

# Water Resources Research

## RESEARCH ARTICLE

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### Key Points:

- Simulated annual maximum and summer median lake chlorophyll-*a* are positively associated with external phosphorus load and air temperature, respectively
- A 2°C rise in simulated air temperature significantly increased summer median, but not annual maximum, chlorophyll-*a*
- Annual maximum chlorophyll-*a* may be more informative than median summer chlorophyll-*a* to assess nutrient load effects on water quality

### Supporting Information:

- Supporting information S1

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## Differential Responses of Maximum Versus Median Chlorophyll-*a* to Air Temperature and Nutrient Loads in an Oligotrophic Lake Over 31 Years

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**Abstract** Globally, phytoplankton abundance is increasing in lakes as a result of climate change and land-use change. The relative importance of climate and land-use drivers has been examined primarily for mesotrophic and eutrophic lakes. However, oligotrophic lakes show different sensitivity to climate and land-use drivers than mesotrophic and eutrophic lakes, necessitating further exploration of the relative contribution of the two drivers of change to increased phytoplankton abundance. Here, we investigated how air temperature (a driver related to climate change) and nutrient load (a driver related to land-use and climate change) interact to alter water quality in oligotrophic Lake Sunapee, New Hampshire, USA. We used long-term data and the one-dimensional hydrodynamic General Lake Model (GLM) coupled with Aquatic EcoDynamics (AED) modules to simulate water quality. Over the 31-year simulation, summer median chlorophyll-*a* concentration was positively associated with summer air temperature, whereas annual maximum chlorophyll-*a* concentration was positively associated with the previous 3 years of external phosphorus load. Scenario testing demonstrated a 2°C increase in air temperature significantly increased summer median chlorophyll-*a* concentration, but not annual maximum chlorophyll-*a* concentration. For both maximum and median chlorophyll-*a* concentration, doubling external nutrient loads of total nitrogen and total phosphorus at the same time, or doubling phosphorus alone, resulted in a significant increase. This study highlights the importance of aligning lake measurements with the ecosystem metrics of interest, as maximum chlorophyll-*a* concentration may be more uniquely sensitive to nutrient load and that typical summer chlorophyll-*a* concentration may increase due to warming alone.

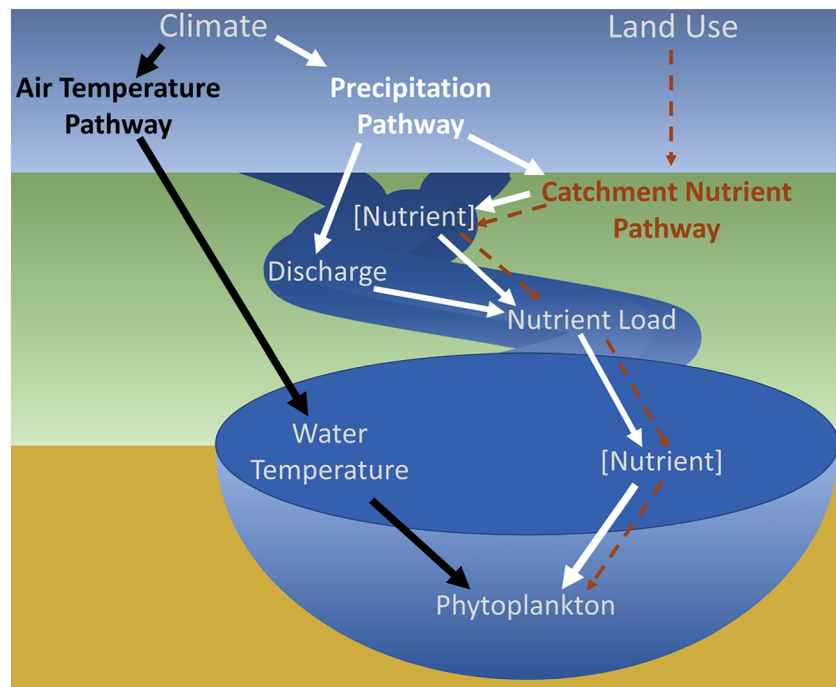
**Plain Language Summary** Clear water lakes are experiencing more frequent water quality problems due to land development and climate change. However, it is challenging to identify how land development and climate change interact to alter water quality because their effects are complex and occurring at the same time. We used three decades of observational data combined with a lake ecosystem simulation model to explore the role of land development and climate change on water quality. Our water quality indicator of focus was phytoplankton, which are small photosynthesizing organisms in the water, often referred to as “algae.” We found that the effects of land use and climate depend on if we look at yearly maximum or average phytoplankton concentrations. Average phytoplankton concentrations during the summer (representing typical summer conditions) increase with either warmer air temperatures or higher nutrient pollution. However, annual maximum phytoplankton concentration (representing phytoplankton “blooms”) only increases with higher nutrient pollution. Typical summer phytoplankton concentrations will likely increase with warmer air temperatures due to climate change alone and increase even further when combined with higher nutrient pollution. To maintain clear water lakes, nutrient pollution should be reduced even more than previously thought to compensate for increasing phytoplankton in a warmer climate.

## 1. Introduction

Lake water quality is often considered to be most influenced by catchment land-use change, whereas climate-induced changes are of secondary importance (Brookes & Carey, 2011; Bucak et al., 2018; Couture et al., 2014, 2018; Jenny et al., 2015). However, since lake water quality is altered through multiple interacting land-use and climate change pathways (Figure 1), it is difficult to tease apart the relative contribution of

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**Figure 1.** Pathways for climate and land use to affect phytoplankton: (1) the Air Temperature Pathway may either stimulate or inhibit phytoplankton growth, for example, warmer surface water may stimulate phytoplankton growth, but earlier onset of thermal stratification may lower nutrient exchange with the hypolimnion, inhibiting phytoplankton growth; (2) the Precipitation Pathway increases stream discharge (potentially increasing overall nutrient load) and increases transport of nutrients from terrestrial landscape (increasing in-stream nutrient concentrations and overall nutrient load); and (3) the Catchment Nutrient Pathway changes nutrient availability and transport from terrestrial landscape (e.g., fertilizer application increases nutrient concentrations in inflow streams; land use development increases impervious surface and erosion). “[Nutrient]” denotes nutrient (nitrogen or phosphorus) concentrations; solid arrows indicate shorter time-scale relationships, and dashed arrows indicate lagged effects as nutrients accumulate in the catchment before being transported to the lake.

each individual driver to overall water quality (Collins et al., 2019; McCullough et al., 2019; Moss et al., 2011). Land-use and land-cover change (e.g., fertilizer application and deforestation) can increase nutrient loads from catchments to lakes through increased stream nutrient concentrations (Bormann et al., 1974; King et al., 2007) via the Catchment Nutrient Pathway (Figure 1). Changes in precipitation frequency or intensity due to climate change can mobilize more terrestrial nutrients and increase stream discharge, consequently increasing total nutrient loads to the lake (Arvola et al., 2015; Jeppesen et al., 2009; Meyer et al., 1999) via the Precipitation Pathway (Figure 1). Additionally, rising air temperatures due to climate change increase surface water temperature, thereby affecting lake biological activity, the duration of summer stratification, and the frequency and duration of hypoxia (De Senerpont Domis et al., 2013; Magee et al., 2019; O’Reilly et al., 2015; Paerl & Huisman, 2008; Woolway et al., 2019) via the Air Temperature Pathway (Figure 1). Due to the interaction between drivers, it is thus possible that altering one pathway may amplify or dampen the lake response and sensitivity to another pathway.

Phytoplankton biomass, and especially its key proxy, chlorophyll-*a* concentration, is useful in assessing lake ecosystem responses to the combined effects of land-use and climate change, since increased nutrients and water temperatures can directly stimulate phytoplankton (Carey, Ibelings, et al., 2012; Trolle et al., 2014; Williamson et al., 2008). As chlorophyll-*a* concentrations increase, there is more variability in the ratio of summer mean versus maximum chlorophyll-*a* concentration (Jones et al., 1979). The increased variability of the ratio of mean-to-maximum chlorophyll-*a* concentration could be because central tendency and maximum chlorophyll-*a* concentration represent different ecosystem responses. Central tendency (e.g., mean or median) chlorophyll-*a* concentration may correspond to typical conditions in the lake, similar to what

would be used to determine trophic state (Carlson, 1977). In contrast, annual maximum chlorophyll-*a* concentration may reflect short-term increases in phytoplankton as a result of a large nutrient loading event or a period of favorable temperature conditions (e.g., Batt et al., 2017). Thus, different summary statistics (e.g., median vs. maximum) of the distribution of chlorophyll-*a* may reveal unique signals of change and may help elucidate the role of different pathways of change in lake ecosystems (Figure 1).

To date, most work assessing the effect of climate and land-use change on phytoplankton biomass or chlorophyll-*a* concentrations has focused on eutrophic lakes and reservoirs, but some recent studies including oligotrophic lakes indicate differential sensitivity to climate and land-use drivers (Hayes et al., 2015; Rigosi et al., 2014). For example, high-nutrient lakes situated in predominantly agricultural catchments can shift from P-limited to N-limited under drought conditions, in contrast to lakes in forested catchments, which tend to be N-limited during drought or nondrought conditions (Hayes et al., 2015). Further, oligotrophic lakes in the northeastern United States are more sensitive to air temperature and precipitation changes than lakes in the same region with higher productivity (McCullough et al., 2019). Given increasing reports of cyanobacterial blooms in oligotrophic lakes in northeastern North America (e.g., Carey et al., 2012; Pick, 2015; Winter et al., 2011) and the rapid loss of oligotrophic freshwater systems (Stoddard et al., 2016), teasing apart the effects of climate and land-use change on oligotrophic lakes is particularly timely.

