Environmental Science & Technology

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Climate Change Impacts on Harmful Algal Blooms in U.S. Freshwaters: A Screening-Level Assessment

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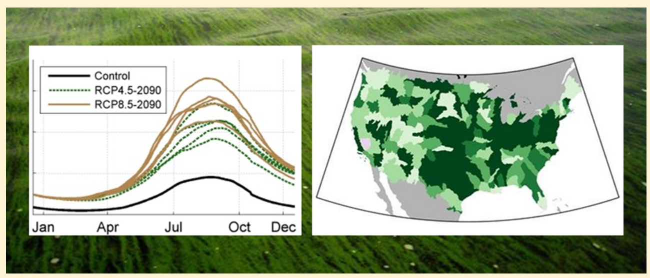
Supporting Information

ABSTRACT: Cyanobacterial harmful algal blooms (CyanoHABs) have serious adverse effects on human and environmental health. Herein, we developed a modeling framework that predicts the effect of climate change on cyanobacteria concentrations in large reservoirs in the contiguous U.S. The framework, which uses climate change projections from five global circulation models, two greenhouse gas emission scenarios, and two cyanobacterial growth scenarios, is unique in coupling climate projections with a hydrologic/water quality network model of the contiguous United States. Thus, it generates both regional and nationwide projections useful as a screening-level assessment of climate impacts on CyanoHAB prevalence as well as potential lost recreation days and associated economic value. Our projections indicate that CyanoHAB concentrations are likely to increase primarily due to water temperature increases tempered by increased nutrient levels resulting from changing demographics and climatic impacts on hydrology that drive nutrient transport. The combination of these factors results in the mean number of days of CyanoHAB occurrence ranging from about 7 days per year per waterbody under current conditions, to 16−23 days in 2050 and 18−39 days in 2090. From a regional perspective, we find the largest increases in CyanoHAB occurrence in the Northeast U.S., while the greatest impacts to recreation, in terms of costs, are in the Southeast.



1. INTRODUCTION

Cyanobacterial harmful algal blooms (CyanoHABs) can affect human health and welfare by degrading the quality of drinking water supplies, thereby complicating treatment for potable water, and forcing activity restrictions at recreational waterbodies. It is estimated that lakes and reservoirs that serve as sources of drinking water for 30−48 million Americans may be periodically contaminated by algal toxins.[1] Although drinking water treatment processes can reduce algal toxins (also called cyanotoxins), they are costly and the removal efficiency can be as low as 60%, potentially leaving water quality compromised.[1−3] For example, nearly 500 000 residents of Toledo, Ohio lost access to their drinking water in August 2014 after testing of water drawn from Lake Erie during a CyanoHAB revealed the presence of cyanotoxins near the city's water treatment plant's intake as well as in the treated water.[4] Cyanobacterial algal toxins were also responsible for nearly half of all reported waterborne disease outbreaks in U.S. untreated recreational freshwater in 2009 and 2010.[5]

Beyond the human health impacts resulting from cyanotoxins in drinking water supplies, CyanoHABs can have a variety of direct deleterious effects on aquatic ecosystems. The blooms result in a loss of water clarity, which suppresses the growth of aquatic plants, negatively affecting invertebrate and fish habitats. From an aesthetic and recreational standpoint, many

Received: March 22, 2017
Revised: June 22, 2017
Accepted: June 26, 2017
Published: June 26, 2017

cyanobacteria can become buoyant and form thick, unsightly surface scums. Under onshore wind conditions, the surface scums can wash up and concentrate on shorelines. Besides detracting from shoreline use and access, upon death their decomposition can lead to strong unpleasant odors, as well as bottom water hypoxia and anoxia. Furthermore, since most cyanobacteria are inedible by zooplankton and planktivorous fish[6−8] they represent a "dead end" in the aquatic food chain. Such sequestered organic carbon prevents waterbodies from supporting stocks of larger fish, crustaceans, and mollusks, and hence CyanoHAB impacts extend to both commercial and recreational fishing. In 2016, such recreational and fishery impacts occurred along beaches in South Florida due to CyanoHABs originating in Lake Okeechobee and flowing through rivers and canals to both Gulf and Atlantic beaches.[9]

These events and their associated impacts may increase in future climates with more frequent extreme precipitation events, which cause higher rates of runoff that carry excess fertilizers and other sources of nutrients into water bodies. Combined with warmer conditions, this increases the likelihood for favorable CyanoHAB-forming conditions. Increased vertical stratification, salinization, and lower pH in waterbodies, all of which are associated with climate change, are also linked to CyanoHAB event frequency, duration, and distribution.[10,11] Changes in climate variability may also play a role in increasing CyanoHAB frequency if increased periods of intense precipitation are followed by periods of drought, leading to longer residence times in reservoirs and allowing more time for bloom formation.[12,13]

In this research, we estimate the potential effect of climate change on the frequency of freshwater CyanoHAB occurrence in the U.S. This research employs a coupled water quantity and quality model of 2119 river basins of the contiguous U.S. (CONUS) to evaluate the effects of climate change. The purpose of this study is to provide a "screening assessment"[14] intended to provide broad insights to support planning, policy, and identify data or methodological gaps to guide future research on this issue that is unavoidably uncertain (through variability of climate, loading input data, biochemical rates, and hydrology, among many other factors). In this vein, our methods are intentionally simplified and are built entirely on well-established and accepted process formulations, kinetic rates, and transport and fate mechanisms, rather than in developing new modeling methods or conducting site-specific, data-intensive calibration. For this reason, we do not intend for these results to inform management of individual waterbodies, but rather to provide insight into cause and effect linkages, similar to previous screening studies.[15] This analysis represents a new component of the Climate Change Impacts and Risk Analysis (CIRA) project,[16] an ongoing effort to quantify and monetize the multisector risks of inaction on climate change and the benefits to the U.S. of global reductions in greenhouse gas emissions.

This study is described in the following sections: Section 2 (Methodological Approach), Section 3 (Sensitivity Analysis), and Section 4 (Results and Discussion). Table 1 provides a list of all acronyms used in the paper. For more details on methods, see the Supporting Information (SI), which includes (1) model framework diagram, (2) selection of GCMs, (3) runoff and water demand modeling, (4) water systems modeling, (5) QUALIDAD-HABs detailed description, (7) additional results, and (8) details on valuation.

