DISSERTATION

THE EFFECTS OF CLIMATE CHANGE ON HIGH ELEVATION LAKE ECOSYSTEMS

Submitted by

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ABSTRACT

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High elevation lakes are an important class of the world's fresh water. Nearly 10% of all lakes globally reside above 2,100 m ASL and almost half of the world's population relies on water from high elevation regions. Also, these lakes provide important cool water habitat refugia for aquatic biota. However, high elevation areas are sensitive to changes in climate and are changing faster than other regions. Likewise, secondary effects of a changing climate like drought, forest fire, and eutrophication threaten lake habitats, exacerbating changes from air warming. Despite the importance of high elevation lakes and their increased threat from climate change, little is known about high elevation lakes and their vulnerability to these threats. The goal of my dissertation was first (Chapter 1) to determine historic changes in lake surface temperatures for a set of high elevation lakes in the Southern Rocky Mountains, USA (SRM). Then, I determined potential future changes to thermal stratification (Chapter 2) and the length of the open water season (Chapter 3) for a subset of lakes in the Rawah Wilderness Area (RWA) within the SRM. For these future predictions, I estimated alterations in lake surface and bottom temperatures from multiple stressors, as well as how these changes may affect aquatic habitat for native and nonnative fish species that reside in the region.

Although historic lake temperature trend analyses are numerous, remote lakes, including many high elevation lakes, are typically underrepresented due to limited availability of long-term datasets. In Chapter 1, I developed a Bayesian modeling technique to analyze sparse data from high elevation lakes that allowed me to estimate lake surface warming across a large region

(SRM). The analysis allowed for inclusion of lakes with few repeated measurements, and observations made prior to 1980 when more intensive lake monitoring began. I accumulated the largest dataset of high elevation lake surface temperatures globally 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.

Like surface temperature trends, many studies have also examined the effects of climate warming on lake thermal stratification, but few have addressed environmental changes concomitant with climate change, such as alterations in water clarity and lake inflow. Although air temperature rise is a predominant factor linked to lake thermal characteristics, climate-driven changes at watershed scales can substantially alter lake clarity and inflow, exacerbating the effects of future air warming on lake thermal conditions. In Chapter 2, I employed the mechanistic General Lake Model (GLM) to simulate future thermal conditions of typical mountain lakes of the western United States. I found that after air temperature, alterations in inflow had the largest effect on lake thermal conditions, changes in wind had the least effect, and large lakes experienced more than double the increase in lake stability than small lakes. Assuming air temperature rise alone, summer stability of mountain lakes of the western United States was predicted to increase by 15-23% at +2°C air temperatures, and by 39-62% at +5°C air temperatures. When accounting for associated changes in clarity and inflow, lake stability was predicted to increase by 208% with +2°C air warming and 318% at +5°C air warming.

Finally, the open water duration at high elevations is increasing at a higher rate than at lower elevations. Earlier snowmelt, resulting in decreased ice cover duration, is having a proportionally higher effect on mountain lakes than other regions. But the effect early melt and increased air temperatures have on mountain lake thermal characteristics and implications for fish is unclear. Mountain lakes exhibit a variety of thermal conditions, altering metabolic requirements for ectotherms. In Chapter 3, I coupled GLM with a fish bioenergetics model to assess potential thermal changes and energetic consequences for native Cutthroat Trout (*Oncorhynchus clarkii* spp.) and nonnative but present Brook Trout (*Salvelinus fontinalis)* in a continuously mixed polymictic and seasonally stratified dimictic mountain lake during early and nominal snowpack melt in the SRM. I found that early snowmelt alone had a larger consumptive demand for all species than an air temperature increase of 2°C, but combined these environmental changes are most effective. Early melt coupled with 5°C air warming could more than double the food requirements for Cutthroat Trout and Brook Trout. Ultimately, food availability may dictate the future success of fish in mountain regions.

My dissertation research expanded the current knowledge of high elevation lake thermal conditions, developed a novel method to utilize sparse datasets, and provided valuable holistic insight to potential future changes in lake thermal structure and habitat suitability for fish while accounting for localized and watershed scale consequences of climate change.

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INTRODUCTION

Lakes interact directly with climate and integrate local watershed characteristics, therefore, changes to the climate system and watershed can alter lake ecosystems (Adrian et al. 2009; Moser et al. 2019). Local weather helps to regulate lake temperatures through latent and sensible heat fluxes (Bonan 2016), as well as propagating mixing via wind (Woolway et al. 2017), thereby governing lake stratification. Alterations in climate (e.g., air temperature warming) can shift lake temperatures (O'Reilly et al. 2015), prolong stratification (Kirillin 2010; Shatwell et al. 2016), and potentially induce stratification in historically unstratified systems (Michelutti et al. 2016). Further, watershed characteristics such as inflows, perennial snow and ice presence, aspect, vegetation cover, and topography, may enhance or hinder a lake's ability to stratify, but the magnitudes of these interactions are less well known. Lake temperatures and stratification drive biological and ecological processes, such as habitat partitioning (Jacobson et al. 2008), metabolic respiration (Brett 1971), predator-prey interactions (Johnson et al. 2017), and production (Arvola et al. 2010). Thus, changes to climate and watersheds, and the implications thereof, can have far-reaching consequences to biota.

Although climate change is often assessed via air temperature and precipitation changes, many secondary consequences occur as a result. Watershed scale alterations, such as forest fires, snowpack alterations, and streamflow changes can all result from climate change (Aponte et al. 2016; Fyfe 2017), with implications for lakes. Lakes integrate landscape scale processes, so the effect of climate change needs to be assessed through a multi-faceted approach. These multiple stressors can induce alterations in lake inflow, clarity, and surface wind (Bixby et al. 2015; Woolway et al. 2017; Sadro et al. 2018), potentially compounding the effects of air temperature increases on lake temperatures and stratification. Therefore, by accounting for climate change using these primary (air temperature) and secondary effects (inflow, clarity, wind), we can improve our understanding of the possible changes to lake ecosystems.

One class of lakes of particular importance regarding climate change effects are mountain lakes. High elevation regions are potentially changing faster than other regions and are susceptible to drastic shifts in snowpack, drought conditions, and forest fires (Pepin et al. 2015; Preston et al. 2016; Sadro et al. 2018). But, mountain lakes are understudied compared to other regions and types of freshwater systems (Catalan and Donato-Rondon 2016). Given that nearly half of the world's population relies on water from high elevation regions (Woodwell 2004), mountain lakes provide thermal refuge for biota (Roberts et al. 2017), and mountain regions are susceptible to climate change, it is imperative to study these lakes and the potential consequences to changing conditions.

Historically, mountain lakes within the Southern Rocky Mountains (SRM), and many others, were fishless (Knapp 1996). Through continued stocking, these lakes have persistent fish populations. But, short growing seasons and cold water limit the productivity and growth potential in these high elevation areas (Bahls 1992). Also, mountain lakes have become important refuge habitats for a native coolwater fish, Cutthroat Trout *Oncorhynchus clarkia,* that are being threatened or displaced at lower elevations by warmer waters and invasive species (Marnell et al. 1987; Roberts et al. 2013). It is not currently known how mountain lake habitats may change under multiple stressors of climate change nor how these changes may alter suitable habitat for fish. Likewise, it unclear how potential changes to mountain lakes may shift physiological and metabolic processes for fish and how these shifts may alter habitat suitability, such as foraging opportunities. By understanding how mountain lakes may be altered under climate change, we can better protect and preserve native coolwater species that rely on this habitat.

In this dissertation, I address how mountain lake temperatures have already changed, to broaden scientific understanding of an understudied class of lakes, and then I predict how mountain lakes may change under the multi-faceted and compounding effects of climate change and watershed scale processes. Finally, I put these predictions in context for fish metabolic and consumptive demands, to better understand the biological consequences to changing mountain lake ecosystems.

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CHAPTER 1 – ESTIMATING LAKE-CLIMATE RESPONSES FROM SPARSE DATA: AN APPLICATION TO HIGH ELEVATION LAKES[1]

1.1 INTRODUCTION

Surface temperature is an important feature of lakes, with physico-chemical 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 CO_2 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 coldwater organisms from accessing the epilimnion, and may create a predation refuge for zooplankton (e.g., Martinez and Bergersen 1991) and fish (e.g.,

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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 been used to document temporal trends in climate-induced warming of lakes (Table 1.1). A wide variety of warming rates has been reported, ranging from <0.0°C decade^{-1} to >1.0°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—0.37°C decade^{-1}; Table 1.1), but a comprehensive understanding of lake responses to climate is still lacking (O'Reilly et al. 2015). Uncertainty in lake-climate responses limits the 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 1.1 represents only about 0.0008% of the ~1.17×10^8 lakes ≥ 0.2 ha on Earth (Verpoorter et al. 2014). Although the quantity of lake surface temperature measurements worldwide is probably

TABLE 1.1 – 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/dec)	Sampling frequency	Data aggregation	Sampling time recorded?	Source
Global	1985-2009	235	3-37,811,900	-404-4,743	0.34	At least monthly	3 month 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 month mean	N/A	Schneider and Hook 2010
Global	1970-2010	26	2-6,800,000	-212-1,987	0.20	1 to many measurements/year	30 day running average	N/A	Kraemer et al. 2015a
Russia	1953-2011	6	1,070-114,000	89.3-138.3	0.30	Daily	10-day average	N/A	Efremova et al. 2016
US Great Lakes	1968-2002	3	1,900,000-8,200,000	75-182.9	0.25-0.84	Several per year	Weekly August mean	N/A	Dobiesz and Lester 2009
Lake Zurich, Switzerland	1947-1998	1	6,500	406	0.24	Monthly	Decadal running mean	Standardized	Livingstone 2003
Wisconsin, USA	1990-2012	142	0.6-53,300	180-537	0.42	3 summer measurements	Monthly mean	N/A	Winslow et al. 2015
Lake Lugano, Italy	1972-2013	1	4,870	271	0.20-0.90	Monthly	Seasonal average	N/A	Lepori and Roberts 2015
Lake Washington, USA	1962-2002	1	8,760	4	0.35	Weekly to monthly	Annual to 5 year running mean	N/A	Winder and Schindler 2004
Italy	1986-2015	5	6,112-36,677	65-257.5	0.17-0.32	Daily to Monthly	Annual and seasonal mean	Standardized	Pareeth et al. 2017

Austria	1965-2009	9	1,079-5,350	115-588	0.40-0.66	Multiple per day	Daily average	Yes, 7, 14 , 19 h	Dokulil 2014
Lake Washington, USA	1964-1998	1	8760	4	0.45	Weekly to biweekly	Monthly average	N/A	Arhonditsis et al. 2004
Lake Tahoe, USA	1970-2002	1	5,010	1,897	0.15	Weekly to biweekly	Monthly, yearly means, 4 year running average	N/A	Coats et al. 2006
Lake Constance, Germany	1962-1998	1	4,720	395	0.17	Monthly profiles	Annual average	N/A	Straile 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, USA	1979-2006	1	8,200,000	182.9	0.34	Several per year	N/A	N/A	Bennington et al. 2010
USA Great Lakes	1979-2006	4	1,900,000-8,200,000	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	1 to many measurements/year	Pooled 30 day running average	N/A	Kraemer et al. 2015b
Austria	1975-2015	3	347-1,421	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 Dokulil 2001
Wisconsin, USA	1911-2014	3	87.4-3,938	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, USA	1981-2015	6	1-1,565	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, USA	1992-2008	6	N/A	N/A	1.1	120 seconds to 14 days	3 month average	Yes	Schneider et al. 2009
USA Great Lakes	1994-2013	5	1,900,000-8,200,000	75-182.9	0.96	Daily	Seasonal mean	N/A	Mason et al. 2016
Ontario, Canada and Wisconsin, USA	1981-2005	12	32-1,091	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 days	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	6,700	'peri-alpine'	0.41	Bi-monthly to monthly	Monthly trend	N/A	Schmid 2016
Lake Erie, USA	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 days	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
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	4,720	395	0.46	Continuous	Annual mean	Yes	Fink et al. 2014

vast, decadal scale monitoring studies that have historically formed the basis of lake warming studies are relatively rare (Table 1.1). Conventional methods for estimating lake warming rely on standardized and repeated measurements so that site-specific, seasonal and short-term inter-annual 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 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 1.1; Figure 1.1). Of the estimated ~11.7 million lakes globally at elevations above 2,100 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 ≥12°C (Livingstone et al. 1999; Novikmec et al. 2013; Woolway et al. 2016; Martinsen et al. 2018),

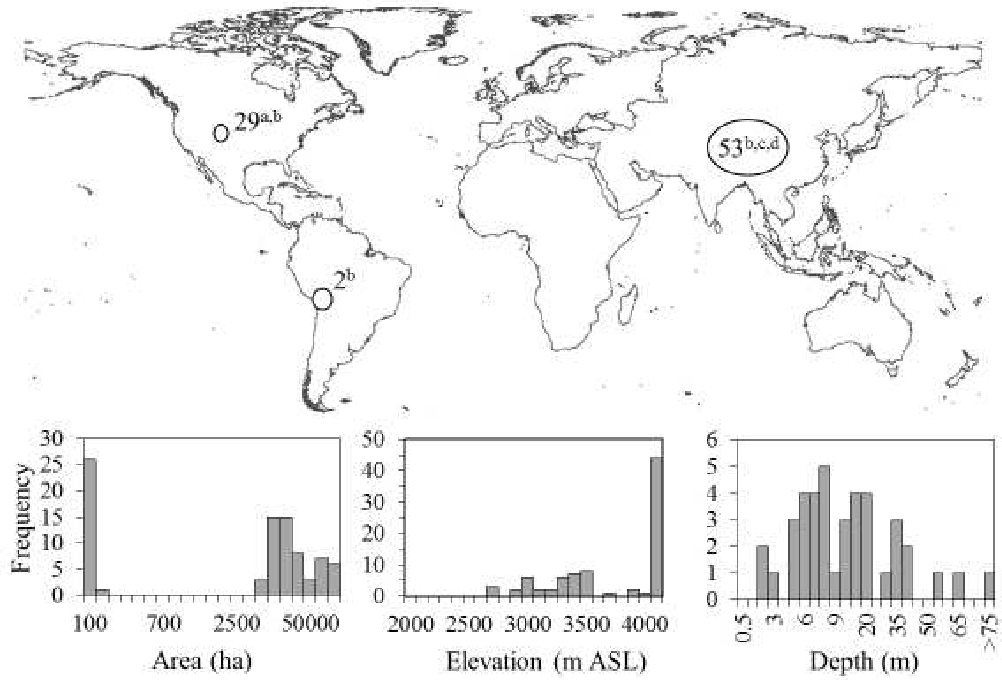

FIGURE 1.1 – Global distribution of high elevation lakes in published studies of lake warming, and their characteristics from Roberts et al. (2017) (a), O'Reilly et al. (2015) (b), Kirillin et al. (2017) (c), and Zhang et al. (2014).

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 1.1. For example, Richardson et al. (2017) required data for ≥50% of years over the period of interest, which encompassed ≥15 years of observations for each lake, while others only included repeated measurement requirements spanning many years (13 year minimum, O'Reilly et al. 2015; 15 year 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 et al. 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 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 a) estimate multi-decadal lake surface temperature trends from sparse data across many high elevation lakes with few repeated observations, and b) 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.

1.2 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, USA to southern Wyoming, USA (Figure 1.2). There are over 2,500 natural lakes in the SRM, of which >95% lie above 2,100 m ASL and >90% are smaller than 10 ha in surface area (Nelson 1988). Since nearly all natural lakes in the SRM are above 2,100 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 ultra-oligotrophic. 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).

