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Modeling temporal and spatial variations of biogeochemical processes in a large subtropical lake: Assessing alternative solutions to algal blooms in Lake Okeechobee, Florida

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ABSTRACT

Study region: Algal blooms (ABs), often exacerbated by excess nutrients from anthropogenic activities, can pose serious risks to public health, fisheries, and ecosystem structure and functions. Lake Okeechobee is located in southcentral Florida (USA), and with a surface area of 1730 km^2, it is the largest subtropical lake in the United States. This lake is shallow, nutrient-rich, and subject to frequent and intense blooms of cyanobacteria, some of which are toxic.
Study focus: In this study, a three-dimensional (3D) model was developed, coupling long-term monitoring data with complex physical, chemical, and ecological processes at fine spatial (15–1000 m horizontal mesh size) and temporal (1 h) resolution. We used this model to understand the influence of environmental factors and nutrient management on ABs dynamics in Lake Okeechobee.
New Hydrological Insights for the Region: The model showed that ABs mostly developed in shallow nearshore regions near canal outlets, and then spread over the lake as a result of prevailing winds and currents. Hypothetical scenario modeling showed that reducing both nitrogen and phosphorus inputs by 50%–75% would be more effective at reducing ABs in the lake than targeting a single nutrient. The model could be used as a tool to assess the effectiveness of different nutrient management strategies in Lake Okeechobee and its watershed, while the framework could be adopted to other large water bodies facing similar issues.

1. Introduction

Lakes and reservoirs provide water for a range of human demands, such as drinking water, irrigation, recreation and tourism (Janssen et al., 2019). Accelerated rates of eutrophication associated with human development in many lake ecosystems around the world are creating water quality issues, including algal blooms (ABs) (Heisler et al., 2008; O'Neil et al., 2012). AB events in lakes are projected to worsen as a result of global warming and continued cultural eutrophication (O'Neil et al., 2012; Paerl et al., 2016; Visser et al., 2016; Beusen et al., 2016). Certain algae types can release toxins that are harmful to human health

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and ecosystems (Anderson et al., 2021). The inhalation or consumption of affected waters can be harmful to animals and humans, and toxins can bioaccumulate in food chains (Berry et al., 2011). Comprehensive water quality management solutions are therefore needed to mitigate the potential for ABs and the associated adverse impacts (Burford et al., 2020). Quantitative modeling has played an important role helping water managers define the drivers for ABs and develop effective approaches to reduce the frequency and intensity of blooms.

Models that define the relationship between environmental factors and ABs have been developed for a number of lakes around the world (Burford et al., 2020; Ralston and Moore, 2020). For example, Bilaletdin et al. (2011) applied a process-based model (AQUATOX) developed by Park et al. (2008), to study the effect of excessive phosphorus loading on eutrophication in Lake Onega (Russia). United States Army Corps of Engineers (USACE) developed the CE-QUAL-ICM model to study eutrophication processes in Chesapeake Bay (USA) (Cerco and Cole, 1992) and concluded that eutrophication models must take into consideration nitrogen, phosphorus, silica, and carbon cycles as well as sedimentation processes (Aldridge, 1995; James and Bierman Jr., 1995; James and Havens, 1996; Havens and James, 1999). James et al. (2008) alluded to the importance of light extinction due to suspended sediment in addition to other processes, with a particular emphasis on Lake Okeechobee. In other modeling efforts, the impacts of climate change on eutrophication and ABs in Lake Taihu, China, have been investigated in Tang et al. (2015, 2016). The modeling efforts revealed the dependency of ABs on water temperature, wind conditions, and nutrient flux into the lake. Recent advances in remote sensing and environmental data science have facilitated the short-term forecasting of algal bloom occurrences (e.g. Tang et al., 2022). Overall, process-based numerical models have become standard in evaluating the nexus of management solution and water quality, but less attention has been focused on broader environmental drivers of ABs in large lakes.