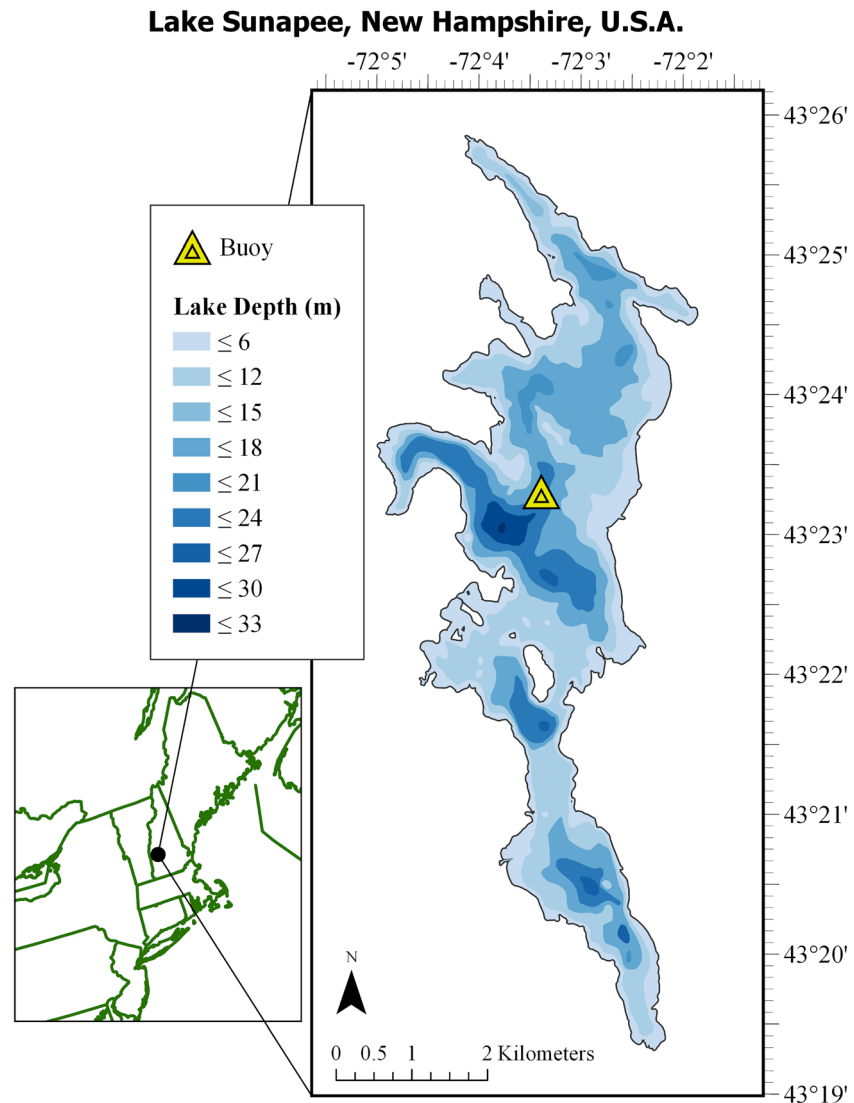
Disentangling the relative role of climate and land use is challenging, given the interaction of different pathways (Figure 1); however, simulation modeling, when used in conjunction with observational data collected across a range of environmental conditions, may further our understanding of the long-term role of multiple drivers on ecosystem processes (Turner & Carpenter, 2017). For example, in oligotrophic Lake Sunapee (NH, USA), chlorophyll-*a* concentrations are generally low, with occasional brief increases (Carey, Ewing, et al., 2012; Carey, Weathers, et al., 2014). Multiple limitations, such as difficulty measuring low concentrations of chlorophyll-*a* with precision, intermittent field monitoring programs that may miss extreme events, and a complicated suite of physical-biological processes that influence the observed temporal patterns of chlorophyll-*a* concentration, contribute to difficulty in assessing multiple drivers in ecosystem analysis (Weathers et al., 2013). However, a well-calibrated simulation model enables us to explore the role of each driver, because environmental drivers can be manipulated independently and their effects on chlorophyll-*a* concentration can be examined through mechanisms instantiated in the model. Simulation models can also provide data at very high temporal resolution relative to empirical data, enabling comparisons of different types of summary statistics—such as central tendencies versus extremes—that are rarely possible with manual field measurements alone.

We evaluated the role of terrestrial nutrient loading and climate on simulated annual maximum and summer median chlorophyll-*a* concentrations by asking two questions: (1) How do simulated annual maximum and summer median chlorophyll-*a* concentrations respond to climate and nutrient-load drivers in an oligotrophic lake? (2) How do simulated annual maximum and summer median chlorophyll-*a* concentrations in an oligotrophic lake respond to projected increases in air temperature and stream inflow nutrient concentration? We used historical climate, stream, and lake monitoring data to calibrate a one-dimensional hydrodynamic model coupled with an aquatic ecosystem model to produce a 31-year reference simulation of water quality in oligotrophic Lake Sunapee, NH to address Question 1. We then applied multiple factorial scenarios of elevated stream nutrient concentrations and air temperature to the calibrated model to address Question 2.

## 2. Materials and Methods

### 2.1. Study Site Description

Lake Sunapee is located on the border of Merrimack and Sullivan counties in New Hampshire, USA (43°24' N, 72°3'W). Lake Sunapee is the sixth largest lake in New Hampshire and is an important drinking water source and recreation area (Sunapee Area Watershed Coalition, 2008). Lake Sunapee has a surface area of 16.55 km<sup>2</sup>, a volume of  $1.88 \times 10^8$  m<sup>3</sup>, residence time of 3.1 years, mean depth of 10 m, maximum depth of 33 m, and maximum fetch of 9.1 km (Carey, Weathers, et al., 2014; Richardson et al., 2017). The lake is dimictic, with ice cover from December or January until late March or April (Bruesewitz et al., 2015), and a mean summertime thermocline maximum depth of 6–8 m (Carey, Weathers, et al., 2014).



**Figure 2.** Location and bathymetry of Lake Sunapee, New Hampshire, USA. Bathymetric map source: Lake Sunapee Protective Association.

The Lake Sunapee Protective Association (LSPA; lake-sunapee.org) is a member of the Global Lake Ecological Observatory Network (GLEON; gleon.org), and deploys and maintains a monitoring buoy located near the deepest point in the lake (Figure 2). The buoy has sensors that measure meteorological data, a water temperature depth profile, and epilimnetic dissolved oxygen concentration at 10- to 15-minute intervals (all data available in Environmental Data Initiative Repository; LSPA et al., 2018; Richardson et al., 2020).

Lake Sunapee is an oligotrophic, clear-water lake with historical chlorophyll-*a* concentrations less than  $5 \mu\text{g L}^{-1}$  (Steiner & Titus, 2017; NHDES, 2017) and dissolved organic carbon concentrations less than  $2.5 \text{ mg L}^{-1}$  (Solomon et al., 2013). The surrounding catchment is approximately 80% forested, 7% wetlands and ponds, 6% developed, 4% agricultural land, and 3% miscellaneous open space, but has been facing increasing development pressure (Cobourn et al., 2018; CSRC 2002; Yang et al., 2018), especially around the perimeter of the lake. The lake has six major inflows, which are estimated to collectively account for roughly 90% of all surface water inputs to the lake (Schloss, 1990). Lake Sunapee air temperature has been increasing at a rate of  $0.42^\circ\text{C}$  per decade since 1979 ( $p$  value  $<0.001$ ; Figure S1 in the supporting information).

## 2.2. Model Description and Driver Data

We used the General Lake Model (GLM) v.2.1.8, a one-dimensional hydrodynamic model coupled with Aquatic EcoDynamics (AED), a lake ecosystem model (Hipsey et al., 2019). GLM and AED are open-source and are available online (<http://aed.see.uwa.edu.au/research/models/GLM/> and <https://github.com/AquaticEcoDynamics/GLM>).

GLM-AED requires many different driver data files and configuration files (Hipsey et al., 2019), including initial water chemistry and temperature, daily stream inflow temperature, volume, and nutrient concentrations (see below), daily lake outflow volume (Ward et al., 2020), and hourly weather. Hourly weather data at the buoy site (see section 2.1 and Figure 2) from 1982 to 2015 were downloaded from the North American Land Data Assimilation System (NLDAS-2) website (Xia et al., 2012). We estimated daily stream inflow volume to the lake based on precipitation from NLDAS-2 and a simple overland flow relationship based on a runoff coefficient and impervious surface area (held constant through the simulation), as well as a snow accumulation and snowmelt model (McCarthy, 2008; USCOE, 1998; Van Mullem et al., 2004). Base flow was added to the precipitation-generated inflow such that their sum produced a total flux sufficient to reproduce the known mean residence time of the lake (3.1 years) (Richardson et al., 2017; Schloss, 1990), given the lake volume. Daily inflow water temperature was modeled using two linear regressions with NLDAS-2 air temperature and stream temperature data (Ewing et al., 2020), one for cold (subzero) air temperatures and one for air temperatures above 0°C (Text S1 and Figures S2–S9). Observed stream temperature and final stream inflow volume and temperature driver data are available in the Environmental Data Initiative repository (Ewing et al., 2020; Ward et al., 2020).

GLM-AED driver data also include daily nutrient concentrations for inflow streams, representing terrestrial and stream nutrient contributions to the lake. Inflow chemistry data were obtained from LSPA's long-term monitoring program, in which measurements of total phosphorus (TP) were available for inflow streams at monthly intervals each summer from 1986–2015 ( $n$  of observed values = 2,692 from 1986 to 2015). Although stream inflow concentrations often co-vary with stream inflow volume, there was no volume-concentration relationship in our observations, so our modeled daily stream concentration was independent of stream inflow volume. On days without observed inflow stream TP concentration, we used the *rmnorm* function in R (R version 3.3.3, R Core Team, 2017) to randomly sample with replacement from a randomly generated normal distribution ( $n = 1,000$ ,  $\mu = 5$ -year moving window mean of observed values,  $\sigma = 5$ -year moving window variance of observed values); we used the 5-year distribution of observations from 1986 to 1991 to bootstrap the years prior to 1986. TP concentrations were divided into fractions based on observations from oligotrophic Ontario Lakes with similar trophic status, bedrock, and land use (Wetzel, 2001): 50% adsorbed P, 2.95% soluble reactive P, 32.7% particulate organic P, and 14.35% dissolved organic P.

On days without observed total nitrogen (TN) inflow stream concentrations, we created a TN:TP mass ratio for every day using the *rmnorm* function in R to randomly sample with replacement from a randomly generated normal distribution of TN:TP ( $n = 1,000$ ,  $\mu =$  mean of observed TN:TP values,  $\sigma =$  variance of observed TN:TP values;  $n$  of observed values = 135, from 2009 to 2012) and then back-calculated TN using the randomly generated TN:TP and previously estimated TP value. In lieu of observational data, we divided TN concentrations into fractions of particulate organic N (40%), dissolved organic N (40%), nitrate (10%), and ammonium (10%), following literature values (reviewed by Wetzel, 2001) and assuming that available N would be lower than organic N pools. Daily dissolved organic carbon (DOC) and particulate organic carbon (POC) values were held constant at  $1.4 \text{ g L}^{-1}$  and  $0.15 \text{ g L}^{-1}$ , respectively, throughout the 31-year simulation ( $n = 132$  from 2004, 2005, and 2009–2013) due to the low number of observations and limited direct comparisons for generating a total organic carbon:TP relationship. Stream nutrient concentration driver data are available in the Environmental Data Initiative repository (Ward et al., 2020).