I collected some lake surface temperature data myeself but most were gathered from state and federal agencies responsible for waters within the SRM. I 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 (Figure 1.2, Table 1.2) to understand variation in surface temperatures due to time of day, day of year, and lake area. I also measured

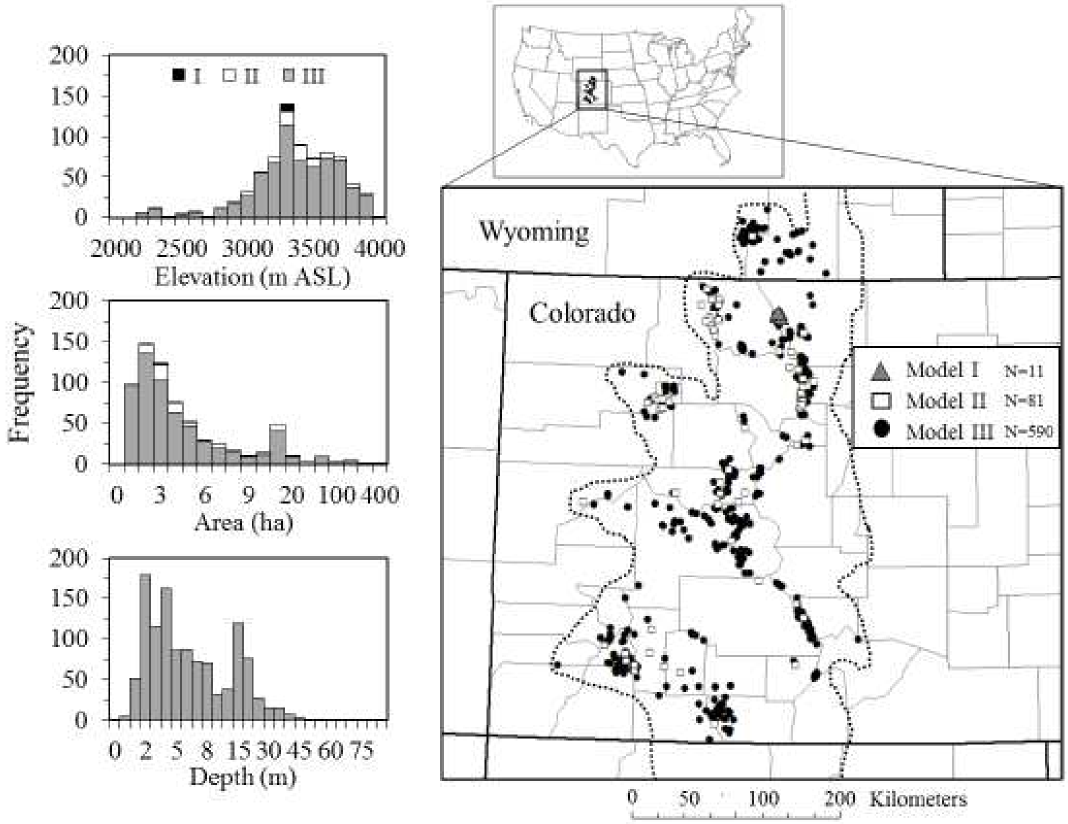

FIGURE 1.2 – Distribution and characteristics of high elevation lakes in the Southern Rocky Mountain, U.S.A. (dotted line) used in the present study. Symbols represent the dataset and corresponding model to which each lake contributed.

dissolved oxygen concentration 1 m from bottom at the deepest location in 8 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 2,100 m, and 3) temperature values were indicative of ice-free conditions (≥ 4°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, I 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 (Figure 1.3). 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 (Figure 1.3). An advantage of the Bayesian approach over traditional ones (e.g., simple linear regression) is that it

TABLE 1.2 – 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	3,275	2.4	4.27
Camp	40.695	-105.928	3,205	4.8	1.10
Lost	40.719	-105.937	3,097	3.7	5.79
Lower Sandbar	40.696	-105.947	3,253	1.5	1.68
McIntyre	40.704	-105.961	3,242	5.9	10.67
Rawah #1	40.696	-105.953	3,250	2.9	2.13
Rawah #2	40.692	-105.951	3,275	2.8	3.96
Rawah #3	40.684	-105.956	3,316	8.5	35.05
Sugarbowl	40.703	-105.968	3,288	3.1	15.24
Upper Camp	40.683	-105.924	3,270	15.4	23.47
Upper Sandbar	40.692	-105.946	3,263	3.3	7.40
Mean	40.696	-105.947	3249	4.9	9.73

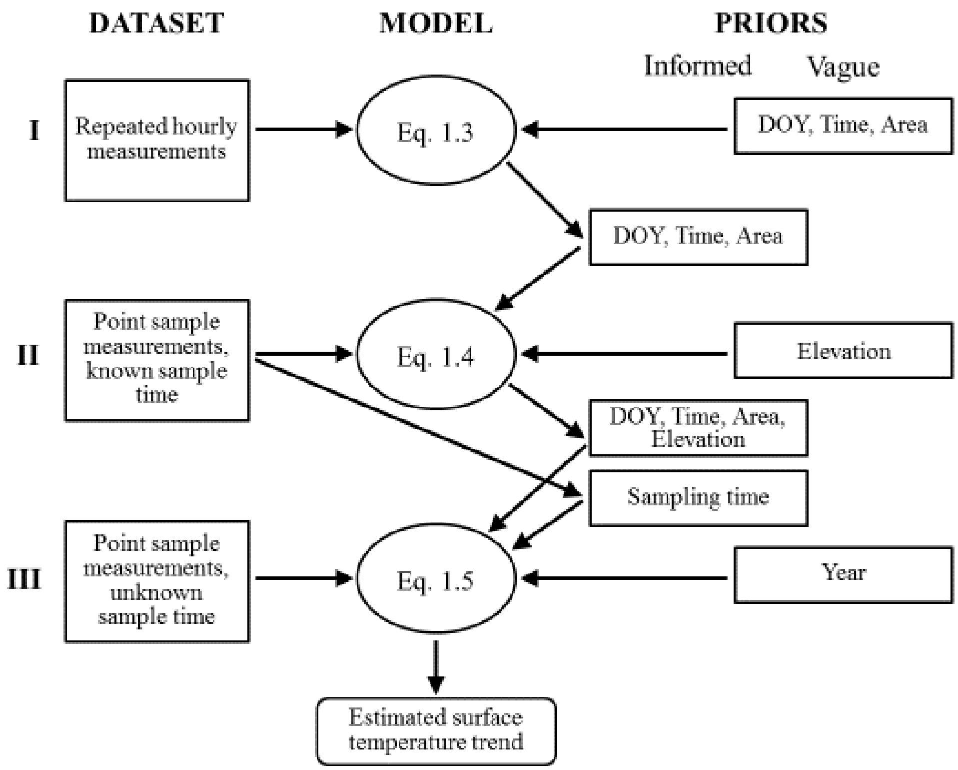

FIGURE 1.3 – Sequential procedure showing each dataset type and priors used for each model. Priors can be informed or vague. Informed priors are derived from previous models or dataset used to inform parameter distributions for future models, while vague priors do not arise from previous data.

treats unobserved quantities as random variables and complex processes can be decomposed into a series of conditional sub-processes. Bayes theorem (eq.1.1) 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.

$$P(\theta|y) \propto P(y|\theta) \times P(\theta) \qquad (1.1)$$

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 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 distribution, whereas ‘Markov Chain’ designates that each random sample 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 sub-problems. 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).

I used a sequential procedure, with three models in hierarchy (Figure 1.3). 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. I 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. Lastly, I calculated Bayesian posterior predictive p-values (PB) of mean and discrepancy: [observation-prediction]^2 to ensure the model accurately gives rise to the data:

$$PB = \mathrm{P}(T\,(\mathbf{y}_{new},\theta\,) \geq T\,(\mathbf{y},\theta\,) \mid \mathbf{y}) \qquad (1.2)$$

where, simulations generating a new dataset, $T\,(\mathbf{y}_{new},\theta\,)$, from the predicted posterior distribution are used to determine the probability that this new dataset is different from the observed, $T\,(\mathbf{y},\theta\,)$ **| 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:

$$y_{it} = \beta_{0_{it}} + \beta_{1_{it}} sin\left(\frac{Time_i}{24} \text{ x } 2\pi\right) + \beta_{2_{it}} cos\left(\frac{Time_i}{24} \text{ x } 2\pi\right) + \beta_{3_{it}} sin\left(\frac{Day_i}{365} \text{ x } 2\pi\right) + \beta_{4_{it}} cos\left(\frac{Day_i}{365} \text{ x } 2\pi\right) + \beta_{5_{it}}(Area_i) \qquad (1.3)$$

where, y_{it} indexes lake surface temperature observation at lake *i* at time *t*, $\mathrm{Time_i}$ is the hourly value for time of observation at lake *i*, while $\mathrm{Day_i}$ is the ordinal day of observation at lake *i*. Area is lake surface area (ha). I 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:

$$y_{it} = \beta_{0_{it}} + \beta_{1_{it}} sin\left(\frac{Time_i}{24} \text{ x } 2\pi\right) + \beta_{2_{it}} cos\left(\frac{Time_i}{24} \text{ x } 2\pi\right) + \beta_{3_{it}} sin\left(\frac{Day_i}{365} \text{ x } 2\pi\right)$$
$$+\beta_{4_{it}} cos\left(\frac{Day_i}{365} \text{ x } 2\pi\right) + \beta_{5_{it}}(Area_i) + \beta_{6_{it}}(Elev_i) \qquad (1.4)$$

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:

$$y_{it} = \beta_{0_{it}} + \beta_{1_{it}} sin\left(\frac{ST_i}{24} \text{ x } 2\pi\right) + \beta_{2_{it}} cos\left(\frac{ST_i}{24} \text{ x } 2\pi\right) + \beta_{3_{it}} sin\left(\frac{Day_i}{365} \text{ x } 2\pi\right)$$
$$+\beta_{4_{it}} cos\left(\frac{Day_i}{365} \text{ x } 2\pi\right) + \beta_{5_{it}}(Area_i) + \beta_{6_{it}}(Elev_i) + \beta_{7_{it}}(Year_i) \qquad (1.5)$$

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, I designate it differently than previous models. ST is estimated from the distribution of known sampling times in model II, allowing me 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

1955-2016 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 I used a normal likelihood.

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

$$DD = \sum_{1}^{365} max\left(\frac{T_{max}-T_{min}}{2} - T_{base}, 0\right) \qquad (1.6)$$

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 I used T_{base} = 4°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. I computed DD each day for the average conditions of dataset III and summed them across the ice-free period.

1.3 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 inter-lake variability (Figure 1.4), 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 <2ºC to >10ºC, while peak summer temperatures ranged from 14-22ºC. 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 (Figure 1.2) during 1985-2015. This dataset contributed a more diverse set of lake elevations (2,295 - 3,820 m ASL) than the dataset for model I, to define distributions for these parameters required for model III. In this dataset, elevation accounted for >10ºC range in peak surface temperature over this area. More than half of the data from model II occurred in one year (1985). Therefore, this dataset did not represent enough interannual variability to include a term for year in model II.

The dataset for model III consisted of 1,493 observations collected from 590 lakes during 1955-2016 (Figure 1.5). This represents the largest dataset ever used to estimate warming rate of high elevation lakes. The lakes were well-distributed across the SRM (Figure 1.2). 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 ~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 years of continuous repeated measurements (Figure 1.5). 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.

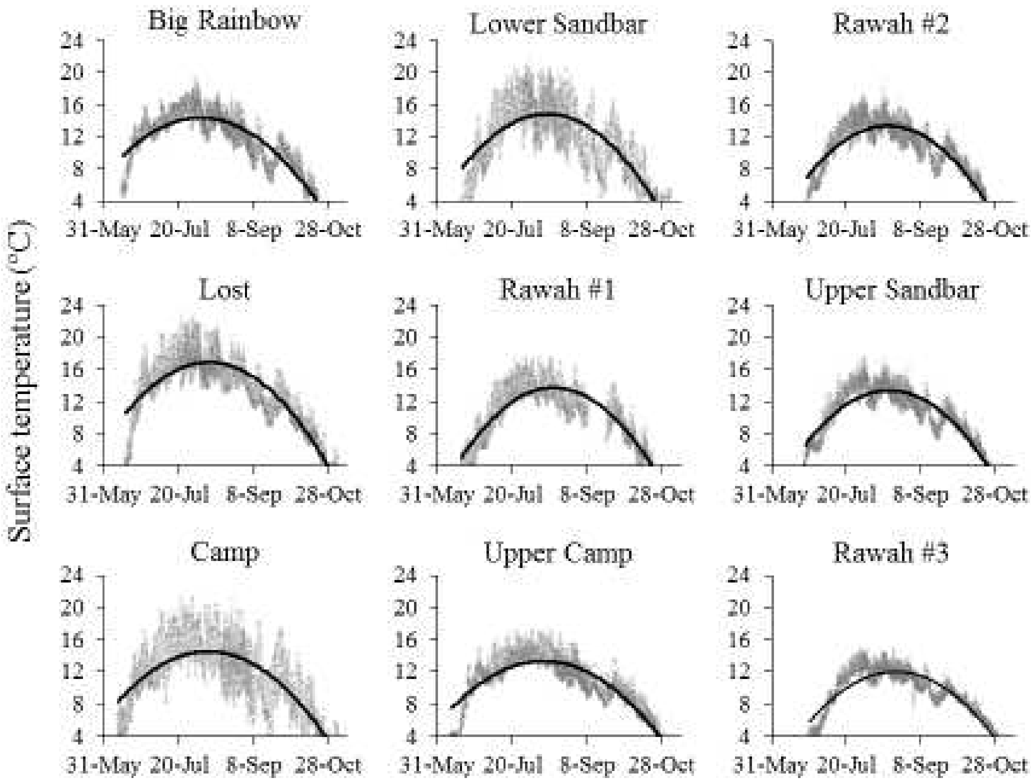

FIGURE 1.4 – Hourly surface temperature measurements of nine neighboring lakes in the Rawah Wilderness Area, Colorado, during the ice-free period of 2015, 2016. McIntyre and Sugarbowl were omitted because 2015 data were not collected. Lakes are ordered by increasing depth, left–right, top–bottom. A second order polynomial was fit to each lake to help the reader visualize peak temperatures and timing of open-water conditions across lakes.

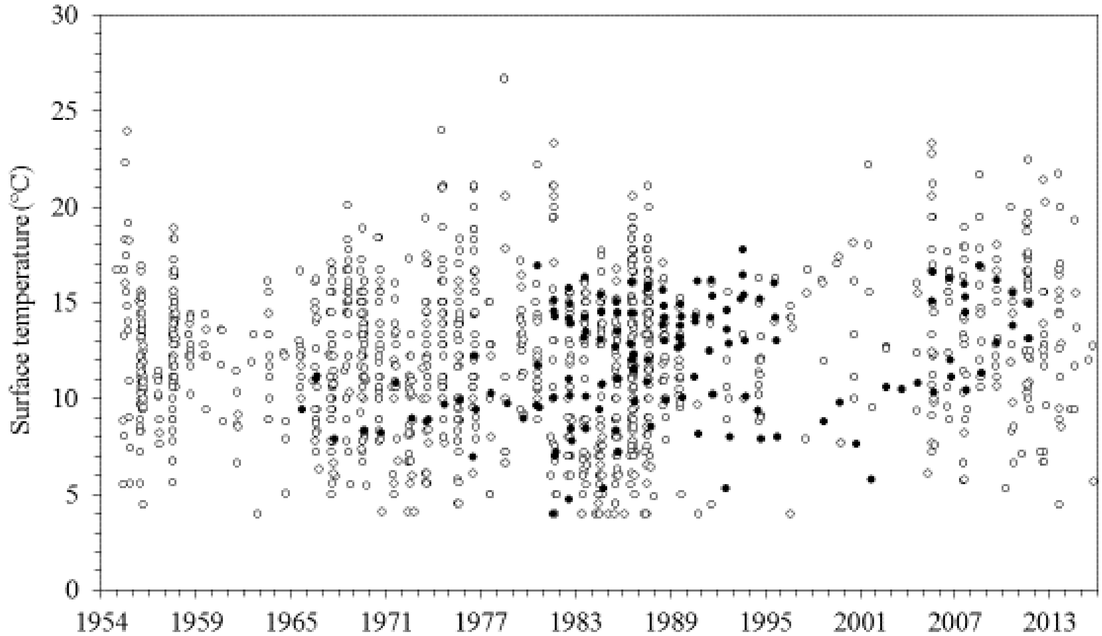

FIGURE 1.5 – Lake surface temperature data for 590 lakes in the SRM during 1956–2016. Open symbols (n = 1354) represent unrepeated temperature measurements, while closed symbols (n = 139) show the subset of lakes where measurements were repeated sufficiently to use conventional trend estimation.

All three models converged and showed no indication of a lack of fit. For model I, I acquired 25,000 MCMC samples 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, I 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 1.3).

My model 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. I estimated that during 1955-2016, surface temperatures increased by 0.81℃, and average regional DD have increased by 14% from 904 DD (CI: 818-991) in 1955 to 1,026 DD (CI: 934-1117) in 2016.

1.4 DISCUSSION

I 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 I used to determine this rate alleviates some conventional data requirements for temperature trend estimation because uncertainties from diel, seasonal and inter-lake variation are explicitly incorporated. This

TABLE 1.3 – Parameter estimates from each model. SD is standard deviation of the estimate. Diagnostic statistics indicated no lack of fit for any models parameters.

		Model I		Model II		Model III	
Parameter	Symbol	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
Std. dev. model	σ	2.06	0.008	5.519	0.400	3.188	0.062

approach allowed me 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 I report continues, these lakes will be on average 1.11ºC warmer by 2100. This increase in surface temperature will result in an estimated 15% increase in DD in the epilimnion from 2016 to 2100. I 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 nonnative species found at lower elevations such as the Smallmouth Bass *Micropterus dolomeiu* (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 I 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 nonnative 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.

My 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). My 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 I documented in Table 1. Investigators have variously used monthly, seasonal, and annual averages to calculate warming rates. However, these different timeframes 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 my study were collected from June through September, it was not necessary to aggregate data over a pre-defined seasonal period to estimate interannual warming because my models included terms for seasonality. This is a significant advantage of my 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, though, 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 years, 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. 2015b; 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. I believe that the six decade time period used in my study partially accounts for my 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). I recognize that, in a broader geographic perspective, my definition of ‘high elevation’ lakes is subjective. The average minimum elevation in the SRM is ~1,780 m ASL, so my high elevation lakes are 320 – 2,169 m above the surrounding lowland landscape. However, generally speaking, temperate 'high 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-Rondan 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 my region against surface warming, similarly to other high elevation regions (Zhang et al. 2014; Sadro et al. 2018). But snowpack in my 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 I 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 I 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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CHAPTER 2 – COMPOUND EFFECTS OF WATER CLARITY, INFLOW, WIND AND CLIMATE WARMING ON MOUNTAIN LAKE THERMAL REGIMES[2]

2.1 INTRODUCTION

Lakes are sensitive to climate (Adrian et al. 2009). One consequence of a warming climate are increased lake temperatures (O'Reilly et al. 2015; Christianson et al. 2019), which can affect the resistance of the water column to mixing (lake stability) (Idso 1973). Indeed, climate change has already been shown to cause changes in stability (Shatwell et al. 2016; Woolway et al. 2017b) and mixing regime (Kirillin 2010; Michelutti et al. 2016; Ficker et al. 2017). These shifts can be ecologically significant because thermal stratification is one of the most prominent physical features of lakes (Dodds and Whiles 2010), and it drives a variety of processes including oxygen dynamics (Blottiere et al. 2017), and physiological rates of aquatic organisms (Brett 1971). Further, prolonged stratification can constrict coldwater habitat by increasing hypoxia in the hypolimnion (bottom layer) while warming and deepening the epilimnion (surface layer) (Stefan et al. 2001; Engelhardt and Kirillin 2014; Massaghi et al. 2017) resulting in a "temperature-oxygen squeeze" for coldwater organisms (Jacobson et al. 2008; Jiang et al. 2012). Even modest changes to stratification can cause major shifts in the phytoplankton and zooplankton populations (Arvola et al. 2010) that are a basis of production in any lake food webs. Consequently, climate-induced changes to lake stratification can disrupt community composition and ecosystem properties (Woodward et al. 2010).

