


Estimating lake–climate responses from sparse data: An application to high elevation lakes

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Abstract

Although many studies demonstrate lake warming, few document trends from lakes with sparse data. Diel and seasonal variability of surface temperatures limit conventional trend analyses to datasets with frequent repeated observations. Thus, remote lakes, including many high elevation lakes, are underrepresented in trend analyses. We used a Bayesian technique to analyze sparse data that explicitly incorporated diel and seasonal variability. This approach allowed us to estimate lake warming in a region of limited knowledge: high elevation lakes (> 2100 m ASL) of the Southern Rocky Mountains, U.S.A. The analysis allowed for inclusion of lakes with few repeated measurements, and observations made before 1980 when more intensive lake monitoring began. We accumulated the largest dataset of high elevation lake temperatures analyzed to date. Data from 590 high elevation lakes in the Southern Rocky Mountains showed a 0.13°C decade⁻¹ increase in surface temperatures and a 14% increase in seasonal degree days since 1955. This result is lower than other regional and global estimates of lake warming; however, it is similar to other high elevation lake studies. Our approach can be applied to other understudied regions, increasing our overall understanding of the effects of climate change on lakes and their temporal dynamics.

Surface temperature is an important feature of lakes, with physicochemical and ecological implications. Surface temperature influences lake mixing regimes (Kraemer et al. 2015a; Michelutti et al. 2016) and the propensity for thermal stratification (Rempfer et al. 2010). Greater surface temperatures allow stratification to develop earlier and last longer (Crossman et al. 2016). These effects can increase stability of the water column, limiting mixing generated from wind or nocturnal convective cooling (Butcher et al. 2015; Sahoo et al. 2015). While warmer surface temperatures can accelerate oxygen production in the photic zone, oxygen solubility is inversely related to temperature so less oxygen is taken up from the atmosphere. Reduced mixing enforced by warm surface temperatures also inhibits oxygen transfer to the hypolimnion, increasing the likelihood of hypoxia (Wilhelm and Adrian 2008; Foley et al. 2012; Golosov et al. 2012). Hypoxia can cause nutrient release from the sediment, leading to algal blooms when the lake mixes again (Peeters et al. 2002;

Wilhelm and Adrian 2008). Warming also increases microbial respiration which can increase the CO₂ emissions from lakes that are already an important component of the global carbon cycle (Cole et al. 2007). Warmer surface temperatures induce earlier spawning in fish and increase metabolic activity, seasonal growth and trophic interactions by preventing cold-water organisms from accessing the epilimnion, and may create a predation refuge for zooplankton (e.g., Martinez and Bergersen 1991) and fish (e.g., Johnson et al. 2017). Sustained warming of lake surface temperatures can make the system less favorable for native species and increase the likelihood of new species becoming established (Lennon et al. 2001; Rahel and Olden 2008). Thus, lake surface temperature mediates complex interactions between physical and chemical factors, with important implications for biogeochemical cycles and biodiversity.

The surface of lakes interacts directly with climate and surface temperature responds rapidly and directly to climatic forcing (Carpenter et al. 2011). Thus, surface temperature is a relatively easy to measure indicator of the climate's thermal influence on lakes (Adrian et al. 2009). Because surface temperature is a fundamental measurement for limnological studies, historical datasets are available globally (Sharma et al. 2015), and lake surface temperature records have frequently

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Table 1. Reported rates of lake surface temperature increase and differences in sampling frequency, data aggregation and whether sampling time was reported. Rate of increase is of average or range reported. Sampling frequency and data aggregation use syntax specific to each study, respectively. N/A is noted for studies which do not report information for respective category.

| Location | Time period | N | Lake area (ha) | Elevation (m ASL) | Rate of increase (°C/decade) | Sampling frequency | Data aggregation | Sampling time recorded? | Source |
|--------------------------|-------------|----------------------|----------------|-------------------|------------------------------|-------------------------------|---|--------------------------|-----------------------------|
| Global | 1985–2009 | 235 | 3–37,811,900 | –404 to 4743 | 0.34 | At least monthly | 3 months mean | N/A | O'Reilly et al. (2015) |
| Global | 1991–2009 | 167 | ≥50,000 | N/A | 0.37 | At least 20 samples per lake | 3 months mean | N/A | Schneider and Hook (2010) |
| Global | 1970–2010 | 26 | 2–6,800,000 | –212 to 1987 | 0.20 | One to many measurements/year | 30 d running average | N/A | Kraemer et al. (2015a) |
| Russia | 1953–2011 | 6 | 1070–114,000 | 89.3–138.3 | 0.30 | Daily | 10-d average | N/A | Efremova et al. (2016) |
| U.S. Great Lakes | 1968–2002 | 31,900,000–8,200,000 | 75–182.9 | 0.25–0.84 | Several per year | Weekly August mean | N/A | N/A | Dobiesz and Lester (2009) |
| Lake Zurich, Switzerland | 1947–1998 | 1 | 6500 | 406 | 0.24 | Monthly | Decadal running mean | Standardized | Livingstone (2003) |
| Wisconsin, U.S.A. | 1990–2012 | 142 | 0.6–53,300 | 180–537 | 0.42 | Three summer measurements | Monthly mean | N/A | Winslow et al. (2015) |
| Lake Lugano, Italy | 1972–2013 | 1 | 4870 | 271 | 0.20–0.90 | Monthly | Seasonal average | N/A | Lepori and Roberts (2015) |
| Lake Washington, U.S.A. | 1962–2002 | 1 | 8760 | 4 | 0.35 | Weekly to monthly | Annual to 5 yr running mean | N/A | Winder and Schindler (2004) |
| Italy | 1986–2015 | 5 | 6112–36,677 | 65–257.5 | 0.17–0.32 | Daily to monthly | Annual and seasonal mean | Standardized | Pareeth et al. (2017) |
| Austria | 1965–2009 | 9 | 1079–5350 | 115–588 | 0.40–0.66 | Multiple per day | Daily average | Yes, 7, 14, 19 h | Dokullil (2014) |
| Lake Washington, U.S.A. | 1964–1998 | 1 | 8760 | 4 | 0.45 | Weekly to biweekly | Monthly average | N/A | Arhonditsis et al. (2004) |
| Lake Tahoe, U.S.A. | 1970–2002 | 1 | 5010 | 1897 | 0.15 | Weekly to biweekly | Monthly, yearly means, 4 yr running average | N/A | Coats et al. (2006) |
| Lake Constance, Germany | 1962–1998 | 1 | 4720 | 395 | 0.17 | Monthly profiles | Annual average | N/A | Straille et al. (2003) |
| Lake Baikal, Russia | 1946–2005 | 1 | 3,150,000 | 455.5 | 0.20 | At least monthly | Seasonal average | N/A | Hampton et al. (2008) |
| Lake Superior, U.S.A. | 1979–2006 | 1 | 8,200,000 | 182.9 | 0.34 | Several per year | N/A | N/A | Bennington et al. (2010) |
| U.S.A. Great Lakes | 1979–2006 | 41,900,000–8,200,000 | 75–182.9 | 0.10–1.6 | Hourly | Seasonal average | Yes | Austin and Colman (2007) | |