## 2.3. Model Calibration and Evaluation

The total simulation period for the Lake Sunapee GLM-AED model was 15 April 1982 to 31 December 2015. The simulation has four distinct periods: (1) a spin-up period from 15 April 1982 to 31 December 1984, (2) a calibration period from 1 January 2005 to 31 December 2009, (3) an evaluation period from 1 January 2010 to 31 December 2013, and (4) the periods of both 1 January 1985 to December 2004 and 1 January 2014 to 31 December 2015 in which no goodness-of-fit metrics were calculated due to limited observational data. We



chose these time periods for calibration and evaluation because they cover a wide range in annual temperature and precipitation and coincide with a time period of sufficient available data for comparison. We ran the model on an hourly time step, simulating vertical whole-water profile conditions at the deepest location of the lake.

Before initializing the full 31-year simulation, we conducted a shorter simulation for calibration of model parameters and evaluation of model fit. We focused on 2005 through 2009 for the calibration phase, which included a range of warm, cool, dry, and wet years. To account for potential effects of initial conditions, we began analyzing model outputs after the simulation ran through one full summer stratified and fall turnover period. Specifically, for the model calibration process, we initiated the model simulation in April 2004, setting the initial water chemistry profile to observed values measured at the buoy site of the lake in April 2004, but we did not use model outputs for calibration until 1 January 2005. Examining model outputs from 2005 through 2009, we systematically adjusted lake physics, nutrient cycling, and phytoplankton growth parameters (Table S1) to improve the model fit with available observed data based on goodness-of-fit metrics (following Bennett et al., 2013; for final parameters and initial condition data sets, see Ward et al., 2020). Due to the coarse temporal resolution of observed P concentrations and chlorophyll-*a* concentration data, we calibrated the model to represent expected annual patterns in P and chlorophyll-*a* concentration in addition to comparing model outputs with infrequent observations. For example, we ensured cyclical patterns of chlorophyll-*a* concentration were recreated in the model (e.g., peaks in late summer, decreases during turnover and ice-cover periods). Then, we fine-tuned the magnitude of chlorophyll-*a* during the summer stratified period using direct comparison with observational data (most of which were collected during the summer stratified period and did not show discernible patterns within each year). For nitrogen, we calibrated the model to anticipated annual cyclical patterns and approximated the magnitude of TN to observed pelagic TN (Cottingham, 2020) and the relative proportion of each constituent to be in agreement with expected ratios in oligotrophic lakes (Wetzel, 2001). During the calibration period (2005–2009), we were only able to make direct comparisons of simulated and observed pelagic N in 2009, due to there being no observational measurements of pelagic N earlier in the calibration period. The simulated TN concentrations were within the range of observed pelagic TN concentrations (Carey, Cottingham, et al., 2014; Cottingham, 2020). Conversely, we calibrated the model to daily values for temperature and dissolved oxygen, as we had high-frequency observations of these variables beginning in 2007 (Richardson et al., 2020).

After final parameter values were established, we calculated the same goodness-of-fit metrics during the 2010–2013 evaluation period. This period was selected for evaluation due to there being adequate observational data for comparisons. Goodness-of-fit metrics were calculated for model output and high-frequency observations of temperature and dissolved oxygen at noon each day during the calibration and evaluation period. Due to limited frequency of observational data for TP, TN, and chlorophyll-*a* concentration, we calculated the same goodness-of-fit metrics used on high-frequency comparisons and compared observed and simulated medians and ranges for the days of observation with expected concentrations in oligotrophic lakes. All goodness-of-fit metrics were calculated using the *hydroGOF* package (Zambrana-Bigiarini, 2017) in R. These included  $R^2$  (best fit = 1), root mean square error (RMSE; which presents model error in the same units as the variable of interest, best fit = 0), percent bias (PBIAS; a measure of bias in predictions with overpredictions positive and underpredictions negative as a % of the magnitude of observations, best fit = 0), Nash-Sutcliffe efficiency (NSE; a high-frequency comparison of model output and observations commonly used in discharge modeling, in which the best fit = 1, a value of 0 indicates the model predictions are as accurate as the mean of observed values, and a negative value indicates the mean of observed values is more accurate than the modeled values), and mean absolute error (MAE; in units of the variable of interest, best fit = 0).

#### 2.4. Reference Simulation Analysis—Question 1: How Do Annual Maximum Versus Median Chlorophyll-*a* Concentrations Respond to Climate and Land-Use Drivers in an Oligotrophic Lake?

To identify which drivers in the Catchment Nutrient Pathway, Precipitation Pathway, and Air Temperature Pathway (Figure 1) were most associated with interannual variability in chlorophyll-*a* concentrations, we assessed model outputs and driver data from the long-term Lake Sunapee GLM-AED simulation. Drivers within each of the three pathways are often interlinked, however, the goal here was to narrow the focus of driver variables, with further exploration of the pathways themselves in section 2.6. We used the final

parameters established during calibration (Ward et al., 2020), initialized the simulation on 15 April 1982, and ran the model through 31 December 2015. The purpose of the 31-year simulation was to explore how the model outputs change across a range of annual conditions. The relationship between drivers and chlorophyll-*a* concentration is likely complex, but for a first step at understanding the interactive effects of climate and land-use pathways on seasonal phytoplankton responses, we summarized daily model outputs to the seasonal scale. We refer to the initial simulation, aimed at reproducing lake conditions over the past 31 years, as the “reference” simulation rather than “baseline” in recognition that the lake is already undergoing ecosystem change (Richardson et al., 2017).

To assess whether different summary statistics of summer chlorophyll-*a* concentration were associated with different drivers as described above, we focused our analysis on annual maximum and summer median chlorophyll-*a* concentration. “Summer” was considered to be from 1 June 1 to 30 September each year. We selected the June through September window since this time period most consistently included summer stratification over the 31 years. Since we predicted that annual maximum and summer median chlorophyll-*a* concentration may respond to different drivers, we analyzed them separately, though they are correlated with each other (Spearman  $\rho = 0.47$ ,  $p < 0.01$ ; Figure S10).

We used a multistep analysis to determine the association between land-use and climate drivers on summer median and annual maximum chlorophyll-*a* concentrations. We grouped potential driver variables into three categories: variables related to the (1) Precipitation Pathway (Figure 1; precipitation), (2) Air Temperature Pathway (air temperature), and (3) combined Catchment Nutrient Pathway and Precipitation Pathways (TN and TP loads) to identify the most associated driver variables within each pathway. For Question 1, we did not assess nutrient concentration separately from load because nutrient concentrations are made ecologically meaningful in combination with discharge, in the form of total nutrient load to the lake (e.g., Carpenter et al., 2018). We examined the role that increases in nutrient concentration in inflow streams could have on chlorophyll-*a* concentration response in Question 2.

We then aggregated each driver to spring (March through May), summer (June through September), water year (previous calendar year 1 October to current calendar year 30 September), and the previous three water years to assess more immediate versus lagged responses in chlorophyll-*a* concentration. The 3-year aggregation was selected due to the 3.1-year hydraulic residence time in the lake (Richardson et al., 2017; Schloss, 1990). We assessed different summary statistics for air temperature, including mean, minimum, and maximum, and used cumulative totals for TN and TP load and precipitation for each time period to identify possible driver-response associations.

We used Spearman correlations to identify which potential driver variables were the most strongly associated with summer median and maximum chlorophyll-*a* concentration. Annual summer median chlorophyll-*a* concentrations can be treated as independent from year to year, though there were weak lag-1 autocorrelations for maximum chlorophyll-*a* concentration that may affect inferences (Figures S11, S12). Nonparametric Spearman correlations were used to account for nonlinearity and potential outliers that bias Pearson correlation estimates ( $r$ ).

## 2.5. Scenario Analysis—Question 2: How Do Maximum Versus Median Chlorophyll-*a* Concentrations in an Oligotrophic Lake Respond to Projected Increases in Air Temperature and Stream Inflow Nutrient Concentration?

To examine the relative contribution of higher stream inflow nutrient concentrations (Catchment Nutrient Pathway) and higher air temperatures (Air Temperature Pathway) to future chlorophyll-*a* concentrations, we generated five scenarios exploring different combinations of changes in air temperature and stream N and P concentrations that are plausible for the Lake Sunapee catchment (Table 1). The five scenarios were applied to the reference 1985–2015 simulation, in which the stream nutrient (TN and TP) concentrations (Catchment Nutrient Pathway, Figure 1; Scenarios 1, 2, 3, and 5, Table 1) and air temperature (Air Temperature Pathway, Figure 1; Scenarios 4 and 5, Table 1) driver data were manipulated, but all other conditions (e.g., stream discharge) were held constant.

The five hindcasted scenarios (Table 1) were based on expected future air temperature and inflow stream nutrient conditions for the Lake Sunapee catchment according to downscaled climate projections (Abatzoglou, 2013; Taylor et al., 2012) and economic development projections (Sunapee Area Watershed

**Table 1**  
*GLM-AED Hindcasted Scenario Descriptions*

Name	Description	Driver data modification
Scenario 1: $TN \times 2$	Increased inflow stream N concentration	Concentration of each fraction of N was doubled in comparison to reference simulation
Scenario 2: $TP \times 2$	Increased inflow stream P concentration	Concentration of each fraction of P was doubled in comparison to reference simulation
Scenario 3: $TNTP \times 2$	Increased inflow stream N and P concentrations	Concentration of each fraction of N and P was doubled in comparison to reference simulation
Scenario 4: $+2^{\circ}C$	Increased air temperature	Air temperature was increased by $2^{\circ}C$ in comparison to reference simulation
Scenario 5: $TNTP \times 2 + 2^{\circ}C$	Increased inflow stream N and P concentrations and air temperature	Concentration of each fraction of N and P was doubled and air temperature was increased by $2^{\circ}C$ in comparison to reference simulation

Coalition, 2008). In Scenario 1:  $TN \times 2$ , Scenario 2:  $TP \times 2$ , and Scenario 3:  $TNTP \times 2$ , we doubled the daily concentration of each fraction of N and P, to result in two times the total N, P, or N and P load, respectively. In Scenario 4:  $+2^{\circ}C$  scenario, we increased each hourly air temperature in the meteorological driver data file by  $2^{\circ}C$ . Finally, we increased air temperature and inflow stream N and P concentrations in Scenario 5:  $TNTP \times 2 + 2^{\circ}C$ , in which the concentration of each fraction of N and P was doubled, thereby doubling the total N and P load, and added  $2^{\circ}C$  to each hourly air temperature in the meteorological driver data. These scenarios were simplistic for the purpose of identifying the potential role of individual drivers in lake ecosystem outcomes. We recognize that changes to these drivers in reality will be more complex (e.g., nutrient loads will not increase uniformly, but likely will be characterized by more extreme peaks and higher background concentrations); however, for model simulations to elucidate lake process dynamics, simplified scenarios can be a useful tool (e.g., Piccolroaz et al., 2015).