Table 1. Acronyms Defined

acronym	definition
AR5	intergovernmental panel on climate change's fifth assessment report
BOD	biochemical oxygen demand
CanESM2	canadian earth system model
CCSM4	community climate system model, version 4
CIRA	climate change impacts and risk analysis
CLIRUN-II	climate runoff model, version 2
CMIP-5	coupled model intercomparison project, phase 5
CONUS	contiguous U.S.
CyanoHABs	cyanobacterial harmful algal blooms
DO	dissolved oxygen
ERF1	enhanced river reach file
GCMs	general circulation models
GHGs	greenhouse gases
GISS-E2-R	goddard institute for space studies modele/russell
HadGEM2-ES	hadley centre global environment model version 2 earth system
HAWQS	hydrologic and water quality system
HUCs	hydrologic unit codes
ICLUSv2	integrated climate and land use scenarios version 2
LOCA	localized constructed analogs
M&I	municipal and industrial
MIROC5	model for interdisciplinary research on climate, version 5
RCPs	representative concentration pathways
SPARROW	spatially referenced regressions on watershed attributes
US Basins	U.S. water resources systems model
WHO	World Health Organization

2. METHODOLOGICAL APPROACH

Our analytical framework builds upon previous work[17] and uses a series of linked models to evaluate the biophysical impacts of climate change on CyanoHAB occurrence in future climates. We assess the impacts of changes in terms of temperature, precipitation, nutrient loadings, water demands, and vertical stratification; however, the modeling does not take into account pH or salinization which we leave to future research. The model chain starts with projections from General Circulation Models (GCMs) for alternative future climates. GCM projections of precipitation, mean temperature, and daily temperature range are input into: (a) a rainfall-runoff model (CLIRUN-II[18]), which is used to simulate monthly runoff in each of the 2,119 8-digit hydrologic unit codes (HUCs) of the CONUS; and (b) a water demand model, which projects water requirements of the municipal and industrial (M&I) and agriculture sectors. Given these runoff and demand projections, a water resources systems model (U.S. Basins[17]) produces a time series of reservoir storage, release, and allocation to the various demands in the system (e.g., M&I, agriculture, environmental flows, transboundary flows, hydropower). We then use a modified version of the QUALIDAD water quality model[19] to incorporate this information on managed flows and reservoir states to simulate a number of water quality characteristics, including cyanobacteria concentrations, in waterbodies. Note that the modeling of cyanobacteria in QUALIDAD is first introduced in this study, while the other modeling processes build on previous work. For this reason, much of the detail on QUALIDAD is included in Section 4 of the SI. Finally, cyanobacteria concentrations are evaluated for their potential recreational impacts in terms of potential days of restricted recreational activity at specific sites, based on recommended thresholds for human health risk.[20]

DOI: 10.1021/acs.est.7b01498
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2.1. Emission Scenarios and Climate Projections. The greenhouse gases (GHG) emissions and climate scenarios used in this analysis are a subset of those generated for the Intergovernmental Panel on Climate Change's Fifth Assessment Report (AR5). For climate forcing, two Representative Concentration Pathways (RCPs) are used: RCP8.5 and RCP4.5. RCP8.5 represents a future with substantial warming caused by higher GHG emissions, which results in a total change in radiative forcing by 2100 (compared to 1750) of 8.5 W/m^2. RCP4.5 represents a future with significant global reductions in GHG emissions, achieving a total radiative forcing of 4.5 W/m^2 by 2100. We use five GCMs of the many generated for the AR5 as part of the Coupled Model Intercomparison Project Phase 5 (CMIP-5): CanESM2, CCSM4, GISS-E2-R, HadGEM2-ES, and MIROC5.[21] These projections were downscaled using a statistically based process that employs a multiscale spatial matching scheme to select analog days from observations across CONUS.[22] This data set, LOCA (Localized Constructed Analogs),[23] results in a $^1/_{16}$ degree resolution for daily maximum temperature, daily minimum temperature, and daily precipitation. For this analysis, all of these variables were aggregated to the 8-digit HUC scale of the CONUS. Furthermore, each climate projection through 2099 is split into four 20-year "eras"—2030 (2020–2039), 2050 (2040–2059), 2070 (2060–2079), and 2090 (2080–2099). Impacts in these future eras are compared to a "Control" scenario, which uses baseline climate over the years 1986–2005, with the added effect of population growth on future water demands and nutrient loadings.

2.2. Biophysical Modeling Overview. The biophysical model simulates CyanoHAB occurrence across the climate baseline and projections. Since CyanoHABs are more likely to form within water bodies that stratify in the summer, the focus of this work is on larger, deeper waterbodies across the CONUS, including over 300 individual reservoirs and 10 natural lakes important for recreation. Smaller reservoirs are aggregated to a single representative reservoir for each of the 8-digit HUCs. To provide a broad sense of the spatial distribution and size of reservoirs in the U.S. Basins model, Figure 1 displays total reservoir storage in each 8-digit HUC.

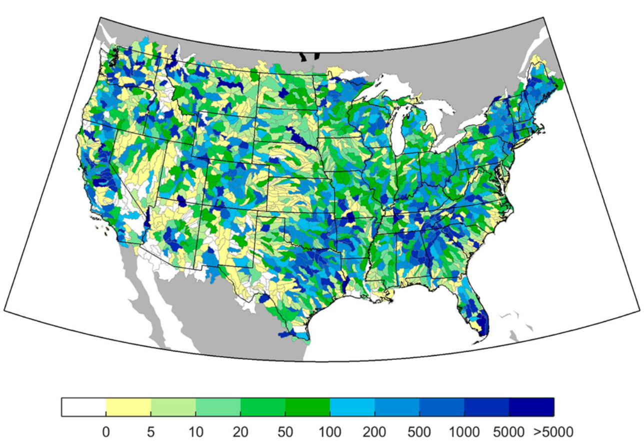


Figure 1. Total reservoir storage in each 8-digit HUC (millions of cubic meters).

The steps for estimating CyanoHAB occurrence in the U.S. include (1) modeling changes in river flow and water demand, (2) simulating changes in reservoir volumes over time using the U.S. Basins water resource systems model (3) estimating the biomass of key phytoplankton functional groups (including cyanobacteria) with QUALIDAD and (4) converting biomass concentration to cell count, a step needed for valuation. Additional detail for (1) and (2) can be found in Boehlert et al. (2015).[17] Due to the computational intensity of the model, one year of mean climate is used for the baseline period and future eras. This is an important caveat because, in this study, we are not addressing effects of interannual variability but rather a long-term mean change.