| | | | | | | | | | |
|---------------------------------------|-----------|----------------------|---------------|---------------|-----------|-------------------------------|---------------------------------------|---------------|---------------------------------|
| Lake Tanganyika, Tanzania | 1912–2013 | 1 | 3,290,000 | 773 | 0.13 | One to many measurements/year | Pooled 30 d running average | N/A | Kraemer et al. (2015b) |
| Austria | 1975–2015 | 3 | 347–1421 | 481–553 | 0.33–0.48 | At least 12/yr | Annual mean | N/A | Ficker et al. (2017) |
| Denmark | 1989–2006 | 20 | N/A | N/A | 1.1 | 19/yr | Seasonal mean | N/A | Jeppesen et al. (2013) |
| Austria | 1911–1990 | 8 | 270–47,600 | 396–750 | 0.11 | Daily | Monthly mean | Early morning | Livingstone and Dokullil (2001) |
| Wisconsin, U.S.A. | 1911–2014 | 3 | 87.4–3938 | 257.86–259.69 | 0.07–0.14 | At least one per year | N/A | N/A | Magee and Wu (2017) |
| Lake Garda, Italy | 1986–2015 | 1 | 36,998 | 65 | 0.20–0.36 | Daily | N/A | Standardized | Pareeth et al. (2016) |
| Wisconsin, U.S.A. | 1981–2015 | 6 | 1–1565 | N/A | 0.13–0.73 | Biweekly | Monthly and seasonal mean | N/A | Winslow et al. (2017) |
| Europe | 1988–2003 | 16 | N/A | N/A | 1.3 | Monthly May to October | Median of yearly means of all lakes | N/A | Weyhenmeyer et al. (2007) |
| Northeast North America | 1985–2014 | 226 | 1.6–20,700 | 3.1–667 | 0.52 | Daily to one/yr | Single profile of peak stratification | N/A | Richardson et al. (2017) |
| Northeast North America | 1975–2014 | 85 | 1.6–20,700 | 3.1–667 | 0.54 | Daily to one/yr | Single profile of peak stratification | N/A | Richardson et al. (2017) |
| Nevada and California, U.S.A. | 1992–2008 | 6 | N/A | N/A | 1.1 | 120 s to 14 d | 3 months average | Yes | Schneider et al. (2009) |
| U.S.A. Great Lakes | 1994–2013 | 51,900,000–8,200,000 | 75–182.9 | 0.96 | Daily | Seasonal mean | Seasonal mean | N/A | Mason et al. (2016) |
| Ontario, Canada and Wisconsin, U.S.A. | 1981–2005 | 12 | 32–1091 | 327–501 | 0.90 | Weekly to monthly | Monthly standardized mean | N/A | Palmer et al. (2014) |
| Northeast North America | 1984–2014 | 3955 | >8 | <1926 | 0.80 | 8–16 d | N/A | N/A | Torbick et al. (2016) |
| Tibet | 1982–2012 | 2 | 52,600–61,000 | 4300 | 0.18–0.24 | N/A | N/A | N/A | Kirillin et al. (2017) |
| Lower Lake Zurich, Switzerland | 1981–2013 | 1 | 6700 | “Peri-alpine” | 0.41 | Bimonthly to monthly | Monthly trend | N/A | Schmid and Koster (2016) |
| Lake Erie, U.S.A. | 1983–2002 | 1 | 2,566,700 | 173 | 0.37 | Several per year | Daily, weekly, monthly averages | N/A | Burns et al. (2005) |
| Southern Rocky Mountains | 1985–2080 | 27 | 1–131 | 2907–3495 | 0.25 | 60 min | Daily mean | N/A | Roberts et al. (2017) |
| Tibetan Plateau | 2001–2012 | 52 | N/A | >2000 | 0.12 | Every 8 d | Yearly average | Yes | Zhang et al. (2014) |
| Lake Lunz, Austria | 1921–2015 | 1 | 68 | 608 | 0.085 | Daily | Monthly, annual average | Yes | Kainz et al. (2017) |
| United Kingdom | 1960–2000 | 4 | N/A | N/A | 0.35 | N/A | Mean summer temperature | N/A | Arvola et al. (2010) |

(Continues)

Table 1. Continued

| Location | Time | | Lake area (ha) | Elevation (m ASL) | Rate of increase (°C/decade) | Sampling frequency | Data aggregation | Sampling time recorded? | Source |
|-------------------------|-----------|---|----------------|-------------------|------------------------------|--------------------|-------------------------|-------------------------|--------------------------|
| | period | N | | | | | | | |
| Austria | 1961–2000 | 4 | N/A | N/A | 0.43 | N/A | Mean summer temperature | N/A | Arvola et al. (2010) |
| Lake Geneva, Europe | 1983–2000 | 1 | 58,000 | 372 | 0.56 | Continuous | Daily and monthly means | N/A | Gillet and Quetin (2006) |
| Lake Constance, Germany | 1981–2011 | 1 | 4720 | 395 | 0.46 | Continuous | Annual mean | Yes | Fink et al. (2014) |

been used to document temporal trends in climate-induced warming of lakes (Table 1). A wide variety of warming rates has been reported, ranging from $< 0.0^{\circ}\text{C decade}^{-1}$ to $> 1.0^{\circ}\text{C decade}^{-1}$. At the regional scale, some of this discordance may be a result of differences in land use, and morphometric and physiographic factors are also important (Adrian et al. 2009; O'Reilly et al. 2015). Estimates of warming rates from global studies are more alike ($0.20\text{--}0.37^{\circ}\text{C decade}^{-1}$; Table 1), but a comprehensive understanding of lake responses to climate is still lacking (O'Reilly et al. 2015). Uncertainty in lake–climate responses limits our ability to predict impacts to lakes themselves and understand the changing functional role of lakes at the global scale, including their role in the global carbon cycle (Tranvik et al. 2009).

