RESEARCH ARTICLE

Thermal regimes of Rocky Mountain lakes warm with climate change

James J. Roberts^{1,2*}, Kurt D. Fausch³, Travis S. Schmidt¹, David M. Walters²

1 Colorado Water Science Center, U.S. Geological Survey, Fort Collins, Colorado, United States of America, **2** Fort Collins Science Center, U.S. Geological Survey, Fort Collins, Colorado, United States of America, **3** Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, United States of America

☞ These authors contributed equally to this work.

* jroberts@usgs.gov

Abstract

Anthropogenic climate change is causing a wide range of stresses in aquatic ecosystems, primarily through warming thermal conditions. Lakes, in response to these changes, are experiencing increases in both summer temperatures and ice-free days. We used continuous records of lake surface temperature and air temperature to create statistical models of daily mean lake surface temperature to assess thermal changes in mountain lakes. These models were combined with downscaled climate projections to predict future thermal conditions for 27 high-elevation lakes in the southern Rocky Mountains. The models predict a $0.25^{\circ}\text{C}\cdot\text{decade}^{-1}$ increase in mean annual lake surface temperature through the 2080s, which is greater than warming rates of streams in this region. Most striking is that on average, ice-free days are predicted to increase by $5.9\text{ days}\cdot\text{decade}^{-1}$, and summer mean lake surface temperature is predicted to increase by $0.47^{\circ}\text{C}\cdot\text{decade}^{-1}$. Both could profoundly alter the length of the growing season and potentially change the structure and function of mountain lake ecosystems. These results highlight the changes expected of mountain lakes and stress the importance of incorporating climate-related adaptive strategies in the development of resource management plans.

OPEN ACCESS

Citation: Roberts JJ, Fausch KD, Schmidt TS, Walters DM (2017) Thermal regimes of Rocky Mountain lakes warm with climate change. PLoS ONE 12(7): e0179498. <https://doi.org/10.1371/journal.pone.0179498>

Editor: João Miguel Dias, Universidade de Aveiro, PORTUGAL

Received: June 2, 2016

Accepted: May 31, 2017

Published: July 6, 2017

Copyright: This is an open access article, free of all copyright, and may be freely reproduced, distributed, transmitted, modified, built upon, or otherwise used by anyone for any lawful purpose. The work is made available under the [Creative Commons CC0](https://creativecommons.org/licenses/by/4.0/) public domain dedication.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: This work was funded by the United States Geological Survey, who provided JJR funding through the Mendenhall Postdoctoral Fellowship Program. Colorado Parks and Wildlife also provided funding to KDF. The funder provided support in the form of salaries for authors JJR, DMW, TSS, but did not have any additional role in the study design, data collection and analysis, decision to publish, or preparation of the

Introduction

Aquatic systems are being altered by anthropogenically driven changes in climatic conditions [1–5]. Changes in climate are causing a wide range of stresses in aquatic systems, and a particularly important one is increasing water temperature, which has been documented in streams and lakes worldwide [5–7]. Lakes are important sentinels of climate change [8,9] and the routes to change in lakes include three primary climate forcing pathways: temperature, precipitation, and incident solar radiation [10]. Rising water temperatures in lakes is a particularly important change because lakes have warmed faster than atmospheric temperatures in some cases [11,12]. Worldwide, the summer surface temperatures of lakes are increasing at an average rate of $0.34^{\circ}\text{C}\cdot\text{decade}^{-1}$ [5]. These high rates of temperature rise are likely to have significant effects on lakes because thermal regime has a strong influence on the structure and

manuscript. The specific roles of these authors are articulated in the 'author contributions' section.

Competing interests: This work was funded by the United States Geological Survey, who provided JJR funding through the Mendenhall Postdoctoral Fellowship Program. Colorado Parks and Wildlife also provided funding to KDF. This commercial affiliation does not alter our adherence to PLOS ONE policies on sharing data and materials.

function of lentic ecosystems [13–15]. Specific lake processes that are susceptible to thermal changes include plankton bloom phenology [16], harmful algal blooms [17], depletion of hypolimnetic dissolved oxygen concentrations [18], and thermal suitability for vertebrates [19,20].

Although changing thermal conditions are predicted for lakes of all sizes and types, the influence of a changing climate on abiotic and biotic conditions of high-elevation mountain lakes remains poorly studied. Small lakes are common features of mountainous landscapes, where headwater systems function as important drivers of watershed processes [21]. One region where headwater lakes are especially important to biogeochemical and hydrologic processes is the southern Rocky Mountains (SRM; [22,23]). Within the SRM, a semi-arid portion of western North America, mountain lakes and corresponding headwater networks influence important water management decisions through their storage and release of snowmelt, an important hydrologic driver of streams, rivers, and reservoirs [24–27]. Air temperatures in the SRM are warming, although these trends are mostly confined to the summer and fall seasons [28], and the magnitude of these changes are elevation dependent [29]. Therefore, understanding how high-elevation mountain lakes respond to climate change is important for water management in the SRM and other regions where anthropogenic needs depend on mountain hydrology.

Mountain lakes and associated headwater regions also provide critical refuge habitats for native species throughout the SRM, many of which are imperiled (e.g., Cutthroat Trout *Oncorhynchus clarkii* spp. and several amphibians; [30–32]). Various aspects of climate change, including warming temperatures, have the potential to alter the unique habitats that these lakes provide. However, the influence of changing climatic conditions on mountain lakes in the SRM has been previously addressed mostly through broad scale generic modeling of North American lakes (i.e., [33–35]) and a limited number of empirically-based studies of individual mountain lakes [28,36]. Thus, uncertainty remains regarding how the thermal conditions of SRM lakes have changed in the past, the magnitude of likely future changes, and the potential landscape-level consequences of these changes for lake-dependent species and ecosystem processes.

Here we use continuous records of surface water temperature for individual lakes and weather station measurements of air temperature to create statistical models of daily mean lake surface temperature. The fine-scale temporal resolution of our predictions facilitates detailed analyses of SRM lake thermal regimes. We combine these statistical models with dynamically downscaled regional climate model predictions to forecast lake surface water temperature trends over the next 70 years, and test the hypothesis that mountain lakes in the SRM are warming in response to climate change. Our model results provide information and models crucial to the creation of climate-smart management and conservation plans for mountain lakes and their biota.

Materials and methods

Temperature data

We compiled data for 27 lakes, the majority of which are in Rocky Mountain National Park (S1 Table), all of which had continuous records at least 2 years long (range: 2 to 15 years). Temperature was recorded every 60 minutes for the entire duration of each continuous lake record. We performed an initial quality check of these data using protocols established for stream temperature data [37]. Only georeferenced data collected within the top 3 meters of the water column or located within the first 250m of the lake inlet or outlet stream were included in our analysis. Hydrogeomorphic site characteristics for each lake (S1 Table) were collected

during logger deployment (maximum depth and elevation) and downloaded from the National Hydrography Dataset Plus Version 2 (surface area and cumulative drainage area; NHDPlusV2; <http://www.horizon-systems.com/nhdplus/>). To use the data collected in Rocky Mountain National Park we received approval for this project from the park and we performed this research under a Scientific Research and Collection Permit (#ROMO-2013-SCI-0009).