QUALIDAD[17,19] uses managed flows and reservoir volumes from U.S. Basins and climate parameters to model several water quality constituents for each 8-digit HUC. These constituents include water temperature, dissolved oxygen (DO), three species of nitrogen (ammonia, nitrate/nitrite, and organic nitrogen), two species of phosphorus (inorganic and organic), and phytoplankton (split into four functional groups, described later). These constituents and their interactions are depicted in Figure 2 and detailed in SI Section 5. To track these water quality constituents within the CONUS framework, each 8-digit HUC is divided into a number of segments based on the Enhanced River Reach File (ERF1) from USGS;[24] see Strzepek et al. (2015)[25] for additional detail. Each constituent is modeled separately in each segment, and upstream to downstream mass transfer is governed using numerical methods documented by Chapra (2011)[26] and Chapra and Canale (2015).[27] Water temperature is modeled with a heat budget approach,[26] that simulates the surface heat exchange of a body of water as well as water sources/sinks (see Strzepek et al. (2015)[25] and the SI Section 5 for more detail). The water temperature model includes two vertical layers in lakes and reservoirs (stratification) and requires mean, minimum, and maximum daily air temperature, wind speed, solar radiation, specific humidity, and air pressure. Changes in air temperature from the GCMs is a primary driver of changes in water temperature. DO, nitrogen, phosphorus, carbon, and phytoplankton are influenced by water temperature via reaction rates. Phytoplankton are also influenced by water temperature via growth rates. Changes in precipitation affect the loading rates (higher precipitation causes more runoff and therefore more loading) as well as the mass balance of constituents via changes in streamflow.

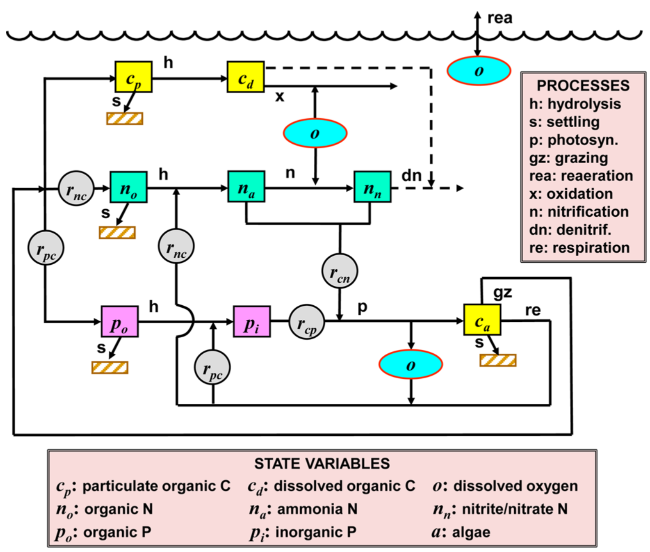
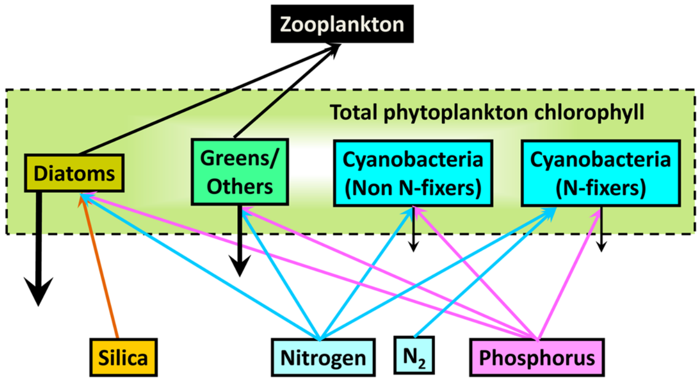


Figure 2. Schematic depicting the QUALIDAD state variables along with the major processes governing their interactions.

2.3. Modeling Cyanobacteria. The earlier version of QUALIDAD simulated the biomass of total phytoplankton as

DOI: 10.1021/acs.est.7b01498
Environ. Sci. Technol. 2017, 51, 8933–8943



Parameter	Diatoms	Greens	Cyano. N_2 fixers	Cyano. Non N_2 fixers	Units
Maximum growth rate	2.75	2.25	0.75	0.9	/d
Plateau minimum temperature	20.27	26.78	29.7	29.7	°C
Plateau maximum temperature	20.27	30.94	-	-	°C
Kappa1	0.00488	0.00465	0.00514	0.00514	
Kappa2	0.0246	0.133	-	-	
Respiration rate	0.1	0.075	0.025	0.025	/d
Respiration temp parameter	1.07	1.07	1.07	1.07	
Grazing death rate	0.1	0.1	0	0	/d
Grazing death temp parameter	1.07	1.07	1.07	1.07	
N half saturation	15	15	0	15	μgN/L
P half saturation	2	2	2	2	μgP/L
DIN preference			15		μgN/L
Light parameter	100	90	60	60	ly/d
Settling velocity	0.2	0.1	0.05	0.05	m/d
Carbon:Chlorophyll (Chlorophyll:Carbon)	60 (16.67)	60 (16.67)	30 (33.33)	30 (33.33)	gC/gA (mgA/gC)

Figure 3. Flow diagram depicting the interactions between nutrients and the four phytoplankton functional groups incorporated into the QUALIDAD framework (top); and key parameters for the four functional groups (bottom). Note that the nitrogen block in the flow diagram represents total available nitrogen (i.e., ammonia and nitrate).

one aggregate group. Although this allows QUALIDAD to be used to predict the gross impacts of eutrophication, it was incapable of simulating the phytoplankton community in greater detail, including the occurrence of cyanobacteria. The phytoplankton assemblage is complex and diverse, and is therefore typically aggregated to a smaller number of functional groups in a modeling framework.[28−30] The model in this study includes four phytoplankton functional groups: diatoms, green algae (or chlorophytes), cyanobacteria (also called blue-green algae), some of which can "fix" nitrogen from the atmosphere (N_2-fixers) and others that cannot fix atmospheric nitrogen (non-N_2-fixers).

The diatoms and green algae (also referred to as "greens") represent the beneficial algae groups. Diatoms prefer cooler water temperatures, have higher growth and respiration rates, require more light, and settle faster than the other phytoplankton groups considered. Green algae grow and settle slower than diatoms, but can tolerate higher temperatures. Both greens and diatoms are commonly a good food source for zooplankton and planktivorous fish[31] and do not generally cause harm when consumed by humans or animals.