Understanding the effect of environmental drivers on ABs is important for identifying the best targets for management of eutrophication issues. Given its size and close relationships to wide range of regional water supply and water quality issues, Lake Okeechobee is an example of a lake deserving of attention. James and Bierman Jr. (1995), James and Pollman (2011), James (2016) used a mass balance model and a dynamic water quality model, namely the Internal Loading Phosphorus Model (ILPM) and the Lake Okeechobee Water Quality Model (LOWQM) to evaluate nutrient management solutions (e.g., large-scale chemical treatment and dredging). An open source model called Lake Operation Optimization of Nutrient Exports (LOONE) was developed by Tarabih et al. (2022) to evaluate water quality control alternatives for the lake. Lumped models like this are important for uncertainty analyses or operational purposes (i.e., gate operations for Lake Okeechobee) since their processing time is relatively short (Dilks and James, 2011; James, 2016). However, a spatially explicit three-dimensional (3D) hydrodynamic model is needed to represent critical hydrodynamic and biogeochemical processes in this complex water system. For instance, although substances in the lake are well mixed in the vertical direction, light penetration and algal growth occur predominantly in the top layer (i.e., 30 cm to 1.2 m depending on the location) (Phlips et al., 1995; Rodusky et al., 2005; James, 2016). Jin et al. (2007) developed the 3D Lake Okeechobee Environment Model (LOEM) and used it to study water quality processes in the lake. LOEM was based on the Environmental Fluid Dynamics Code (EFDC) (Hamrick, 1992), which does not have 3D flexible computational mesh capabilities. This limitation makes it difficult to simulate the littoral zone in detail, especially those canals in the northern and western sites of Lake Okeechobee. Overall, the lessons learned from decades of research in this lake are also relevant to other similar shallow, large subtropical lakes.

In this study, we explored the relationships among hydrodynamics, nutrient fluxes, and ABs in large subtropical lakes, within the context of a case study of Lake Okeechobee, using a high spatial and temporal numerical model. Lake Okeechobee is not only an important lake in Florida but is also an interesting example of a highly engineered system with multiple regulated inflows and outflows. Through this study, we aimed to answer three important, management-related questions: (1) What are the main factors causing ABs in Lake Okeechobee? (2) How much of a reduction in nutrient imports and/or legacy sediments is needed to reduce the occurrence of ABs? (3) What magnitude of nutrient input reduction would be required to reduce ABs? The open source Delft3D-FLOW module was used to simulate the hydrodynamic conditions of the lake. Hydrodynamic modeling results were used to drive a water quality — ecological Delft3D-WAQ model to calculate algal production. Modeling results were compared against observed data for model calibration and validation. We then tested several alternative solutions to investigate how phytoplankton concentrations change with regard to changes in nutrient concentrations using *Chlorophyll-a (Chl-a)* as a surrogate for phytoplankton biomass.

2. Study area

Lake Okeechobee is located in southcentral Florida, USA (center location at 26.9690° N, 80.7976° W). With a surface area of 1730 km^2, it is the largest freshwater lake in the U.S. outside of the Great Lakes (Fig. 1). Though of natural origin, Lake Okeechobee has functioned as a reservoir since the construction of a dike that surrounds around 230 km of its perimeter. Among six main tributaries, only Fisheating Creek is not diked and flow is not regulated. The lake is an important source of water for nearby cities as well as for the Everglades National Park, the Loxahatchee National Wildlife Refuge, and the Everglades Agricultural Area. The lake also plays a critical role in regional flood control. Water levels and outflows are controlled by a complex network of hydraulic structures (i.e., culverts, gates, locks, and pumps) operated by the USACE and the South Florida Water Management District (SFWMD), guided by the Lake Okeechobee Regulation Schedule (LORS) (USACE, 2008) and the forthcoming Lake Okeechobee System Operating Manual (LOSOM) (USACE, 2022).