We acquired air temperature records from the snow telemetry (SNOTEL) network and created a database of the 21 SRM SNOTEL sites nearest the lakes with temperature data. Daily summaries of average air temperature ($^{\circ}\text{C}$) were downloaded from the SNOTEL webportal (<http://www.wcc.nrcs.usda.gov/snow/>) and used to calculate the 7-day running mean of daily air temperature (hereafter, mean weekly temperature). We used this metric as the independent variable to create water temperature models of daily mean lake surface temperatures for each lake and, in turn, to predict past and future lake temperatures.

Model development

We created a separate model of daily mean lake surface temperature for each lake. We used air temperature from the nearest SNOTEL site (via Euclidian distance) and selected data to match the period of lake temperature record. We used mean weekly air temperature as a predictor of daily mean lake surface temperature (Fig 1A), and created predictive models using non-linear logistic regression [38,39]. This modeled relationship represents how air temperature and lake surface temperature co-vary, with extreme low air temperature rarely driving lake temperature below 0°C and an asymptotic upper limit of lake temperature controlled by evaporative cooling [39]. Model parameters were fit using a non-linear least-squares loss function and the Gauss-Newton algorithm. All models were fit using SYSTAT 12 software (Chicago, IL). We evaluated model fit using the Nash Sutcliffe Coefficient (NSC; [40]) where a perfect model fit receives a value of 1 and a poor model fit can receive negative values. The NSC is a more effective measure than the Root Mean Squared Error for evaluating the fit of non-linear models [39].

Lake temperature predictions

Reconstructing lake temperature. We employed these non-linear models to predict past lake surface temperature (reconstructing) using the entire air temperature time series (1986–2014) from the SNOTEL sites. These reconstructions serve as baseline conditions for assessing projected future thermal conditions for each lake (Fig 1B).

Projections of lake temperature. We used the model developed for each lake to project future thermal conditions from dynamically downscaled climate projections [41]. The spatial resolution of these climate projections is 15x5-km grid cells, and projections are available for short-term (2035–2045) and long-term (2075–2085) time horizons. We used daily output of surface air temperature from the PSU/OSU GENMOM (GNM; [42]) and MPI ECHAM5 (ECH; [43]) climate models, which were dynamically downscaled using a regional climate model (RegCm3; [41]) under the A2 emission scenario from the IPCC AR4 (International Panel of Climate Change) which assumes a medium-to-high emissions future [44]. The A2 emission scenario is most similar to the RCP 8.5 carbon scenario used in the newest IPCC AR5 efforts [45]. Moreover, the GNM and ECH climate models were the only two models from Hostetler et al. [41] that provided daily output suitable for our analysis. We compared daily air temperatures measured at each SNOTEL site used in this study with temperatures predicted from each climate model within the overlaying grid cell of each SNOTEL site for 2010–2012 (the only overlapping years available) and created an average monthly correction factor. We applied this additive monthly correction factor to all climate projections before

Fig 1. Lake temperature modeling process. Schematic of the process used to create models of lake surface temperature and predicted future thermal conditions of southern Rocky Mountain lakes. Input variables are shown in ovals and the model of surface temperature and model output are in rectangles. Thermal metrics include the warmest 30-day running mean of daily mean water temperature (M30AT), the mean annual surface temperature (MAT), the mean summer surface water temperature (MST), and number of ice-free days (IFD). The gray polygon in B indicates upper and lower bounds of the predictions derived from uncertainty analysis (see [Materials and Methods](#)).

<https://doi.org/10.1371/journal.pone.0179498.g001>

predicting lake surface temperature (Fig 1B). These future air temperatures were summarized as weekly mean temperatures and used as input into each lake-specific model to predict future daily surface water temperature.

We performed an uncertainty analysis using each of the two climate models to create a new data-series of highest and lowest predicted daily mean air temperatures, since the highest and lowest value for a given day were not consistently associated with one model. Using this dataset

of predicted high and low daily air temperature we calculated mean weekly high and low air temperatures. We then used these to predict high and low daily surface water temperature for each lake, which defined the upper and lower bounds of our predictions (Fig 1B).

Lake thermal metrics

We used the daily values of lake surface temperature reconstructed and predicted from forecasting to calculate four lake thermal metrics (Fig 1). The first is a measure of fish habitat quality [31] and represents the warmest 30-day running mean of daily mean water temperature (M30AT). The other three metrics are the mean annual surface water temperature (MAT), the mean summer surface water temperature (mean for June–August of each year; MST), and the number of ice-free days (sum of days with a daily mean lake surface temperature $\geq 4^{\circ}\text{C}$ for each year; IFD). This estimate of IFD is based on lake hydrodynamics and assumes that when the lake surface water is 4°C (i.e., the value at which liquid water is most dense) the entire water column is iso-thermal with no ice cover [46]. We summarize these thermal metrics at three different time horizons: current (2004–2014), 2040s (2035–2045), and 2080s (2075–2085). We also used the annual predictions of these metrics to examine trends (i.e., rates of change) in our thermal metrics from 1986–2002 (depending on the record of the closest SNO-TEL site) through 2085 using linear regression ($\alpha = 0.05$), with year as the independent variable. We used the slopes from these linear regressions to represent the rate of change for each temperature metric, and present all results as rates of change $\cdot \text{decade}^{-1}$. These statistical analyses were performed using SYSTAT 12 (Chicago, IL) software.

Fish thermal habitat quality. We assessed the thermal habitat quality for native fishes (Cutthroat Trout) in these mountain lakes using eco-physiological thresholds defined in the literature. Roberts et al. [31] related M30AT to growth and recruitment of Cutthroat Trout in SRM streams and defined five eco-physiological states which are directly relevant to thermal habitat quality of mountain lakes for these fish. Briefly, a M30AT below 8.0°C is too cold for growth and survival of young trout. Temperatures in the 8.0 – 9.0°C range are cold enough to restrict the survival of young trout up to age-1. However, higher temperatures (9.1 – 18.0°C) are optimal for growth and recruitment of trout, while even warmer temperatures (18.1 – 19.9°C) can reduce growth. Finally, temperatures in excess of 20.0°C limit or stop growth of Cutthroat Trout [31]. We use these eco-physiological thresholds to evaluate the fish thermal habitat quality in these 27 mountain lakes and examine changes through the 2080s.

Results

Model development

The models of surface temperature for each of the 27 lakes had an average NSC value of 0.83, although the model parameters and fit varied among lakes (NSC range 0.68–0.91; S2 Table). The average model parameter for maximum temperature (α) was 20.1°C , the average parameter for minimum temperature (μ) was 0.0°C , the average γ (i.e., parameter defining slope between α and μ) was 0.3, and the average β (i.e., the parameter defining inflection point) was 12.0°C (S2 Table; see [38] for more details of model equation and parameters). The variation of these parameter values among water bodies supports our decision to fit individual models for each lake.