Although many studies have examined how climate change can alter lake stratification and thermal regimes (e.g., Butcher et al. 2015; Kraemer et al. 2015; Edlund et al. 2017), most

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

A few studies have incorporated some of these interdependencies by addressing how clarity (Rose et al. 2016), wind (Woolway et al. 2017b), inflow (Rimmer et al. 2011), or lake size (Butcher et al. 2015; Winslow et al. 2015) can mediate effects of climate warming on lake stability. However, their relative importance and interactive effects are difficult to determine without considering them simultaneously. Further, climate change can also drive changes in water clarity, inflow, and wind, compounding effects of warming on lake stability (Adrian et al.

2009). For instance, climate change can be linked to global phenomena such as increasing forest fire frequency and intensity (Aponte et al. 2016). Forest fires can increase runoff, and sediment and nutrient delivery to lakes, which can directly and indirectly reduce water clarity (Bixby et al. 2015). Climate change is also altering precipitation patterns and affecting snowpack amount and melt timing in snowmelt-dominated regions, changing the volume and timing of spring runoff, and therefore, lake inflows (Barnett et al. 2005) and temperature (Sadro et al. 2019). Climate-induced depletion of perennial snowpack and glaciers, a worldwide concern (Hall and Fagre 2003; Radic et al. 2013), may exacerbate the effects of reduced annual runoff (Bliss et al. 2014; Huss and Hock 2018). Finally, atmospheric stilling has already occurred in many parts of the globe (Vautard et al. 2010), reducing surface wind energy inputs to lakes and prolonging stratification (Woolway et al. 2017b). Thus, climate change has multi-faceted effects on lake stability that should be considered together to better anticipate how lakes and their biota will respond to climatic and related environmental change.

Mountain lakes are particularly sensitive to climate change (Williamson et al. 2009; IPCC 2013) and climate-related environmental stressors like drought, forest fire, and perennial snow and ice retreat. But because they are usually remote, this class of lakes has been understudied. About 10% of the world’s lakes lie above 2,100 m in elevation (Verpoorter et al. 2014) and are widely distributed across the globe (Catalan and Donato-Rondón 2016), but relatively few studies have examined effects of climate change on mountain lakes compared to their low elevation counterparts (Christianson et al. 2019). The remoteness of mountain lakes has also isolated them from many other anthropogenic environmental stressors such as land use change, development and invasive species. Thus, these lakes can be important refuge habitats for native aquatic species (Roberts et al. 2017). More information about how the thermal regime and stratification of mountain lakes may change in the future is needed to protect these relatively pristine ecosystems and the rare fauna that inhabit them.

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

2.2 METHODS

2.2.1 Study Setting

Field observations were collected in the Rawah Wilderness Area (RWA) located in northern Colorado, USA (Figure 2.1). The RWA covers 31,565 ha within the Roosevelt National Forest in the Medicine Bow Mountain Range and contains 25 named natural lakes ranging in size from 1 ha to 15 ha and with depths of 1 m to 45 m. Elevations in the RWA ranges from 2,560 m to 3,960 m above sea level. The RWA resides in the Southern Rocky Mountains (SRM) that host about 2,500 mountain lakes. Collectively, the western U.S. contains ~16,000 mountain lakes (Bahls 1992). The mountain lakes of the region share a number of characteristics that suggest that they may respond similarly to climate change. Most of these lakes are small (< 30 ha in surface area; Bahls 1992). Though latitude- and elevation-dependent, the growing season is short; in the SRM, lakes are typically ice-covered from October to June.

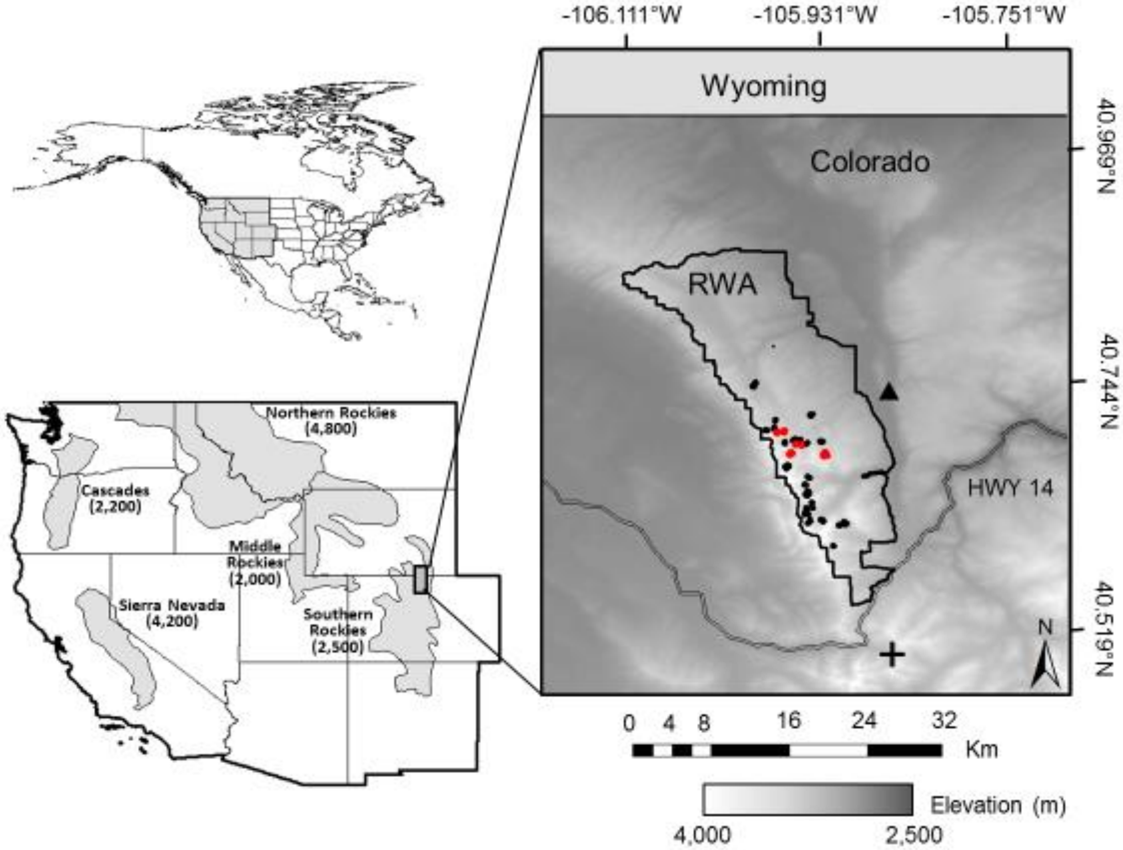

FIGURE 2.1 – Mountainous regions of the western U.S. with the approximate number of mountain lakes present in each, and location of the lakes (red) in the Rawah Wilderness Area where field sampling occurred. The location of the weather station used to gather climatological data (triangle) and site of the Michigan River stream gauge (cross) used for this study is also shown.

Historically, the hydrology of the region and inflows to lakes have been driven by winter snow accumulation and summer runoff from snowmelt (Poff and Ward 1990; Sadro et al. 2018). Mountain lakes of the western U.S. are highly oligotrophic (Bahls 1992) but atmospheric deposition of anthropogenic nitrogen is increasing (Baron et al. 2012). Wildfire is another pervasive climate-related disturbance to mountain lakes throughout the western U.S.

2.2.2 Field Observations

I gathered detailed measurements from six lakes in the RWA from June to September 2016 (Table 2.1). I chose lakes for my study that represented a relatively wide range of lake area, depth and clarity. Five of the six RWA lakes remained stratified throughout the summer, but the shallowest lake (Big Rainbow) was polymictic (Figure 2.2). Strong diel temperature fluctuations (< 2°C to > 10°C) occurred in all of the lakes, with cooling of the surface water at night. Temperature of the epilimnion (within 1 m of the surface) and hypolimnion (within 1 m of the bottom) were recorded hourly with Onset HOBO Pendant UA-002-08 data loggers placed in the middle, deepest part of each lake. Dissolved oxygen concentration (mg/L) was measured once on August 17, 2016 at each lake using an Onset HOBO U26 dissolved oxygen sensor 1 m off the bottom at the deepest part of each lake. I measured water clarity at least monthly with a standard 20-cm diameter Secchi disk. Three of the six study lakes had observable surface inflows; an Onset HOBO Pendant UA-002-08 data logger was deployed in each to collect hourly inflow temperature.

Weather data were collected from a variety of sources or computed from established relationships. Because my study occurred in a Wilderness Area, the nearest existing weather stations were about 50 km away. At the beginning of my study I set up an Onset U30 remote weather station immediately adjacent to the RWA and <10 km from the study lakes (Figure 2.1).

TABLE 2.1 – Physiographic and morphometric characteristics of six study lakes in the Rawah Wilderness Area, Colorado. Secchi depth reported is the average value from at least two samples gathered from July 15 – August 31, 2016.

Lake name	Latitude (°N)	Longitude (°E)	Elevation (m ASL)	Area (ha)	Maximum depth (m)	Secchi depth (m)
Big Rainbow	40.693	-105.941	3,275	2.4	4.3	0.8
Upper Sandbar	40.692	-105.946	3,263	3.3	7.4	3.2
McIntyre	40.704	-105.961	3,242	5.9	10.7	4.4
Sugarbowl	40.703	-105.968	3,288	3.1	15.2	3.6
Upper Camp	40.683	-105.924	3,270	15.4	23.5	3.1
Rawah #3	40.684	-105.956	3,316	8.5	35.1	2.7
Mean	40.696	-105.947	3249	4.9	9.7	3.0

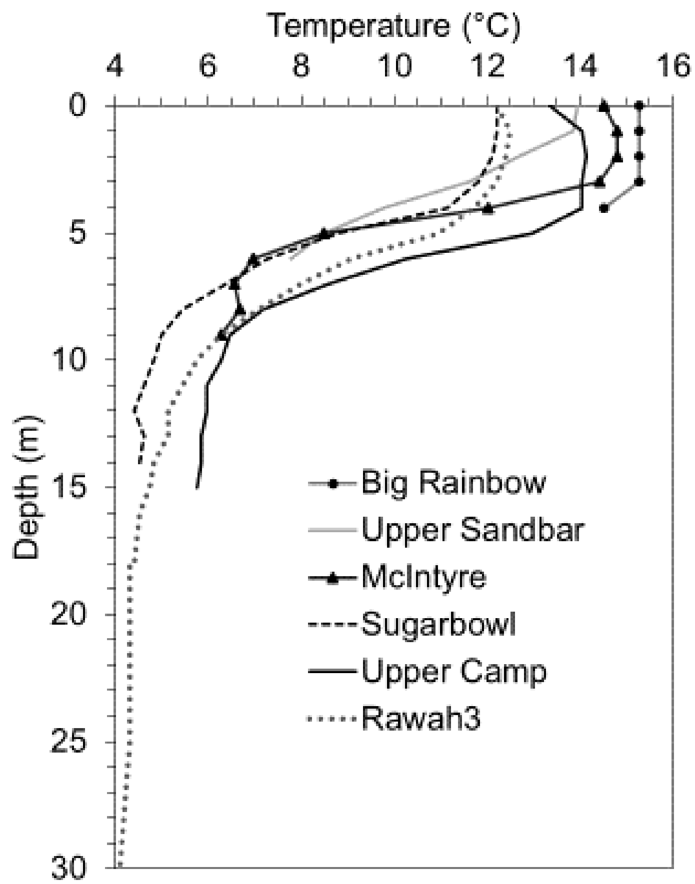

FIGURE 2.2 – Temperature profiles for six lakes in the Rawah Wilderness Area measured at 07:00 h on the day of maximum stratification (July 30, 2016).

The weather station collected five weather metrics every hour: air temperature (°C), wind speed (m/s), relative humidity (%), precipitation (rain; mm), and solar radiation (W/m^2). To use accurate near-lake air temperatures for modeling I estimated the air temperature lapse rate to account for the 600 m elevation difference from the weather station and lakes. To do this, I deployed air temperature loggers near the study lakes at two sites. After accounting for the temperature lapse rate, there was good agreement with the weather station and near lake air temperatures. Cloud fraction was calculated using the standardized ASCE Penman-Monteith method which uses the ratio of sampled solar radiation to calculate clear-sky radiation to estimate cloud fraction daily (ASCE-EWRI Task Committee Report 2005).

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

2.2.3 Simulation Modeling

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

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

The model was calibrated to match the thermal and mixing regimes observed in each RWA lake during 2016. Although GLM allows for inflow, lake inflows can be difficult to quantify, so calibration of GLM is often accomplished by omitting inflow or treating inflow as a free parameter (Read et al. 2014; Bueche and Vetter 2015; Magee and Wu 2016; Fenocchi et al. 2017; Bruce et al. 2018). In my case, as in many mountain areas, established stream gauges were sparse, and installing stream gauges in a wilderness area was prohibited. Instead, I allowed inflow to vary during model calibration to maximize the fit between observed and predicted thermal conditions. Because warming of these lakes typically begins when spring snowmelt declines (Sadro et al. 2018), I modeled thermal regimes during the post-runoff, open water period. I validated predicted low flow conditions by comparing them to 1) summer stream flows measured from a nearby site at a similar elevation (Michigan River near Cameron Pass, CO; 3,168 m ASL), 2) stream flows at similar elevations across the SRM (NHD dataset described below), and 3) in-situ inflow estimates from four lakes in the RWA with surface inflow measured using the float method (Hauer and Lamberti 1996) on August 17, 2016. Outflows were set to equal inflows because water level in the lakes did not change during my study.

Simulations began on July 15, when snowmelt runoff normally subsides. The duration of the simulations was six weeks, ending on August 31. Many mountain lakes in the region enter fall mixis shortly after this date. Goodness of fit of the model's predicted temperatures for each lake was assessed using root mean square error (RMSE):

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^{N}(Pred_i - Obs_i)^2}{N}} \qquad (2.1)$$

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

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

$$\mathrm{RTRM} = \frac{[(1-6.63*10^{-6}(BT-4)^2)-(1-6.63*10^{-6}(ST-4)^2)]*10^6}{8} \qquad (2.2)$$

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

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

The final set of simulations addressed how air temperature rise interacts with the broader range of mountain lake characteristics found across the western U.S. Summer inflow data were obtained from the National Hydrography Dataset (NHD) gathered from the Western U.S. Stream Flow Metrics website (RMRS 2019). I used stream flow data for stream segments located at elevations above 2,100 m for the four major river basins of the SRM (Upper Colorado, Rio Grande, Arkansas, and Lower Missouri) to represent the regional range of inflow. Lake clarity, area and depth data were obtained for almost 2,000 mountain lakes in the western U.S. from the EPA National Lakes Assessment datasets for years 1985, 2007, and 2012 (USEPA 2019), and supplemented with data from a database of 1,300 natural lakes in Colorado (Colorado Parks and Wildlife, unpublished). The 10^{th}, 50^{th}, and 90^{th} percentiles for each characteristic were used to represent low/small, medium and high/large levels of inflow, water clarity, and lake size (Table 3). Lake size categories were defined by the percentiles for both area and depth, except that I used 3.9 m as the shallowest depth because GLM was difficult to calibrate at shallower depths.

Thus, small lakes were characterized as 3.9 m in depth and 0.81 ha in area, medium lakes were defined as 5.8 m in depth and 2.99 ha in area, and large lakes were defined as 20 m in depth and 11.98 ha in area. Each combination of characteristics and levels was simulated at nominal air temperatures, and at +2°C and +5°C warming scenarios.

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

2.3 RESULTS

2.3.1 Field Observations

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

2.3.2 Simulation Modeling

There was good correspondence between observed temperatures and temperatures predicted by GLM for all six lakes. The average RMSE across lakes was ≤ 1.26°C (Table 2.2). Generally, RMSE was lower for bottom temperatures than surface temperatures, but only by ~0.3°C on average. Results for the clearest lake (McIntyre) showed the largest surface RMSE (1.86°C) and bottom RMSE (1.48°C), while results for the largest and deepest lake (Rawah #3) had the smallest surface temperature RMSE (0.90°C), and second smallest for bottom temperature RMSE (0.51°C). The RMSE of surface-bottom temperature difference was also low, and similar to RMSE of surface temperatures across lakes. Inflows estimated during calibration ranged 0.04-0.30 $m^3 s^{-1}$ (Table 2.2), which falls within the range of the 10th and 90th percentile of stream flows in the NHD within the elevation range of the SRM (Table 2.3). Also, a nearby stream gauge in the Michigan River had a similar average flow (0.05 $m^3 s^{-1}$) over the time period of this study. Further, the difference between the average calibrated inflows of the study lakes and the average measured inflows of four RWA lakes was only 0.03 $m^3 s^{-1}$.

Air temperature rise alone caused a substantial increase in water column stability (Figure 2.3). On average, across all six RWA lakes, a 2°C increase in air temperature resulted in a 34% increase in stability, while a 5°C increase in air temperature increased stability by 81%. Stability increases were greater in the largest lakes. The relative increase in stability in the +2°C scenario in the deepest lake (Rawah #3) was similar to the relative increase in stability in the two smallest lakes in the +5°C scenario.

TABLE 2.2. Results of GLM calibration for the six Rawah Lakes, including inflow, and Root Mean Square Error (RMSE) for fitted surface temperature, bottom temperature, and the difference between surface and bottom temperature.

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

TABLE 2.3. Some characteristics of mountain lakes in the western U.S. Described inflows are from stream segments within the four major river basins of the Southern Rocky Mountains. The CPW source denotes unpublished data used by permission from Colorado Parks and Wildlife.