Cyanobacteria represent the other two functional phytoplankton groups as described above—N_2-fixers and non-N_2-fixers—and are prokaryotic, ancient life forms. Compared to greens and diatoms, cyanobacteria generally thrive at higher temperatures and lower light levels, and they grow and settle more slowly.[32] They are also largely inedible, providing low-quality food for zooplankton[7,33,34] and can produce toxins that can harm or even kill grazing zooplankton.[35−37]

Since diatoms prefer cooler water, cyanobacteria are generally in competition with the greens during the times of year when the epilimnion (top layer of a stratified water body) is warm. This is particularly true in nutrient-enriched waterbodies. Both types of cyanobacteria can regulate their buoyancy, a key to their competitive advantage over the greens by monopolizing light in the photic (light penetrating) zone of a lake or reservoir. The cyanobacteria N_2-fixer group has the added benefit of being able to "fix" dissolved atmospheric nitrogen (N_2). This means they do not solely depend on dissolved combined nitrogen forms in the water (ammonia and nitrate). The cyanobacterial non-N_2-fixers, which include the genera *Microcystis*, the most commonly reported cyanobacteria in a recent national wide surveillance of blooms,[38] also grow somewhat faster than the cyanobacteria N_2-fixers, especially at higher temperatures.

In most lakes and reservoirs, a typical phytoplankton successional pattern evolves during the growing season: in the spring, growth begins with diatoms, progresses to greens, and, if nutrients are abundant, concludes with the dominance of cyanobacteria and development of blooms (CyanoHABs) in the summer and fall.[39] The prevalence of each of these groups, as well as their total biomass, is influenced by the lake or reservoir system's trophic state, which is largely a function of nutrient levels. Thus, the seasonal succession is primarily governed by the interplay of temperature and nutrient levels. For systems with high phytoplankton biomass or turbidity, the competition is further influenced by light limitation which depends on the depth of solar radiation penetration in the water column. QUALIDAD employs simple process representations

DOI: 10.1021/acs.est.7b01498
Environ. Sci. Technol. 2017, 51, 8933−8943

to simulate the seasonal dominance of these four phytoplankton functional groups as a function of temperature, nutrients, and light.

For example, Paerl and Otten (2013)[37] have developed a plot of the temperature dependence of specific growth rates for the main phytoplankton functional groups. The points presented in Paerl and Otten (2013)[37] are fit with an asymmetric bell-shaped curve originally developed by Cerco and Cole (2014)[40] but modified here to also accommodate a constant maximum "plateau" that is necessary to adequately fit some functional groups:

$$k_{g,\max}(T) = k_{g,\max} e^{-\kappa_1 (T - T_1)^2} \quad T \le T_1 \tag{1}$$

$$k_{g,\max}(T) = k_{g,\max} \quad T_1 \le T \le T_2 \tag{2}$$

$$k_{g,\max}(T) = k_{g,\max} e^{-\kappa_2 (T - T_2)^2} \quad T > T_2 \tag{3}$$

Here, $k_{g,\max}(T)$ = the maximum photosynthesis rate [/d] at water temperature T (°C)], κ_1 and κ_2 are parameters that determine the rate of decline of growth for temperatures below and above the optimal temperature, respectively, and T_1 and T_2 are the lower and upper temperatures defining the range of the plateau (°C). If $T_1 = T_2$, the model simplifies to an asymmetrical bell curve. The plateau version of the asymmetric bell curve (as opposed to the version without the plateau) was used here because it represents the relationship of temperature with growth presented by some of the graphs in Paerl and Otten (2013).[37] The parameters, T and κ, were fit using these data points presented in Paerl and Otten.[37] Note that for cyanobacteria, Paerl and Otten's data indicate a drop-off at very high temperatures (≥38 °C). Although this suggests a physiological limit occurs at very high temperatures, data below 38 °C were better represented by a plateau starting at ~30 °C.

Michaelis–Menten formulas and half-saturation constants are used to parametrize nutrient limitation. Self-shading is modeled with the Beer–Lambert law and commonly used formulas relating light extinction to phytoplankton chlorophyll concentration. Both were originally developed in the early 1970s[41,42] and are now standard in process-oriented water quality models.[43]

The interrelationship of these processes for the phytoplankton functional groups and the key parameter values that define the characteristics of the functional group are summarized in Figure 3. Note that the selected parameters represent our best estimates of the most likely values based on the range from the literature, tempered by our professional experience. Hence, we do not expect that they would yield accurate results for any particular lake; but rather that they represent expert opinion consistent with a screening approach.

2.4. Converting from Biomass to Cell Count. The biophysical water quality model, QUALIDAD, produces daily biomass concentrations in mass units of mgC/L. However, in the U.S., national and state-level guidance and regulations for drinking water supplies and recreational waters for the protection of public health use cyanobacteria cell count. Converting from biomass to cell count is not trivial because of the variety of cell shapes and sizes of cyanobacteria. Consistent with our screening-level approach, we develop a simple conversion scheme that conforms with current standards established by the World Health Organization (WHO).[20] Specifically, the WHO has established provisional health guidelines for recreational exposure to CyanoHABs as follows:

level	description	N_c, cells/mL	a_p, μgChla/L
1	risk of short-term impacts like skin irrigations and gastrointestinal illness	20 000	10
2	risk of longer-term, more serious illnesses in addition to the short-term health impacts	100 000	50

The chlorophyll guideline applies for the case where cyanobacteria dominate the phytoplankton. Further, notice that these values scale linearly as 2000 cell/mL per μgChla/L. Using the ratio of chlorophyll to carbon ratio from Figure 3 (33.333 μgChla/mgC), this can be translated into carbon units as follows:

$$N_c\left(\frac{\text{cells}}{\text{mL}}\right) = 2000\frac{\text{cells/mL}}{\mu\text{gChla/L}} \times c_p\left(\frac{\text{mgC}}{\text{L}}\right) \times 33.33\frac{\mu\text{gChla}}{\text{mgC}}$$
$$= 66\,667\frac{\text{cells/mL}}{\text{mgC/L}} \times c_p\left(\frac{\text{mgC}}{\text{L}}\right)$$

Here, N_c is the resulting concentration in terms of cell count and c_p is the output from QUALIDAD. There is undoubtedly a high level of uncertainty in this relationship, which is an important caveat to the results. Nevertheless, it provides a means to express the water quality model projections in a format consistent with the magnitudes of the WHO provisional guidelines and with our screening approach.