A reason for uncertainty about how lakes respond to climate may be the extremely limited cumulative sample size of existing studies. The total number of lakes listed in Table 1 represents only about 0.0008% of the $\sim 1.17 \times 10^8$ lakes ≥ 0.2 ha on Earth (Verpoorter et al. 2014). Although the quantity of lake surface temperature measurements worldwide is probably vast, decadal scale monitoring studies that have historically formed the basis of lake warming studies are relatively rare (Table 1). Conventional methods for estimating lake warming rely on standardized and repeated measurements so that site-specific, seasonal, and short-term interannual variation in thermal patterns can be accounted for in trend estimates. Sustaining such monitoring studies is difficult so they tend to occur on larger, easily accessed, notable systems. This limits our inference about lake–climate responses and does not take advantage of data from shorter term, less intensive lake temperature studies typical of smaller and more remote lakes. For example, small, high elevation lakes are abundant worldwide (Downing et al. 2006; Verpoorter et al. 2014) and they may respond to climate differently and, therefore, be warming at different rates than other lakes (Hauer et al. 1997; Thompson et al. 2005; Winslow et al. 2015), but they are relatively underrepresented in lake–climate studies (Table 1; Fig. 1). Of the estimated ~ 11.7 million lakes globally at elevations above 2100 m (Verpoorter et al. 2014), < 100 have been analyzed for surface temperature trends.

The paucity of studies on high elevation lakes may be because high elevation lakes can be difficult to access, so surface temperature records are often sparse and difficult to use for trend estimates. Even with the increased use of advanced remote sensing technology to evaluate changes in lake surface temperature (Riffler et al. 2015; Woolway and Merchant 2017), high elevation lakes remain understudied. Further, remoteness and variable ice-off dates make standardizing temperature measurements to a particular date or even time of day difficult. However, because the ice-free season is brief and variable, small differences in sampling date among years can have marked effects on observed surface temperature and trend estimates. These typically small and shallow lakes can also exhibit diel temperature fluctuations of $\geq 12^{\circ}\text{C}$

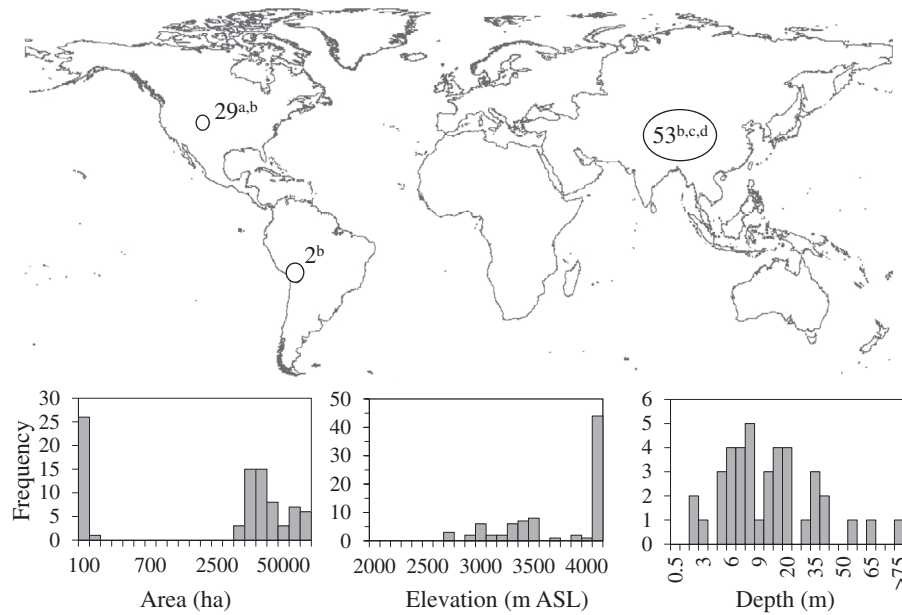


Fig. 1. Global distribution of high elevation lakes in published studies of lake warming, and their characteristics from Roberts et al. (2017) (a), O’Reilly et al. (2015) (b), Kirillin et al. (2017) (c), and Zhang et al. (2014) (d).

(Livingstone et al. 1999; Novikmec et al. 2013; Woolway et al. 2016; Martinsen et al. 2018), which can be an order of magnitude greater than reported decadal warming rates. Therefore, sparse datasets that are not composed of replicated

measurements that minimize the influence of diel and seasonal variability have not been used in traditional long-term trend estimates, as is evident in Table 1. For example, Richardson et al. (2017) required data for $\geq 50\%$ of years over the

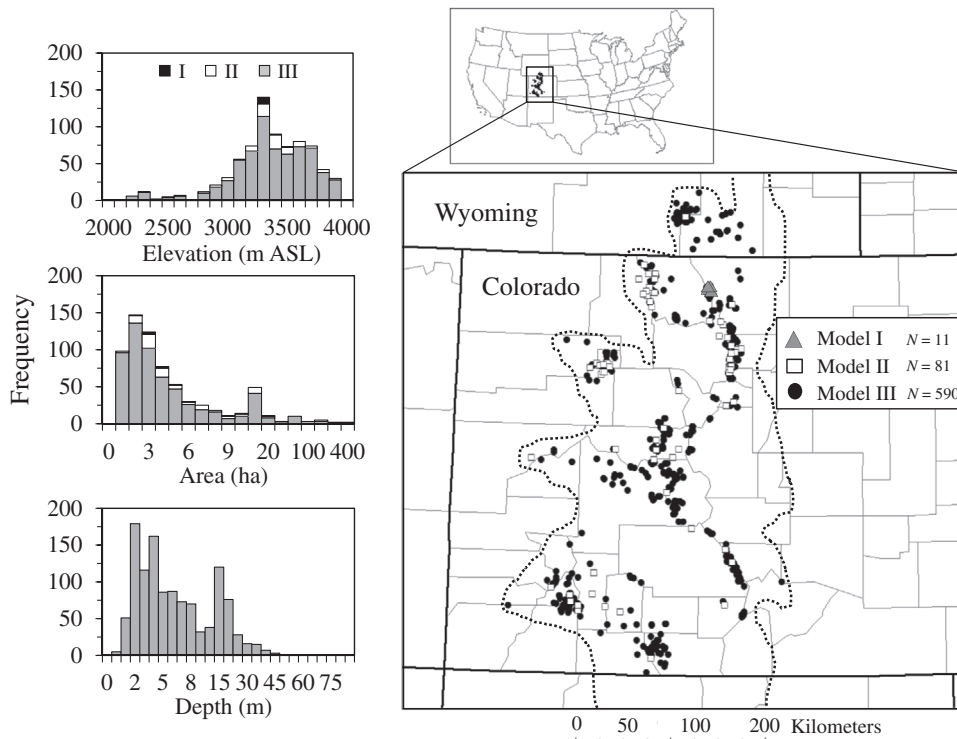


Fig. 2. Distribution and characteristics of high elevation lakes in the Southern Rocky Mountain, U.S.A. (dotted line) used in the present study. Symbols represent the dataset and corresponding model to which each lake contributed.

