, mountain lakes outside the SRM may differ in other characteristics (e.g., finescale climate or water chemistry). For example, lakes in the RWA could be considered slightly more turbid than other mountain lakes. It is possible that glacial flour or dissolved organic carbon input from surrounding vegetation may be decreasing clarity more than in other systems. Also, mountain lakes larger than we simulated are present throughout the region. Thus, our results should be viewed in this lake size context. We also acknowledge that climate change has already altered mountain lake ice-off dates (Preston et al. 2016; Sadro et al. 2018) so future studies of mountain lake stability should examine the interactive effects of earlier ice-off and stratification with other lake characteristics.

Although GLM has been applied successfully to a very wide range of lake characteristics using the same parameterizations we used (Hipsey et al. 2012; Rose et al. 2016; Bruce et al. 2018), validating our model with high resolution data from lakes in other mountain ranges would be informative. High resolution data are difficult to obtain in remote locations and were not available for the RWA beyond the period used in this study. We also found that it was difficult to calibrate the model to lakes < 3.9 m deep. It may be that the influence of sediment warming and possible nocturnal heat release may be contributing to the lack of fit of GLM in these shallow lakes (Fang and Stefan 1996). Finally, given the importance of inflow in our simulations, more comprehensive data on surface and subsurface inflows (see Caine 1989) would be useful. Permanent stream gages are probably rare in the vicinity of mountain lakes, especially those, like the RWA lakes, that are within federally-designated wilderness areas, so it will be useful for future studies to employ portable stream flow loggers or water level loggers that could be used to measure lake inflows.

The number of studies demonstrating the effects of climate change on lake thermal properties is expansive. However, studies that focus on effects of air temperature rise alone underestimate the impacts of climate change on lakes because of the compound effects of other climate-related stressors. Lake thermal models provide a means to investigate the relative importance of a suite of lake-specific and climate-related factors. The structure and function of GLM makes it a widely applicable tool, and indeed this model has been used in a large number of lake studies across the globe (Bruce et al. 2018). When coupled with improved forecasts of environmental change lake models like GLM can make better predictions of the impacts of climate-related stressors on the physical characteristics of lakes and resulting habitat suitability for aquatic organisms. Climate change has many direct and indirect consequences for lake systems. Combating climate change and preparing for its effects on lakes necessitates a holistic understanding of the compound effects of climate-related stressors and their consequences.

Acknowledgements We thank Ben Galloway, Casey Barby, Brendon Sucher, Austin Coward, and William Pate for help collecting field data. We also thank A. Scott Denning for help and guidance through the conceptualization of the manuscript. This project was supported by NSF Grant No. DGE-0966346 "I-WATER: Integrated Water, Atmosphere, Ecosystems Education and Research Program" and a private gift to Colorado State University, Account Number 6-464540. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. government.

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