Lake temperature predictions

We used the measured and predicted air temperature in our models of lake temperature to predict daily lake surface temperature during past, current, and future periods for each of the

Table 1. Trends in thermal conditions for southern Rocky Mountain lakes. Predicted change in lake surface temperature metrics for 27 southern Rocky Mountain lakes. Metrics were calculated using the lake-specific non-linear models of daily mean lake surface temperature, mean weekly air temperatures from SNOTEL sites, and future mean weekly air temperature predicted from climate models [41]. Rates of change $\cdot \text{decade}^{-1}$ were calculated by linear regression using annual measures of each metric as a function of year. Upper and lower bounds of these predictions from our uncertainty analysis are shown in parentheses.

Lake	Increase per decade			M30AT 2080s (°C; i.e., Warmest 30days)
	Mean summer (°C; MST)	Mean annual (°C; MAT)	Ice free days (IFD)	
Adams Lake	0.52 (0.32, 0.72)	0.27 (0.14, 0.40)	6.4 (3.9, 8.5)	16.1 (14.6, 16.9)
Arrowhead Lake	0.36 (0.15, 0.43)	0.17 (0.09, 0.25)	6.7 (3.9, 8.3)	10.7 (09.3, 11.3)
Bear Lake	0.29 (0.17, 0.38)	0.17 (0.08, 0.25)	5.2 (3.3, 7.1)	11.7 (10.8, 12.1)
Big Cow Lake	0.54 (0.34, 0.72)	0.23 (0.12, 0.31)	6.2 (4.0, 7.5)	13.7 (12.1, 14.5)
Bluebird Lake	0.60 (0.48, 0.71)	0.27 (0.18, 0.36)	6.1 (4.1, 7.1)	13.7 (13.0, 14.1)
Boundary Lake	0.47 (0.31, 0.64)	0.24 (0.13, 0.35)	6.4 (3.9, 8.4)	14.2 (12.9, 14.8)
Caddis Lake	0.42 (0.25, 0.58)	0.21 (0.11, 0.30)	6.5 (4.2, 8.2)	12.7 (11.2, 13.5)
Crystal Lake	0.44 (0.27, 0.60)	0.22 (0.12, 0.32)	6.4 (4.1, 8.2)	13.4 (12.1, 14.1)
Dream Lake	0.43 (0.27, 0.56)	0.25 (0.13, 0.35)	5.3 (3.2, 7.3)	15.8 (14.8, 16.3)
Fern Lake	0.59 (0.37, 0.80)	0.34 (0.21, 0.47)	6.8 (4.1, 9.2)	16.2 (14.7, 17.4)
Gem Lake	0.50 (0.34, 0.67)	0.23 (0.14, 0.33)	6.0 (4.3, 7.2)	14.3 (13.0, 14.9)
Jewel Lake	0.64 (0.39, 0.83)	0.26 (0.15, 0.36)	6.3 (4.1, 7.4)	15.4 (13.5, 16.4)
Lake Husted	0.55 (0.34, 0.75)	0.27 (0.14, 0.39)	5.9 (3.4, 7.9)	16.6 (15.0, 17.4)
Lake Louise	0.46 (0.29, 0.63)	0.22 (0.11, 0.33)	5.9 (3.4, 7.7)	13.8 (12.5, 14.5)
Lake Nanita	0.41 (0.26, 0.56)	0.24 (0.12, 0.36)	4.8 (2.8, 7.1)	16.3 (15.1, 17.0)
Little Cow Lake	0.55 (0.35, 0.74)	0.23 (0.13, 0.33)	5.9 (4.0, 7.3)	14.3 (12.7, 15.1)
Lost Lake	0.48 (0.31, 0.66)	0.26 (0.13, 0.39)	5.4 (3.1, 7.7)	16.7 (15.5, 17.4)
Lower Hutcheson Lake	0.45 (0.28, 0.62)	0.23 (0.12, 0.34)	6.5 (3.9, 8.3)	13.7 (12.4, 14.3)
Odessa Lake	0.33 (0.21, 0.44)	0.19 (0.10, 0.27)	5.5 (3.6, 7.4)	12.4 (11.5, 12.9)
Pear Lake	0.56 (0.37, 0.74)	0.29 (0.16, 0.43)	6.0 (3.5, 8.4)	17.3 (16.0, 18.0)
Pettingell Lake	0.32 (0.23, 0.42)	0.25 (0.13, 0.37)	4.4 (1.5, 7.1)	17.3 (16.7, 17.6)
Sandbeach Lake	0.57 (0.37, 0.77)	0.33 (0.18, 0.48)	5.7 (3.2, 8.2)	19.5 (18.1, 20.2)
Spruce Lake	0.49 (0.31, 0.68)	0.28 (0.14, 0.42)	4.5 (2.0, 6.9)	19.4 (17.8, 20.3)
Timber Lake	0.55 (0.36, 0.78)	0.26 (0.14, 0.39)	5.9 (3.6, 7.7)	17.1 (15.4, 18.0)
Trappers lake	0.43 (0.28, 0.55)	0.28 (0.16, 0.39)	5.8 (2.3, 8.3)	17.6 (15.5, 18.8)
Upper Hutcheson Lake	0.41 (0.25, 0.57)	0.21 (0.11, 0.31)	6.4 (3.8, 8.3)	12.2 (10.1, 14.4)
Ypsilon Lake	0.42 (0.26, 0.57)	0.23 (0.12, 0.34)	5.9 (3.7, 7.9)	14.0 (12.2, 15.8)
Mean (SE)	0.47 (0.02)	0.25 (0.01)	5.9 (0.1)	15.0 (0.4)

<https://doi.org/10.1371/journal.pone.0179498.t001>

27 lakes, the slopes at all lakes are significant at $\alpha = 0.05$ (Fig 1B). The current (2004–2014) MAT among lakes of 3.9°C (range 2.2–6.4) increased to 5.5°C (3.4–7.9) by the 2080s. On average, MAT increased $0.25^{\circ}\text{C} \cdot \text{decade}^{-1}$ from 1986 through 2085 resulting in a 41% mean increase over current conditions by the 2080s (Table 1). In contrast, the magnitude of change in MST was roughly double that predicted for MAT. The current MST of 9.8°C (5.9–13.7) increased to 12.7°C (8.3–16.8) by the 2080s, a 30% mean increase, resulting in an overall rate of increase of $0.47^{\circ}\text{C} \cdot \text{decade}^{-1}$ (Table 1). Large increases in IFD are also predicted. The current mean IFD of 128 days (86–184) increased to 165 days (131–217) IFD by the 2080s. The mean overall rate of change for IFD was $5.9 \text{ days} \cdot \text{decade}^{-1}$, resulting in 37 more days without ice cover by the 2080s compared to current conditions (2004–2014), a 29% increase (Table 1; Fig 2). Finally, the thermal suitability of SRM lakes for native fishes also changed. The current M30AT for these lakes is 12.1°C on average (7.8–15.8; S1 Table), whereas the mean M30AT predicted for the 2080s is 15.0°C , an increase of 2.9°C or 24% from current conditions (Table 1).