Characteristic	Number of waters	10^{th} percentile	Median	90^{th} percentile	Source
Surface area (ha)	1,909	0.81	2.99	11.98	USEPA 2019; CPW
Maximum depth (m)	1,712	1.5	5.8	20.0	USEPA 2019; CPW
Secchi depth (m)	472	1.96	5.00	10.74	USEPA 2019
Inflow (m^3s^{-1})	56,829	0.001	0.015	0.593	RMRS 2019

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

The sensitivity analysis confirmed that water temperatures and stability of the RWA lakes were most responsive to air temperature change (Figure 2.4). The effect of air temperature was positive and higher air temperatures increased stability and water temperatures more than the same proportional reduction in air temperatures reduced stability and water temperatures. Stability and surface temperatures were negatively related to inflow, and the changes were larger for reduced inflow than for increased inflow. Bottom temperatures were positively related to inflow. Thus, warmer and drier conditions will have compound effects on water column stability and water temperatures in the RWA lakes. Changes in lake clarity and wind speed produced smaller effects. The effect of changes to water clarity were variable and lake-specific, but changes were generally <10% of the nominal value. However, climate-related changes in water clarity could be much greater than the 20% perturbations in my simulations (McEachern et al. 2000; Rose et al. 2016). In general, stability and water temperatures were negatively related to changes in wind speed, and <10% of the nominal value. Because of the low sensitivity of lake thermal structure to wind relative to other factors, I did not include wind in further analyses.

I performed 3,888 simulations representing all combinations of RWA lake areas, depths, clarity and inflow under nominal, +2°C, and +5°C air temperature scenarios.

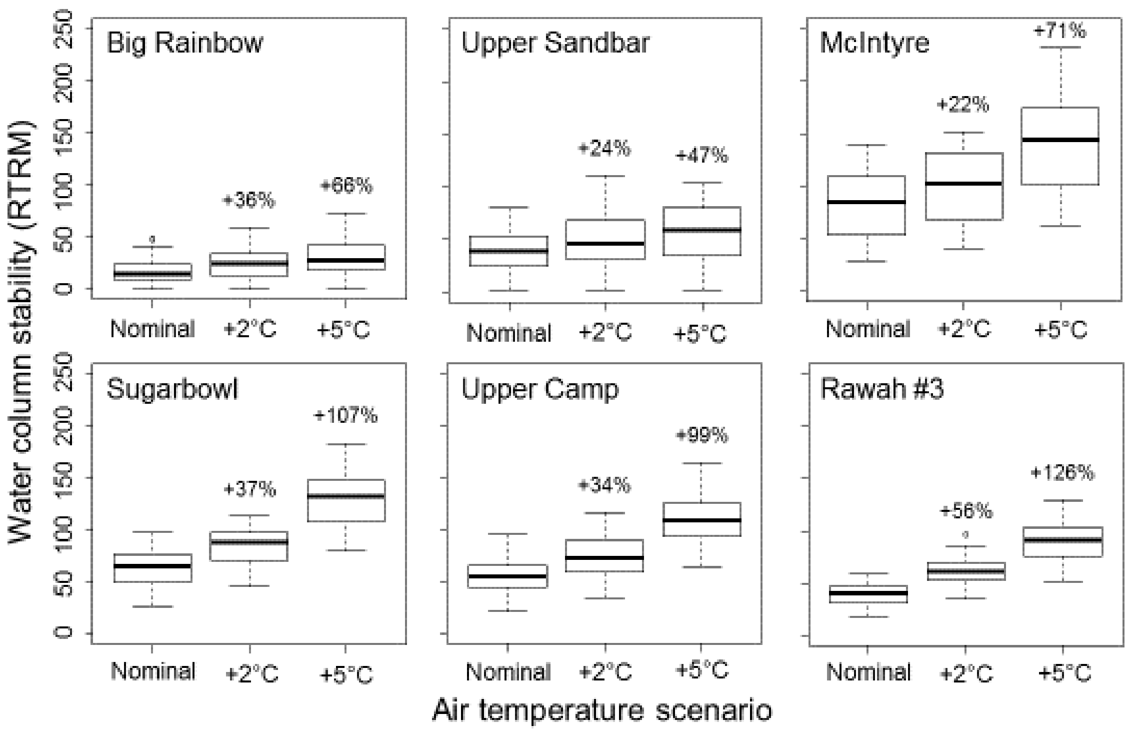

FIGURE 2.3 – Boxplots showing predicted water column stability (aveRTRM) of the six study lakes under nominal, +2°C, and +5°C air temperature scenarios. Percentages show the change in stability relative to nominal conditions.

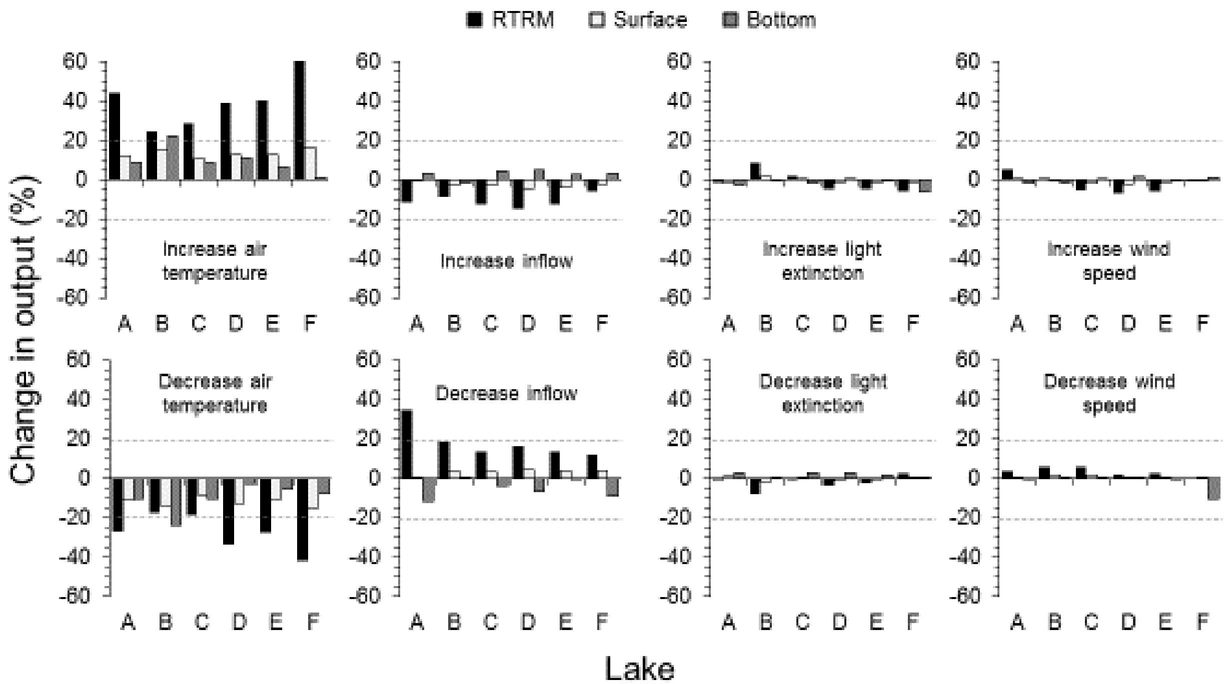

FIGURE 2.4 – Results of a sensitivity analysis assessing the effects of a ±20% change in air temperature, inflow volume, clarity, and wind speed on predicted surface temperature, bottom temperature and stability (aveRTRM) for the six study lakes: Big Rainbow (A), Upper Sandbar (B), McIntyre (C), Sugarbowl (D), Upper Camp (E), and Rawah #3 (F).

In general, lake stability increased with lake area and depth and decreased with Secchi depth and inflow, and the relationships appeared to be asymptotic (Figure 2.5). Under nominal air temperatures, inflow produced the greatest variation in aveRTRM (74%). Variations in aveRTRM due to depth (67%) and area (63%) were similar, and greater than the variation due to water clarity (44%). These patterns were similar in the increased air temperature scenarios. Across the range of lake characteristics average stability increased by 24% and minimum stability increased by 57% on average with a +2°C change in air temperature and increased by an average of 71% and 173% respectively with a +5°C change in air temperature. Depth produced the greatest relative increase in minRTRM (> 1000%), and clarity produced the lowest relative increase (22%). The effect of depth on aveRTRM and minRTRM was greatest for depths < 20 m; increases in depth above about 20 m had almost no effect on lake stability metrics.

Across the range of RWA lake characteristics, the multiple regression analysis showed that air temperature, area, depth, clarity, and inflow were all significant predictors of lake stability (AICc = -4790.46, AIC weight = 1, $R^2 = 0.91$, $p < 0.001$) (Table 2.4). Residual diagnostics also supported the full model, with no non-normality or residual dependence. Of the climate-related factors, air temperature had the largest effect, followed by clarity and then inflow. With other parameters held constant, a 20% change in air temperature resulted in an average 32.42% change in aveRTRM. A 20% change in clarity or inflow resulted in 4.62% and 4.46% changes in aveRTRM, respectively. Although actual changes in these factors would be region- and time- specific, their cumulative effects are important. For example, change in lake stability was predicted to be 28% higher with reductions in clarity and inflow coupled with air temperature increase (41.50%), compared to effects of a 20% increase in air temperature alone. Lake area and depth were also important.

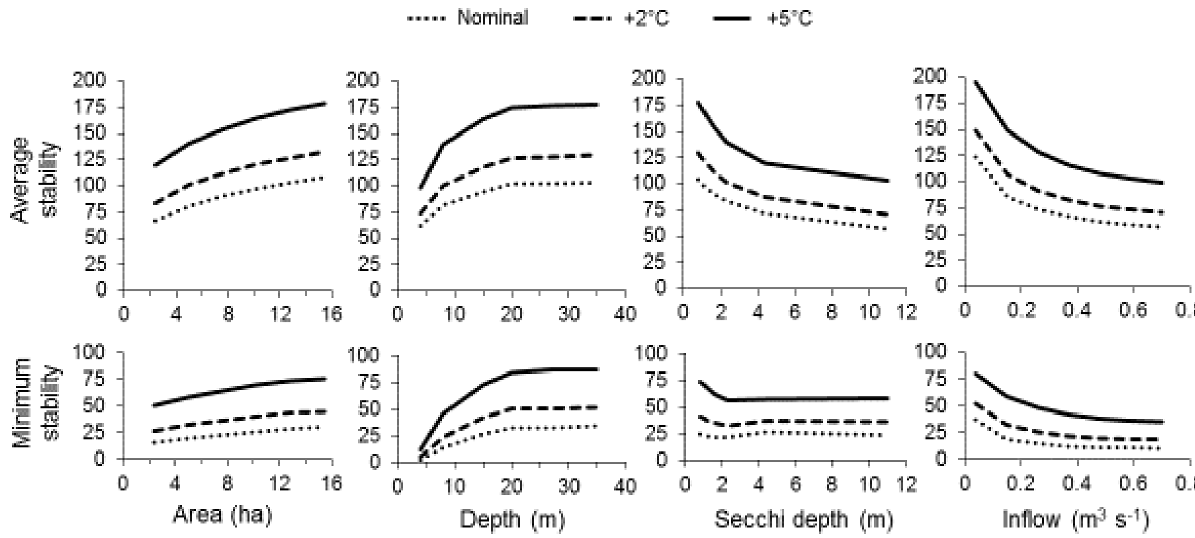

FIGURE 2.5 – Predicted effects of lake area, depth, Secchi depth, and inflow on average (aveRTRM) and minimum (minRTRM) water column stability under three air temperature scenarios. Ranges of the independent variables correspond to the ranges found in the RWA lakes and the western United States.

TABLE 2.4 – Results of multiple regression analysis to investigate relationships among lake stability (aveRTRM), air temperature and lake characteristics. ∆AICc is difference between the Akaike information criterion of the given model and the model with the lowest AICc; AICc weight (w_i) indicates the probability of the particular model being the best in the candidate set.

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

A 20% change in depth or area resulted in a 5.24% and 4.47% change in aveRTRM, on average, indicating that the response of lake stability to climate-related factors will be mediated by lake morphometry.

Expanding my inference to the range of mountain lake characteristics in the western U.S., generally, larger lakes had higher stability under all air temperature scenarios, water clarities and inflows than smaller lakes (Figure 2.6). On average, the stability of large lakes was predicted to increase more under +2°C (23%) and +5°C (62%) air temperatures scenarios than the stability of small lakes that was predicted to increase by 15% at +2°C and 39% at +5°C, on average. Lakes with the lowest inflow were predicted to increase in stability by 20% at +2°C and 59% at +5°C, on average, while the lakes with the highest inflow were predicted to increase in stability by 19% at +2°C and 40% at +5°C. Air temperature rise had a similar relative effect on stability of clear and turbid lakes. The clearest lakes were predicted to increase by 21% at +2°C and 53% at +5°C compared to the most turbid lakes that were predicted to increase by 17% at +2°C and 49% at +5°C, on average. Overall, the largest relative change in stability from air temperature rise occurred in large, clear lakes with high inflows (112% at +5°C), demonstrating the influence that clarity and inflow can have on lake stability.

Changes to lake stability resulting from air temperature rise were compounded by concurrent reductions to water clarity or inflow. In fact, step changes in inflow or clarity from high to moderate or moderate to low had larger effects on stability than the effect of air temperature rise predicted in climate change scenarios (Figure 2.6). For example, if clarity declined from high to moderate at +2°C then aveRTRM was predicted to increase by 53%, and by 92% at +5°C, on average, and a shift from moderate to low clarity at +2°C increased aveRTRM by 66% and 113% at +5°C, on average.

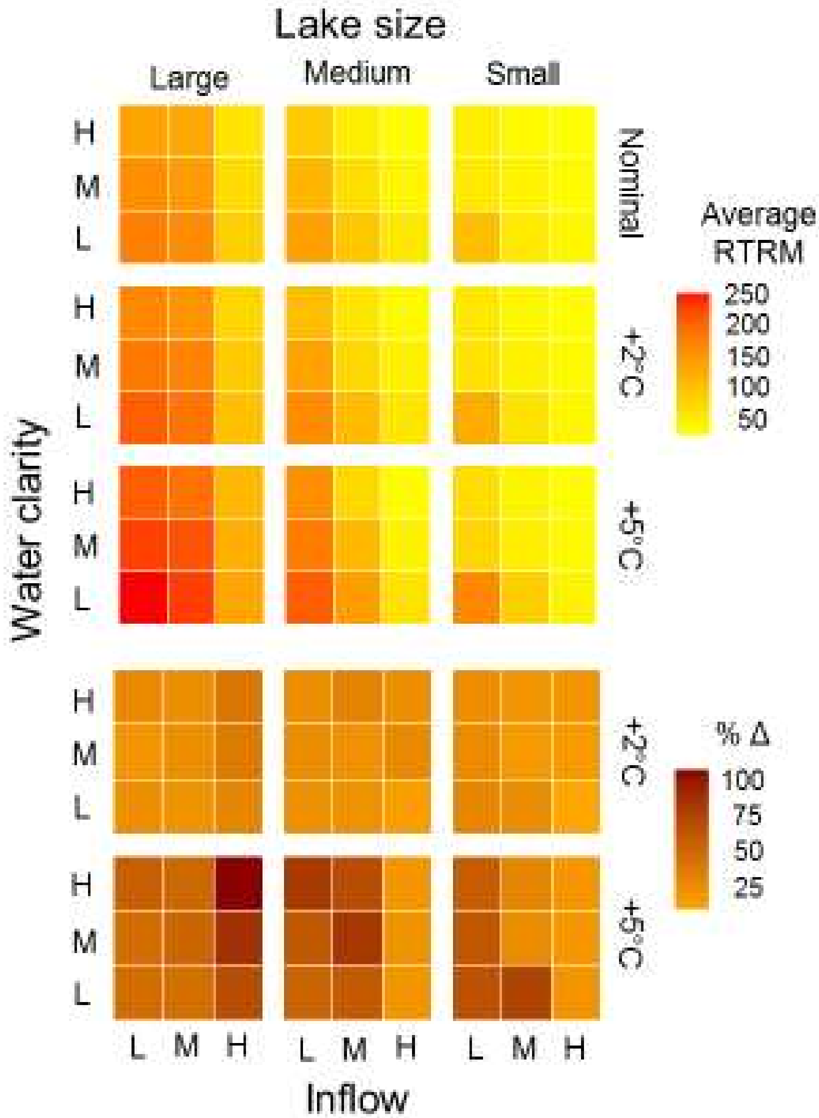

FIGURE 2.6 – Predicted cumulative effects of air temperature, lake size, clarity and inflow on lake stability (aveRTRM). Categories for lake characteristics were defined as the 10th, median, and 90th percentiles for mountain lakes in the western U.S. Top panel compares stability under nominal, +2°C and +5°C air temperature scenarios, and the bottom panel shows the relative change (%) in stability resulting from air temperature rise.

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

Lake size had a similar effect on lake surface and bottom temperatures (Figure 2.7), where generally, larger lakes had higher surface temperatures than small lakes. However, surface temperatures of small lakes increased more with air temperature rise than in large lakes. On average, the surface temperatures of small lakes were predicted to increase by 12% at +2°C and 16% at +5°C, whereas large lake surface temperatures were predicted to increase at only 9% at +2°C and 12% at +5°C. Thus, lake surface temperatures may become more homogenous across lake sizes as air temperatures rise. Under nominal air temperatures, the range of lake surface temperature spanned 7.3°C, while at +2°C it spanned 6.8°C and at +5°C the span in surface temperatures declined to 5.8°C. Bottom temperatures in small lakes were also more responsive to air temperature rise than in large lakes. On average, bottom temperatures of small lakes were predicted to increase by 12% at +2°C and 16% at +5°C, while only 2% at +2°C and 1% at +5°C in large lakes; however, unlike surface temperatures, some scenarios resulted in decreased bottom temperatures. Generally, high turbidity and low inflow resulted in smaller bottom temperatures. Larger lakes also had decreasing bottom temperatures under air warming predominantly more than small lakes.