period of interest, which encompassed ≥ 15 yr of observations for each lake, while others only included repeated measurement requirements spanning many years (13 yr minimum, O'Reilly et al. 2015; 15 yr minimum, Schneider and Hook 2010). Sampling frequency has varied, from at least 1 per year (Magee and Wu 2017) to hourly (Austin and Colman 2007) in each lake. Satellite observations can allow for more frequent measurements than usually available in remote lakes, but these data are more recent (post 1970s) and can only be collected on larger lakes to minimize the effect of shoreline (Schneider and Hook 2010). Investigators have usually aggregated data by averaging measurements within weeks, months, or seasons to smooth out short-term variation (Dokulil 2014; O'Reilly et al. 2015; Winslow et al. 2015). In some cases, yearly or greater averages are used (Livingstone 2003; Coats et al. 2006; Zhang et al. 2014). The aggregated data are then used to derive trend estimates. In the case of remote lakes with sparse data, trend analyses would need to incorporate seasonal and diel effects in a different way than for lakes with more continuous temperature records.

New quantitative tools to exploit the vast amount of discontinuous or unreplicated lake temperature measurements already collected, and to account for error associated with short-term temperature variation would improve our overall understanding of how all types of lakes are responding to a changing climate. By incorporating diel and seasonal variability directly into the analysis, data from lakes sampled irregularly can be included, greatly increasing the number of lakes that can be examined for the effects of climate change. The goals of this study were to (1) estimate multidecadal lake surface temperature trends from sparse data across many high elevation lakes with few repeated observations, and (2) evaluate the hypothesis that high elevation lakes have warmed at a different rate than other lake types. Bayesian methods were used to draw on current knowledge of diel and seasonal variation for inclusion as priors. The approach also accounted for

uncertainty in time of day that measurements occurred because this is frequently not reported or accounted for in trend analyses.

Methods

The data for this study were obtained from lakes in the Southern Rocky Mountains (SRM), which extend about 650 km from northern New Mexico, U.S.A. to southern Wyoming, U.S.A. (Fig. 2). There are over 2500 natural lakes in the SRM, of which $> 95\%$ lie above 2100 m ASL and $> 90\%$ are smaller than 10 ha in surface area (Nelson 1988). As nearly all natural lakes in the SRM are above 2100 m ASL, this was used to define "high elevation" so that the largest number of lakes was included in the study. These lakes are mostly of glacial origin, and classified as oligotrophic or ultraoligotrophic. Some are seepage lakes with little to no overland inflow or outflow (Pennak 1969), but the hydrology of most of them is dominated by runoff from annually variable snowmelt (Hauer et al. 1997). The vast majority of these lakes were historically fishless (Hauer et al. 1997), but most that can support fish have been stocked with salmonids (*Oncorhynchus* and *Salvelinus* spp.; Nelson 1988).

We collected some lake surface temperature data ourselves but most were gathered from state and federal agencies responsible for waters within the SRM. We deployed Onset HOBO temperature loggers in the top 1 m of the epilimnion that recorded hourly measurements at 11 lakes in the Rawah Wilderness in northern Colorado (Fig. 2; Table 2) to understand variation in surface temperatures due to time of day, day of year, and lake area. We also measured dissolved oxygen concentration 1 m from bottom at the deepest location in eight lakes in the Rawahs during late August in 2016. The median area of the Rawah lakes was very similar to those for the other 590 lakes in the overall dataset. Agency data were included if the lake was: (1) natural, (2) located above 2100 m,

Table 2. Characteristics of 11 lakes in the Rawah Wilderness Area, Colorado, used to estimate diel and seasonal variation in lake surface temperature (model 1).

| Lake name | Latitude N | Longitude E | Elevation (m ASL) | Area (ha) | Maximum depth (m) |
|---------------|------------|-------------|-------------------|-----------|-------------------|
| Big Rainbow | 40.693 | -105.941 | 3275 | 2.4 | 4.27 |
| Camp | 40.695 | -105.928 | 3205 | 4.8 | 1.10 |
| Lost | 40.719 | -105.937 | 3097 | 3.7 | 5.79 |
| Lower Sandbar | 40.696 | -105.947 | 3253 | 1.5 | 1.68 |
| McIntyre | 40.704 | -105.961 | 3242 | 5.9 | 10.67 |
| Rawah #1 | 40.696 | -105.953 | 3250 | 2.9 | 2.13 |
| Rawah #2 | 40.692 | -105.951 | 3275 | 2.8 | 3.96 |
| Rawah #3 | 40.684 | -105.956 | 3316 | 8.5 | 35.05 |
| Sugarbowl | 40.703 | -105.968 | 3288 | 3.1 | 15.24 |
| Upper Camp | 40.683 | -105.924 | 3270 | 15.4 | 23.47 |
| Upper Sandbar | 40.692 | -105.946 | 3263 | 3.3 | 7.40 |
| Mean | 40.696 | -105.947 | 3249 | 4.9 | 9.73 |

and (3) temperature values were indicative of ice-free conditions ($\geq 4^\circ\text{C}$; Wetzel 2001; Roberts et al. 2017). Depth at samples were not available for agency measurements, but were all regarded as “surface” temperatures. For each lake, we also recorded latitude (UTM northing), elevation (m ASL), and surface area (ha) because these factors could affect lake surface temperature. Due to the remoteness of these lakes, other characteristics such as water clarity, lake depth, or residence time, were not available for most lakes.

Lake surface temperature observations were grouped into three mutually exclusive and increasingly sparse datasets (Fig. 3). Due to sparsity of data, individual lakes were not considered sampling units; rather individual measurements were considered sampling units. The first dataset included only lakes with hourly temperature measurements and was used to develop a model accounting for time of day that temperature was measured, as well as seasonal and lake size effects (model I). The second dataset consisted of lakes with point sample measurements and known sampling time; these data were used to develop a model to account for effects of elevation, as well as lake area, on temperature (model II). The third, and largest but sparsest dataset included lakes with point sample measurements, but sampling time was unknown and there were few repeated measurements at a given lake (model III). This dataset and model III were used to estimate the secular warming trend over the time period of the dataset, accounting for all temporal, lake size, and elevation effects, and unknown sampling time.