Fig 2. Future thermal conditions of southern Rocky Mountain lakes. Location, relative size, and juxtaposition of each study lake. Maps show portions of the Flat Tops Wilderness (A.) and Rocky Mountain National Park (B.) within the Southern Rocky Mountains.

Model predictions of M30AT in the 2080s are shown in color for each of the 27 lakes, and the predicted increase in the number of ice-free days (IFD) over seven decades (circles). The three lakes that are labeled were used to present our uncertainty analysis (see Fig 3).

<https://doi.org/10.1371/journal.pone.0179498.g002>

The uncertainty analysis showed that both the upper and lower bounds for all the thermal metrics are predicted to increase for all the lakes through the 2080s (Table 1; Fig 3). However, with time, the spread of the upper and lower bounds also increased about the mean trends for these three thermal metrics. The variation in the trend was greatest for MAT, for which the upper and lower bounds averaged $\pm 45\%$ lower and higher (0.13–0.36, respectively), than the mean rate for all the lakes of $0.25^{\circ}\text{C} \cdot \text{decade}^{-1}$. Variation was less for IFD, for which the average bounds were $\pm 36\%$ lower and higher (3.51–7.79) than the mean rate of $5.9 \text{ days} \cdot \text{decade}^{-1}$, and even less for MST, for which the average bounds were $\pm 35\%$ lower and higher (0.30–0.63) than the mean rate of $0.47^{\circ}\text{C} \cdot \text{decade}^{-1}$. Across the gradient of thermal conditions, the thermal metrics of a representative warm lake (Sandbeach Lake) increased at greater rates and were more variable than a cool (Ypsilon Lake) or cold (Odessa Lake) lake.

Fish thermal habitat quality. Current mean M30AT for these 27 lakes is 12.1°C , on average, which is considered optimal [31] for recruitment and growth of native Cutthroat Trout (S1 Table). However, Arrowhead Lake is currently too cold for young fish survival and Caddis Lake is currently cold enough to decrease the survival of young fish (S1 Table). By the 2080s the models predict that none of these 27 lakes will be too cold for growth and survival of young fish, although two will be too warm. The models predict a mean M30AT of 15.0°C for the 27 lakes in the 2080s, which is considered optimal for growth and survival. Nevertheless, two individual lakes, Spruce Lake and Sandbeach Lake will be warm enough to reduce the growth rate of adult cutthroat trout by the 2080s (Table 1).

Discussion

The surface temperature and IFD of high-elevation lakes in the SRM have already increased with warming climatic conditions, and are projected to increase more in the coming decades. The magnitude of these changes are greater than reported trends for lakes worldwide. For example, the predicted MST increase of $0.47^{\circ}\text{C} \cdot \text{decade}^{-1}$ is more than a 0.10°C greater than the predicted increase of $0.34^{\circ}\text{C} \cdot \text{decade}^{-1}$ for nighttime summer surface temperature measured for lakes worldwide [5]. However, our results indicate that temperature increases are unlikely to be great enough by the 2080s to make most of these lakes thermally unsuitable for native top predators (i.e., Cutthroat Trout) in these systems. Nevertheless, the magnitude of these changes is substantial. For example, the 30% and 41% predicted increases in MST and MAT, respectively, are likely to have unexpected consequences for abiotic characteristics, biogeochemical processes, and trophic dynamics of these important SRM headwater habitats, and hold the potential to cause ecological surprises [47,48] in the food webs of these mountain lakes.

The most striking thermal change for these high-elevation lakes is the 29% increase (i.e., a mean increase of 37 days) in IFD by the 2080s. Increasing length of the ice-free season has been observed and predicted for lakes worldwide, based on long records of lake and river surface freeze and thaw dates [49,50]. For example, a comprehensive assessment of ice cover for freshwater systems in the northern hemisphere observed (1822–1995) a $1.7 \text{ day decade}^{-1}$ increase in ice free days in 11 lakes (a subset of the water bodies included in the study; [49]). Our forecasted average increase in ice free days ($5.9 \text{ days} \cdot \text{decade}^{-1}$) is much greater than that observed in the recent past; nevertheless, the higher rates we predicted are supported by other models of future increases, such as an increase of 10–26 ice-free days in Canadian lakes by

Fig 3. Trends in southern Rocky Mountain lake thermal regimes. Example plots of thermal change (1988–2015) and the uncertainty analysis for these rates of change in three thermal metrics for three representative lakes. These lakes span the range of

relative thermal regimes observed which include cold (Odessa Lake; a-c), cool (Ypsilon Lake; d-f), and warm (Sandbeach Lake; g-i). Thermal metrics presented are the mean annual lake surface temperature (a,d,g), the mean summer lake surface temperature (b,e,h), and number of ice-free days (c,f,i). Green trend lines represent the upper and lower bounds of future thermal trends. These bounds are calculated using the highest and lowest projected mean weekly air temperatures from both climate models combined.

<https://doi.org/10.1371/journal.pone.0179498.g003>

2055 [51]. Another study using models of generic lakes across the contiguous United States predicted that a scenario where atmospheric CO₂ concentrations doubled (no time period specified) from past levels (i.e., 1961–1979) could result in 90 more ice free days in lakes, depending on location [34]. An empirical study of one watershed in the SRM also supports our results, reporting that ice is thawing 2.1 days · decade⁻¹ earlier (average decadal rate, 1981–2014; [36]), which is similar to half (2.95 days · decade⁻¹) the change we predict for IFD. These changes in length of IFD are also likely to influence important ecological processes occurring during ice-cover, processes that are understudied and are important drivers of the ecosystem functions in temperate lakes [52]. Our study is the first to model the change in IFD for relatively cold, high-elevation lakes, and shows that these lakes will also lose ice at a drastic rate, similar to those predicted for lakes at lower elevations.

Our models predict that these lakes will warm at a faster rate than streams and rivers within the Rocky Mountain region. The MST in streams in the upper Columbia River drainage (Northern Rocky Mountains) is predicted to increase 2.1 °C by the 2080s [53], substantially lower than our model predicted MST increase of 2.9 °C. Likewise, we predict that lake M30AT will increase 2.9 °C by the 2080s, nearly three-fold higher than the increase of 1.1 °C predicted for high-elevation streams in the upper Colorado River basin [31]. The greater increase in lake temperatures when compared to streams and rivers in the SRM underscores the need to determine which thermal properties are driving ecosystem processes in these high-elevation lakes, to allow a better understanding of the ecological consequences of these thermal changes.