It is well-known that the lake has become progressively more eutrophic since the construction of the dike in the first half of the 20th century, in part because of nutrient inputs from urban and agricultural development in the lake's watersheds (Khare et al., 2019; Tarabih and Arias, 2021). Over time, a thixotropic mud layer containing legacy nutrients has developed especially in the deeper zone of the lake (Fisher et al., 2001, 2005; Vogel et al., 2016). As a shallow lake, during windy periods, phosphorus attached to

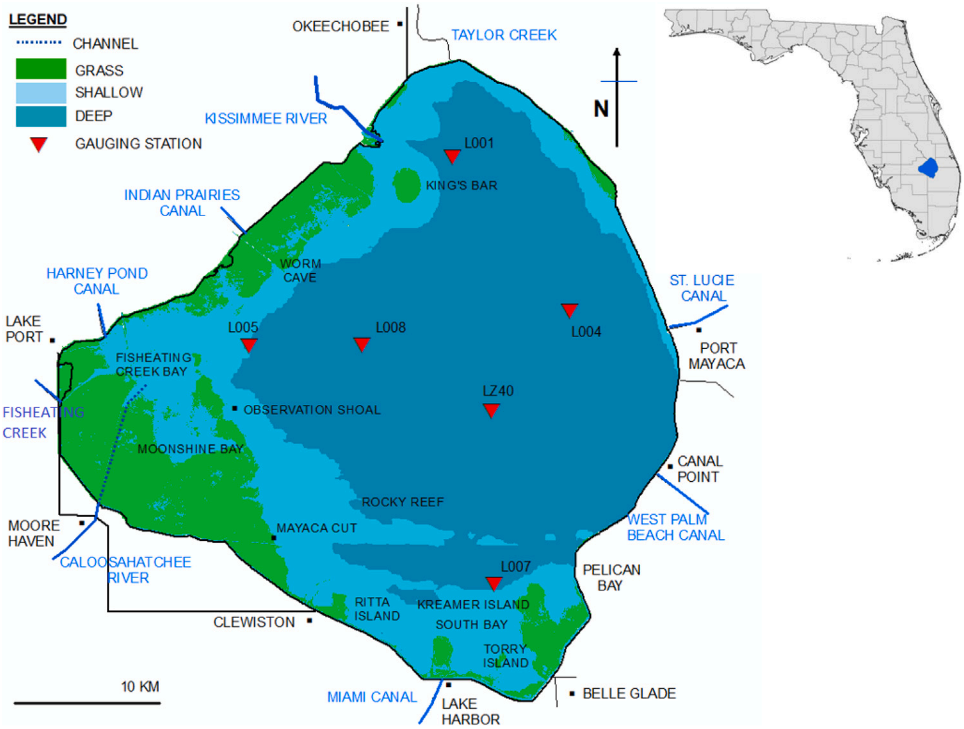

Fig. 1. Overview map of Lake Okeechobee and the location of the six main sampling locations used in this study. Kissimmee River, Taylor Creek Nubbin Slough, Fisheating Creek, and Indian Prairie are the main sources of water besides rainfall, and water is withdrawn from the lake via Caloosahatchee River, St. Lucie Canal, Miami Canal, West Palm Beach Canal, and some other smaller canals. The inset shows the location of Lake Okeechobee in the State of Florida.

sediment particles is stirred up and becomes accessible to algae in the water column, but too much sediment may cause an inverse relationship of phosphorus and algae owing to light limitation (Phlips et al., 1995; Søballe, 1998). Large-scale algal blooms have continued to occur along with the accumulation of legacy phosphorus in this benthic mud layer. Missimer et al. (2020) conducted a literature review and concluded that it would be very difficult to restore the lake without removing the legacy nutrients.

The rising tropic status of Lake Okeechobee has led to increasing incidents of intense harmful algal blooms dominated by cyanobacteria, a trend that has been observed in many lakes in Florida (Canfield et al., 1989). Part of the rising threats from cyanobacteria blooms has been prominence of the toxic species *Microcystis aeruginosa* (Rosen et al., 2017; Paerl et al., 2020), which is particularly noted for prolific production of the hepatoxin microcystin (Chorus and Welker, 2021).