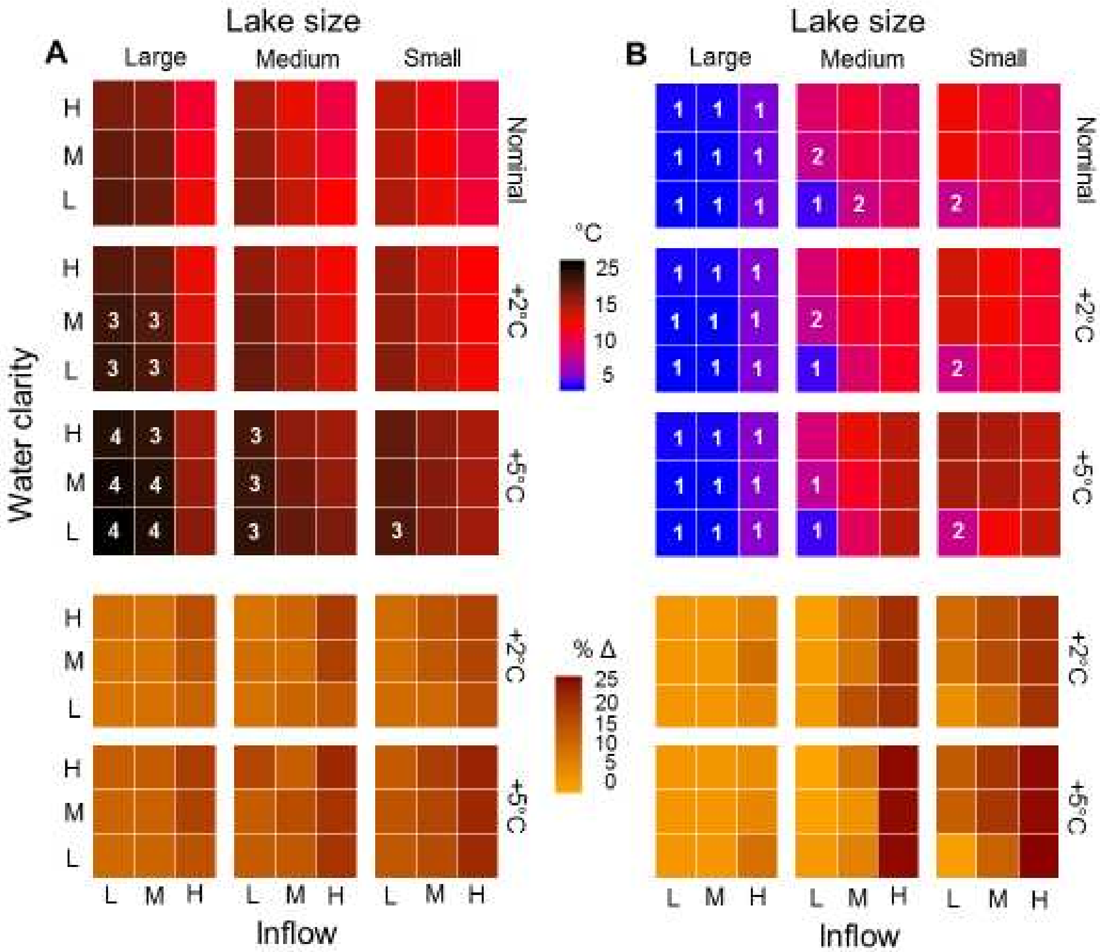

FIGURE 2.7 – Predicted cumulative effects of air temperature, lake size, clarity and inflow on lake surface (A) and bottom (B) temperatures (M30AT). Categories for lake characteristics were defined as the 10th, median, and 90th percentiles for mountain lakes in the western U.S. Top panel compares lake temperatures under nominal, +2°C and +5°C air temperature scenarios, and the bottom panel shows the relative change (%) lake temperatures resulting from air temperature rise. Combinations of lake conditions with predicted temperatures be harmful for Cutthroat Trout (trout) are indicated as follows: (1) too cold for growth and survival of young trout, (2) restricted growth for trout up to age-1, (3) reduced growth for adult trout, and (4) limited to no growth of adult trout.

Large lakes of all clarities at low and moderate inflows had slightly decreasing bottom temperatures with rising air temperatures, whereas only low inflow, low clarity small lakes had decreasing bottom temperatures at +5°C.

As with stability, including effects of changing clarity and inflow produced greater change in surface and bottom temperatures than under air warming alone. If clarity decreased from high to moderate then surface temperatures increased by 15% at +2°C and 32% at +5°C, on average, while a shift from moderate to low clarity resulted in surface temperature increases of 14% at +2°C and 30% at +5°C (Figure 2.7). Decreasing inflow from high to moderate resulted in surface temperature increases of 35% at +2°C and 53% at +5°C, on average, and a decrease in inflow from moderate to low was predicted to increase surface temperatures by 20% at +2°C and 34% at +5°C. The largest increase in surface temperature was predicted when clarity and inflow both changed from high to moderate, resulting in an increase of 43% at +2°C and 61% at +5°C. Bottom temperature changes were more complex and demonstrated the collective influences of lake size, clarity, and inflow. Generally, bottom temperatures in large lakes changed very little (<2% on average), compared to medium and small lakes where changes were larger and could be positive or negative. For example, in medium sized lakes, clarity changes combined with air increases led to decreased bottom temperatures at low inflow (-31% on average) and increased bottom temperatures at high inflow (35% on average). But at moderate inflows, bottom temperatures in medium sized lakes increased when clarity decreased from high to moderate, and bottom temperatures decreased when clarity shifted from moderate to low. The only reduction in bottom temperatures of small lakes occurred at low inflow with a clarity change of moderate to low (-36% on average). The largest overall change occurred in small lakes where reducing clarity and inflow from high to moderate led to a 32% increase in bottom temperatures at +2°C and 56% increase at +5°C.

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

2.4 DISCUSSION

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

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

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

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

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

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

In the RWA lakes, it appeared that such a tipping point is reached at a daily minimum RTRM of ~30. This corresponded to a daily minimum surface-bottom temperature difference of only about 2°C. When stability was below this threshold stratification was brief and intermittent and the lakes continued to mix periodically throughout the summer. Lakes that sustained a ≥ 2°C difference in surface and bottom temperatures during diurnal cooling stayed stratified for longer periods throughout the summer. Others have found that this RTRM value corresponds to the development of a metalimnion and limited mixing of the water column (Kortmann et al. 1982; Barbiero et al. 1997). In my nominal scenario, the minRTRM of 30 was reached at a maximum depth of about 20 m, on average across all lake types and conditions. This means that under current conditions, lakes that were at least 20 m deep remained stratified throughout the summer. However, under certain conditions, such as high turbidity and low inflow, much smaller lakes can reach this stability threshold. On average, across the >3,500 possible combinations of turbidities, water clarities, inflows, and lakes sizes present in the RWA, my simulations showed that the maximum depth associated with a minRTRM of 30 drops from 20 m to about 8 m under a +5°C air warming scenario. Based on the range of maximum depths in my regional dataset, this implies that climate change could cause an additional 26% of mountain lakes to develop prolonged stratification. Also, my simulations show that, generally, minRTRM is changing much more than averageRTRM under climate and environmental change.

Many investigators have used temperature difference between surface and bottom layers to define the likelihood of prolonged stratification. However, RTRM is a more appropriate method for evaluating lake stability because RTRM considers water density differences rather than an absolute temperature difference between surface and bottom (Kortmann et al. 1982). Because water density changes nonlinearly with temperature, stability metrics that explicitly incorporate temperature effects on density will become more useful as lakes become warmer in the future. Rising temperatures can increase lake stability even when temperature differences between surface and bottom layers do not change. For example, when lake surface temperature is

13°C, a 2°C surface-bottom temperature difference results in RTRM < 30, while the same surface-bottom temperature difference results in RTRM > 30 at a surface temperature of 15°C. The particular RTRM threshold for stratification is site-specific. For example, lakes in areas with strong winds, and lakes with high surface area to depth ratio or high inflows may require larger RTRM values to experience persistent stratification. However, because even small changes in temperatures can lead to considerable changes in RTRM, especially at higher temperatures, air temperature rise will likely shift the mixing regimes of some mountain lakes. These changes to stability could be intensified by concomitant decreases in lake clarity and/or inflows.

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

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

This study has some potential limitations. First, I calibrated my model to a relatively small set of mountain lakes in the Southern Rocky Mountains. Although mountain lakes across the western U.S. share some basic characteristics (e.g., morphometry, trophic state, hydrology), and thus my primary conclusions should be applicable outside the SRM, other characteristics may differ (e.g., finescale climate or water chemistry). Validating my model with high resolution data from lakes in other mountain ranges would be informative. I also found that it was difficult to calibrate the model to lakes < 3.9 m deep. It may be that the influence of sediment warming and possible nocturnal heat release may be contributing to the lack of fit of GLM in these shallow lakes (Fang and Stefan 1996). Finally, given the importance of inflow in my simulations, more comprehensive data on surface and subsurface inflows (see Caine 1989) would be useful. Permanent stream gauges are probably rare in the vicinity of mountain lakes, especially those, like the RWA lakes, that are within federally-designated wilderness areas, so it will be useful for future studies to employ portable stream flow loggers or water level loggers that could be used to measure lake inflows.

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

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CHAPTER 3 – COMBINED EFFECTS OF EARLY SNOWMELT AND CLIMATE WARMING ON MOUNTAIN LAKE TEMPERATURES AND FISH ENERGETICS[3]

3.1 INTRODUCTION

Effects of climate-induced variation in the magnitude and timing of snowmelt are well-studied in lotic systems (e.g., Martinec 1975; Brubaker and Rango 1996; Yarnell et al. 2010), particularly in the western United States and other regions where rivers exhibit a snowmelt hydrograph (Poff and Ward 1990). Snowmelt can be an important contributor to stream flow, but it also buffers stream temperatures from atmospheric warming (Lisi et al. 2015). Reduced snowpack and earlier melting allow rivers to warm sooner, affecting phenology, energetic costs, and consumptive requirements of lotic ectotherms like fishes (Railsback and Rose 1999; Lisi et al. 2015). These hydrologic effects on water temperature and physiology are compounded by rising air temperatures that allow rivers to reach higher seasonal maxima (Wenger et al. 2011). Changes to snowmelt can also affect lakes with inflows but much less is known about how lake temperatures and lacustrine biota respond to this component of climate change, or how such hydrologic changes will interact with rising air temperatures.

Many studies have demonstrated that worldwide lakes are becoming warmer and more strongly stratified (Adrian et al. 2009; Kirillin 2010; Schmid et al. 2014; O'Reilly et al. 2015; Michelutti et al. 2016; Christianson et al. 2019; Christianson et al. in review). These changes to lake thermal regimes have important implications for lentic ecosystem structure and function. Warming raises metabolic rates of aquatic organisms and increases their oxygen and food

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requirements (Ficke et al. 2007). However, warming also reduces water column mixing which can prolong stratification (Adrian et al. 2009; Woolway and Merchant 2019), lead to reduced oxygen availability (Jankowski et al. 2003), and segregate predators from their prey (Johnson et al. 2017). Warming can also reduce the ability of lakes to sequester CO_2 (Yvon-Durocher et al. 2010), an important role of lakes in the global carbon cycle (Tranvik et al. 2009). Further, climate warming has decreased the duration of ice cover in temperate lakes (Magnuson et al. 2000; Dibike et al. 2011; Sharma et al. 2019). Together these effects are increasing growing season degree-days and annual energetic demands for fish and other aquatic organisms (Roberts et al. 2017; Honsey et al. 2018). Thus, it is important to understand how various aspects of climate change are driving lake warming and stratification patterns.

Although the effects of climate change on lakes are ubiquitous, the magnitude of change in lake temperature and ice cover duration varies across regions and lake types (Magnuson et al. 2000; Luoto and Nevalainen 2013; O'Reilly et al. 2015; Christianson et al. 2019). For example, lakes at high elevation (>2,100 m ASL) are experiencing greater air temperature rise (Pepin et al. 2015; Preston et al. 2016) and reductions in ice cover duration than in their lower elevation counterparts (Thompson et al. 2005b; Roberts et al. 2017). Given that high elevation lakes are usually colder, have longer ice-covered periods and therefor, shorter growing seasons than lakes at low elevations, climate-induced changes can have disproportionately large effects on high elevation lake thermal regimes. The duration of ice cover in high elevation lakes is closely linked to the processes that govern snowmelt dynamics (Magnuson et al. 2000; Preston et al. 2016; Sadro et al. 2018; Sadro et al. 2018b). Low snowpack can result in earlier snowmelt (Yarnell et al. 2010; Musselman et al. 2017), which has been linked to shorter ice cover duration (Parker et al. 2008; Preston et al. 2016) and higher summer temperatures (Sadro et al. 2018). Generally, across western North America, less precipitation has been falling as snow (Berg and Hall 2017) and annual snowpack has been declining (Fyfe et al. 2017). Partly as a result of reduced snowpack, snowmelt dates are retreating in many high elevation areas (Mote et al. 2005; Barnett et al. 2005; Musselman et al. 2017). Concomitantly, ice-off dates have shifted earlier, and open water duration has increased in high elevations lakes, including those in the Southern Rocky Mountains (SRM), USA (Preston et al. 2016; Roberts et al. 2017). However, relatively few studies have examined effects of altered snowmelt and ice cover dynamics on high elevation lake temperatures and the energetics implications for their biota, including fishes.

Historically, fish did not occur in most high elevation lakes of the western United States (Knapp 1996), but due to habitat degradation, the presence of introduced species at lower elevations, and a desire to create new sport fishing opportunities, managers transplanted both native and nonnative species of trout to more remote, isolated and relatively pristine lakes at higher elevations (Bahls 1992). Consequently, high elevation lakes in the region have become important refuge habitat for native coldwater species of conservation concern, such as Cutthroat Trout *Oncorhynchus clarkii* (Marnell et al. 1987; Roberts et al. 2013). These lakes also continue to be popular with anglers seeking these fish as well as introduced species such as Brook Trout *Salvelinus fontinalis* (Meyer and Schill 2007). While predicted increases in seasonal thermal maxima are not expected to exceed physiological optimum temperatures for these species (Bear et al. 2007; Christianson et al. in review), warmer and longer growing seasons resulting from reduced snowpack may increase the amount of food required to meet metabolic demands (Borgstrom 2001) in these highly oligotrophic, food-limited lakes (Bahls 1992). Thus, climate change has the potential to intensify existing competitive interactions between trout species (Dunham et al. 2002; McGrath and Lewis 2007; Benjamin and Baxter 2012) and amplify the trophic effects of fish on native fauna in high elevation lakes (Knapp 1996; Eby et al. 2006). Management of sport fisheries and conservation of native fauna in high elevation lakes would benefit from forecasts of the effects of changes to snowmelt, growing season length and warming on energetics of cold- and coolwater fish species.

The objectives of this study were to 1) use a thermodynamic model for lakes to predict how earlier snowmelt and warmer air temperatures will affect thermal regimes of high elevation lakes and 2) use a fish bioenergetics model to predict effects on metabolic costs and consumptive demand of Cutthroat Trout and Brook Trout.

3.2 METHODS

3.2.1 Study Area

The focus of this study was lakes in the Rawah Wilderness Area (RWA) of north central Colorado (Figure 3.1). These glacial lakes range in elevation from 3,100 - 3,500 m ASL. As is true of most high elevation lakes across the western United States the RWA lakes are small (<20 ha), and many of them are paternoster lakes connected by a stream (Bahls 1992; Horne and Goldman 1994). The hydrology of the RWA is also similar to other montane areas of the western United States, with inflows dominated by snowmelt dynamics (Poff and Ward 1990). Historically, the ice-free season for high elevation lakes in Colorado lasted from June until October (Roberts et al. 2017). Based on my sampling and modeling (Christianson et al., in review) I estimate that about one third of the 25 named lakes in RWA are currently polymictic, and the remainder are dimictic. Because changes to inflow magnitude and timing, as well as warmer air temperatures, could increase the chances for polymictic lakes to stratify, I chose one polymictic lake (Rawah #2) and one dimictic lake (Rawah #3) for detailed study and comparison (Figure 3.1).

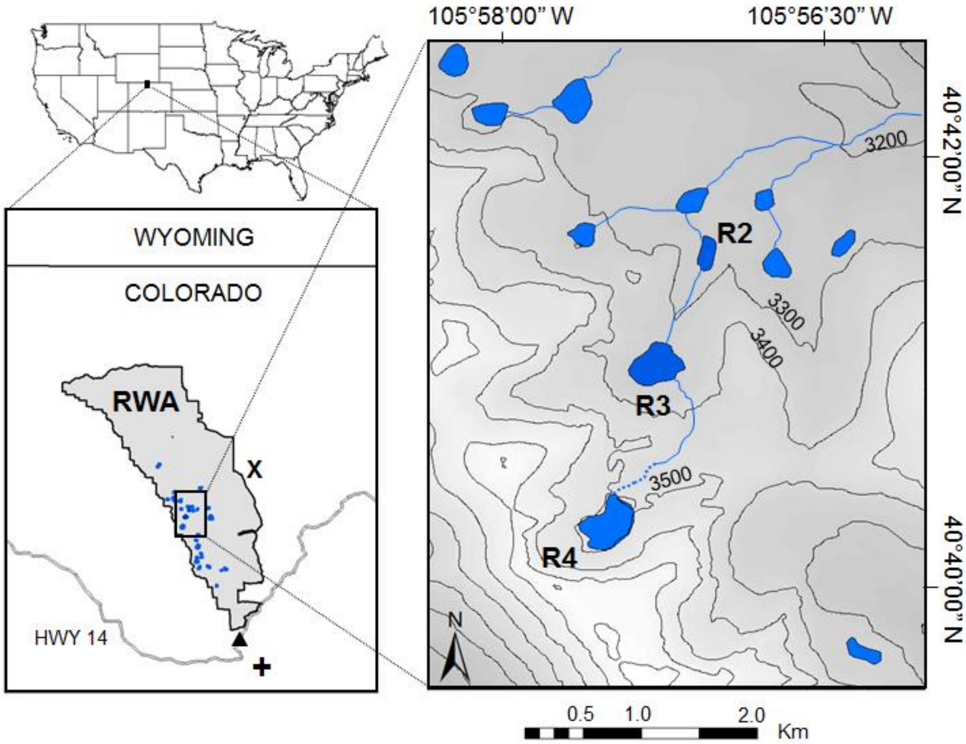

FIGURE 3.1. Rawah Wilderness Area (RWA) of northern Colorado, U.S. with location of the lakes in blue (R2 = Rawah #2, R3 = Rawah #3 and R4 = Rawah #4) and approximate elevation topography (m ASL). The locations of the weather station (X), SNOTEL site (triangle) and the Michigan River stream gauge (cross) are also shown.