2.5. Water Quality Input Data. Loadings enter the system as point and nonpoint sources. Agricultural nonpoint source loadings were developed using data available from the Spatially Referenced Regressions on Watershed Attributes (SPARROW) model.[44] These included total annual nitrogen and phosphorus from fertilizer application, as well as biochemical oxygen demand (BOD) outputs from livestock. The transport of nonpoint loadings through the landscape to the main river reaches and reservoirs were modeled using the Hydrologic and Water Quality System (HAWQS).[45] Municipal contributions for each constituent were assumed to be point sources and are based on per-capita export coefficients.[43] These annual municipal loadings increase over time based on U.S. population projections developed using the Integrated Climate and Land Use Scenarios version 2 (ICLUSv2) model.[46,47] Using the UN Median Variant projection for the U.S.,[48] ICLUSv2 was applied to generate county-level population projections between 2000 and 2100.

3. SENSITIVITY ANALYSIS

When performing a site-specific modeling study to support a reservoir or watershed scale management or regulatory decision, a number of analyses are typically conducted to accurately identify model parameters and assess the reliability of model simulations.[49,50] These include calibration, confirmation, sensitivity analysis, and uncertainty analysis. In contrast, many of these procedures are inappropriate for a multisystem (i.e., cross-sectional) screening analyses of the type presented here.

For example, a sensitivity analysis generates information on how parameter uncertainty affects interpretation of model results and identifies those parameters that have the greatest impact on the model outcomes. Whereas this is de rigueur for a site-specific application, it is not as appropriate for the current type of application dealing with numerous systems with a wide

DOI: 10.1021/acs.est.7b01498
Environ. Sci. Technol. 2017, 51, 8933–8943

range of hydrologic, morphometric, and biochemical characteristics. For example, the processes governing nutrient recycle in the upper layers of a thermally stratified, long-residence-time lake (e.g., hydrolysis, decomposition, grazing, sedimentation etc.) would have a strong impact on its summer water quality. In contrast, for shallow, fast flushing systems, water quality would be more strongly influenced by summer inflows due to storm events. Thus, there is no single set of significant parameters across all lakes.

For a screening-level modeling application, a sensitivity analysis should be governed by the types of planning or management questions being addressed. In this study, we focused on assessing how climate-induced water temperature increases will impact regional cyanobacterial prevalence across the continental United States (CONUS).

Three principal factors have the strongest influence on the results of our water quality model for cyanobacterial prevalence in this context: water temperature, nutrient concentrations, and uncertainty in cyanobacteria growth at high temperatures.

Since the results from this analysis focus on cyanobacteria concentration estimations for climate scenarios with increasing temperature over time, the relationship between cyanobacteria growth and water temperature is paramount. Furthermore, records and observations of cyanobacteria growth at the higher temperatures projected by these scenarios in the latter half of the 21st century are scarce. To address this uncertainty, we include an additional set of results using the linear increase in growth rate at higher temperatures (instead of the plateau) from Canale and Vogel (1974).[39] We refer to these two sets of results as the "Plateau-Growth" and "Linear-Growth" scenarios for the plateau and linear cases, respectively (see Figure 4).

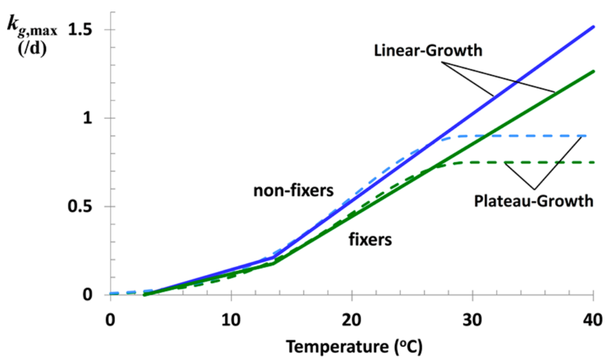


Figure 4. Plot of maximum growth rate versus temperature for the two cyanobacteria groups-- cyanobacteria non-N_2-fixers (nonfixers) and cyanobacteria N_2-fixers (fixers)—and the two growth scenarios—Linear-Growth and Plateau-Growth.

Our sensitivity analysis consists of running the model over various temperatures and inorganic phosphorus (Pi) and nitrogen (Ni) levels, using a median reservoir size and climate (from the baseline) across the CONUS. For each model run, we present results for both the Plateau- and Linear-Growth scenarios. We model each reservoir as a closed system (i.e., flow-in and flow-out are set to zero), and maintain constant nutrient levels and temperature for each individual run. The system is solved for conditions in the epilimnion (top layer) and run from the mid-April to the end of September, which coincides with the primary cyanobacteria growth season and the water recreation season in North America. Figure 5(a) shows the mean concentrations of the four phytoplankton

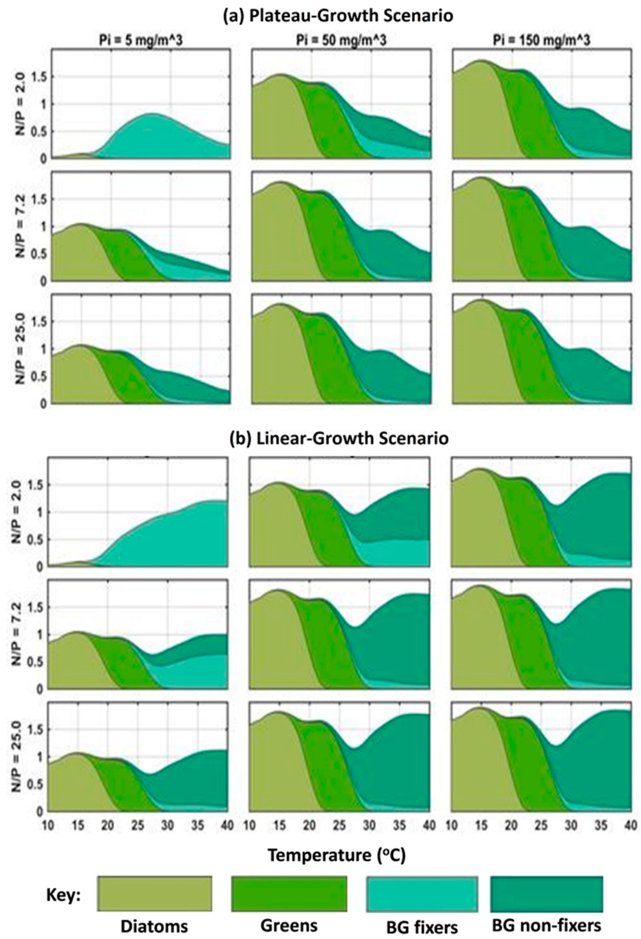


Figure 5. Phytoplankton concentrations (mgC/L) of the four functional groups (Diatoms, Greens, cyanobacteria N_2 fixers (BG fixers), and cyanobacteria non-N_2-fixers (BG nonfixers), for various temperatures (*x*-axis), inorganic phosphorus (Pi; columns), and ratios of inorganic nitrogen to inorganic phosphorus ratio (N/P; rows) using the (a) Plateau-Growth and (b) Linear-Growth scenarios.