3. Methods

In order to simulate complex processes in Lake Okeechobee, we relied on coupling Delft3D-FLOW and Delft3D-WAQ [see Deltares, 2019]. The hydrodynamic Deflt3D-FLOW module solves the momentum and continuity equations using an unstructured finite volume method, and Delft3D-WAQ solves the advection–diffusion equations together with an extensive water quality library for different biogeochemical processes. For Delft3D-WAQ, we simulated several biogeochemical cycles, including oxygen, nitrogen, phosphorus, sediment settling and resuspension, algal growth and competition, carbon components, silica (Si), and other ions (i.e., Fe^{3+}, Mn^{2+}, and SO_4^{2-}). Fig. 2 shows the main biogeochemical processes considered. More details on each process and data used in this study are described in the sub-sections below.

3.1. Lake hydrodynamics

Inputs to Delft3D-FLOW include lake bathymetry data, bottom surface roughness coefficient (Manning's n), canal flows, climatic forcings (precipitation, evaporation, wind velocity, wind direction, air temperature, and humidity), and water temperature. The most recent bathymetry data (released in 2014) were downloaded from SFWMD's Geospatial Services Section (www.sfwmd.gov) at 5 ft (1.52 m) of horizontal spatial resolution. The Hebert Hoover dike acted as a hard (closed) boundary surrounding the computational domain, including 7623 flexible (orthogonal and triangular) mesh cells. The mesh resolution ranged from 15 m for the near-shore zones and southwest marshes to 1000 m for the off-shore deeper water zones (Supplemental Information Fig S1). The range of mesh size was chosen based on balancing computational costs and level of details of the model domain. The vertical dimension was subdivided into five layers using the sigma-layer approach, which scales the thickness of each layer proportional to the total water

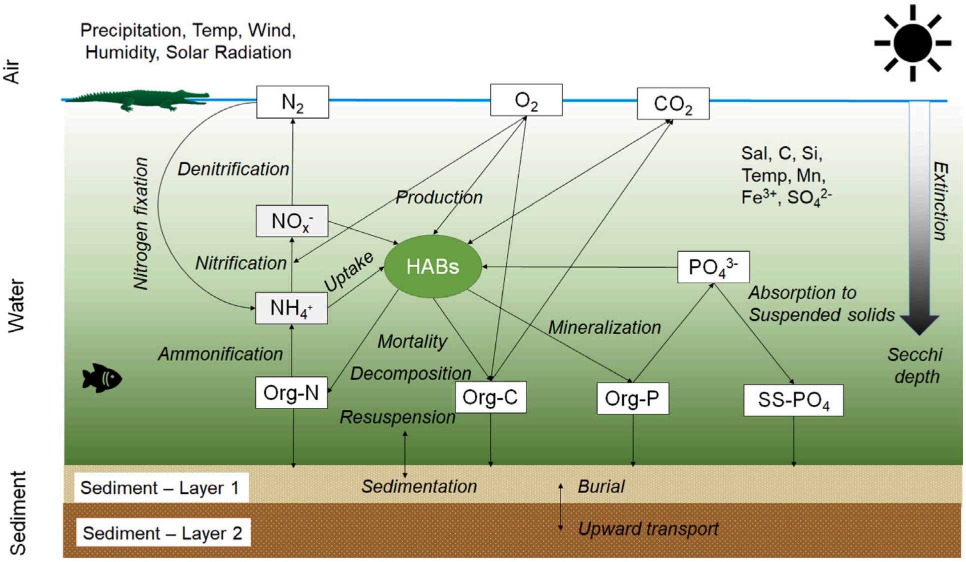

Fig. 2. Overview of modeling framework, including main physical and biogeochemical processes considered.

depth. Typically, lake water balance was obtained by including inflows, outflows, rainfall and evapotranspiration (from open water and wetland) (Bilaletdin et al., 2011). Sporadic emergency water abstraction in the form of pumping activities in the southern part of the lake, infiltration, and leakage were not considered.