These datasets and models were used in a Bayesian model framework (Fig. 3). An advantage of the Bayesian approach over traditional ones (e.g., simple linear regression) is that it treats unobserved quantities as random variables and complex processes can be decomposed into a series of conditional sub-processes. Bayes theorem (Eq. 1) can be expressed as the proportionality of the posterior distribution to the joint distribution. The posterior distribution is defined as the probability of parameter values (θ) conditional on the observed data (y), while the joint distribution is defined as the probability of the data conditional on the parameters multiplied by the probability of the prior distribution of the parameters.

$$P(\theta|y) \propto P(y|\theta) \times P(\theta) \tag{1}$$

In this manner, the parameter estimates are updated from a set of observations describing the posterior predictive distribution of the parameters. This approach also allows for the inclusion of parameters with little to no information (e.g., time of day temperature was measured), by defining vague priors for these distributions. The posterior distributions of these parameters can then be used as informed priors for subsequent models (Hobbs and Hooten 2015). A Markov Chain Monte Carlo (MCMC) method is used to fit the model to data. The “Monte Carlo” designation estimates properties of parameter distributions via random samples from a prior distribution, whereas “Markov Chain” designates that each random sample

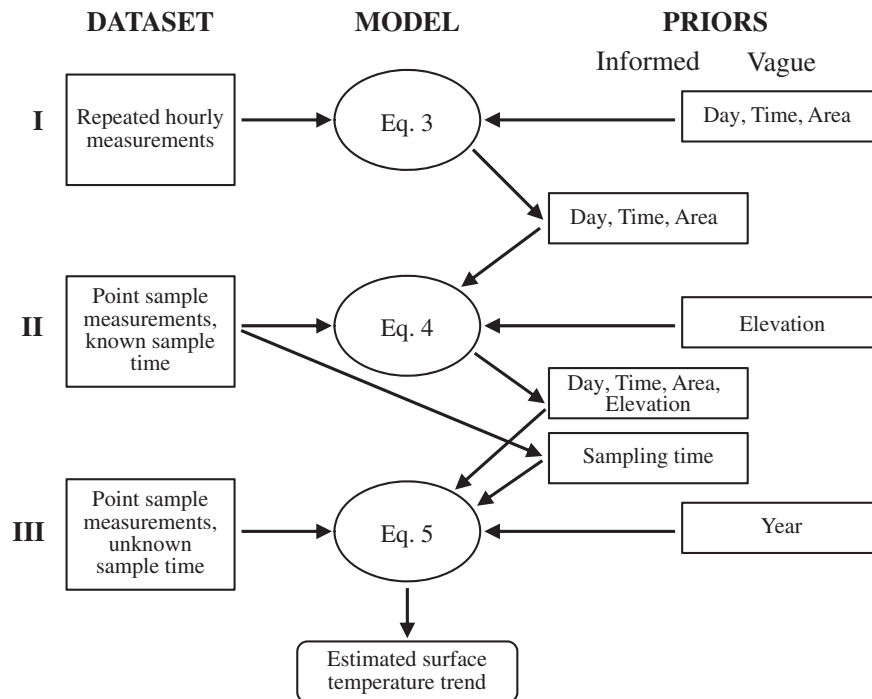


Fig. 3. Sequential procedure showing each dataset type and priors used for each model. Priors can be informed or vague. Informed priors are derived from previous models or dataset used to inform parameter distributions for future models, while vague priors do not arise from previous data.

is generated from the previous sample in a “chain.” The MCMC algorithm iterates through each parameter individually assuming the other parameters are known, turning a complex problem into a series of simpler subproblems. A posterior distribution that provides inference for the parameter values is approximated from numerous iterations of sampling through the MCMC (Van Ravenzwaaij et al. 2016).

We used a sequential procedure, with three models in hierarchy (Fig. 3). Each model drew on the previous model’s results as informed priors for parameters which were initially vague. Later models were updated from the former model’s means and covariance among each coefficient. Models increased in complexity, accounting for more uncertainty and sources of variability in surface temperature. The “rjags” package in R vs 3.3.2 (R core team, 2017) was used to develop and fit each model. We checked for convergence of three MCMC chains through visual inspection and Gelman and Rubin convergence diagnostics (Gelman and Rubin 1992; Brooks and Gelman 1998) using the “gelman.diag” function of the “coda” package in R. A Gelman and Rubin diagnostic value above 1.1 indicated lack of fit, while values at or near 1 indicated no lack of fit. Last, we calculated Bayesian posterior predictive p -values (PB) of mean and discrepancy: $[\text{observation-prediction}]^2$ to ensure the model accurately gives rise to the data:

$$\text{PB} = P(T(\mathbf{y}_{\text{new}}, \theta) \geq T(\mathbf{y}, \theta) | \mathbf{y}) \quad (2)$$

where, simulations generating a new dataset, $T(\mathbf{y}_{\text{new}}, \theta)$, from the predicted posterior distribution are used to determine the probability that this new dataset is different from the observed, $T(\mathbf{y}, \theta) | \mathbf{y}$, in terms of the statistic T . Extreme values of PB < 0.1 or > 0.9 indicate lack of fit, while values near 0.5 indicate no lack of fit of the model (Hobbs and Hooten 2015).

Model I captured diel and seasonal variation in surface temperature while accounting for lake area, providing informed priors for these factors in subsequent models. A combined sine and cosine function was used to model temporal variation:

$$y_{it} = \beta_{0_{it}} + \beta_{1_{it}} \sin\left(\frac{\text{Time}_i}{24} \times 2\pi\right) + \beta_{2_{it}} \cos\left(\frac{\text{Time}_i}{24} \times 2\pi\right) + \beta_{3_{it}} \sin\left(\frac{\text{Day}_i}{365} \times 2\pi\right) + \beta_{4_{it}} \cos\left(\frac{\text{Day}_i}{365} \times 2\pi\right) + \beta_{5_{it}} (\text{Area}_i) \quad (3)$$

where, y_{it} indexes lake surface temperature observation at lake i at time t , Time_i is the hourly value for time of observation at lake i , while Day_i is the ordinal day of observation at lake i . Area is lake surface area (ha). We used vague priors for initial β values, assuming normal distributions to allow for all positive and negative values bounded within the distribution. Data for this model used temperatures from 11 neighboring lakes with high resolution continuous measurements to minimize extraneous influence of site characteristics on surface temperature variability.

Because lakes in the SRM occur over a wide range of elevations, model II captured this effect on surface temperature,

while incorporating effects of diel and seasonal variation. Latitude was not included in model II or III due to high correlation of the beta estimates (0.994) of latitude and elevation. Model II used the coefficient means and covariance results from Model I as informed priors for coefficients β_1 - β_5 :

$$y_{it} = \beta_{0_{it}} + \beta_{1_{it}} \sin\left(\frac{\text{Time}_i}{24} \times 2\pi\right) + \beta_{2_{it}} \cos\left(\frac{\text{Time}_i}{24} \times 2\pi\right) + \beta_{3_{it}} \sin\left(\frac{\text{Day}_i}{365} \times 2\pi\right) + \beta_{4_{it}} \cos\left(\frac{\text{Day}_i}{365} \times 2\pi\right) + \beta_{5_{it}} (\text{Area}_i) + \beta_{6_{it}} (\text{Elev}_i) \quad (4)$$

where, y_{it} indexes lake surface temperature observation at lake i at time t . Time, Day, and Area are the same as in model I, and Elev (elevation, m ASL) is added. A vague prior was used for β_6 . The data for this model included point sample observations with known sampling time at a wide range of elevations across the SRM.