functional groups over August and September over various nutrient and temperature conditions using the Plateau-Growth scenario. The columns show three levels of total nutrients signified by the inorganic phosphorus concentrations (5, 50, and 150 mg/m^3) and the rows show three inorganic nitrogen to inorganic phosphorus ratios (2, 7.2, and 25) denoting increasing phosphorus limitation. For context, the median inorganic phosphorus of all reservoirs in CONUS in the historical simulation is about 130 mg/m^3 and the median N/P ratio is about 9.2. Each of these panels includes many runs with incrementally increasing temperature from 10 to 40 °C. Similarly, Figure 5(b) shows the same 9-paneled graphic for the Linear-Growth scenario.

The diatoms dominate at lower temperatures, peaking at about 15 °C. Then, as temperature increases, the greens dominate, ranging from about 20 to 28 °C with the cyanobacteria dominating above 30 °C. At low N/P ratios and low total nutrient levels (panels in the upper left), we see that the cyanobacteria N_2-fixers tend to dominate over the non-N_2-fixers due to the added advantage of fixing nitrogen from the atmosphere when dissolved nitrogen levels (ammonia and nitrate) in the water are low. Except for these cases where nitrogen levels are low, the cyanobacteria non-N_2-fixers tend to dominate due to slightly higher growth rates. In the Plateau-Growth scenario,

DOI: 10.1021/acs.est.7b01498
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we can see that cyanobacteria concentrations start to decline above about 33 °C due to higher rates of respiration while the growth rates have plateaued. In the Linear-Growth scenario, the cyanobacteria concentrations do not decline at higher temperature but continue to increase until past 35 °C when they start to flatten.

This sensitivity analysis illustrates that the model performs as expected based on the behaviors documented in the literature and described in Section 2.2. For example, the seasonal succession patterns for the four phytoplankton groups are consistent with observed patterns in lakes and reservoirs. Also aligning with expectations, the sensitivity analysis demonstrates that the behavior of the model is strongly influenced by both water temperature and nutrient concentrations. Due to uncertainty in cyanobacteria growth rates at higher temperatures, the analysis also shows the importance of considering the uncertainty of cyanobacteria growth at higher temperatures (as shown with the two growth scenarios used here).

4. RESULTS AND DISCUSSION

The following section presents results and findings based on the model outputs for reservoirs and lakes across the contiguous United States. Although the analysis included five GCMs, in the following maps we present results from two of these for simplicity: GISS-E2-R and HadGEM2-ES. Due to the strong relationship between cyanobacteria growth and temperature, we have selected these two GCMs because GISS-E2-R projects the lowest increases in air temperature by 2090, while HadGEM2-ES projects the highest. Also, we focus on RCP 8.5 because this scenario presents the stronger signal. Note that in order to isolate climate impacts from the effects of population growth, the projected changes are all expressed relative to the Control scenario, which uses historical climate with the effects of population growth, as previously mentioned.

Figure 6 shows the changes in reservoir and lake surface-layer temperatures. We present these at the 4-digit HUC level, which

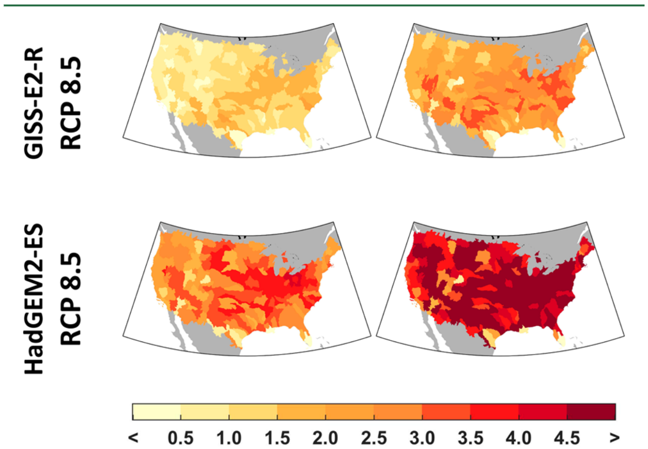

Figure 6. Changes in mean annual projected waterbody surface temperature (°C) for both the GISS-E2-R and MIROC5 climate models, two eras, and RCP 8.5, aggregated to the 4-digit HUC weighted by surface area.

are aggregated by weighting each waterbody within the 4-digit HUCs by surface area. These changes in water temperature are primarily influenced by changes in air temperature. GISS-E2-R projects moderate increases in water temperature with 2050 projections ranging from less than 0.5 °C to an increase of about 2 °C around the Great Lakes for RCP8.5. In 2090, these increases are larger, reaching above about 3 °C in some areas for RCP8.5 but only around 2 °C for RCP4.5. Alternatively, HadGEM2-ES projects significantly larger increases, ranging from the RCP4.5−2050 projection with increases around 2 °C to the RCP8.5−2090 projection with increases reaching 5 °C.

Figure 7 depicts the changes in cyanobacteria concentrations annually for the surface layer of reservoirs and lakes at the 4-digit HUC level, weighted by surface area. Note that the surface layer is set to a 5m depth, except for reservoirs and lakes with a mean depth less than 5m. Given that these are averages over large areas (about 11 waterbodies in each 4-digit HUC), and depth, these increases in concentration are potentially low estimates, i.e. conservative, as cyanobacteria can concentrate near the surface due to buoyancy, or along shores downstream of lateral winds, within either case potentially resulting in concentrations about 100 times larger.[20]

Due largely to the differences in projected air temperatures, GISS-E2-R generally shows less increase in cyanobacteria concentrations than HadGEM2-ES. In the Plateau-Growth scenario, most of the increases are in the East and Midwest, with decreases generally found in the West where nutrient concentrations are projected to decline due to changes in loadings.