The  $+2^{\circ}C$  scenario represents additional temperature warming above the already-observed  $1.4^{\circ}C$  warming that occurred in the Sunapee catchment from 1981 to 2015 (Figure S1), representing a total of  $3.4^{\circ}C$  warming over reference 1981 air temperatures by the end of the simulation period. This  $2^{\circ}C$  warming above current conditions is expected at Lake Sunapee by 2050 according to the RCP 8.5 prediction, and by 2066 in the RCP 4.5 prediction, averaged across downscaled global climate models (Abatzoglou, 2013; Taylor et al., 2012). The  $TPTN \times 2$  scenario is within the range of expected changes to inflow stream nutrient concentration in the catchment given local zoning and development (Sunapee Area Watershed Coalition, 2008).

We ran each scenario from 1982 through 2015 and assessed differences between the 31-year distribution of annual maximum and summer median chlorophyll-*a* concentration. We compared 31-year annual distributions of annual maximum and summer median chlorophyll-*a* concentrations to assess the effects of each scenario across a range of weather and loading conditions using Anderson-Darling tests (Razali & Wah, 2011) with a Bonferroni correction in R (R version 3.3.3, R Core Team, 2017).

## 2.6. Confirmation of Conceptual Driver Pathways With Scenario Model Output

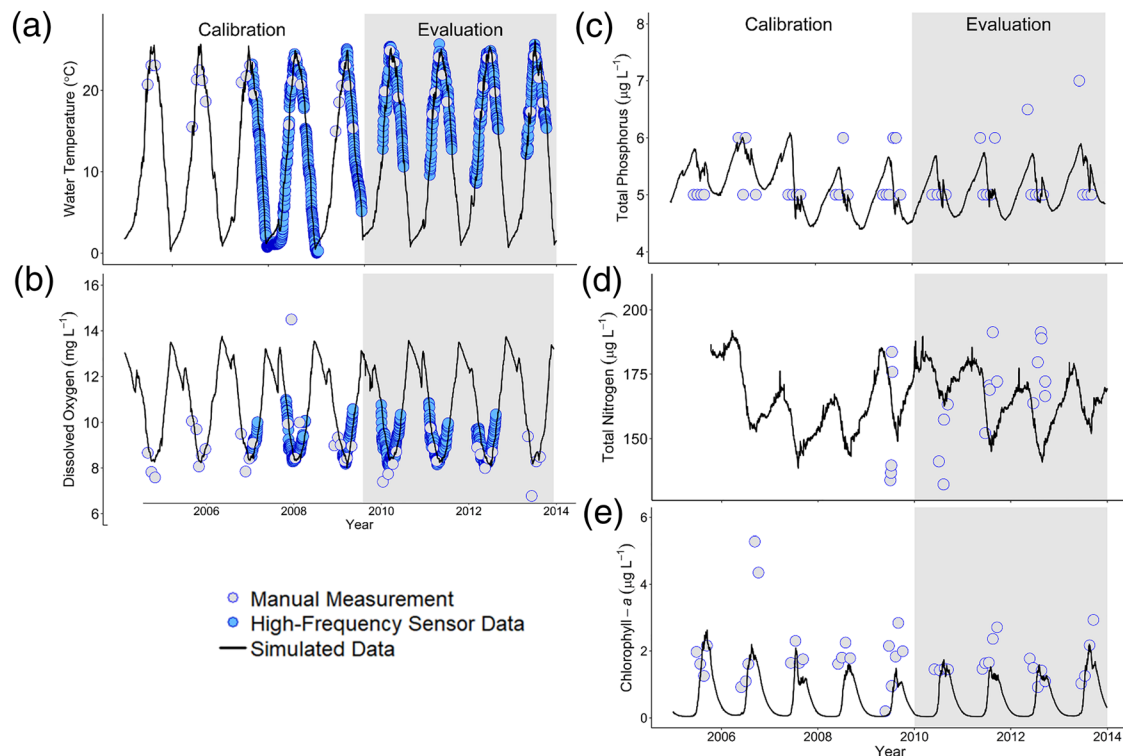
To explicitly link the detailed model outputs with the conceptual driver pathways (Figure 1), we examined the relationships between the driver variables identified in the reference analysis (section 2.4), mediating variables (e.g., epilimnetic nutrient concentration and phytoplankton nutrient uptake), and the response variables (summer median and annual maximum chlorophyll-*a* concentration) across scenarios (section 2.5). The goal of this analysis was to leverage results from both Question 1 and Question 2 to determine if the driver variables associated with the Air Temperature Pathway and Catchment Nutrient Pathway (Figure 1) that were identified as important in the reference simulation analysis actually influenced annual and summer chlorophyll-*a* concentrations in the model as conceptualized in Figure 1. For this analysis, we examined relationships between driver data variables (e.g., nutrient loads), mediating variables that were simulated in the model (i.e., the variables that responded to changes in the driver variables and altered our focal response variables; e.g., epilimnetic P concentration and phytoplankton P uptake), and simulated focal response variables (annual maximum and summer median chlorophyll-*a* concentration) with Spearman correlations.

## 3. Results

### 3.1. Model Calibration and Evaluation

The GLM-AED model simulated water temperature and dissolved oxygen dynamics during the calibration (2005–2009) and evaluation (2010–2013) phase that closely tracked the observed data (Figures 3a and 3b).





**Figure 3.** Simulated and observed surface (0–6 m) mean water temperature (a); simulated and observed dissolved oxygen 1 m below the surface (b); simulated and observed surface (0–6 m) mean total phosphorus (c); simulated and observed surface (0–6 m) mean total nitrogen (d); and simulated and observed surface (0–3 m) mean chlorophyll-*a* (e). The white panel background is the calibration phase and gray panel background is the evaluation phase (for goodness-of-fit metrics, see Table 2). The method detection limit for total phosphorus observations in panel (c) was  $5 \mu\text{g L}^{-1}$ .

The goodness-of-fit metrics for high-frequency sensor data comparisons (water temperature and dissolved oxygen; Table 2, Figure 3) were within the range of previous GLM-AED simulations on north temperate lakes (e.g., Kara et al., 2012; Snorheim et al., 2017). In both simulated and observed data, surface water temperature warmed to  $\sim 25^{\circ}\text{C}$  in the summer and cooled to  $0^{\circ}\text{C}$  in the winter (Figure 3a). Simulated dissolved oxygen at 1 m decreased in the summer to  $\sim 8.5 \text{ mg L}^{-1}$  and increased in the winter to  $\sim 12.5 \text{ mg L}^{-1}$  (Figure 3b).

GLM-AED simulated mean epilimnetic phosphorus, nitrogen, and chlorophyll-*a* concentrations during the calibration (2005–2009) and evaluation (2010–2013) phase were within the range expected for oligotrophic lakes (Figures 3c, 3d, and 3e). Given the low number of field observations for epilimnetic TP, TN, and chlorophyll-*a* concentrations, as well as the absence of subseasonal patterns in observational data, we compared medians and ranges of simulated and observed TP, TN, and chlorophyll-*a* concentrations on the days of observation in addition to the goodness-of-fit metrics (Table 2). Simulated epilimnetic TP (Figure 3c;  $5.1\text{--}6.2 \mu\text{g L}^{-1}$ ; median =  $5.6 \mu\text{g L}^{-1}$ ,  $n = 40$ ) was similar to observed epilimnetic TP ( $5.0\text{--}7.0 \mu\text{g L}^{-1}$ ; median =  $5.0 \mu\text{g L}^{-1}$ ,  $n = 40$ ), and simulated epilimnetic TN (Figure 3d;  $143\text{--}170 \mu\text{g L}^{-1}$ ; median =  $162 \mu\text{g L}^{-1}$ ,  $n = 21$ ) was similar to observed epilimnetic TN ( $127\text{--}191 \mu\text{g L}^{-1}$ ; median =  $167 \mu\text{g L}^{-1}$ ,  $n = 21$ ). Simulated surface chlorophyll-*a* concentration (Figure 3e;  $0.1\text{--}2.2 \mu\text{g L}^{-1}$ ; median =  $0.9 \mu\text{g L}^{-1}$ ,  $n = 41$ ) was less than observed surface chlorophyll-*a* concentration ( $0.2\text{--}5.3 \mu\text{g L}^{-1}$ ; median =  $1.64 \mu\text{g L}^{-1}$ ,  $n = 41$ ). Overall, the model represented oligotrophic lake conditions well (e.g., mean chlorophyll-*a*  $< 2.6 \mu\text{g L}^{-1}$  and TP  $< 12 \mu\text{g L}^{-1}$ , Carlson, 1977; Figure 3). The model adequately represented the central tendencies of observed chlorophyll-*a* concentration but did not predict the peaks and slightly overpredicted TP (Table 2). The C:N in the lake was approximately 1:8 throughout the simulation, with particulate N composing the largest fraction of TN, similar to observations of littoral TN in Lake Sunapee. We note that our observed TP concentrations were very low (often below laboratory method detection limits and limits of quantitation).