The lakes are < 1 km apart so they experience the same weather conditions, but the outflow from Rawah #3 flows into Rawah #2. Rawah #3 is situated at 3,316 m ASL, has a maximum depth of 35 m and a surface area of 8.5 ha. Rawah #3 has an inflow also. Rawah #2 is situated at 3,275 m ASL, has a maximum depth of 4 m and surface area of 2.8 ha. Both lakes contain naturally reproducing Brook Trout and Cutthroat Trout are stocked biennially to sustain those populations; no other fish species are present (Colorado Parks and Wildlife, unpubl.).

3.2.2 Data Collection and Hydroclimate Scenarios

I deployed water temperature and weather data loggers to gather the information required to calibrate a thermodynamic lake model (described below) for the study lakes. Onset HOBO Pendant UA-002-08 data loggers were used to collect hourly surface, bottom, and inflow temperatures of both lakes during May through August 2016. I deployed an Onset U30 remote weather station on the eastern border of the wilderness area, about 10 km from the study lakes, to collect air temperature (°C), wind speed (m/s), relative humidity (%), precipitation (rain; mm), and solar radiation (W/m^2) (Christianson et al., in review). Cloud cover was calculated as a ratio of sampled solar radiation to clear-sky radiation (ASCE-EWRI Task Committee Report 2005), and cloud cover was then used to calculate longwave radiation. A comparison with long-term records from the 1980s showed that weather in 2016 reasonably represented nominal weather conditions for the study area (Christianson et al., in review).

Because of the remoteness of RWA lakes, little is known about ice-off dates, but snowpack melt (hereafter snowmelt) is linked to ice-out in other high elevation lakes (Parker et al. 2008; Sadro et al. 2018). I used the date that snowpack was exhausted (SWE = 0; hereafter, the "snowmelt date") to approximate the initiation of lake surface warming (Figure 3.2).

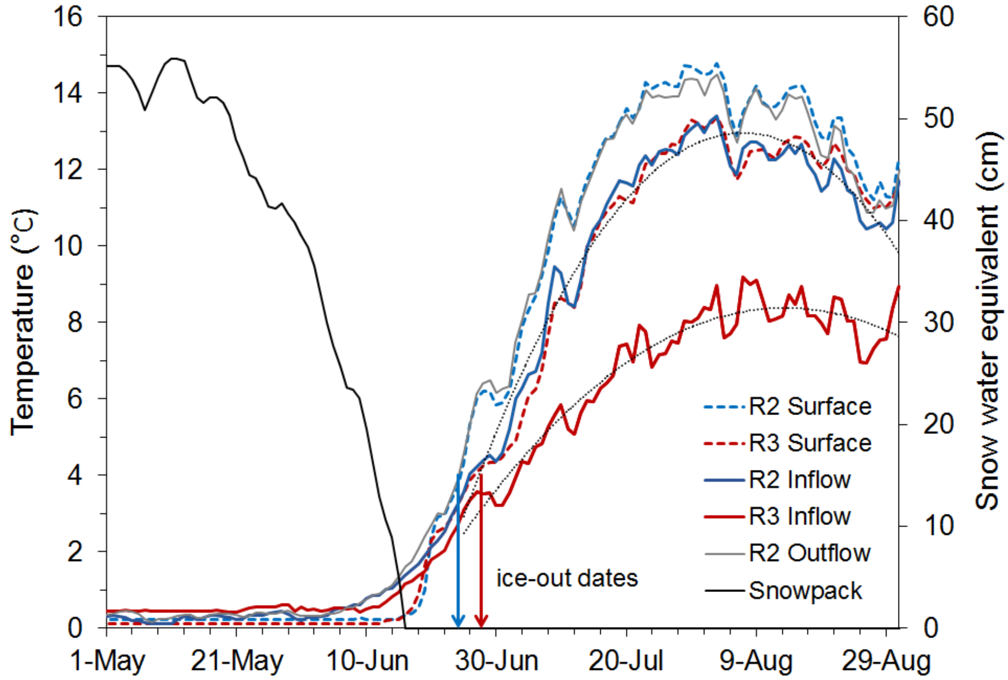

FIGURE 3.2. Daily snowpack depth (snow water equivalent; SWE) and lake surface temperatures and inflow temperature for Rawah #2 and Rawah #3 in 2016, as well as outflow temperature for Rawah #2. Date of ice-out in each lake is indicated. Polynomial functions fit to the inflows are shown as dotted lines.

Ice-off date was assumed to occur when lake surface temperatures reached 4°C (Wetzel 2001; Roberts et al. 2017). Four SNOTEL sites surround the RWA but maximum snow water equivalents (SWE) and melt rates were similar across all stations; I used snowpack/snowmelt data from the "Joe Wright" (551) SNOTEL site that was located at an elevation of 3,571 m and < 0.5 km from the RWA boundary (Figure 3.1; https://www.wcc.nrcs.usda.gov/snow/). SNOTEL data from 1980-2016 also allowed me to characterize the variability in snowpack and snowmelt dates and configure simulation scenarios. SNOTEL records showed that the snowmelt date in 2016 (June 16) was close to the long-term average (June 17, SD = 11 days, n = 37 years), again suggesting that 2016 was a reasonable representation of nominal hydroclimatic conditions for the study area.

The lowest snowpack and earliest snowmelt date on record occurred in 2012 (Figure 3.3); data from that year were used to represent the early-snowmelt scenario. Annual snowpack (maximum SWE) was positively correlated with snowmelt date ($r = 0.80$, $N=36$, $p= <0.01$; Figure 3.3), confirming that variation in snow deposition accounted for much of the annual variation in snowmelt dates. It was also clear that snowmelt date was associated with lake warming (Figure 3.2). In 2016, both lakes began warming shortly after snow depth reached zero, but it took over a week longer to reach ice free conditions. Rawah #2 became ice free nine days after SWE reaching zero, while Rawah #3 took 11 days to become ice-free.

As in other federally-designated wilderness areas, stream gauges do not exist in the RWA, so I used streamflow data from the gauge closest to the RWA (Michigan River; Figure 3.1) and at a similar elevation (3,167 m ASL; RMRS 2019) to characterize the timing of the descending limb of the hydrograph of lake inflows under nominal (2016) and early snowmelt (2012) conditions (Figure 3.4).

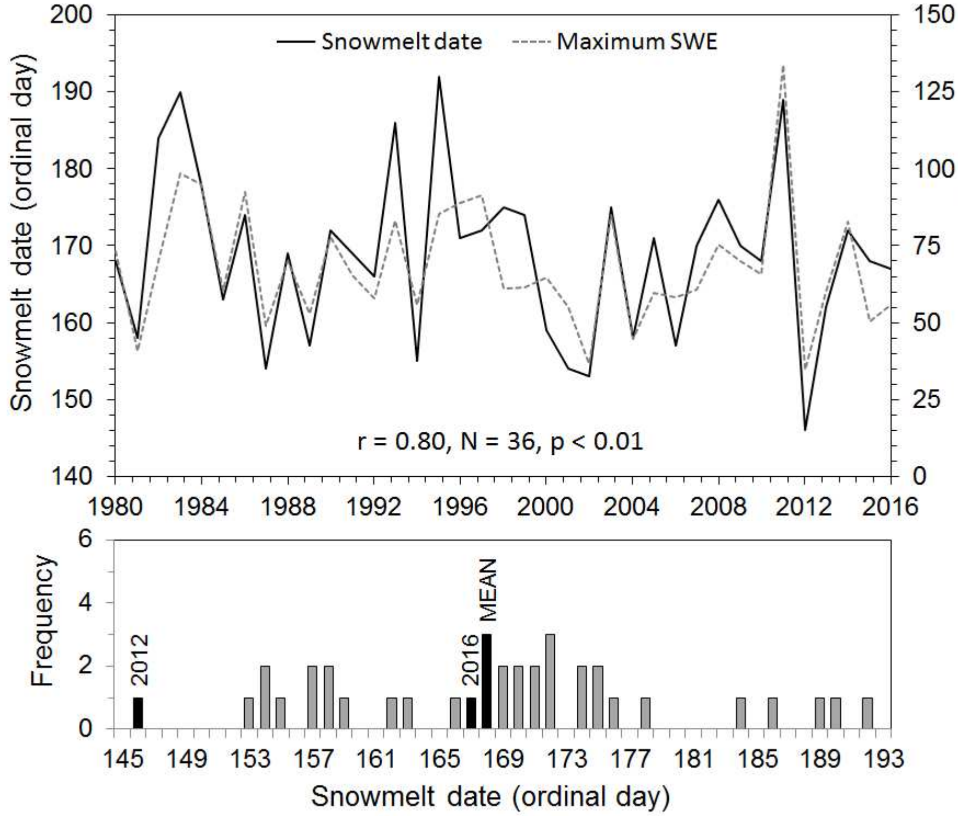

FIGURE 3.3. Day of year when snowpack reached zero (snowmelt date; solid line), and yearly maximum snowpack depth (SWE; dashed line). A frequency histogram of snowmelt dates is also shown.

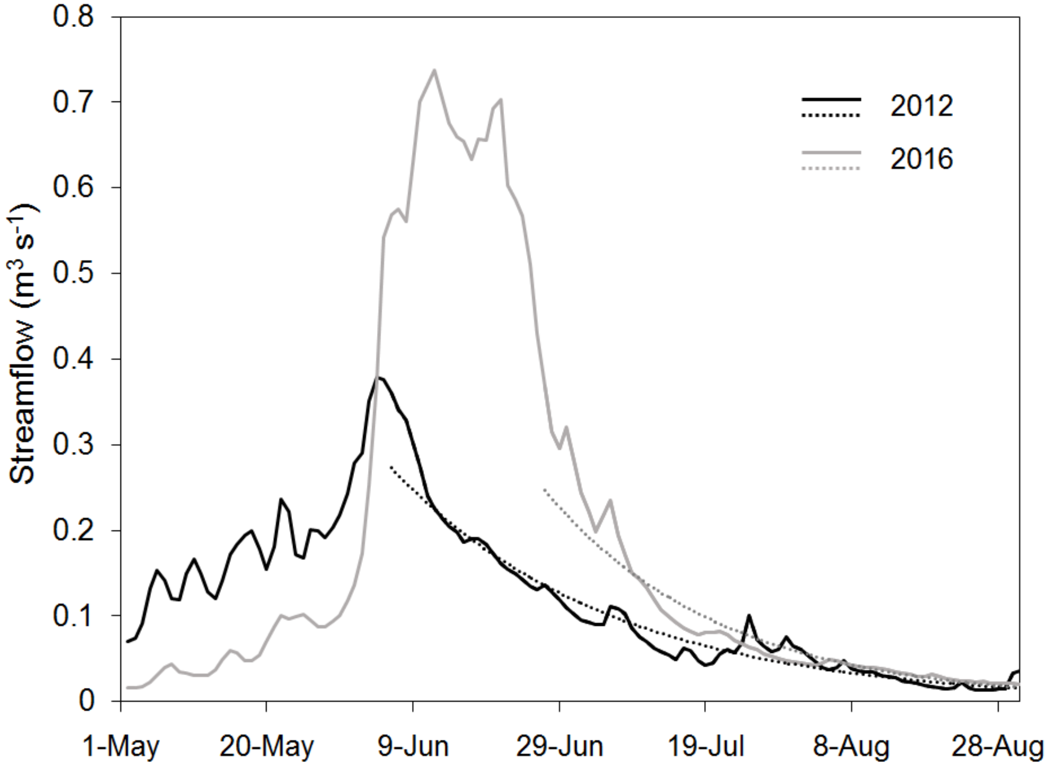

FIGURE 3.4. Streamflow from the Michigan River gauge for 2012 and 2016 (solid lines). Fitted exponential decay functions are shown for the duration of the open-water period each year (dotted lines).

An exponential decay function (Martinec 1975) was fitted to the gauge data for these two years. This decay function was of the form:

$$Q = R_0 e^{-Kt} \quad (3.1)$$

where, Q is daily inflow (m^3 sec^{-1}), R_0 is initial daily runoff, K is the coefficient of exhaustion, and t is day. Total inflow to each lake was estimated during model calibration (Christianson et al. in review), and that discharge entered the lakes according to each year's exponential decay function. I used temperatures of inflows to Rawah # 2 and Rawah #3 recorded in 2016 to represent nominal inflow temperatures. Rawah #2 inflow temperatures were close to Rawah #3 surface temperatures (Figure 3.2), so Rawah #3 surface temperature was used as Rawah #2 inflow temperature. For Rawah #3 inflow temperature during early snowmelt, I fit a second order polynomial to the nominal daily inflows ($R^2 > 0.96$; Figure 3.2) and shifted them to the earlier snowmelt date. Weather conditions in 2016 were used for nominal and early snowmelt scenarios.

I simulated effects of air temperature rise with two scenarios: a) nominal temperatures +2°C and b) nominal temperatures +5°C. These increases represent a) the most probable and b) the extreme predictions of air warming for this region, corresponding to representative concentration pathways (RCP) 4.5 and 8.5 (IPCC 2013). Nominal (2016) air temperatures were increased by these amounts for each warming scenario. I increased the temperature of inflows to Rawah #3 in warming scenarios using an adjustment of 0.44°C per 1°C increase in air temperature (Mohensi et al.1999; Rieman and Isaak 2010). Predicted surface temperatures in Rawah #3 were used for Rawah #2 inflow temperatures.

3.2.3 Thermodynamic Modeling

I used the General Lake Model ver. 3.1.1 (GLM; Hipsey et al. 2012) in R ver. 3.3.2 (R Core Team 2016) to simulate surface and bottom temperatures in the study lakes under nominal conditions (2016) and under altered hydroclimate scenarios. The GLM is a one dimensional, process-based thermodynamic model that simulates water temperature profiles while accounting for dynamic processes like mixing, inflows, outflows, and the surface energy balance. The model has been used worldwide for a variety of lake types and conditions (Hipsey et al. 2017; Bruce et al. 2018; Winslow et al. 2017). I used recommended parameter values (Hipsey et al. 2017); inputs included a time series of meteorological data, and lake-specific data (depth, area, latitude, longitude, light attenuation coefficient and inflow temperature and discharge).

First, I calibrated GLM to match 2016 (nominal) temperatures in each lake by minimizing the root mean square error (RMSE) of measured and simulated epilimnion and hypolimnion temperatures:

$$\mathrm{RMSE} = \sqrt{\frac{\sum_{i=1}^{N}(Pred_i - Obs_i)^2}{N}} \qquad (3.2)$$

where N is the number of observations, $Pred_i$ is the predicted daily average temperature, and Obs_i is the observed daily average temperature. Each lake was simulated starting at ice-off; Rawah #2 became ice-free on June 25, and Rawah #3 became ice-free on June 27 (Figure 3.2). Simulations continued until August 31st when my field work concluded, and the lakes were close to turnover. I then used the calibrated model to simulate effects of alternative snowmelt date and air temperature scenarios and compared the results to nominal conditions. Ice-off dates for the earlier snowmelt simulations accounted for the same delay between snowmelt date and ice-free date as during nominal conditions and were June 4 in Rawah #2 and June 6 for Rawah #3.

In total, I simulated lake temperatures in six hydroclimate scenarios: nominal conditions, nominal +2°C, nominal +5°C, early snowmelt with nominal air temperatures, early snowmelt with +2°C air temperatures, and early snowmelt with +5°C air temperatures. Each scenario was applied to each lake and surface and bottom temperatures were tracked. Because Rawah #2 is very shallow, surface-bottom temperature differences were small so I averaged them, assuming that the lake would remain polymictic (Christianson et al., in review). In Rawah #3 simulations I predicted temperatures of the epilimnion. The overall thermal effects of each scenario were quantified by calculating growing degree-days for the simulation period:

$$DD = \sum_{i=1}^{N} max\left(T_{daily_i} - T_{base_i}, 0\right) \qquad (3.3)$$

where DD is cumulative degree days, N is the number of days in the simulation, T_{daily} are daily average simulated temperatures and T_{base} is baseline temperature. I used T_{base} = 5ºC because this temperature represents the minimum temperature for spawning of salmonids and has been used in other degree day analyses for trout (Coleman and Fausch 2007). The number of days in simulations differed because starting dates varied with snowmelt date. Because the open water season extends beyond August 31st, but my simulations did not, I estimated the remaining open water degree days by fitting a second order polynomial function to the simulated lake temperature for each scenario and using this function to calculate degree days until the polynomial function reached 4ºC (Coleman and Fausch 2007). Although this approach does not account for natural variability to the remainder of the growing season, it represents a generalized average and allows me to evaluate degree days for the entire season. These seasonal total DD allow me to assess thermal requirements for juvenile trout, where 800 DD is considered the minimum requirement for juvenile Cutthroat Trout survival (Coleman and Fausch 2007).