Although temperature itself is a dominant driver of biological processes [13], the timing and seasonal fluctuations of water temperature are likely as important, or more important. Although the predicted average summer temperatures (M30AT) are unlikely to have acute effects, such as extirpation, for many taxa in SRM lakes, the potential chronic effects of changes in thermal regime may greatly influence the physical habitats of these biota and ecosystem processes that support them. For example, the warming surface water temperatures are unlikely to influence hypolimnetic temperatures [54], but related abiotic conditions such as hypolimnetic volume will likely decrease as thermocline depth increases [2,55]. Primary producers, which form the trophic base of food webs in these lakes, are likely to be strongly influenced by warming temperatures. Potential consequences include increases in frequency and severity of harmful algal blooms [17,56], and earlier spring phytoplankton blooms [57]. In the SRM, shifts to earlier ice-off dates are increasing chlorophyll *a* values (an indicator of phytoplankton production), suggesting that this thermal metric is an important driver of SRM lake primary production [36]. Climate change induced alterations of phytoplankton dynamics [58] can also lead to decreases in hypolimnetic dissolved oxygen concentration [18,59] and, consequently, reduced densities of benthic invertebrates [60]. Pelagic invertebrates are also influenced by warming thermal conditions of lakes through changes in zooplankton phenology [16] and increases in zooplankton productivity [61,62]. Climate driven thermal changes in SRM lakes may interact synergistically with elevated rates of atmospheric nitrogen deposition in high-elevation landscapes [63,64], with the potential to alter nutrient dynamics [65,66] in these normally oligotrophic systems, pushing them toward mesotrophic or eutrophic states [67].

High-elevation lakes, like those in the SRM, provide critical fish habitat, and changes to thermal characteristics are likely to alter fish life histories. Although it is unknown how many

of these lakes were naturally fishless, owing to extensive stocking of native and non-native fishes initiated around the turn of the 20th century [68,69], it is likely that some of the lakes in our analysis were fishless. Of the 27 lakes in our analysis, 23 currently have fish populations. One critical life history event for fish in high-elevation lakes is the movement between lakes and connecting streams for spawning. The phenology of spawning migrations can be shifted earlier for spring spawning fish [70] and later for fall spawning fish [71] when adult fish are exposed to increasing temperature in lake-stream networks. Earlier spawning events can result in a longer growing season for young-of-the-year fish. However, the growth and survival of young fish is a function of both temperature and prey availability [20,72]. Shifts in the timing of spawning events could result in a trophic mismatch of prey availability and demand during early life history events for fish [73,74], but such a phenomenon requires heterogeneity in seasonal warming rates [75]. The differences in warming rates between high-elevation SRM streams [31] and those reported for SRM lakes in this study indicate heterogeneity in warming rates and therefore, the potential for climate driven trophic mismatches during early fish life history. Paradoxically, the growth potential of adult fish in SRM high-elevation lakes may actually increase because these systems are currently quite cold, but this will vary by species and also be dictated by how prey (i.e., lower trophic levels) respond to these changing thermal conditions.

Although our results indicate a warming trend in overall thermal regimes of high-elevation SRM lakes, our study has potential limitations. First, the rates of change we present are based on climate projections using a medium to high emission scenario, which may be higher than those predicted under lower emissions. Using multiple emission scenarios would not influence the direction of these changes, but could alter the magnitudes of rates of change that our models predicted. Second, our focus on lake surface temperature does not address potential changes to other limnological features such as water column stratification and thermocline depth. Third, collection of more detailed data on drivers of ice cover phenology (e.g., timing and amount of snowfall or rain; [36]) could help refine predictions of ice dynamics in mountain lakes. Likewise, gathering basic physiographic data for lakes such as detailed bathymetry and continuous vertical thermal profiles would allow future studies of mountain lake temperature regimes to include more detailed processes such as water residence time, timing of runoff, and mixing dynamics (*sensu* [2,51]). These more detailed processes are particularly important to ice-off timing in SRM lakes which is likely driven by air temperature along with the timing and amount of snowfall or rain [36]. Finally, there are potential biases in the SNOTEL air temperature data caused by changes in sensor type and placement at SNOTEL sites, which mainly influenced daily maximum and minimum air temperature values [76]. This bias was strongest for minimum temperatures (warmer), whereas the bias in maximum temperature was weaker and varied by season (cooler in summer and warmer in winter). For our analysis we used SNOTEL daily mean air temperature, which was not addressed in the previously mentioned bias analysis [76]. We suggest that this bias is likely small, possibly influencing the magnitude but not the direction of these trends.

Although our results predict striking changes in the thermal regime of SRM high-elevation lakes, data were available for a relatively small sample of lakes arrayed in two fairly restricted regions of the SRM in Colorado. Thus, it is unlikely that we have characterized the full range of lake thermal response across the SRM landscape. Given the affordability and availability of commercial temperature loggers, the scope of future studies could be easily expanded to include collection of continuous lake temperatures. Additionally, new lake temperature data could easily be added to our predictive model approach (*sensu* [38]) to further explore the influence of climate change on high-elevation lakes. Ideally, a more comprehensive database of continuous temperatures could be used to create models for mountain lakes similar to the

useful resources already available for mountain stream networks (e.g., NorWeST; <http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html>). Mountain lakes are important headwater sources of relatively pristine habitat for ecological communities and water for human uses, so understanding how changing climatic conditions are influencing these lakes is paramount to creating climate-smart management strategies for water resources and the biota that inhabit them.

Supporting information

S1 Table. Physio-chemical characteristics of the southern Rocky Mountain lakes in this analysis. Hydrogeomorphic characteristics of the 27 lakes with continuous records of lake surface temperature. Mean weekly air temperatures from SNOTEL sites were also used with our models of lake surface temperature to calculate the current (2004–2014) thermal conditions (M30AT).
(DOCX)

S2 Table. Lake surface temperature model parameters and fit. Summary of lake temperature data (period of record) used to parameterize models of surface temperature and the parameter values for lake surface temperature models* (sensu [38]). The Nash-Sutcliffe Coefficient (NSC; 1 = perfect fit) is a measure of model fit for non-linear logistic regression models [38].
(DOCX)

S1 File. Daily mean lake surface water temperatures. Water temperatures (°C) collected from each of the 27 SRM lakes, summarized as daily mean lake surface water temperature. These water temperature data were used with air temperature from the closest SNOTEL station to fit models of daily lake surface temperature [sensu 38].
(CSV)

S2 File. Mean weekly air temperature values from the closest SNOTEL station for each study lake. The mean weekly air temperature (°C) values from the closest SNOTEL station to each of 27 SRM lakes. This included both observed data (1998–2013) and monthly corrected projections from downscaled regional climate models (2035–2045, 2075–2085; [41]). These observed data were used to fit models of daily mean lake surface temperature. Both the observed and projected air temperature data were also used to reconstruct and forecast daily mean lake surface temperature.
(CSV)

S3 File. Annual values for the four lake thermal metrics from each study lake. The annual values of the four lake surface temperature metrics (°C) used to summarize the response of each of the 27 SRM lakes to changes climatic conditions. These four metrics include meant annual lake surface temperature (MAT), mean summer lake surface temperature (MST), number of ice-free days (IFD), and maximum 30-day mean summer lake surface temperature (M30AT).
(CSV)

Acknowledgments

We thank C. Kennedy and K. Rogers for providing lake temperature data, and D. Shaw, E. Martin, and A. Herdrich for database development. We would also like to thank J. Read (USGS internal reviewer), Joao Miguel Dias (handling editor), and two anonymous reviewers for providing comments of earlier versions of this manuscript. This research was subjected to

USGS review and is approved for publication. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author Contributions

Conceptualization: JJR KDF TSS DWM.