**Table 2**

Goodness-of-Fit Metrics for Comparing Observed and Simulated GLM-AED Data for Lake Sunapee, NH, USA: Coefficient of Determination From Linear Regression ( $R^2$ ), Root Mean Square Error (RMSE), Percent Bias (PBIAS), Nash-Sutcliffe Efficiency (NSE), Mean Absolute Error (MAE); and  $n$  is the Number of Observed Measurements

Variable	Observation	Model period	$n$	$R^2$	RMSE	PBIAS	NSE	MAE
Temperature (°C) (0–6 m)	Buoy (daily max)	Calibration	781	0.99	1.25	6.0	0.98	1.05
		Evaluation	480	0.97	0.84	2.4	0.96	0.72
	Manual	Calibration	26	0.81	1.5	1.6	0.69	1.21
		Evaluation	14	0.85	1.34	1.3	0.74	1.10
Dissolved Oxygen ( $\text{mg L}^{-1}$ ) (1 m)	Buoy (daily mean)	Calibration	415	0.57	0.43	−0.4	0.51	0.36
		Evaluation	278	0.57	0.42	0.4	0.48	0.34
	Manual	Calibration	26	0.07	1.34	1.9	0	0.77
		Evaluation	21	0.53	0.67	5.1	−0.04	0.51
Total P ( $\mu\text{g L}^{-1}$ ) (0–6 m)	Manual	Calibration	26	0.02	0.64	8.2	−1.62	0.55
		Evaluation	14	0.14	0.69	6.0	−0.11	0.64
Total N ( $\mu\text{g L}^{-1}$ ) (0–6 m)	Manual	Calibration	10	0.38	26.72	11.6	−1.06	24.16
		Evaluation	11	0.64	29.49	−13.9	−5.25	26.30
Chlorophyll- $a$ ( $\mu\text{g L}^{-1}$ ) (0–3 m)	Manual	Calibration	27	0.19	1.36	−54	−0.94	1.08
		Evaluation	14	0.12	1.11	−50	−2.46	0.95

Note. Each goodness of fit metric was calculated comparing model outputs and observational data for the time period (Calibration 2005–2009 or Evaluation 2010–2013) of interest.

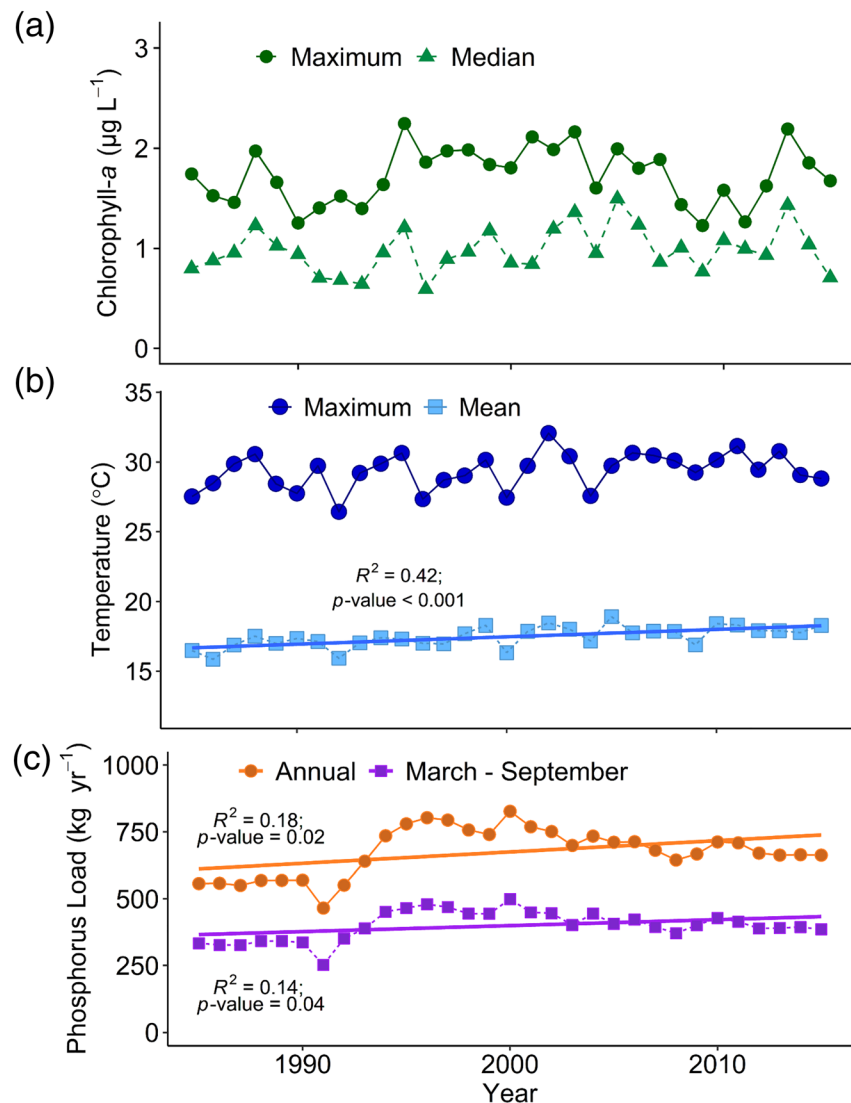
### 3.2. Driver Data and Primary Response Variable Trends Over Simulation Period

Over the 31-year reference simulation, simulated June–September median and annual maximum chlorophyll- $a$  concentration did not increase or decrease (Figure 4a), following historical records of Lake Sunapee (Steiner & Titus, 2017; NHDES, 2017): the temporal trend for simulated summer median chlorophyll- $a$  had  $R^2 = 0.02$ ,  $p = 0.18$ ; annual maximum chlorophyll- $a$  had  $R^2 = -0.02$ ,  $p = 0.50$ . Simulated June–September median chlorophyll- $a$  concentration ranged from 0.6 to 1.4  $\mu\text{g L}^{-1}$  (mean = 1.0  $\mu\text{g L}^{-1}$ ; SD = 0.23) over the 31 years. Simulated annual maximum chlorophyll- $a$  concentration ranged from 1.2 to 2.2  $\mu\text{g L}^{-1}$  among years (mean = 1.7  $\mu\text{g L}^{-1}$ ; SD = 0.29).

There was an increasing trend in observed June–September mean air temperature and external phosphorus load from 1985 to 2015, but there was no significant change in annual maximum air temperature (Figures 4b and 4c). Observed June–September mean air temperature ranged from 15.9 to 18.9°C (mean = 17.5°C; SD = 0.74), and increased over the simulation period at a rate of 0.05°C yr<sup>−1</sup> ( $R^2 = 0.42$ ,  $p < 0.001$ ; Figure 4b). Observed annual maximum air temperature ranged from 26.4°C to 32.08°C (mean = 29.4°C; SD = 1.29;  $R^2 = 0.10$ ,  $p = 0.50$ ). Most external P entered the lake between March and September of each year. Total annual external P load ranged from 465 to 826 kg (mean = 674 kg, SD = 89.8), and increased over the simulation period at a rate of 4.2 kg yr<sup>−1</sup> ( $R^2 = 0.18$ ,  $p = 0.02$ ). March–September external phosphorus (P) load ranged from 252 to 499 kg (mean = 399 kg; SD = 55 kg), and increased at a rate of 2.2 kg yr<sup>−1</sup> ( $R^2 = 0.14$ ,  $p = 0.04$ ; Figure 4C).

### 3.3. Question 1: Reference Simulation Analysis—Relationships Between Annual Maximum Versus Median Chlorophyll- $a$ Concentration and Climate and Catchment Load Drivers

Simulated annual maximum and summer median chlorophyll- $a$  concentrations were sensitive to different drivers (Table 3). Simulated annual maximum chlorophyll- $a$  concentration was the most strongly correlated with 3-year sum of external March–September TP load (Table 3; Spearman rho = 0.65,  $p < 0.001$ ,  $n = 31$ ). In contrast, simulated annual median chlorophyll- $a$  concentration was most strongly correlated with June–September maximum air temperature (Table 3; Spearman rho = 0.67,  $p < 0.001$ ,  $n = 31$ ) (Table S2). A subset of the driver variables analyzed with the strongest response variable relationships and additional representative driver variables from each pathway are presented in Table 3; Spearman correlation results for all driver variables tested are listed in Table S2.



**Figure 4.** Time series of simulated summer maximum (circle, solid line) and median (triangle, dashed line) chlorophyll-*a* concentrations aggregated on an annual scale in the surface (0–3 m) over the 31-year simulation (a); annual maximum (circle, solid line) and summer mean air (square, dashed line) temperature from North American Land Data Assimilation System (NLDAS-2) website (Xia et al., 2012) (b); and annual (circle, solid line) and March through September (square, dashed line) external phosphorus load (c).

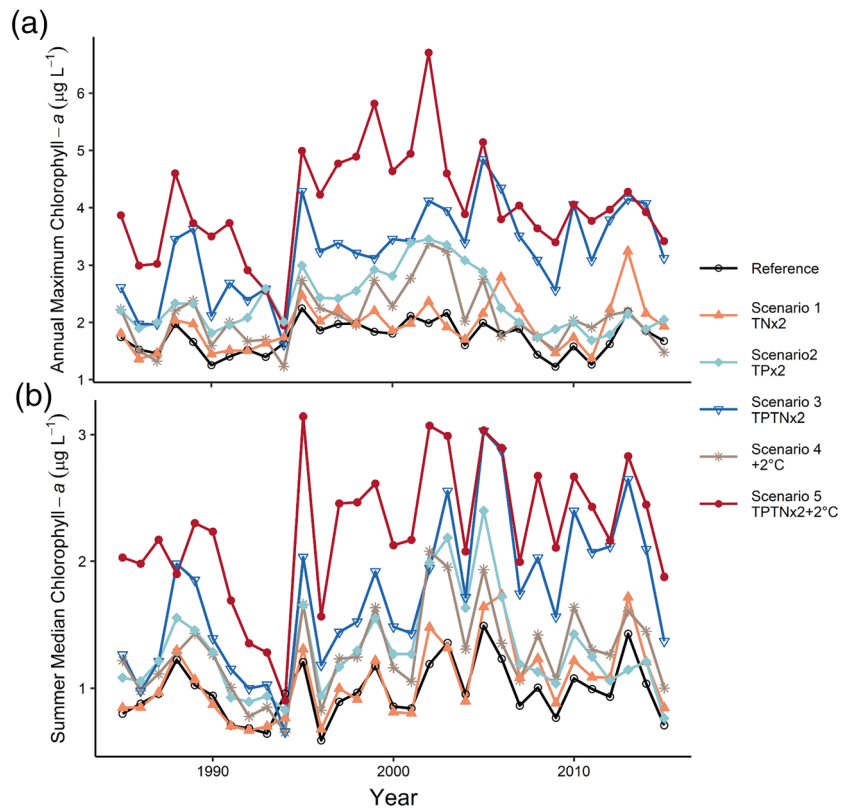
### 3.4. Question 2: Scenario Analysis—Response of Maximum Versus Median Chlorophyll-*a* Concentrations to Projected Increases in Stream Inflow Nutrient Concentration and Air Temperature

Increases in combined nitrogen and phosphorus inflow concentrations had a stronger effect on both summer median and annual maximum chlorophyll-*a* concentrations than temperature or single nutrient additions alone (Figures 5 and 6). In each year of the 31-year simulation, summer median chlorophyll-*a* concentration was 0.9 to 2.1 times higher in Scenario 3: TNTP  $\times 2$  than in Scenario 4:  $+2^{\circ}\text{C}$  (Figures 5 and 6). Similarly, annual maximum chlorophyll-*a* concentration was 1.1 to 2.5 times higher in Scenario 3: TNTP  $\times 2$  than in Scenario 4:  $+2^{\circ}\text{C}$  (Figures 5 and 6). Further, summer median chlorophyll-*a* concentrations were 0.8 to 2.3 times higher in Scenario 3: TNTP  $\times 2$  than in Scenario 1: TN  $\times 2$  or Scenario 2: TP  $\times 2$  (Figures 5 and 6). Similarly, Scenario 3: TNTP  $\times 2$  exhibited annual maximum chlorophyll-*a* concentrations between 0.8 and 2.2 times higher than annual maximum chlorophyll-*a* concentrations in Scenario 1: TN  $\times 2$  or Scenario 2: TP  $\times 2$  (Figure 5).