Model III is the final expansion of the first two models:

$$y_{it} = \beta_{0_{it}} + \beta_{1_{it}} \sin\left(\frac{\text{ST}_i}{24} \times 2\pi\right) + \beta_{2_{it}} \cos\left(\frac{\text{ST}_i}{24} \times 2\pi\right) + \beta_{3_{it}} \sin\left(\frac{\text{Day}_i}{365} \times 2\pi\right) + \beta_{4_{it}} \cos\left(\frac{\text{Day}_i}{365} \times 2\pi\right) + \beta_{5_{it}} (\text{Area}_i) + \beta_{6_{it}} (\text{Elev}_i) + \beta_{7_{it}} (\text{Year}_i) \quad (5)$$

where, Year_i is the year of observation at lake i and ST_i is sampling time for observation at lake i . Because sampling time is now unknown for this model, we designate it differently than previous models. ST is estimated from the distribution of known sampling times in model II, allowing us to incorporate diel variability even when sampling time was not reported, as was frequently the case. The coefficient for year ($\beta_{7_{it}}$) reports the average yearly surface temperature trend from 1955 to 2016 across all lakes. Coefficients 1–6 were informed priors from model II, while $\beta_{7_{it}}$ had a vague prior for year. In all models, we used a normally distributed likelihood.

The posterior distribution of model III was used to derive quantities of interest while incorporating parameter uncertainty. We derived degree days during the ice-free season as a more temporally integrative and biologically meaningful measure of lake warming in a given year:

$$\text{DD} = \sum_1^{365} \max\left(\frac{T_{\text{max}} - T_{\text{min}}}{2} - T_{\text{base}}, 0\right) \quad (6)$$

where, DD is cumulative degree days, T_{max} and T_{min} are maximum and minimum daily temperatures and T_{base} is baseline temperature. If the mean daily temperature was below T_{base} then DD = 0. Although we used $T_{\text{base}} = 4^\circ\text{C}$ because this temperature represents ice-free conditions, it is also the minimum temperature for growth of salmonids (Piper et al. 1982), the predominant fish family in the high elevation lakes of the SRM. Thus, this measure of warming could also be interpreted

as an estimate of growing degree days for salmonids. We computed DD each day for the average conditions of dataset III and summed them across the ice-free period.

Results

The dataset for model I consisted of more than 37,000 hourly surface temperature observations from the 11 Rawah lakes in 2015–2016. Although these lakes were located within 6 km of each other, they exhibited a wide range of diel, seasonal, and interlake variability (Fig. 4), making this a good dataset for defining distributions of these parameters for use in models II, and III. In general, smaller lakes showed greater diel variation and higher peak summer temperatures than larger lakes. Diel variation ranged from $< 2^{\circ}\text{C}$ to $> 10^{\circ}\text{C}$, while peak summer temperatures ranged from 14°C to 22°C . The lowest peak temperature was observed in the highest elevation lake, and the highest peak temperature was observed in the lowest elevation lake, indicating that both lake size and elevation were important determinants of lake surface temperature.

The dataset for model II consisted of 113 observations from 81 lakes distributed across the SRM in Colorado and Wyoming (Fig. 2) during 1985–2015. This dataset contributed a more diverse set of lake elevations (2295–3820 m ASL) than the dataset for model I, to define distributions for these parameters required for model III. In this dataset, elevation accounted

for $> 10^{\circ}\text{C}$ range in peak surface temperature over this area. More than half of the data from model II occurred in 1 yr (1985). Therefore, this dataset did not represent enough inter-annual variability to include a term for year in model II.

The dataset for model III consisted of 1493 observations collected from 590 lakes during 1955–2016 (Fig. 5). This represents the largest dataset ever used to estimate warming rate of high elevation lakes. The lakes were well-distributed across the SRM (Fig. 2). Although no temperature measurements were available from the portion of the SRM extending into northern New Mexico. However, this northern New Mexico region represents only $\sim 17\%$ of the total area of the SRM (Fenneman 1931) and permanent lakes are rare there (Wright 1964). Despite the large number of observations, this dataset would be considered sparse by contemporary standards. For example, there were no lakes in the dataset with at least one observation per year for at least 50% of the time series. To meet this standard, a minimum of 18,290 observations would have been required. There were only three lakes in the dataset with > 10 yr of continuous repeated measurements (Fig. 5). These lakes were relatively close together without measurements available before 1965 or after 2012, and do not represent the diversity of lake sizes and elevations in the SRM region.

All three models converged and showed no indication of a lack of fit. For model I, we acquired 25,000 MCMC samples