Data curation: JJR.

Formal analysis: JJR.

Funding acquisition: JJR.

Methodology: JJR.

Project administration: JJR.

Visualization: JJR.

Writing – original draft: JJR.

Writing – review & editing: JJR KDF TSS DWM.

References

- Schneider P, Hook SJ. Space observations of inland water bodies show rapid surface warming since 1985. *Geophysical Research Letters*. 2010; 37: L22405. <https://doi.org/10.1029/2010gl045059>
- Read JS, Wilson LA, Hansen GJA, Hoek JVD, Hanson PC, Bruce LC, et al. Simulating 2368 temperate lakes reveals weak coherence in stratification phenology. *Ecological Modelling*. 2014; 291: 142–150. <https://doi.org/10.1016/j.ecolmodel.2014.07.029>
- Leppi J, DeLuca T, Harrar S, Running S. Impacts of climate change on August stream discharge in the Central-Rocky Mountains. *Climatic Change*. 2012; 112: 997–1014. <https://doi.org/10.1007/s10584-011-0235-1>
- Isaak DJ, Wollrab S, Horan D, Chandler G. Climate change effects on stream and river temperatures across the northwest U.S. from 1980–2009 and implications for salmonid fishes. *Climatic Change*. 2012; 113: 499–524. <https://doi.org/10.1007/s10584-011-0326-z>
- O'Reilly CM, Sharma S, Gray DK, Hampton SE, Read JS, Rowley RJ, et al. Rapid and highly variable warming of lake surface waters around the globe. *Geophysical Research Letters*. 2015; 42. <https://doi.org/10.1002/2015gl066235>
- Heino J, Virkkala R, Toivonen H. Climate change and freshwater biodiversity detected patterns, future trends and adaptations in northern regions. *Biological Reviews*. 2009; 84: 39–54. <https://doi.org/10.1111/j.1469-185X.2008.00060.x> PMID: 19032595
- Schmid M, Hunziker S, Wuest A. Lake surface temperatures in a changing climate: a global sensitivity analysis. *Climatic Change*. 2014; 124: 301–315. <https://doi.org/10.1007/s10584-014-1087-2>
- Adrian R, O'Reilly CM, Zagarese H, Baines SB, Hessen DO, Keller W, et al. Lakes as sentinels of climate change. *Limnology and Oceanography*. 2009; 54: 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283 PMID: 20396409
- Williamson CE, Saros JE, Schindler DW. Sentinels of change. *Science*. 2009; 323: 887–888. <https://doi.org/10.1126/science.1169443> PMID: 19213905
- Williamson CE, Saros JE, Vincent WF, Smol JP. Lakes and reservoirs as sentinels, integrators, and regulators of climate change. *Limnology and Oceanography*. 2009; 54: 2273–2282. https://doi.org/10.4319/lo.2009.54.6_part_2.2273
- Schneider P, Hook SJ, Radocinski RG, Corlett GK, Hulley GC, Schladow SG, et al. Satellite observations indicate rapid warming trend for lake in California and Nevada. *Geophysical Research Letters*. 2009; 36: 1–6. <https://doi.org/10.1029/2009GL040846>
- Austin JA, Colman SM. Lake Superior summer water temperatures are increasing more rapidly than regional air temperatures: A positive ice-albedo feedback. *Geophysical Research Letters*. 2007; 34: n/a-n/a. <https://doi.org/10.1029/2006GL029021>
- Magnuson JJ, Crowder LB, Medvick PA. Temperature as an ecological resource. *American Zoologist*. 1979; 19: 331–343. <https://doi.org/10.1093/icb/19.1.331>

14. Paerl HW, Millie DF. Physiological ecology of toxic aquatic cyanobacteria. *Phycologia*. 1996; 35: 160–167. <https://doi.org/10.2216/i0031-8884-35-6S-160.1>
15. Lapierre J-F, Seekell DA, del Giorgio PA. Climate and landscape influence on indicators of lake carbon cycling through spatial patterns in dissolved organic carbon. *Global Change Biology*. 2015; 21: 4425–4435. <https://doi.org/10.1111/gcb.13031> PMID: 26150108
16. Williamson CE, Salm C, Cooke SL, Saros JE. How do UV radiation, temperature, and zooplankton influence the dynamics of alpine phytoplankton communities? *Hydrobiologia*. 2010; 648: 73–81. <https://doi.org/10.1007/s10750-010-0147-5>
17. Michalak AM, Anderson EJ, Beletsky D, Boland S, Bosch NS, Bridgeman TB, et al. Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. *Proceedings of the National Academy of Sciences of the United States of America*. 2013; 110: 6448–6452. <https://doi.org/10.1073/pnas.1216006110> PMID: 23576718
18. Jankowski T, Livingstone DM, Buhner H, Forster R, Niederhauser P. Consequences of the 2003 European heat wave for lake temperature profiles, thermal stability, and hypolimnetic oxygen depletion: Implications for a warmer world. *Limnology and Oceanography*. 2006; 51: 815–819. <https://doi.org/10.4319/lo.2006.51.2.0815>
19. Sharma S, Vander Zanden MJ, Magnuson JJ, Lyons J. Comparing climate change and species invasions as drivers of coldwater fish population extirpations. *Plos One*. 2011; 6. <https://doi.org/10.1371/journal.pone.0022906> PMID: 21860661
20. Kao Y- C, Madenjian CP, Bunnell DB, Lofgren BM, Perroud M. Potential effects of climate change on the growth of fishes from different thermal guilds in Lakes Michigan and Huron. *Journal of Great Lakes Research*. 2015; 41: 423–435. <https://doi.org/10.1016/j.jglr.2015.03.012>
21. Sadro S, Nelson CE, Melack JM. The influence of landscape position and catchment characteristics on aquatic biogeochemistry in high-elevation lake-chains. *Ecosystems*. 2012; 15: 363–386. <https://doi.org/10.1007/s10021-011-9515-x>
22. Campbell DH, Baron JS, Tonnessen KA, Brooks PD, Schuster PF. Controls on nitrogen flux in alpine/subalpine watersheds of Colorado. *Water Resources Research*. 2000; 36: 37–47. <https://doi.org/10.1029/1999wr900283>
23. Hartman MD, Baron JS, Ewing HA, Weathers KC. Combined global change effects on ecosystem processes in nine US topographically complex areas. *Biogeochemistry*. 2014; 119: 85–108. <https://doi.org/10.1007/s10533-014-9950-9>
24. Clow DW. Changes in the timing of snowmelt and streamflow in Colorado: a response to recent warming. *Journal of Climate*. 2010; 23: 2293–2306. <https://doi.org/10.1175/2009JCLI2951.1>
25. Nijssen B, O'Donnell GM, Hamlet AF, Lettenmaier DP. Hydrologic sensitivity of global rivers to climate change. *Climatic Change*. 2001; 50: 143–175. <https://doi.org/10.1023/a:1010616428763>
26. Barnett TP, Adam JC, Lettenmaier DP. Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature*. 2005; 438: 303–309. <https://doi.org/10.1038/nature04141> PMID: 16292301
27. Serreze MC, Clark MP, Armstrong RL, McGinnis DA, Pulwarty RS. Characteristics of the western United States snowpack from snowpack telemetry (SNOTEL) data. *Water Resources Research*. 1999; 35: 2145–2160. <https://doi.org/10.1029/1999WR900090>
28. Baron JS, Schmidt TM, Hartman MD. Climate-induced changes in high elevation stream nitrate dynamics. *Global Change Biology*. 2009; 15: 1777–1789.
29. McGuire CR, Nufio CR, Bowers MD, Guralnick RP. Elevation-dependent temperature trends in the Rocky Mountain Front Range: changes over a 56- and 20-year record. *PLoS One*. 2012; 7: e44370. <https://doi.org/10.1371/journal.pone.0044370> PMID: 22970205
30. Muths E, Bailey LL, Watry MK. Animal reintroductions: An innovative assessment of survival. *Biological Conservation*. 2014; 172: 200–208. <https://doi.org/10.1016/j.biocon.2014.02.034>
31. Roberts JJ, Fausch KD, Peterson DP, Hooten MB. Fragmentation and thermal risks from climate change interact to affect persistence of native trout in the Colorado River basin. *Global Change Biology*. 2013; 19: 1383–1398. <https://doi.org/10.1111/gcb.12136> PMID: 23505098
32. Isaak DJ, Young MK, Luce CH, Hostetler SW, Wenger SJ, Peterson EE, et al. Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*. 2016; 113: 4374–4379. <https://doi.org/10.1073/pnas.1522429113> PMID: 27044091
33. Hostetler SW, Small EE. Response of North American freshwater lakes to simulated future climates. *Journal of the American Water Resources Association*. 1999; 35: 1625–1637. <https://doi.org/10.1111/j.1752-1688.1999.tb04241.x>