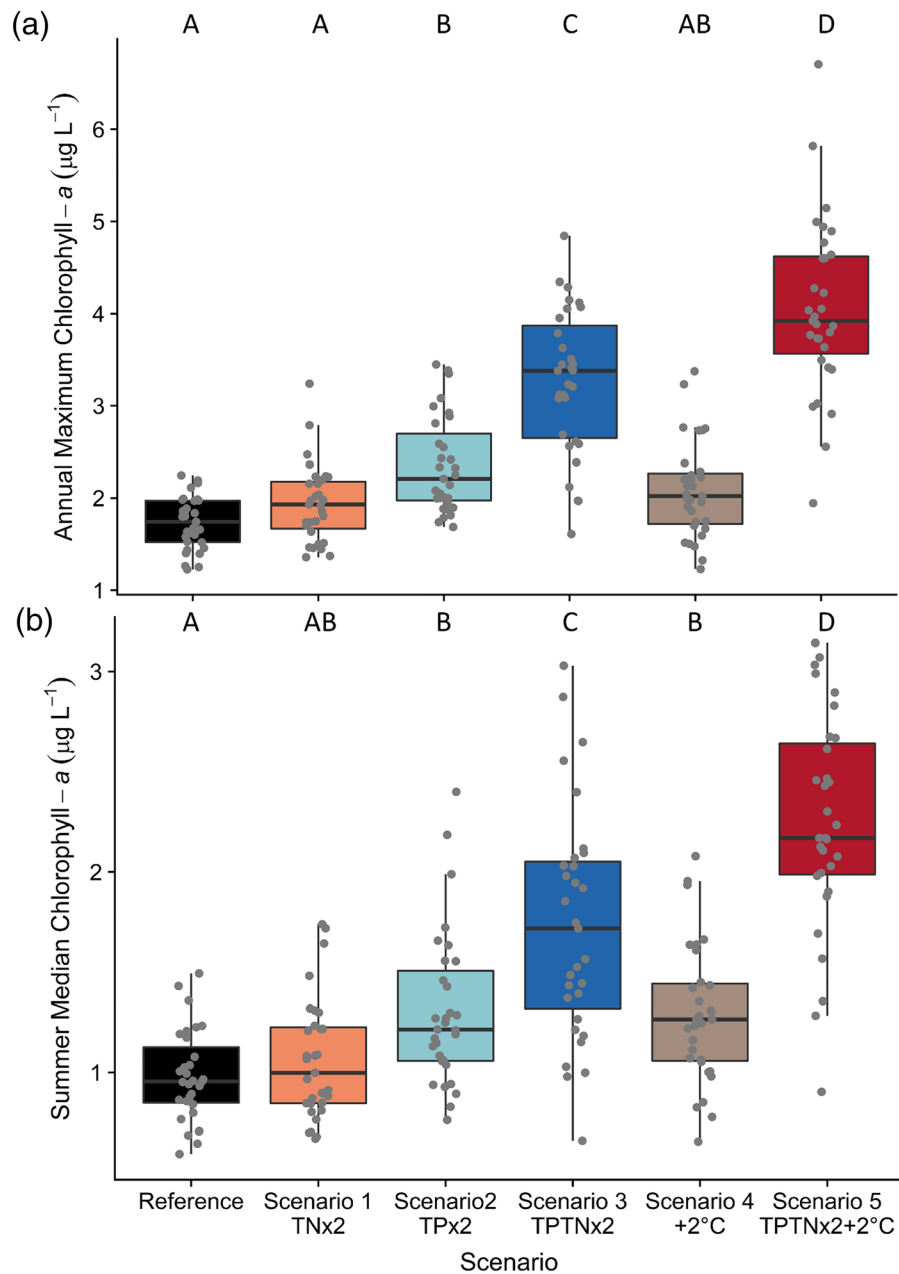
**Table 3**  
Spearman Correlation Coefficients for Driver Variable Aggregations and Annual Maximum and Summer Median Chlorophyll-*a*

Category	Variable	Annual max Chl- <i>a</i>	Summer median Chl- <i>a</i>
Air Temperature (climate driver: Air Temperature Pathway in Figure 1)	Mean of 3 years June–September maximum temperature	0.21	0.47 <sup>**</sup>
	<b>Annual maximum temperature</b>	0.29	<b>0.67<sup>***</sup></b>
Total Nutrient Load (combined land-use + climate driver: Catchment Nutrient Pathway & Precipitation Pathway in Figure 1)	<b>Sum 3-yr March–September TP</b>	<b>0.62<sup>***</sup></b>	0.26
	<b>Sum 3-yr March–May TP</b>	<b>0.58<sup>***</sup></b>	0.22
	<b>Sum 3-water years TP</b>	<b>0.62<sup>***</sup></b>	0.27
	Sum 3-yr March–September TN	0.25	0.21
	Sum 3-water years TN	0.33	0.29
	March–May TP	0.48 <sup>**</sup>	0.10
	March–May TN	0.11	−0.06
Total Precipitation (climate driver: Precipitation Pathway in Figure 1)	Sum 3-yr March–May	0.09	0.03
	Sum 3-yr Jun–Sept	−0.35 <sup>**</sup>	0.21
	Sum 3-yr March–September	−0.25 <sup>*</sup>	0.19
	June–Sept	−0.35 <sup>*</sup>	0.22
	Water year	−0.25	0.17

Note. Three-year metrics include the year of response and previous 2 years. Bold text denotes significance of  $p < 0.001$ . Spearman correlation results with all driver variables are listed in Table S2. Water year is from October 1 through September 30.  
Significance value of  $p < 0.05$ . Significance value of  $p < 0.01$ . Significance value of  $p < 0.001$ .



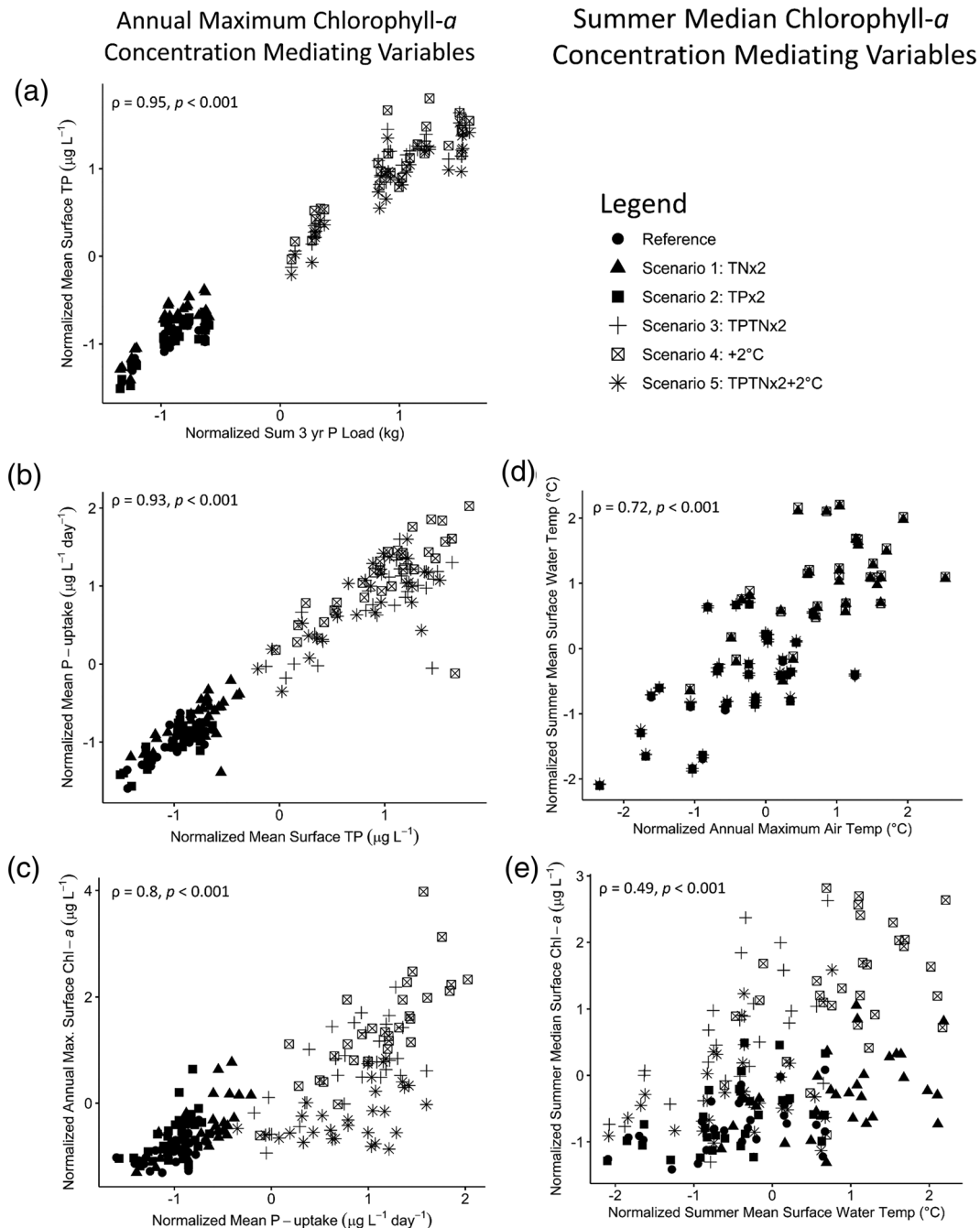
**Figure 5.** Time series of annual maximum and summer median chlorophyll-*a* for all scenarios (Reference = historical simulation; Scenario 1:  $TN \times 2 = 2 \times$  total nitrogen external load; Scenario 2:  $TP \times 2 = 2 \times$  total phosphorus external load; Scenario 3:  $TPTN \times 2 = 2 \times$  total phosphorus and total nitrogen external load; Scenario 4:  $+2^\circ C =$  air temperature warming; Scenario 5:  $TPTN \times 2 + 2^\circ C = 2 \times$  total phosphorus and total nitrogen external load plus air temperature warming) for annual maximum chlorophyll-*a* concentrations (a) and summer median chlorophyll-*a* concentrations (b).