3.2.4 Bioenergetics Effects

I assessed the effects of earlier snowmelt and air temperature scenarios on physiological responses of the fishes using the temperature output from each scenario in a bioenergetics model. Bioenergetics models are based on the second law of thermodynamics which implies that the energy consumed by a fish (its ration) is balanced by the energy expended for metabolism, wastes, and growth (Brett and Groves 1979; Deslauriers et al. 2017):

$$C = M + W + S + G \quad (3.4)$$

where C is consumption, M is metabolism, W is waste products, S is somatic growth and G is gonadal growth. Model parameters are species-specific and physiological relationships are functions of temperature and body size. Units for each term are typically in joules per day but mass equivalents can be computed from the energy density of the fish and its food (e.g., Johnson et al. 2017). These models have been used to address a wide variety of ecological questions, but commonly they have been used to evaluate how diet or environmental conditions affect fish growth, or to quantify effects of a predator on its prey (Hewett and Johnson 1987; Hanson et al. 1997; Deslauriers et al. 2017). Under a given set of environmental conditions, the amount of growth (somatic or gonadal) a fish can attain, its "scope for growth," is a function of its consumption and metabolic losses:

$$SFG = C - (M + W) \quad (3.5)$$

where SFG is scope for growth, C is consumption, M is metabolism, and W is waste products. When SFG = 0 no energy is available to allocate to growth or reproduction, but the fish must consume enough food to compensate for losses to metabolism and wastes (the maintenance ration). Thus, setting SFG = 0 is a sensible way to quantify the effects of environmental change on minimum energy requirements for a fish, when future food availability and consumption rate are unknown. Any growth or reproduction would require additional energy intake, above this baseline.

I used Bioenergetics 4.0 ver. 1.1.1 (Deslauriers et al. 2017) in R to model the effects of hydroclimate scenarios on the energetics of two cold-adapted salmonid species present in the study lakes and common in high elevation lakes of the region: Cutthroat Trout and Brook Trout. Historically, these species have been the top two species stocked in Colorado mountain lakes for decades (Nelson 1988). Bioenergetics simulations lasted from ice out until August 31, and I tracked daily respiration rate (J/g/d) and the total amount of food required for maintenance over the simulation period (SFG = 0). I simulated one size class (171 g wet weight) of fish of each species. Trout in mountain lakes of the RWA and across the SRM are typically small, reaching reproductive maturity by this size (Nelson 1988; Young 1995; Downs 1995; Kennedy et al. 2003; Belk et al. 2009), and this size is representative of catchable trout (~250 mm TL) vulnerable to fishing (Nelson 1987). Diets of fish in small, mountain lakes are dominated by invertebrates, including amphipods, dipterans, and zooplankton (Cavalli et al. 1997; Carlisle and Hawkins 1998; Schindler et al. 2001). Energy densities of these taxa range 2,050 – 4,090 J/g wet mass (James et al. 2012) so I used a value of 3,000 J/g for generic prey energy density in my simulations. Energy density of the fish was set to 4,000 J/g (Johnson et al. 2017).

Lastly, I assessed the relative effects of air temperature rise and growing season length on fish energetics in a regression framework. I used cumulative per capita consumption as the response, and predictors were lake (Rawah #3 or Rawah #2), trout species (Brook Trout or Cutthroat trout), air temperature scenario (nominal, +2°C, or +5°C), and length of the growing season. Lake and species were included as discrete variables (0 or 1). The response was log-transformed to account for non-normality. I used AIC model selection employing the 'dredge' function of the 'MuMin' package in R. Residual diagnostic plots were examined to assess normality and variance of the errors. Covariance was also assessed by using the 'vcov' function in R.

3.3 RESULTS

3.3.1 Thermodynamic Modeling

After model calibration simulated water temperatures were in good agreement with observed temperatures for both lakes. The RMSE for Rawah #3 was 1.22°C for surface temperatures, and 0.14°C for bottom temperatures, and the RMSE for Rawah #2 was 1.12°C for surface, and 1.27°C for bottom temperatures. Simulated inflow volumes and temperature coefficients in the calibrated GLM simulations are provided in Table 3.1.

Air temperature increases and early snowmelt both affected lake surface temperatures (Figure 3.5). Air warming had a larger effect on average and maximum surface temperatures than early snowmelt. Early snowmelt increased surface temperatures by ~0.8°C, on average, but air warming increased surface temperatures by 1.3°C at +2°C, and 2.4°C at a +5°C, on average. Rawah #2 was warmer than Rawah #3 by 0.7°C, on average. Maximum surface temperatures differed between the two lakes. Maximum surface temperatures in Rawah #2, which was polymictic, were 14.8°C, 16.2°C, and 17.6°C, under nominal, +2°C, and +5°C air temperatures, respectively. Maximum surface temperatures in Rawah #3 (dimictic) were 15.4°C, 16.6°C, and 18.1°C for the three air temperature scenarios.

Early snowmelt allowed for warming to begin sooner in both lakes, accumulating more heat early in the summer, while nominal snowmelt buffered against early lake surface warming (Figure 3.5). However, by the end of summer lake surface temperatures were only about 1°C higher in the early vs. nominal snowmelt scenarios. Differences in surface temperatures between snowmelt scenarios were greater throughout the summer and slightly higher at the end of summer in Rawah #3. Spring warming and fall cooling were more rapid in Rawah #2 under both snowmelt scenarios.

TABLE 3.1. Values of coefficients used to simulate lake inflow temperature and volume. Values correspond to a second order polynomial for temperature: $Temp = at^2 + bt + c$, where t is the ordinal day starting at May 26th, i.e., when snow depth reached zero in 2012, and an exponential decay for volume: $Flow = R_0 e^{-Kt}$, where t is the same as temperature, R_0 is initial flow and K is the extinction coefficient. Rawah #3 surface temperatures were used for Rawah #2 inflow temperatures.

Inflow parameter	Snowmelt scenario	Model coefficient	Air warming scenario	Lake: Rawah #2	Lake: Rawah #3
Volume	nominal	*Ro*		2.7	2.2
		K		-0.072	-0.072
	early	*Ro*		2.7	2.2
		K		-0.057	-0.057
Temperature	nominal	a	nominal		-0.0022
			+2°C		-0.0022
			+5°C		-0.0022
		b	nominal		0.3541
			+2°C		0.3541
			+5°C		0.3541
		c	nominal		-6.1194
			+2°C		-4.1194
			+5°C		-1.1194
	early	a	nominal		-0.0014
			+2°C		-0.0014
			+5°C		-0.0014
		b	nominal		0.21
			+2°C		0.21
			+5°C		0.21
		c	nominal		0.5
			+2°C		1.38
			+5°C		2.7

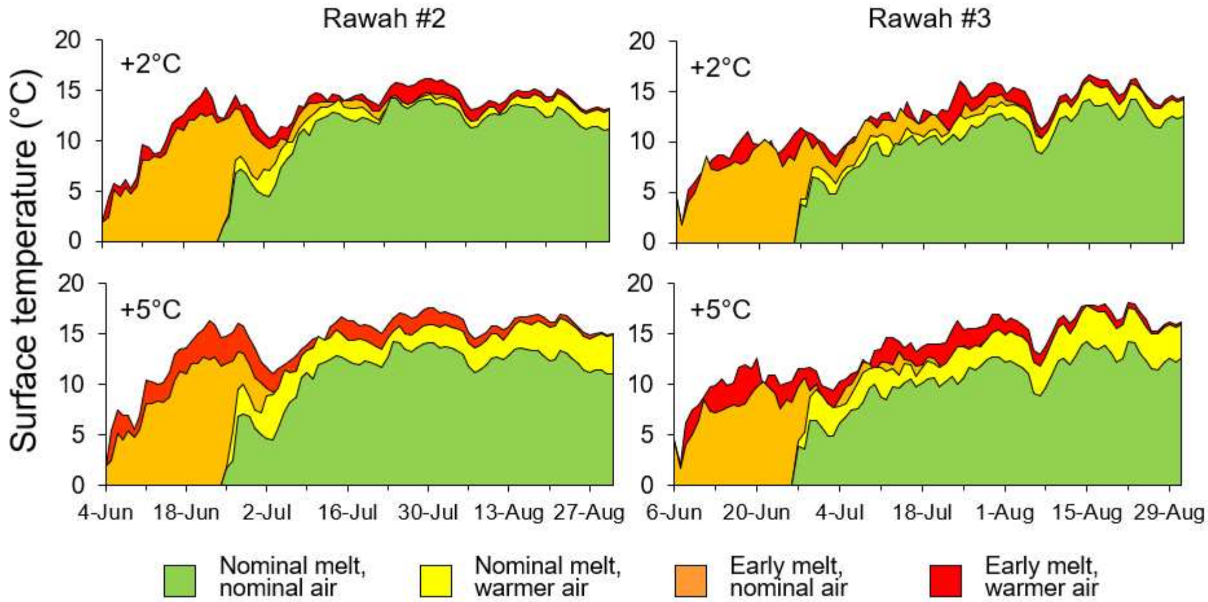

FIGURE 3.5. Predicted effects of air temperature and snowmelt scenarios on lake surface temperatures of Rawah #2 (left) and Rawah #3 (right).

Early snowmelt also resulted in more heat accumulation over the open water season than did increased air temperature (Figure 3.6). Averaged across lakes, early snowmelt increased growing degree days by 42%, while a 2°C increase in air temperatures only increased growing degree days by 12%, and a 5°C increase in air temperatures only increased growing degree days by 26%. Early snowmelt and air warming together increased average growing degree days by 54% at +2°C and 70% at +5°C. Growing degree days accumulated by the end of August were always higher in Rawah #2, due earlier ice out and onset of warming. However, Rawah #2 also cooled more quickly in the fall so by the end of the season total growing degree days was higher in Rawah #3 under all hydroclimate scenarios. Earlier snowmelt and warming both produced higher proportional increases in growing degree days at Rawah #3 than at Rawah #2, suggesting that stratification may have made Rawah #3 surface temperatures more sensitive to climate change effects than surface temperatures in the polymictic lake. Both lakes exceeded the minimum growing degree day threshold for survival of juvenile Cutthroat Trout, even under nominal conditions.

3.3.2 Bioenergetics Effects

Under nominal conditions, Brook Trout had lower median daily respiration rates than Cutthroat Trout in both lakes, and Brook Trout had a wider range of daily respiration rates in all scenarios (Figure 3.7). In general, air temperature rise had a larger effect on daily metabolic costs than did snowmelt recession. Daily respiration rates increased slightly for both species in the early snowmelt scenario, and much more in the air warming scenarios.

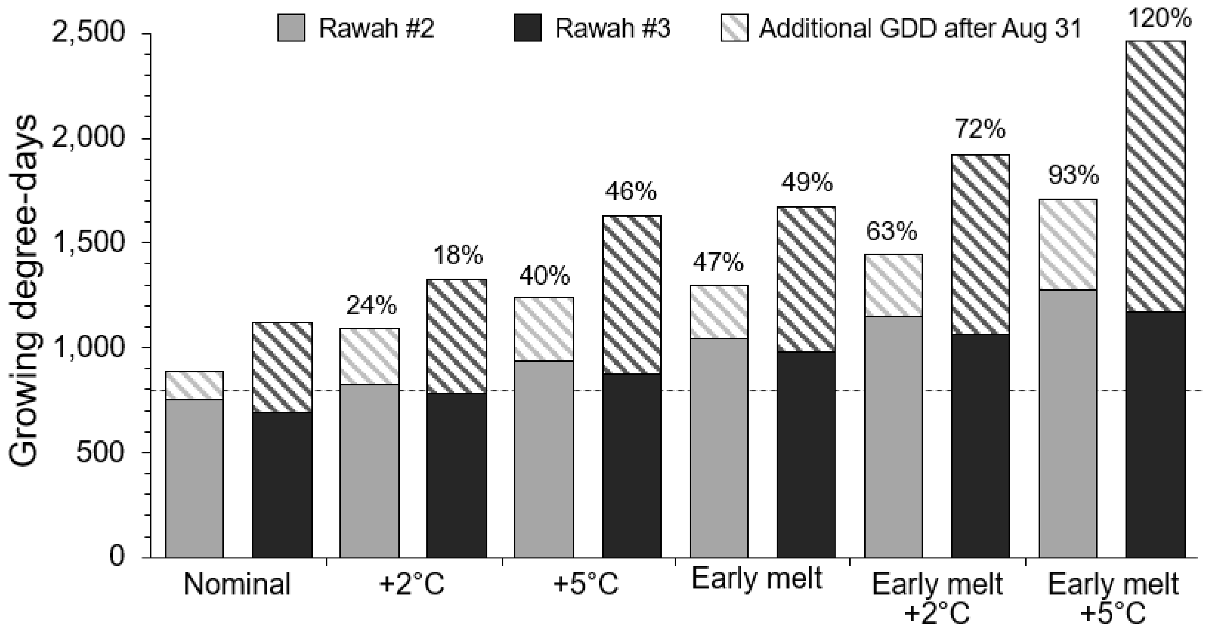

FIGURE 3.6. Predicted growing degree days in the study lakes under nominal conditions vs. increased air temperature and earlier snowmelt scenarios. Percentages show relative change from nominal conditions for the simulation period. Growing degree days extrapolated past the simulation period are also shown to estimate total seasonal growing degree days. The minimum growing degree day threshold for survival of juvenile Cutthroat Trout (Coleman and Fausch 2007) is shown as a dashed line.

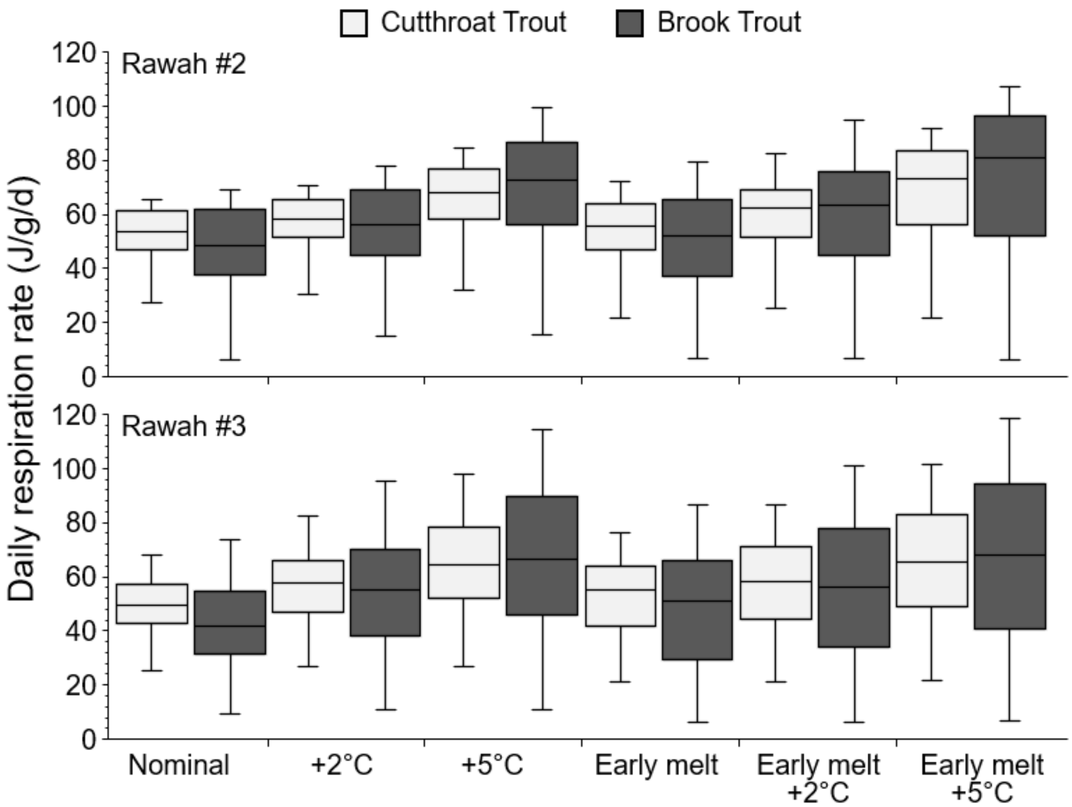

FIGURE 3.7. Seasonal mean specific respiration rates of Cutthroat Trout and Brook Trout during the growing season in both study lakes and under six hydroclimate scenarios.

Averaged across species and lakes, respiration rate increased by 15% and 38% in the +2°C and +5°C air temperature scenarios, respectively, compared with only by 9% in the early snowmelt scenario. Average respiration rates increased by 25% at +2°C and 46% at +5°C in combination with early snowmelt. In most scenarios, the median daily respiration rate was higher in Rawah #2, but only slightly greater than in Rawah #3, which had a larger range in daily respiration rates.

Unlike daily respiration rates, earlier snowmelt had a larger effect on cumulative metabolic costs (measured as the seasonal maintenance ration) than air temperature rise, and the effect was greater for Brook Trout (Figure 3.8). Both species of trout would need to consume more food to compensate for the effects of earlier snowmelt than for the effects of warmer air temperatures. Across lakes, the average maintenance ration with +2°C and +5°C warming increased by 13.8% and 21.9% for Cutthroat Trout and 23.8% and 37.4% for Brook Trout. The average increase in food required with earlier snowmelt was 43.4% for Cutthroat Trout and 52.3% for Brook Trout. Combined effects of +5°C warming and earlier snowmelt could approximately double the minimum food requirements for these two species (92% for Cutthroat Trout and 133% for Brook Trout).

Regression analysis showed that total metabolic cost (cumulative consumption) was well-explained by air temperature changes, length of the growing season, and species (AICc = 232.09, AIC weight = 0.85, $R^2 = 0.97$, $p < 0.001$). The AIC selection procedure indicated that lake could be dropped from the final model. Residual diagnostics did not indicate non-normality or residual dependence. The coefficient for air temperature, $\beta = 0.075$ (95% CI: 0.066 – 0.083), was higher than the coefficient for growing season length, $\beta = 0.018$ (95% CI: 0.016 – 0.020). Holding other predictors constant, a one degree increase in air temperature resulted in a 7.8% increase in cumulative consumption.