34. Fang X, Stefan HG. Simulations of climate effects on water temperature, dissolved oxygen, and ice and snow covers in lakes of the contiguous United States under past and future climate scenarios. *Limnology and Oceanography*. 2009; 54: 2359–2370. https://doi.org/10.4319/lo.2009.54.6_part_2.2359
35. Fang X, Stefan HG, Eaton JG, McCormick JH, Alam SR. Simulation of thermal/dissolved oxygen habitat for fishes in lakes under different climate scenarios—Part 2. Cold-water fish in the contiguous US. *Ecological Modelling*. 2004; 172: 39–54. [https://doi.org/10.1016/s0304-3800\(03\)00285-0](https://doi.org/10.1016/s0304-3800(03)00285-0)
36. Preston DL, Caine N, McKnight DM, Williams MW, Hell K, Miller MP, et al. Climate regulates alpine lake ice cover phenology and aquatic ecosystem structure. *Geophysical Research Letters*. 2016; 43: 5353–5360. <https://doi.org/10.1002/2016gl069036>
37. Dunham JB, Chandler GL, Rieman BE, Martin D. Measuring stream temperature with digital loggers- A user's guide. General Technical Report RMRS-GTR-150WWW. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 2005. pp. 15.
38. Mohseni O, Erickson TR, Stefan HG. Sensitivity of stream temperatures in the United States to air temperatures projected under a global warming scenario. *Water Resources Research*. 1999; 35: 3723–3733. <https://doi.org/10.1029/1999WR900193>
39. Mohseni O, Stefan HG, Erickson TR. A nonlinear regression model for weekly stream temperatures. *Water Resources Research*. 1998; 34: 2685–2692. <https://doi.org/10.1029/98WR01877>
40. Nash JE, Sutcliffe JV. River flow forecasting through conceptual models part I—A discussion of principles. *Journal of Hydrology*. 1970; 10: 282–290. [https://doi.org/10.1016/0022-1694\(70\)90255-6](https://doi.org/10.1016/0022-1694(70)90255-6)
41. Hostetler SW, Alder JR, Allan AM. Dynamically downscaled climate simulations over North America: methods, evaluation and supporting documentation for users. U.S. Geological Survey Open-File Report 2011–1238. 2011. pp. 64.
42. Alder JR, Hostetler SW, Pollard D, Schmittner A. Evaluation of a present-day climate simulation with a new coupled atmosphere-ocean model GENMOM. *Geoscientific Model Development*. 2011; 4: 69–83. <https://doi.org/10.5194/gmd-4-69-2011>
43. Roeckner E, Bauml G, Bonaventura L, Brokopf R, Esch M, Giorgetta M, et al. The atmospheric general circulation model ECHAM5. Part I: Model description. Hamburg, Germany. 2003: Max Planck Institute for Meteorology. 127 p.
44. IPCC. Climate change 2007: the physical science basis. 2007: Intergovernmental Panel on Climate Change (<http://www.ipcc.ch>).
45. IPCC, editor Climate change 2013: the physical science basis. contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge, United Kingdom and New York, NY. 2013: Cambridge University Press. 1535 p.
46. Wetzel RG. *Limnology: Lake and river ecosystems*; Wetzel RG, editor. San Diego. 2001: Academic Press. 1006 p.
47. Lindenmayer DB, Likens GE, Krebs CJ, Hobbs RJ. Improved probability of detection of ecological "surprises". *Proceedings of the National Academy of Sciences of the United States of America*. 2010; 107: 21957–21962. <https://doi.org/10.1073/pnas.1015696107> PMID: 21098660
48. Doak DF, Estes JA, Halpern BS, Jacob U, Lindberg DR, Lovvorn J, et al. Understanding and predicting ecological dynamics: Are major surprises inevitable? *Ecology*. 2008; 89: 952–961. <https://doi.org/10.1890/07-0965.1> PMID: 18481520
49. Magnuson JJ, Robertson DM, Benson BJ, Wynne RH, Livingstone DM, Arai T, et al. Historical trends in lake and river ice cover in the northern hemisphere. *Science*. 2000; 289: 1743–1746. <https://doi.org/10.1126/science.289.5485.1743> PMID: 10976066
50. Sharma S, Magnuson JJ, Batt RD, Winslow LA, Korhonen J, Aono Y. Direct observations of ice seasonality reveal changes in climate over the past 320–570 years. *Scientific Reports*. 2016; 6: 25061. <https://doi.org/10.1038/srep25061> PMID: 27113125
51. Shuter BJ, Minns CK, Fung SR. Empirical models for forecasting changes in the phenology of ice cover for Canadian lakes. *Canadian Journal of Fisheries and Aquatic Sciences*. 2013; 70: 982–991. <https://doi.org/10.1139/cjfas-2012-0437>
52. Hampton SE, Galloway AW, Powers SM, Ozersky T, Woo KH, Batt RD, et al. Ecology under lake ice. *Ecology Letters*. 2017; 20: 98–111. <https://doi.org/10.1111/ele.12699> PMID: 27889953
53. Isaak DJ, Young MK, Nagel DE, Horan DL, Groce MC. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. *Global Change Biology*. 2015; 21: 2540–2553. <https://doi.org/10.1111/gcb.12879> PMID: 25728937
54. Winslow LA, Read JS, Hansen GJA, Hanson PC. Small lakes show muted climate change signal in deepwater temperatures. *Geophysical Research Letters*. 2015; 42: 355–361. <https://doi.org/10.1002/2014gl062325>