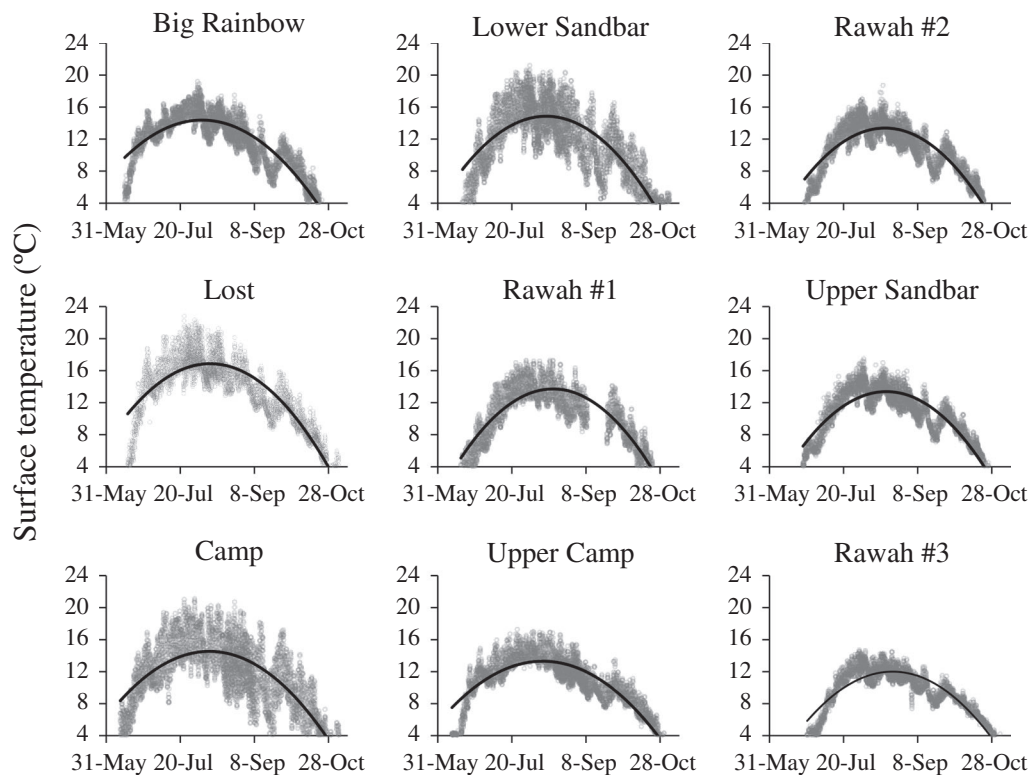


Fig. 4. Hourly surface temperature measurements of nine neighboring lakes in the Rawah Wilderness Area, Colorado, during the ice-free period of 2015, 2016. McIntyre and Sugarbowl were omitted because 2015 data were not collected. Lakes are ordered by increasing depth, left–right, top–bottom. A second order polynomial was fit to each lake to help the reader visualize peak temperatures and timing of open-water conditions across lakes.

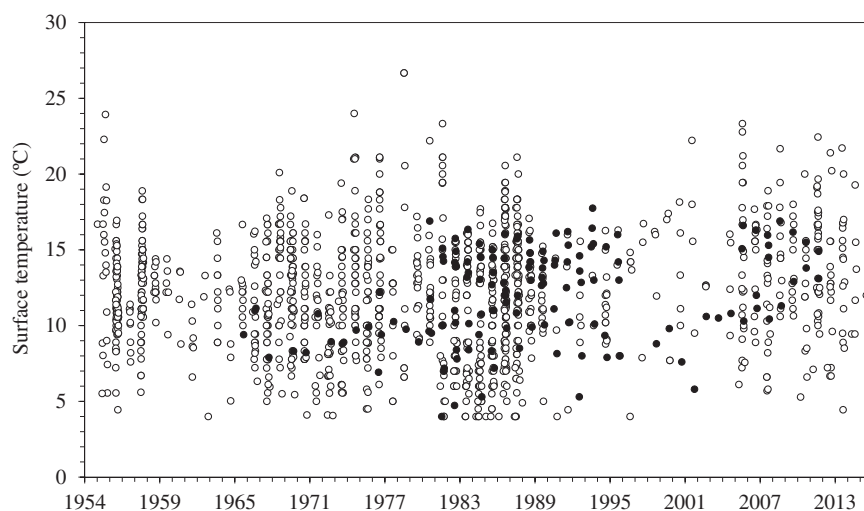


Fig. 5. Lake surface temperature data for 590 lakes in the SRM during 1956–2016. Open symbols ($n = 1354$) represent unrepeated temperature measurements, while closed symbols ($n = 139$) show the subset of lakes where measurements were repeated sufficiently to use conventional trend estimation.

and discarded 10,000 as burn-in. The MCMC algorithm for model I converged with a Gelman–Rubin Diagnostic of 1.0 for all parameters. The Bayesian p -value of 0.49 for mean and 0.50 for discrepancy demonstrated no lack of fit in model I. For model II, we acquired 100,000 MCMC samples and discarded 50,000 as burn-in, and reached convergence (Gelman–Rubin Diagnostic value of 1.0–1.01 for all parameters). A Bayesian p -value of 0.50 for mean and 0.52 for discrepancy showed no lack of fit. Model III converged while acquiring 300,000 MCMC samples and discarding 150,000 as burn-in (Gelman–Rubin Diagnostic value of 1.0 for all parameters), while the Bayesian p -values were 0.50 for mean and 0.51 for discrepancy. Coefficients for diel variation in model III showed an annual average sinusoidal temperature variation of 2.4°C daily across the SRM, compared to an average diel variation of 3.3°C in 2015–2016 in the Rawah lakes (model I). The coefficients for area and elevation in model III showed inverse relationships with temperature (Table 3).

Our modeling estimated that average annual surface temperature of high elevation lakes in the SRM have warmed at the rate of 0.13°C decade⁻¹ (95% credible interval [CI]: 0.03–0.23°C decade⁻¹) since 1955. We estimated that during 1955–2016, surface temperatures increased by 0.81°C, and average regional DD have increased by 14% from 904 DD (CI: 818–991) in 1955 to 1026 DD (CI: 934–1117) in 2016.

Discussion

We found that the average surface temperature of high elevation lakes of the SRM warmed at a rate of 0.13°C decade⁻¹ during 1955–2016. The Bayesian approach we used to determine this rate alleviates some conventional data requirements for temperature trend estimation because uncertainties from diel, seasonal, and interlake variation are explicitly

incorporated. This approach allowed us to estimate warming in the largest dataset on high elevation lakes compiled to date and improve the understanding of warming in an underrepresented class of the world's lakes. If the trend we report continues, these lakes will be on average 1.11°C warmer by 2100. This increase in surface temperature will result in an estimated 15% increase in DD in the epilimnion from 2016 to 2100. We expect that the effects of warming will be mixed for high lake biota. Generally, surface temperatures will become more favorable for *Oncorhynchus* spp. such as the native Cutthroat Trout (Bear et al. 2007, but see some exceptions in Roberts et al. 2017), but these warmer temperatures will make these lakes more vulnerable to invasions by non-native species found at lower elevations such as the Smallmouth Bass *Micropterus dolomieu* (McKinley et al. 2000; Sharma et al. 2007). Warmer surface temperatures can also prolong stratification and the duration of the open water season. These conditions could exacerbate the hypolimnetic hypoxia that we observed in some of the study lakes included in this analysis (Tranvik et al. 2009). Warmer surface temperatures coupled with reduced oxygen availability in the hypolimnion can create a temperature-oxygen squeeze for cold-adapted species (Jacobson et al. 2008; Jiang et al. 2012). The combined effect of these climate change impacts would reduce habitat for the non-native and cold-adapted Lake Trout *Salvelinus namaycush* and Opossum Shrimp *Mysis diluviana*, some of the primary predators, and competitors, respectively, of native fishes in high elevation lakes of the SRM. The full ecological implications of warming for the understudied lakes of the SRM need to be studied further, as diversity in lake types and conditions of the SRM could present differing biological responses to future warming.