Interestingly, in the Plateau-Growth scenario we find areas of larger decreases in the West for high-temperature scenarios than in scenarios with less increase in temperature. For example, HadGEM2-ES RCP8.5−2090, the scenario with the largest temperature increases, shows the largest decreases in certain areas in the West. This phenomenon occurs when the growth of cyanobacteria plateaus (at water temperatures exceeding 30 °C) while the respiration rate continues to increase with temperature, eventually causing decreases in cyanobacterial concentrations. We find that this phenomenon of decreasing cyanobacterial concentrations at higher temperatures occurs when light and nutrient limitations restrict growth to about 15% of maximum. We do not find this behavior in the Linear-Growth scenario because growth continues to increase along with respiration as temperature increases. It is important to note that these regions where the difference between the growth scenarios is high (especially where there is a difference in sign), the uncertainty related to growth parameters is considerable and therefore we have less confidence about the resulting projections. However, the converse is also true; that the regions where the two growth scenarios agree, the results are more robust, independent of the growth scenarios.

Figure 8 shows the population-weighted aggregated cyanobacteria concentration across the year for the 2090 era. The cyanobacteria concentrations of each reservoir and lake are weighted by 8-digit HUC population, as a first-order proxy for human impacts. Note that since these are aggregated across CONUS, individual reservoirs and lakes will be both higher and lower than shown. In the Control scenario, the aggregate concentrations are slightly lower than 20 000 cells/mL at the peak in August and September. In the projected climate scenarios, these peaks rise above 38 000 cells/mL on the low-end and above 70 000 on the high-end. In the Plateau-Growth scenario, the aggregate concentrations show less of a spread across the climate scenarios than in the Linear-Growth scenario, where increasing temperatures above 30 °C continue to increased growth rate.

Since this study focuses on cyanobacteria, we did not do an in-depth analysis on greens or diatoms. However, generally speaking, in already-warm climates, increasing temperatures

DOI: 10.1021/acs.est.7b01498
Environ. Sci. Technol. 2017, 51, 8933−8943

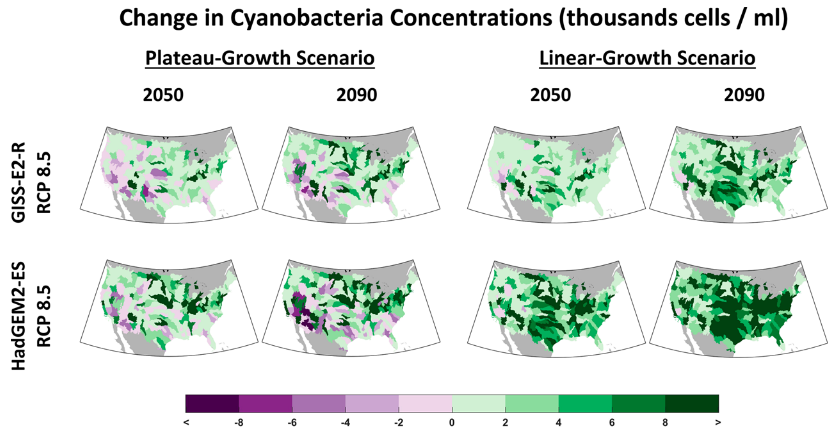

Figure 7. Changes in waterbody surface cyanobacteria (thousands of cells/mL) for the Plateau-Growth (left) and Linear-Growth (right) scenarios for the GISS-E2-R and MIROC5 climate models under RCP 8.5 in 2050 and 2090, aggregated to the 4-digit HUC level, weighted by waterbody surface area.

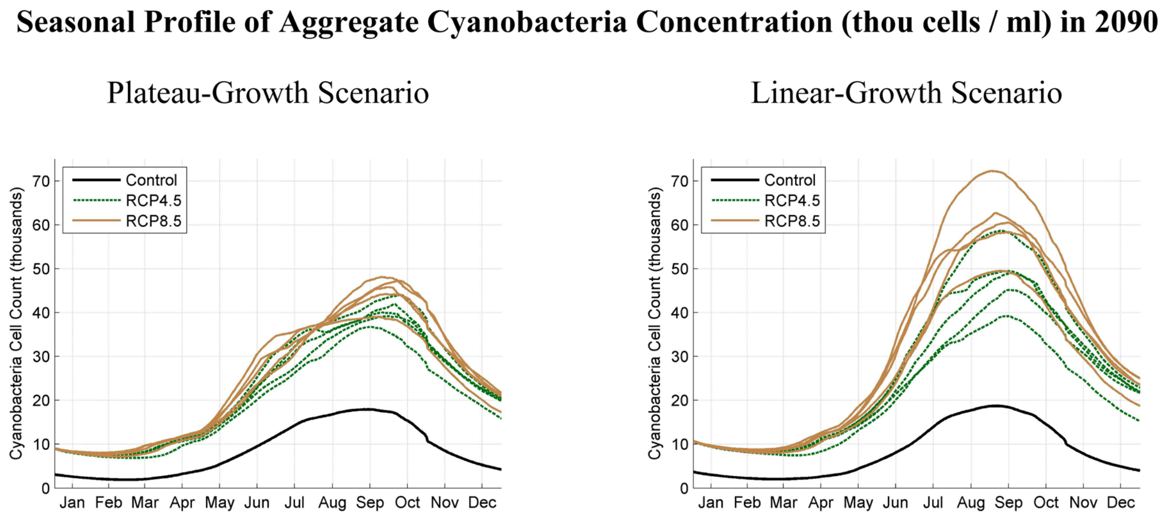

Figure 8. Population-weighted aggregate cyanobacteria concentration (in thousands cells/mL) for all scenarios in 2090. Each line represents results from one of the five GCMs (10 lines total, where each GCM has one RCP8.5 and one RCP4.5).

Table 2. Change in the Mean Number of Days Per Year Per Waterbody, Aggregated by Population, Above 20 000 cells/mL and 100 000 Cells/mL Thresholds for All Climate and Forcing Scenarios[a]

		20 000 cells/mL				100 000 cells/mL			
		plateau		linear		plateau		linear	
		2050	2090	2050	2090	2050	2090	2050	2090
RCP 4.5	CanESM2	9	9	12	13	6	6	9	9
	CCSM4	8	11	12	17	7	8	11	12
	GISS-E2-R	4	4	7	8	4	3	7	5
	HadGEM2-ES	12	17	19	27	8	9	13	15
	MIROC5	10	12	14	19	8	9	12	14
RCP 8.5	CanESM2	11	23	15	34	7	14	10	20
	CCSM4	9	20	14	30	8	10	11	17
	GISS-E2-R	6	11	9	19	5	6	9	11
	HadGEM2-ES	14	23	25	44	8	13	15	24
	MIROC5	10	22	14	32	7	12	11	19

[a]The incremental green shading is used to highlight those with higher values.

cause both diatoms and greens to decrease in concentration in most reservoirs and lakes, although this depends heavily on nutrient conditions. Alternatively, in relatively colder lakes, diatoms start to grow earlier and persist later in the season.