**Figure 6.** Distributions of 31-year annual maximum and median chlorophyll-*a* for five land use and climate scenarios (Reference = historical simulation; Scenario 1:  $TN \times 2 = 2 \times$  total nitrogen external load; Scenario 2:  $TP \times 2 = 2 \times$  total phosphorus external load; Scenario 3:  $TPTN \times 2 = 2 \times$  total phosphorus and total nitrogen external load; Scenario 4:  $+2^\circ\text{C} =$  air temperature warming; Scenario 5:  $TPTN \times 2 + 2^\circ\text{C} = 2 \times$  total phosphorus and total nitrogen external load plus air temperature warming); a unique letter above a boxplot denotes a significantly different distribution from other scenarios (Bonferroni-corrected  $p < 0.002$ , Anderson-Darling test) for annual maximum chlorophyll-*a* concentrations (a) and summer median chlorophyll-*a* concentrations (b).

Warmer air temperature had a significant effect on summer median chlorophyll-*a* concentrations at both ambient and elevated nutrient inflow concentrations, but only increased annual maximum chlorophyll-*a* concentration at elevated nutrient inflow concentrations (Figure 6). Specifically, combined warmer air temperatures and increased nitrogen and phosphorus nutrient inflow concentrations (Scenario 5:  $TNTP \times 2 + 2^\circ\text{C}$ ) increased both annual maximum and summer median chlorophyll-*a* concentrations in comparison to Scenario 3:  $TPTN \times 2$  (Bonferroni-corrected  $p < 0.002$ ; Figure 6). However, warmer air temperatures (Scenario 4:  $+2^\circ\text{C}$ ) significantly affected summer median (Bonferroni-corrected  $p < 0.002$ ; Figure 6b), but not annual maximum chlorophyll-*a* concentrations, in comparison to the reference





**Figure 7.** Spearman correlations between simulation output of driver variable (external TP load), mediating variables (surface water TP concentration, P uptake), and annual maximum chlorophyll-*a* concentration (a–c); between driver variable (air temperature), mediating variable (water temperature), and summer median chlorophyll-*a* concentration (d–e).

simulation (Bonferroni-corrected  $p = 0.01$ ; Figure 6a). In the air temperature scenario (Scenario 4: +2°C), onset of thermal stratification was an average of 6 days earlier, thermocline depth was an average of 1.1 m lower, and summer surface water temperature was an average 1.3°C warmer than in the Reference simulation.

### 3.5. Confirming Driver Pathways

In the reference simulation analysis (section 3.3, Table 3), external P load was identified as the driver variable most associated with annual maximum chlorophyll-*a* concentration. We confirmed that the

Catchment Nutrient Pathway was the likely primary pathway by which external P load affected annual maximum chlorophyll-*a* concentration in the reference simulation, as indicated by the significant relationships between (1) total TP load and surface TP concentration (Figure 7a; Spearman  $\rho = 0.95$ ,  $p < 0.001$ ), (2) surface TP concentration and phytoplankton P uptake (Figure 7b; Spearman  $\rho = 0.93$ ,  $p < 0.001$ ), and (3) phytoplankton P uptake and annual maximum chlorophyll-*a* concentration (Figure 7c; Spearman  $\rho = 0.80$ ,  $p < 0.001$ ).

In the reference simulation analysis (section 3.3), air temperature was identified as the driver most associated with summer median chlorophyll-*a* concentration (Table 3). We confirmed that the Air Temperature Pathway was the likely primary pathway by which air temperature affected summer median chlorophyll-*a* concentration response, as indicated by the significant relationship between (1) air temperature and water temperature (Figure 7d; Spearman  $\rho = 0.72$ ,  $p < 0.001$ ), and (2) water temperature and summer median chlorophyll-*a* concentration (Figure 7e; Spearman  $\rho = 0.49$ ,  $p < 0.001$ ).

#### 4. Conclusions

By pairing long-term empirical data and a simulation model, our study revealed that climate and land-use drivers had different effects on median and maximum chlorophyll-*a* concentrations in Lake Sunapee, highlighting the complexity of overall lake ecosystem responses to global change. Lake ecosystems have nonlinear and interrelated biogeochemical processes, in which high variability in meteorological and nutrient load drivers can interact with phytoplankton dynamics to result in variable chlorophyll-*a* concentrations within and among years (Carey et al., 2016; Carpenter & Kitchell, 1987). Based on the results of our retrospective modeling and scenario analysis (section 3.3, Table 3), we focus on the Air Temperature Pathway and Catchment Nutrient Pathway in the discussion below (Figure 1), though we recognize the importance of the Precipitation Pathway (Collins et al., 2019), particularly as related to its interaction with the Catchment Nutrient Pathway through increased extreme precipitation events leading to sediment mobilization and increased nutrient loads to lakes (Carpenter et al., 2018; Sinha et al., 2017).

##### 4.1. Time Scales of Influence

Our primary reference simulation result—that median chlorophyll-*a* concentration was significantly positively associated with *summer* air temperature while maximum chlorophyll-*a* concentration was significantly positively associated with *three-year* external P load (Table 3)—supports evidence that ecosystem drivers operate simultaneously on different time scales (*sensu*; Rinaldi & Scheffer, 2000). The Air Temperature Pathway (Figure 1) operates at daily and seasonal scales by altering the physical environment for phytoplankton through effects on water temperature (Liu et al., 2019), thermal stratification, mixing, and temperature-mediated biogeochemical reactions (Hamilton & Schladow, 1997). In contrast, given the 3-year residence time of Lake Sunapee, phytoplankton response to land-use change (Catchment Nutrient Pathway, Figure 1) operates over the course of years, resulting in time lags between land-use changes in the catchment, nutrient loads to the lake, and chlorophyll-*a* concentration. Consequently, it logically follows that chlorophyll-*a* concentration was differentially sensitive to these two pathways at different time scales.

In lake ecosystems and their catchments, as well as in GLM-AED model simulations, the pathways highlighted in Figure 1 are integrated, thereby resulting in ecological signals (e.g., chlorophyll-*a* concentration) with multiple time scales of variability. We found that annual maximum chlorophyll-*a* concentration in the reference simulation was most associated with 3-year external TP load (Table 3) and that increasing temperature alone (Scenario 4: +2°C) did not significantly change annual maximum chlorophyll-*a* concentration (Figure 6). The association of annual maximum chlorophyll-*a* concentration with the previous 3 years of external TP loading was in contrast to the expectation that peak phytoplankton biomass is most sensitive to within-year drivers (e.g., Batt et al., 2017). However, because annual maximum chlorophyll-*a* concentration did significantly increase in response to temperature at elevated TN and TP loads (compare Scenario 3 and Scenario 5 in Figure 6), it is possible that changes in multiyear drivers (e.g., years of elevated TN and TP loading) create ambient conditions that interact with daily or seasonal drivers (e.g., optimal air temperatures) to promote high chlorophyll-*a* concentrations. This relationship could be an example of “accumulative carryover” (Ryo et al., 2019), in which longer-term increases in TN and TP loading create the conditions upon which optimal air temperature conditions are able to stimulate phytoplankton to a greater extent than if the 3-year TN and TP loads had been lower. While linking the year-to-year

variability within a single simulation directly to the interaction of 3-year external TP load and daily air temperature is beyond the scope of our analysis, the divergence among Scenarios 3 and 5, but not between Scenario 4 and the reference simulation (Figure 6), supports our hypothesis of interactions between longer-term and shorter-term drivers (Rinaldi & Scheffer, 2000; Ryo et al., 2019). The relationship between drivers at different timescales could include lagged effects from extreme years (e.g., droughts and heat waves), though this is also beyond the scope of our analysis. However, taken together, our reference simulation analysis and scenario results suggest that the underlying causes of peak phytoplankton concentrations are likely a combination of daily and multiyear drivers (as outlined in Figure 1).

The ability to tease apart ecosystem drivers with different time scales of influence on chlorophyll-*a* concentration was only possible via a study that spanned many years. If we only analyzed 1 year of the 31-year reference simulation, our inferences about the drivers of chlorophyll-*a* concentrations in Lake Sunapee likely would not have been applicable to other years (Figure 4). Similarly, multiple years were needed to interpret the scenarios, as individual years exhibited different driver conditions and chlorophyll-*a* concentration responses (Figure 5). A sensitivity analysis (Figures S13 and S14) reveals that, on average, 15–20 simulation years were needed in the scenario distributions analysis to replicate the significant differences observed among all the scenarios for annual and summer chlorophyll-*a* concentration. The clarity of the long-term synoptic view apparent in the comparison of scenarios across 31 years (Figure 6) demonstrates the power of, and need for, long-term analysis for assessing complex ecosystem responses to drivers of change (e.g., Dodds et al., 2012; Hampton et al., 2019; Likens, 1988).

#### 4.2. Underlying Mechanisms

The model simulation results provide insights into the potential mechanisms by which changes in air temperature and nutrient load drivers affected chlorophyll-*a* concentrations. Although GLM-AED is a deterministic model, it is not possible to trace an emergent lake ecosystem property, such as epilimnetic chlorophyll-*a* concentration, to its climate or land-use drivers through the model simulation equations because of the interdependency of model processes, high temporal and spatial (vertical) resolution of process interactions, and nonlinear dynamics. A common solution to this problem is to evaluate model output for broad relationships known to be ecologically relevant, such as nutrient availability and phytoplankton biomass, following Snorheim et al. (2017).