Our estimate of lake warming is lower than some recent global average estimates. O'Reilly et al. (2015) estimated a rate

of 0.34°C decade⁻¹, but that study included just 12 high elevation lakes out of 235 lakes in the dataset and only the summer time period. Schneider and Hook (2010) estimated a global rate of 0.37°C decade⁻¹, but their study from satellite observations included only lakes ≥ 50,000 ha and for two annual time periods (July–September and January–March). Our estimate falls in the middle of estimates for other high elevation lakes distributed across two continents (0.12–0.25°C decade⁻¹; Zhang et al. 2014; Kirillin et al. 2017; Roberts et al. 2017). Thus, it appears that globally, high elevation lakes have warmed at a slower rate than other lake types. More inclusive studies with more lakes are needed to know if this is a general phenomenon, or an outcome of the limited scope of existing studies. For example, a number of factors can account for differences in lake warming trend estimates, including: biases induced by data aggregation, time frame of the estimate, geographic factors, and the particular set of lakes chosen.

Conventional approaches, at least for temperate lakes with a strong seasonal temperature cycle, usually aggregate data across an interval within a year to compute an annual average value and then compute a warming rate across years. Disparities in data aggregation may explain some of the range of lake warming rates that we documented in Table 1. Investigators have variously used monthly, seasonal, and annual averages to calculate warming rates. However, these different time-frames can lead to differing warming rates. For example, summer warming rates can be higher than annual average rates (Hampton et al. 2008; Roberts et al. 2017), but studies have not been consistent in the months used to compute “summer” warming rates. Hampton et al. (2008) and Roberts et al. (2017) used June–August temperatures, but Schneider and Hook (2010) and O’Reilly et al. (2015) used July–September data. Although most of the data for our study were collected from June through September, it was not necessary to aggregate data over a predefined seasonal period to estimate inter-annual warming because our models included terms for seasonality. This is a significant advantage of our analysis

because it allows for more data, including sparse datasets without a consistent annual measurement period, to be included in long-term analyses.

Regardless of the data aggregation approach, although, warming trend estimates will depend on the particular years in the dataset because climate change has not been a linear process. For example, Efremova et al. (2016) argued that major lake temperature change occurred beginning in the late 1970s to the mid-1980s. Likewise, over the last 100 yr, warming since the 1980s has been unprecedented in some regions (Woolway et al. 2017). Lake surface temperature trends encompassing many decades prior to this period would, therefore, be lower than estimates beginning closer to the 1980s. This is evident in Table 1, where four of the longest duration studies (Livingstone and Dokulil 2001; Kraemer et al. 2015*b*; Magee and Wu 2017; Kainz et al. 2017) comprise the majority of trend estimates of 0.15°C decade⁻¹ or lower. Similarly, the four studies with the largest trend estimates (≥ 1°C decade⁻¹; Weyhenmeyer et al. 2007; Schneider et al. 2009; Jeppesen et al. 2013; Mason et al. 2016) are among the shortest duration studies. We believe that the six decade time period used in our study partially accounts for our lower than average trend estimate. Future analyses may refine trend estimates, including evaluating possible nonlinearity. Because new data will accumulate slowly, methods like ours that allow researchers to go further back in time and incorporate older but sparser datasets are useful for understanding the temporal dynamics of the climates effect on lake surface temperatures.

Just as lake warming rate has varied through time, climate change has not affected all lakes equally. Local influences like morphometry, elevation, and catchment characteristics interact with regional drivers of climate (Adrian et al. 2009). We recognize that, in a broader geographic perspective, our definition of “high elevation” lakes is subjective. The average minimum elevation in the SRM is ~1780 m ASL, so our high elevation lakes are 320–2169 m above the surrounding lowland landscape. However, generally speaking, temperate “high

Table 3. Parameter estimates from each model. SD is standard deviation of the estimate. Diagnostic statistics indicated no lack of fit for any model’s parameters.

| Parameter | Symbol | Model I | | Model II | | Model III | |
|-----------|-----------|----------|-------|----------|-------|-----------|------------------------|
| | | Estimate | SD | Estimate | SD | Estimate | SD |
| Intercept | β_0 | 1.55 | 0.056 | 51.949 | 6.194 | 0.808 | 10.290 |
| Sin(Time) | β_1 | -1.181 | 0.015 | -1.182 | 0.015 | -1.191 | 0.015 |
| Cos(Time) | β_2 | -0.224 | 0.015 | -0.224 | 0.015 | -0.226 | 0.015 |
| Sin(Day) | β_3 | -7.951 | 0.050 | -7.960 | 0.053 | -8.381 | 0.052 |
| Cos(Day) | β_4 | -9.769 | 0.043 | -9.782 | 0.045 | -10.184 | 0.045 |
| Area | β_5 | -0.067 | 0.003 | -0.060 | 0.003 | -0.042 | 0.002 |
| Elevation | β_6 | -- | -- | -0.015 | 0.002 | -0.008 | 2.944×10 ⁻⁴ |
| Year | β_7 | -- | -- | -- | -- | 0.013 | 0.005 |
| Time | ST | -- | -- | -- | -- | 12.11 | 0.51 |
| SD model | σ | 2.06 | 0.008 | 5.519 | 0.400 | 3.188 | 0.062 |

elevation” lakes tend to have small watersheds and represent extreme environments with short growing seasons coupled with long ice cover duration and lower surface temperatures, relative to their lower elevation counterparts in a given region (Catalan and Donato-Rondón 2016). A key feature of high elevation lakes in the SRM is that they are distinctly snowmelt driven systems (Hauer et al. 1997). It appears that melting snowpack in the spring and perennial ice/snow during summer have buffered lakes in our region against surface warming, similarly to other high elevation regions (Zhang et al. 2014; Sadro et al. 2018). But snowpack in our region is diminishing and melting earlier, while glaciers are receding (Hoffman et al. 2007; Clow 2010) so lake warming patterns may undergo another abrupt change in the future.

While the number of published studies on lake warming is substantial, collectively they represent a tiny fraction of world lakes. The relatively small sample size of most studies, and non-random selection of lakes, has probably contributed to the lack of consensus in lake warming rates. The median number of lakes included in the 41 studies we report in Table 1 was four. Further, the available studies are confined to lakes where regular and standardized monitoring has been possible. Thus, remote lakes, including many high elevation lakes, as well as small lakes, and lakes in less developed parts of the world, are not well-represented in the literature. The modeling framework we employed may be useful in many regions where detailed time series are relatively rare, but sparser datasets are available for many aquatic systems. Also, with the advent of satellite observations widely available for many decades, this approach may allow better warming estimates for large lakes globally. Given the importance of warming to lakes, their biota and even the global carbon cycle, analyses that can be used to exploit existing, sparse datasets would be valuable and provide a more complete picture of how all lakes have already responded to a changing climate, and make better forecasts of future impacts to a diversity of lakes types.

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Conflict of Interest

None declared.

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