Table 2 shows the change in the mean number of days per year above two thresholds: 20 000 cells/mL and 100 000 cells/mL. These thresholds are based on recommendations from the WHO guidelines.[20] The number of days above the threshold is

DOI: 10.1021/acs.est.7b01498
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averaged across waterbodies, weighted by population, used here as a first-order metric of importance for both recreation and municipal water supply. According to the WHO guidelines for recreational exposure, 20 000 cells/mL is the suggested level at which cyanobacteria presents a moderate risk to human health. The 100 000 cells/mL threshold represents the point at which cyanobacteria levels are at "very high" risk of harmful consequences.[20]

For the baseline scenario, this metric is about 7 days per year per waterbody and is near zero for the 20 000 cell/mL and 100 000 cells/mL thresholds, respectively. The lowest increases in number of days are produced from the GISS-E2-R GCM, and the highest is produced by the HadGEM2-ES GCM due, primarily, to their respective projected increases in air temperature. Note that the patterns and magnitudes of the projected changes in precipitation are similar for these two GCMs. For the 20 000 cells/mL threshold, the mean number of additional days ranges from about 4 to 44 in 2090 across all five GCMs, two climate forcing scenarios, and two growth scenarios. In 2090, a warming climate under RCP 4.5 results, on average, in the equivalent of about an additional half a month above 20 000 cells/mL, whereas RCP 8.5 results in an additional month.

From a regional perspective, the Northwest shows the least impact, where precipitation generally increases without nutrient increases, and temperature projections are generally less than other regions. We find the greatest overall impacts in the Northeast, where there are noteworthy increases in the occurrence of cyanobacteria concentrations exceeding the 100 000 cells/mL threshold. We also find noteworthy increases in cyanobacteria in the Great Plains, especially in the additional number of days above the 20 000 cells/mL threshold.

As mentioned, a partial estimate of the value lost in the recreation sector is described in detail in the SI. This was evaluated across 279 reservoirs and lakes within the CONUS. We find that lost recreation visitation varied across climate forcing scenarios, cyanobacterial growth scenarios, and time from 1.2 million to 5.3 million visitor-days per year for reservoirs for which recreation visitation data were available, with the higher estimate corresponding to the Linear-Growth scenario and RCP 8.5 by 2090. This results in lost annual recreation value ranging from \$57 million to \$245 million. From a regional perspective, the largest impacts occurred in the Southeast, ranging from \$57 million to \$110 million annually by 2090 due primarily to a higher visitation rates in the baseline. Drinking water impacts were not addressed in terms of valuation, although these impacts are likely to be important, especially if municipal water treatment facilities without options to treat cyanotoxins or alternative sources experience higher levels of CyanoHABs at source water intakes.

As with all modeling endeavors, there are limitations and caveats. We have taken a screening-level approach to modeling the biophysical system. First, all waterbodies are modeled as well mixed systems (although during stratification these are split into two vertical layers). Given that cyanobacteria may concentrate vertically over specific depth ranges or horizontally due to lateral winds, the estimates presented here will be less than the potential maxima (see Backer et al. (2015)[38] for concentrations observed under current climate). In addition, we do not model cyanobacteria toxicity, which varies based on several factors and is not necessarily directly correlated with cyanobacteria concentrations. Since cyanobacteria range in shape and size, there is also uncertainty involved in converting from biomass to cell-count. Also, the model does not explicitly account for potential physiological or ecological adaptations that could occur as a result of the heightened temperatures projected by the climate models.

Improved future projections would benefit from additional research and data. Results from the Linear- and Plateau-Growth scenarios differ considerably, which indicates that uncertainty in the growth of cyanobacteria at higher temperatures matters significantly for the future and is not well understood. It is quite likely that very high temperatures will begin to become inhibitory to growth, even with cyanobacteria. However, because we are limited by available data in this regard, extrapolation much beyond 37 °C is highly uncertain at this time. For this reason, we strongly urge that laboratory and/or field studies be conducted to quantify the impact of very high water temperatures (>35 °C) on both the growth and respiration rate of cyanobacteria.

These considerations aside, we believe that our analysis offers useful screening-level estimates of the potential impact of climate-induced temperature rise on the prevalence and economic impact of CyanoHABs for U.S. surface waters. Given adequate hydrologic, demographic, and nutrient supply estimates, a more comprehensive global assessment could be conducted by extending our methodological approach to other parts of the planet. Since the approach is driven by mass-balance and known processes, this kind of screening-level analysis would be easier to apply to other countries and regions of the world than a more complex and calibration-driven approach that would rely more heavily on large quantities of accurately measured data for calibration. Our study underscores the findings of numerous U.S. and global scientific assessments that the ecological and economic impacts of climate change extend well beyond rises in air temperatures. In particular, it illustrates that some regions, such as the Southeast and Northeast U.S., will be especially vulnerable to future elevated water temperatures due to other mitigating factors such as changes in hydrology and increased nutrient loadings.

■ ASSOCIATED CONTENT

Ⓢ Supporting Information

The Supporting Information is available free of charge on the ACS Publications website at DOI: 10.1021/acs.est.7b01498.

> Model framework diagram; Rationale for selection of climate models; Runoff and water demand model descriptions; Water systems model description; QUAL-IDAD-HABs detailed model description; Additional Results; Valuation methods and results (PDF)

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Notes

The authors declare no competing financial interest.

■ ACKNOWLEDGMENTS

We acknowledge the financial support of the U.S. Environmental Protection Agency's (EPA's) Climate Change Division (Contract No. EP-BPA-12-H-0024) and the U.S. National

Science Foundation (Projects 1230543 and 1240851), and access to reservoir datasets from the U.S. Army Corps of Engineers. Technical contributions were provided by Jacqueline Willwerth. Aubrey Scott and Martin Auer of Michigan Technological University, and David Schindler and Michael Patterson provided scholarship and data from the IISD/ELA that informed this paper. We also acknowledge that the final paper benefitted greatly from the perceptive comments, criticisms, and suggestions of the three reviewers. Data used to produce the results of this paper can be obtained through the corresponding author, Brent Boehlert. The views expressed in this article are solely of the authors, and do not necessary represent those of their employers.

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