The strong associations between driver variables (e.g., external P load and air temperature), mediating variables that were simulated in the model (i.e., the variables that responded to changes in the driver variables and altered our focal response variables, such as epilimnetic P concentration and water temperature), and simulated focal response variables reveal the likely mechanistic driver pathways of chlorophyll-*a* concentration in Lake Sunapee (Figures 1 and 7; section 3.5). However, each driver pathway is not isolated from other potential pathways. For example, epilimnetic P concentration was modified in our scenarios via increased inflow stream P concentration (as a proxy for the Catchment Nutrient Pathway, e.g., chronic P additions from septic systems); however, increased erosion due to extreme precipitation could also increase inflow stream P concentration. Thus, our analysis is not intended to be exhaustive assessment of potential driver pathways of change in lake ecosystems, but rather to add to a growing understanding of the role of interacting driver pathways within the context of regional and local climate change (McCullough et al., 2019). While warming air temperatures will likely increase median chlorophyll-*a* concentrations in Lake Sunapee via warmer water temperatures (following Collins et al., 2019; Figure 7), warming air temperatures will also alter lake thermal stratification strength and timing (Kraemer et al., 2015; Woolway et al., 2019), and in turn, hypolimnetic dissolved oxygen concentrations and internal nutrient load dynamics (Marcé et al., 2010; North et al., 2014). Additionally, the interactive effect of multiple drivers of change (i.e., that temperature may have greater effect on annual maximum chlorophyll-*a* concentration at elevated TN and TP loads, Figure 6) highlights the need to understand how the pathways interact across a wide range of conditions.

The specific response of lake variables to pathways of change are mediated through lake-specific characteristics. For example, the Air Temperature Pathway can be mediated by DOC concentration, in which high DOC limits light penetration, thereby buffering the lake water temperature from rising air temperature (Read & Rose, 2013). The DOC-light penetration relationship also affects thermocline depth and is itself mediated by lake size, in which thermocline depth in larger lakes is less dependent on DOC-driven light limitation due to a stronger effect of wind-driven mixing of the epilimnion (Zwart et al., 2016). In sum,

interacting pathways and lake-specific characteristics must be taken into account when interpreting the broad relationships observed in the Reference simulation and scenario testing model output.

Ecosystem models, in conjunction with observational data, reveal potential interactions that would be challenging to observe using empirical data alone. Emergent model simulation patterns inform our understanding of how lake ecosystems may function given our process-based knowledge. For example, in the scenario testing (section 3.4), annual maximum chlorophyll-*a* concentration increased more in the combined increased external TP and TN load scenario than in the increased external TP alone scenario (Figure 6), suggesting that co-limitation or serial limitation (Lewis et al., 2020) may play important roles governing chlorophyll-*a* concentrations in this ecosystem.

Dissolved inorganic nitrogen (DIN) to TP mass ratios in the scenarios demonstrate how Lake Sunapee's nutrient limitation may change in the future, following Bergström (2010)'s previous application of DIN:TP to identify limiting nutrients in oligotrophic lakes. In most years of the Reference simulation, DIN:TP is between 1.5 and 3.4 (Figure S15), a ratio at which co-limitation is expected (Bergström, 2010). In Scenario 1: TN  $\times$  2 and Scenario 2: TP  $\times$  2, the DIN:TP in most years shifts above 3.4 and below 1.5, indicating likely P-limitation and N-limitation, respectively, in response to nutrient addition. In the warming scenarios (Scenario 4: +2°C and Scenario 5: TPTN  $\times$  2 + 2°C), DIN:TP shifts toward N-limitation, in comparison to the Reference simulation and Scenario 3: TPTN  $\times$  2, respectively. Thus, it is not surprising that we observed co-limitation in the scenario results, which both supports previous studies conducted in other low-nutrient systems (Bergström, 2010; Lewis & Wurtsbaugh, 2008; Oleksy, 2019; Paerl et al., 2016; Saros et al., 2010) and informs future empirical work in Lake Sunapee.

Further, the significant difference in annual maximum chlorophyll-*a* concentration between Scenario 3: TPTN  $\times$  2 and Scenario 5: TPTN  $\times$  2 + 2°C and lack of significant difference between the reference simulation and Scenario 4: +2°C (Figure 6) indicate that temperature may have a larger effect on annual maximum chlorophyll-*a* concentration at higher TP concentrations. Separately, summer median chlorophyll-*a* concentration in the reference analysis was not associated with nutrient load, but significantly increased in Scenario 3: TPTN  $\times$  2, indicating that both the Air Temperature Pathway and Catchment Nutrient Pathway are important for summer median chlorophyll-*a* concentration response. These findings were made possible by our long-term ecosystem modeling approach with combined reference simulation analysis and scenario testing.

### 4.3. Modeling Oligotrophic Lake Dynamics

Our calibrated model tended to slightly overestimate total phosphorus concentrations and underestimate chlorophyll-*a* concentrations, potentially identifying limits to our ability to simulate phytoplankton dynamics in oligotrophic lakes. The phosphorus uptake and growth rate algorithms developed for GLM-AED may function better in mesotrophic or eutrophic lakes, where this model and similar other models have primarily been applied (e.g., Bruce et al., 2006; Gal et al., 2009; Kara et al., 2012; Snorheim et al., 2017). For example, phytoplankton may take up and store nutrients more rapidly than expected by current model algorithms due to their scavenging of organic N and P at lower inorganic nutrient concentrations (McKew et al., 2015). Further, warmer temperatures may facilitate increased nutrient uptake at low inorganic N to P ratios in oligotrophic lakes (Oleksy, 2019). Improving the representation of organic nutrient scavenging and other adaptations of phytoplankton taxa to oligotrophic conditions would potentially improve overall model fit of nutrient and chlorophyll-*a* concentrations in low-nutrient lakes.

Modeling low-nutrient systems such as Lake Sunapee is also challenging because lake nutrient samples are often near detection levels. Thus, water quality metrics often show few or no detectable patterns over time (Richardson et al., 2017). Although a water quality monitoring program has existed at Lake Sunapee for over 30 years (NHDES, 2017), most years have only three or four measurements of summer chlorophyll-*a* concentration, limiting our ability to validate hourly model output with observational data. Historical data sparsity emphasizes the importance of long-term modeling studies, where we can leverage limited observational data with our process understanding of ecosystem functioning to make inferences about ecosystem dynamics.

As oligotrophic freshwater systems become less common (Stoddard et al., 2016), it is important to understand *a priori* the role of climate and land use in driving lakes to a trophic state change. Thus, improving our ability to understand lake ecosystems when many metrics are at or below method detection limits is

critical. Future work in this area could include using mechanistic understanding from experiments to improve process-based models (e.g., Carpenter et al., 2011), paleoecological examination of lake dynamics (e.g., Jenny et al., 2015), and further long-term simulation modeling to tease apart the sensitivity of lakes to processes relevant in oligotrophic lake ecosystems.

#### 4.4. Managing Oligotrophic Lakes

This study may inform lake monitoring programs. Our results indicate that median chlorophyll-*a* concentration may increase due to higher air temperature or nutrient load, but maximum chlorophyll-*a* will likely only increase with a higher nutrient load. Thus, the upper bound of chlorophyll-*a* concentrations is likely determined by the nutrient supply, which is generally expected in nutrient-limited oligotrophic lakes. Additionally, given that air temperatures are expected to increase in many regions due to climate change, maximum chlorophyll-*a* concentration is potentially a more sensitive metric in oligotrophic lakes for assessing nutrient load restrictions than median chlorophyll-*a* concentration.

Our work also highlights that oligotrophic lakes may be particularly sensitive to the combined threat of climate and land-use change. Similar to findings in other studies (e.g., Ho et al., 2019), there is mounting evidence that oligotrophic lakes are particularly sensitive to a changing climate separate from land-use-induced increases in nutrient load (Carey, Ibelings, et al., 2012; McCullough et al., 2019; Oleksy, 2019; Sadro et al., 2019). Our scenario analysis indicates that increased nutrient load in combination with higher air temperature had the greatest effect on chlorophyll-*a* concentration (Figure 6), furthering the evidence of the dual threat of climate and land-use change. This is similar to other studies finding interactive effects of climate and other eutrophication drivers (Jeppesen et al., 2010; Moss et al., 2011; Oleksy, 2019; Trolle et al., 2011). Therefore, it is likely that nutrient load reduction targets to achieve water quality goals should be even lower in a changing climate, following earlier work by Jeppesen et al. (2009), Brookes and Carey (2011), and Kosten et al. (2012).

Oligotrophic lake ecosystems provide essential ecosystem services (Batabyal et al., 2003), which makes it imperative to figure out how to maintain oligotrophic lake systems into the future in the face of their decline (Stoddard et al., 2016). Two main findings from this study provide context for managing oligotrophic lakes: (1) the differential response of maximum versus median chlorophyll-*a* concentration to nutrient loading and air temperature highlights the need to consider different aggregation metrics when assessing oligotrophic lake ecosystem response to changing drivers, and (2) the interaction between air temperature and nutrient load imply that even more ambitious nutrient load reductions may be required in a warming climate to achieve water quality goals. Given the rapid loss of oligotrophic lakes and the potential for interactive threats associated with climate and land-use change, this study sets the stage for future research and provides useful perspective on how to manage oligotrophic lakes in the face of climate and land-use change.

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#### Data Availability Statement

Data sets for this research are available in these in-text data citation references: Ward et al. (2020), (CC BY license, public access available at [environmentaldatainitiative.org](https://environmentaldatainitiative.org)), Richardson et al. (2020), (CC BY license, public access available at [environmentaldatainitiative.org](https://environmentaldatainitiative.org)), Ewing et al. (2020), (CC BY license, public access available at [environmentaldatainitiative.org](https://environmentaldatainitiative.org)), Cottingham (2020) (CC BY license, public access available at [environmentaldatainitiative.org](https://environmentaldatainitiative.org)), Xia et al. (2012), (U.S. Public Domain, public access available at [disc.gsfc.nasa.gov/](https://disc.gsfc.nasa.gov/)), MRLC (2018), (U.S. Public Domain, public access available at [mrlc.gov/](https://mrlc.gov/)), CSRC (2002) (no license information provided, public access available at [granit.unh.edu/](https://granit.unh.edu/)). Models used in this research are available online (<http://aed.see.uwa.edu.au/research/models/GLM/> and <https://github.com/AquaticEcoDynamics/GLM>).

#### Conflict of Interest

The authors declare no real or perceived conflicts of interest.

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