55. Fang X, Alam SR, Stefan HG, Jiang L, Jacobson PC, Pereira DL. Simulations of water quality and oxythermal cisco habitat in Minnesota lakes under past and future climate scenarios. *Water Quality Research Journal of Canada*. 2012; 47: 375–388. <https://doi.org/10.2166/wqrjc.2012.031>
56. Markensten H, Moore K, Persson I. Simulated lake phytoplankton composition shifts toward cyanobacteria dominance in a future warmer climate. *Ecological Applications*. 2010; 20: 752–767. <https://doi.org/10.1890/08-2109.1> PMID: 20437961
57. Peeters F, Straile D, Lorke A, Livingstone DM. Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. *Global Change Biology*. 2007; 13: 1898–1909. <https://doi.org/10.1111/j.1365-2486.2007.01412.x>
58. Parker BR, Vinebrooke RD, Schindler DW. Recent climate extremes alter alpine lake ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*. 2008; 105: 12927–12931. <https://doi.org/10.1073/pnas.0806481105> PMID: 18725641
59. Scavia D, David Allan J, Arend KK, Bartell S, Beletsky D, Bosch NS, et al. Assessing and addressing the re-eutrophication of Lake Erie: Central basin hypoxia. *Journal of Great Lakes Research*. 2014; 40: 226–246. <https://doi.org/10.1016/j.jglr.2014.02.004>
60. Granados I, Toro M. Recent warming in a high mountain lake (Laguna Cimera, Central Spain) inferred by means of fossil chironomids. *Journal of Limnology*. 2000; 59: 109–119. <https://doi.org/10.4081/jlimnol.2000.s1.109>
61. Gauthier J, Prairie YT, Beisner BE. Thermocline deepening and mixing alter zooplankton phenology, biomass and body size in a whole-lake experiment. *Freshwater Biology*. 2014; 59: 998–1011. <https://doi.org/10.1111/fwb.12322>
62. Domis LND, Elser JJ, Gsell AS, Huszar VLM, Ibelings BW, Jeppesen E, et al. Plankton dynamics under different climatic conditions in space and time. *Freshwater Biology*. 2013; 58: 463–482. <https://doi.org/10.1111/fwb.12053>
63. Baron JS, Caine N. Temporal coherence of two alpine lake basins of the Colorado Front Range, USA. *Freshwater Biology*. 2000; 43: 463–476. <https://doi.org/10.1046/j.1365-2427.2000.00517.x>
64. Mast MA, Clow DW, Baron JS, Wetherbee GA. Links between N deposition and nitrate export from a high-elevation watershed in the Colorado Front Range. *Environmental Science & Technology*. 2014; 48: 14258–14265. <https://doi.org/10.1021/es502461k> PMID: 25383864
65. Elser JJ, Andersen T, Baron JS, Bergstroem A- K, Jansson M, Kyle M, et al. Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science*. 2009; 326: 835–837. <https://doi.org/10.1126/science.1176199> PMID: 19892979
66. Bergstrom AK, Blomqvist P, Jansson M. Effects of atmospheric nitrogen deposition on nutrient limitation and phytoplankton biomass in unproductive Swedish lakes. *Limnology and Oceanography*. 2005; 50: 987–994. <https://doi.org/10.4319/lo.2005.50.3.0987>
67. Wolfe AP, Van Gorp AC, Baron JS. Recent ecological and biogeochemical changes in alpine lakes of Rocky Mountain National Park (Colorado, USA): a response to anthropogenic nitrogen deposition. *Geobiology*. 2003; 1: 153–168. <https://doi.org/10.1046/j.1472-4669.2003.00012.x>
68. Love Stowell SM, Kennedy CM, Beals SC, Metcalf JL, Martin AP. The genetic legacy of more than a century of stocking trout: a case study in Rocky Mountain National Park, Colorado, USA. *Canadian Journal of Fisheries and Aquatic Sciences*. 2015; 72: 1565–1574. <https://doi.org/10.1139/cjfas-2015-0009>
69. Metcalf JL, Love Stowell S, Kennedy CM, Rogers KB, McDonald D, Epp J, et al. Historical stocking data and 19th century DNA reveal human-induced changes to native diversity and distribution of cutthroat trout. *Molecular Ecology*. 2012; 21: 5194–5207. <https://doi.org/10.1111/mec.12028> PMID: 22998121
70. Wedekind C, Kung C. Shift of spawning season and effects of climate warming on developmental stages of a grayling (*Salmonidae*). *Conservation Biology*. 2010; 24: 1418–1423. <https://doi.org/10.1111/j.1523-1739.2010.01534.x> PMID: 20561001
71. Warren DR, Robinson JM, Josephson DC, Sheldon DR, Kraft CE. Elevated summer temperatures delay spawning and reduce redd construction for resident brook trout (*Salvelinus fontinalis*). *Global Change Biology*. 2012; 18: 1804–1811. <https://doi.org/10.1111/j.1365-2486.2012.02670.x>
72. Penaluna BE, Dunham JB, Railsback SF, Arismendi I, Johnson SL, Bilby RE, et al. Local variability mediates vulnerability of trout populations to land use and climate change. *Plos One*. 2015; 10. <https://doi.org/10.1371/journal.pone.0135334> PMID: 26295478
73. Einum S, Fleming IA. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution*. 2000; 54: 628–639. <https://doi.org/10.1111/j.0014-3820.2000.tb00064.x> PMID: 10937238
74. Letcher BH, Dubreuil T, O'Donnell MJ, Obedzinski M, Griswold K, Nislow KH. Long-term consequences of variation in timing and manner of fry introduction on juvenile Atlantic salmon (*Salmo salar*) growth,

- survival, and life-history expression. *Canadian Journal of Fisheries and Aquatic Sciences*. 2004; 61: 2288–2301. <https://doi.org/10.1139/f04-214>
75. Straile D, Kerimoglu O, Peeters F. Trophic mismatch requires seasonal heterogeneity of warming. *Ecology*. 2015; 96: 2794–2805. <https://doi.org/10.1890/14-0839.1.sm> PMID: [26649399](https://pubmed.ncbi.nlm.nih.gov/26649399/)
76. Oyler JW, Dobrowski SZ, Ballantyne AP, Klene AE, Running SW. Artificial amplification of warming trends across the mountains of the western United States. *Geophysical Research Letters*. 2015; 42: 153–161. <https://doi.org/10.1002/2014gl062803>