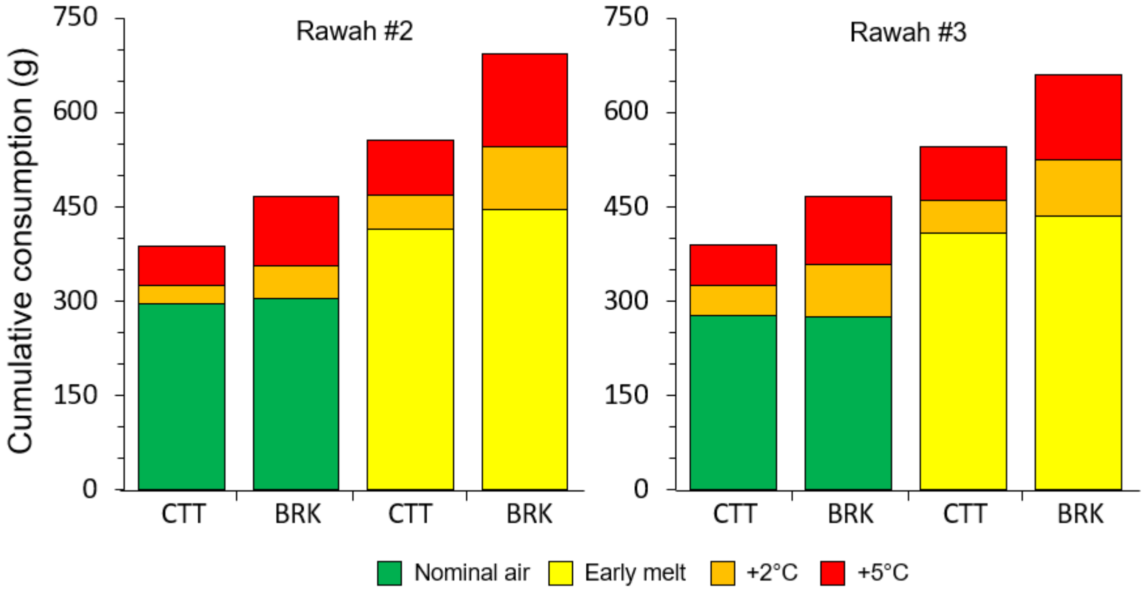

FIGURE 3.8. Predicted cumulative consumptive demand of Cutthroat Trout (CTT) and Brook Trout (BRK) during the growing season in both study lakes and under six hydroclimate scenarios.

A one day increase in the open water season resulted in a 1.8% increase in cumulative consumption. Thus, a four day increase in the open water season is equivalent to the effect of a one degree increase in air temperature.

3.4 DISCUSSION

Many studies of the effects of climate change on lakes generally have focused on the effects of air temperature rise (Missaghi et al. 2017; Woolway et al. 2017). My findings suggest that future predictions may underestimate the impact of climate change on lake temperatures, growing season length and fish energetic demands if reduced snowpack and earlier snowmelt dates coincide with rising air temperatures. I found that just a four day increase in the open water season would be needed to equal the effect of a one degree increase in air temperature. Similarly, an increase in growing season length alone could equal the effects of moderate increases to air temperature. In my simulations, air temperature rise was constrained to a maximum of 5°C, based on RCP 8.5, while a 2°C increase is considered more likely to occur in the future. But on the other hand, growing season length increased by 21 days in my simulations, based on historical observations, and could be more in the future, so changes to growing season length have the potential to affect seasonal heat accumulation more than air temperature rise. The largest effect, however, will be when a long growing season coincides with increased air temperature.

Air temperature rise itself may hasten snowmelt through sensible heat exchange, but also via greater occurrence of rain on snow events (Berg and Hall 2017). Even during large snowpack years, rain on snow and increased air temperatures may drive early melt. Further, when coupled with increased air temperature and rain events, low snowpack years could result in melt dates earlier than have been observed so far. Although snowpack has decreased for some regions (Fyfe et al. 2017), generally, future snowpack is uncertain (Kharin et al. 2013). However, due to the possibility that air increases will drive earlier average melt regardless of snowpack conditions, early snowmelt and longer growing seasons are likely to become more frequent if air temperatures continue to climb.

Another study in the SRM estimated a recession in mountain lake ice-off date of 2.1 days/decade (Preston et al. 2016). If this trend is applicable to my lakes, it would mean that by 2100, the new average ice-off date would occur within about 4 days of 2012, the most extreme year on record. Shorter periods of snow cover and warmer growing seasons could also have indirect effects on mountain lakes such as more forest fires, and decreased stream flows (Hoffman et al. 2007; Clow 2010; Aponte et al. 2016). These watershed impacts can affect lake clarity and inflows (Barnett et al. 2005; Bixby et al. 2015) and amplify direct effects of air temperature rise on lake temperatures (Christianson et al., in review). For example, air warming combined with reduced clarity and inflow could be double the effects of air warming alone (Christianson et al., in review). Thus, in combination with earlier snowmelt and air warming, secondary climate change effects could cause unprecedented increases in lake temperature. And, because many mountain lakes are connected by streams to form paternoster systems, rising lake temperatures will have implications for downstream stream and lake temperatures as well.

As I showed, streamflow from melting snowpack buffers lakes from warming, but this effect is diluted if inflows are received from an upstream lake. I found that inflows from my upstream lake (R3) to the downstream lake (R2) were more than 4°C warmer in late summer than the inflows to R3. Thus, the presence of lakes can significantly alter downstream stream temperatures, and these lakes can amplify the effect of warmer air temperatures on streams, especially in years with low snowpack and earlier snowmelt. Therefore, studies on the effect of climate change on mountain stream temperatures, and the effectiveness of the "cold-water climate shield" for salmonid refugia (Isaak et al. 2015) should consider the presence of lakes, and the indirect effect of earlier snowmelt on stream temperature change.

Climate change could also affect the availability of thermal refugia for fish within the lakes themselves. The direct and indirect effects of warmer and longer growing seasons can intensify lake stratification (Christianson et al., in review), increasing the opportunity for hypoxia to develop in the hypolimnion (Jankowski et al. 2006). Many of the lakes in my study area already exhibit hypoxia during late August (Christianson et al., in review). Thus, longer growing seasons in the future may restrict lacustrine fish to warmer surface waters, with implications for their energy budgets.

Overall, I found that early snowmelt alone had a larger effect on total energy demand of fishes than even the most extreme commonly accepted predictions of air temperature rise, primarily due to its effects on the growing season. Early snowmelt was predicted to have relatively modest effects on daily energy demand because summer lake temperatures rose by only about 1°C over temperatures exhibited during an average snowmelt year. However, early snowmelt allowed lake warming to begin three weeks earlier and result in the accumulation of almost double the number of growing degree days for trout in my study lakes. The longer growing season and higher number of growing degree days meant that trout would need to consume almost 50% more food just to meet basic metabolic demands, and considerably more food to gain surplus energy to devote to growth and reproduction. On average, my study lakes already achieved the minimum number of growing degree days needed to support reproduction and survival of young Cutthroat Trout based on a threshold reported by Coleman and Fausch (2007) for Colorado. Increases to growing degree days due to earlier snowmelt could provide additional opportunity for juvenile fish to grow and survive, but only if sufficient food resources are present.

Air temperature rise had larger effects on daily energy demand than early snowmelt. Despite this, the cumulative effect over the growing season was generally less than the effects of early snowmelt. The effect of a 2°C increase in daily air temperatures increased average daily energy demand by an amount similar to that caused by earlier snowmelt, but if daily air temperatures rose by 5°C then average daily respiration rates exceeded those under early snowmelt. Cumulative energy demand of Brook Trout was slightly more sensitive to air temperature rise than Cutthroat Trout, and a 5°C increase in air temperatures could have a slightly greater effect for that species than earlier snowmelt. Maximum lake temperatures were close to the optimum for growth of both species (~14°C) and well below maximum temperature for growth (~20°C) (Schofield et al. 1993; Bear et al. 2007) in all scenarios. This implies that growth of trout in these lakes in the future will not be temperature limited but could be food limited.

Our predictions of the effects of climate change on the growing season and fish energy demands have important implications for growth and survival of these sport fish, but also for their competitive interactions. If food is sufficient, the longer growing season resulting from early snowmelt could allow trout to grow more. Indeed, other work showed that another coldwater salmonid, Brown Trout *Salmo trutta*, grew 50% more in an alpine lake during low snowpack/early snowmelt years (Borgstrøm 2001). Historic growth rates of Cutthroat Trout and Brook Trout in the RWA lakes are moderate, with fish achieving 314 mm and 289 mm by age 5, respectively (Nelson 1987), which is slightly below the generally accepted fisheries “quality” size for these species (Neumann et al. 2012). Thus, faster growth could be achievable and would be appreciated by anglers.

Effects of climate change on food production in these mountain lakes have not been investigated so it is unknown how future fish growth will actually be affected. Most mountain lakes in the region are oligotrophic (Bahls 1992), but warmer temperatures and longer growing seasons could increase primary and secondary production, potentially increasing food availability for fish. Oleksy et al. (in review) demonstrated that recent warming combined with nitrogen deposition in the SRM increased the production of benthic algae. Food for fish could increase if amphipods, dipterans and other benthic invertebrates common in mountain lake fish diets respond to increases in primary production. If food production lags behind expected climate-driven increases in trout consumptive demand, then competitive interactions that are well documented for these two species (Kennedy et al. 2003) could intensify, and growth and survival may decrease. More research is needed to forecast how thermal effects of a changing climate will affect mountain lake productivity, and therefor how fish populations may respond.

The observed range of snowmelt dates for this region was greater than six weeks, and the SD was just under two weeks. The extreme scenario I simulated occurred once in 37 years. Thus, natural variability in snowmelt date is already high, but very early snowmelt has been rare. Natural year-to-year variation in snowmelt has been a feature of these systems, but a directional change toward earlier snowmelt could have an additive effect on fish energetics because both species can live for more than 5 years in these lakes (Nelson 1987). Successive years of early snowmelt and high consumptive demand could impact reproduction and survival if food is scarce but could result in substantial increases in size at age if food availability increases with growing degree days.

3.5 CONCLUSIONS

I showed that low snowpack resulting in early snowmelt can increase mountain lake temperatures, heat accumulation, growing season length, and fish consumptive demand, and that these effects could be more than twice as strong as expected climate-driven changes in air temperature. Changes to these lake and biotic features would be even more powerful if snowmelt recession and air temperature rise coincide in the future. Uncertainty in how mountain lake productivity will be affected by climate change makes it difficult to know if climate change will be beneficial or detrimental to fish populations. Given potential increases in food requirements for fish, but poor ability to forecast changes in food availability, managers will need to monitor fish growth rates to determine if reductions in stocking rates or other actions are necessary to maintain desired fish growth rates as the climate changes. The higher sensitivity of lake thermal conditions and fish energy requirements to snowpack dynamics also highlights the need to include changes to snowfall and snowmelt in forecasting the effects of climate change on mountain lakes and their biota.

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CONCLUSION

Historically, only a small fraction of the world's lakes has been analyzed for temperature trends and effects of climate change, and of those, high elevation lakes were generally neglected from these studies. This dissertation contributes to the literature and general research behind temperature trends and climate change effects on mountain lakes. I developed a new method to utilize sparse data, which allowed me to determine warming of lakes in the Southern Rocky Mountains to be 0.13ºC/decade. Because new datasets accumulate slowly, it is likely that methods like the one presented will become increasingly beneficial to researchers that wish to utilize vast datasets readily available, while gaining a more complete understanding of how lakes are currently responding to climate change.

My research also determined that changes in air temperature are likely the most influential factor currently affecting mountain lakes. But, secondary effects of climate change, which can alter inflow, clarity and wind, may become increasingly important as they compound the effects of air warming. Changes to inflow and clarity combined with air warming may result in lake stratification changes that are double that of air warming alone. Compounding secondary effects of climate change need to be considered in lake-climate change predictions for a holistic perspective to future change.

Finally, the predicted changes to mountain lake thermal conditions will have implications for biota. It is likely that coolwater species, like some trout, will have more suitable future habitat. And although air temperature is the driving factor behind changing thermal conditions, the duration of the open water season likely plays a larger role affecting fisheries. Timing of ice out, which is closely linked to snowpack conditions, dictates the length of the growing season for aquatic organisms. Even small changes to the length of the open water season can have considerable effects on the metabolic and consumptive demands of trout. Therefore, the cumulative effect of a longer open water duration will likely be more important for the management of mountain lake fisheries than the magnitude of air temperature increases. But, ultimately, food availability will be a key factor controlling the success of fish in mountain lakes.

APPENDIX

TABLE A.1 – Temperature profiles for Big Rainbow for select days in 2016. Data was collected from a buoy string with HOBO Onset data loggers in the center of the lake at 12:00 h.

Depth (m)	Temperature (°C) July 10	July 24	August 7	August 21
0	14.613	16.141	14.9	14.804
1	14.325	15.76	14.517	13.654
2	14.23	15.664	14.134	13.461
3	13.846	15.091	13.461	12.594
4	13.365	14.613	12.98	12.11

TABLE A.2 – Temperature profiles for McIntyre for select days in 2016. Data was collected from a buoy string with HOBO Onset data loggers in the center of the lake at 12:00 h.

Depth (m)	Temperature (°C) July 10	July 24	August 7	August 21
0	12.883	15.378	14.421	14.23
1	13.076	15.282	14.038	13.942
2	12.013	14.804	13.846	13.654
3	10.651	14.421	13.654	13.269
4	7.882	11.236	13.173	12.98
5	7.079	8.182	9.768	12.401
6	6.166	6.573	7.582	8.68
7	5.552	6.37	6.775	7.682
8	10.259	6.166	7.179	7.983
9	5.244	5.962	6.37	7.079

TABLE A.3 – Temperature profiles for Rawah #2 for select days in 2016. Data was collected from a buoy string with HOBO Onset data loggers in the center of the lake at 12:00 h.

Depth (m)	Temperature (°C) July 10	July 24	August 7	August 21
0	11.722	14.325	13.558	13.654
1	11.236	14.038	13.076	12.69
2	10.651	13.461	12.69	12.401
3	10.161	13.269	12.401	12.11

TABLE A.4 – Temperature profiles for Rawah #3 for select days in 2016. Data was collected from a buoy string with HOBO Onset data loggers in the center of the lake at 12:00 h.

Depth (m)	Temperature (°C) July 10	July 24	August 7	August 21
0	9.472	13.076	12.69	13.173
1	9.669	12.787	12.787	12.98
2	9.077	12.207	12.013	12.401
3	8.879	11.722	11.722	12.013
4	8.581	11.236	11.431	11.819
5	7.582	10.455	11.041	11.625
6	6.775	9.373	10.846	11.139
7	6.064	7.983	9.965	10.553
8	5.655	6.674	8.282	7.682
9	5.45	5.86	6.573	6.37
10	5.244	5.141	5.757	5.757
11	5.244	5.037	5.347	5.45
12	5.141	4.831	5.141	5.244
13	5.141	4.831	4.934	4.934
14	4.831	4.727	4.727	4.727
15	4.727	4.519	4.623	4.519
16	4.727	4.415	4.519	4.415
17	4.727	4.415	4.415	4.415
18	4.519	4.311	4.311	4.311
19	4.519	4.311	4.311	4.311
20	4.519	4.311	4.311	4.311
25	4.415	4.207	4.207	4.207
30	4.207	4.102	4.102	4.102

TABLE A.5 – Temperature profiles for Sugarbowl for select days in 2016. Data was collected from a buoy string with HOBO Onset data loggers in the center of the lake at 12:00 h.

Depth (m)	Temperature (°C) July 10	July 24	August 7	August 21
0	9.373	12.207	12.11	11.528
1	10.161	12.69	12.594	12.98
2	9.669	12.401	12.304	12.594
3	9.077	11.625	12.013	12.11
4	7.882	10.748	12.013	12.304
5	6.674	7.782	10.259	11.334
6	6.064	6.674	7.682	9.176
7	5.45	5.962	6.573	7.481
8	5.141	5.45	5.757	5.962
9	4.519	4.831	4.831	4.934
10	4.415	4.623	4.623	4.727
11	4.207	4.415	4.519	4.519
12	4.311	4.519	4.623	4.623
13	4.311	4.519	4.519	4.519

TABLE A.6 – Temperature profiles for Upper Camp for select days in 2016. Data was collected from a buoy string with HOBO Onset data loggers in the center of the lake at 12:00 h.

Depth (m)	Temperature (°C)			
	July 10	July 24	August 7	August 21
0	13.558	15.473	15.091	14.517
1	12.401	14.325	13.942	13.076
2	12.401	14.23	13.75	13.076
3	12.207	13.75	13.461	12.594
4	12.11	12.69	12.98	12.497
5	10.846	11.819	12.594	12.304
6	8.978	10.455	12.013	12.11
7	6.978	9.176	9.077	9.866
8	6.674	7.582	7.079	8.282
9	6.268	7.079	6.674	7.481
10	6.064	6.877	6.471	7.079
11	5.757	6.37	6.166	6.573
12	5.757	6.166	6.166	6.573
13	5.757	6.064	6.064	6.37
14	5.757	5.962	6.166	6.471
15	5.552	5.757	5.962	6.268

TABLE A.7 – Temperature profiles for Upper Sandbar for select days in 2016. Data was collected from a buoy string with HOBO Onset data loggers in the center of the lake at 12:00 h.

Depth (m)	Temperature (°C)			
	July 10	July 24	August 7	August 21
0	10.651	13.75	12.787	12.98
1	10.748	13.846	12.98	13.076
2	8.978	12.013	12.497	12.401
3	7.882	10.944	12.207	12.207
4	6.775	9.176	11.431	11.625
5	6.166	8.082	9.176	10.846
6	5.962	7.582	8.282	9.077

TABLE A.8 – Secchi and turbidity values for each lake collected in 2015 and 2016. Values are average summer (July, August, September) measurements each year. Also shown are oxygen measurements sampled from one meter off the substrate in the deepest part of each lake. Oxygen was sampled once during 2016 during August 16-17.

Lake	Secchi (m)		Turbidity (NTU)		Oxygen
	2015	2016	2015	2016	(mg/L)
Big Rainbow	1.0	0.8	1.90	4.60	4.8
McIntyre		4.4		1.31	
Rawah #2	Bottom	Bottom	0.34	1.34	7.4
Rawah #3	2.4	3.5	0.45	0.98	2.1
Sugarbowl		3.6		1.21	
Upper Camp	2.9	2.5		1.91	2.4
Upper Sandbar	3.2	3.4	0.70	1.68	1.6