3.2. Oxygen cycle

Oxygen is a fundamental component of most aquatic biogeochemical cycles and was therefore included in this study. In some of the previous Lake Okeechobee modeling studies, oxygen cycling was ignored because the lake is shallow (the average depth of the lake is approximately three meters) and, thus the lake was assumed to be primarily aerobic. Nonetheless, historical data over the period 2008–2021 showed that the concentrations of NO_2^- plus NO_3^- (from here on called NO_x^-) were sometimes below 0.01 mg/L, suggesting either algal uptake or denitrification under anoxic conditions. Jin et al. (2007) also considered dissolved oxygen (DO) in their model. Thus, we explicitly considered oxygen cycling in the lake, including chemical oxygen demand (COD), biochemical oxygen demand (BOD) and sediment oxygen demand (SOD). In Delft3D-WAQ, the reaeration of oxygen into water is dependent on water temperature, salinity intrusion, and wind speed (see Eq. (1)) (Deltares, 2019), but biochemical processes in the lake are expected to have little effects on water temperature and salinity. Thus, we added these two variables as time series data instead of simulating them directly.

$$\begin{cases} Rrear = klrear \times (Coxs - Cox)/H \\ klrear = \frac{a \times v^b}{H^c} + d \times W^2 \\ Coxs = f(T, SAL) \end{cases} \tag{1}$$

where: $Rrear$ is the reaeration rate [$gO_2m^{-3}d^{-1}$]; $klrear$ is reaeration transfer coefficient in water [d^{-1}]; Cox is the actual dissolved oxygen concentration [gO_2m^{-3}]; $Coxs$ is the saturation dissolved oxygen concentration [gO_2m^{-3}]; H is depth of the water column [m]; a, b, c and d are coefficients (obtained from model calibration); W is wind speed at 10 m height [ms^{-1}]; T is water temperature [^oC]; SAL is salinity [kgm^{-3}].

3.3. Phosphorus and nitrogen cycles

Atmospheric deposition, nitrification, denitrification, nitrogen fixation, ammonification, and uptake by algae were assumed to be responsible for transformations among four nitrogen forms: organic nitrogen, ammonia NH_4^+, nitrite-nitrate NO_x^-, and nitrogen gas N_2. Regarding the phosphorus cycle, we considered organic phosphorus and ortho-phosphate (PO_4^{3-}) as well as the adsorption of PO_4^{3-} to suspended solids and bed sediments beside atmospheric deposition. In all of these nutrient-related processes, hydrolysis and algal dynamics contributed to chemical consumption, transformation, and decomposition. Atmospheric deposition values (23.3 kg of organic phosphorus, 661.7 kg of ammonia, 714.6 kg of nitrate-nitrite and 2003 kg of organic nitrogen per day) were taken from James (2016). Overall, the mass balances for dissolved PO_4^{3-}, NO_x^-, and NH_4^+ in the water column are calculated as follows:

$$\frac{\Delta PO_4^{3-}}{\Delta t} = loads + transport \pm sorption + mineralization \pm precipitation/ dissolution - primary\ production + autolysis + atmospheric\ deposition \pm sediment\ exchange\ flux \tag{2}$$

$$\frac{\Delta NO_x^-}{\Delta t} = loads + transport + nitrification - denitrification - primary\ production + atmospheric\ deposition \pm sediment\ exchange\ flux \tag{3}$$

$$\frac{\Delta NH_4^+}{\Delta t} = loads + transport - nitrification + ammonification - primary\ production + atmospheric\ deposition \pm sediment\ exchange\ flux \tag{4}$$

Equations for other forms of phosphorus and nitrogen are described in detail in Deltares (2019).

3.4. Algae life cycle

In this study, we modeled the dominant types of phytoplankton organisms in Lake Okeechobee, grouped into cyanobacteria spp., green algae, and diatoms as reported in previous studies (Cichra et al., 1995; Havens et al., 1996; Phlips et al., 2020; Paerl et al., 2020; Tarabih and Arias, 2021). Most major blooms in the lake are dominated by cyanobacteria, with *Microcystis aeruginosa*, *Dolichospermum spp.*, and *Aphanizomenon spp.* among the most prevalent cyanobacteria genera. Dominance of cyanobacteria in blooms is a common feature in eutrophic lakes in Florida (Canfield et al., 1989). The pattern of cyanobacterial dominance extends to many shallow eutrophics around the world (Dokulil and Teubner, 2000). Overall, we simulated algal growth, respiration, transport, settling, resuspension, and mortality, but grazing was not considered. Havens et al. (1996) conducted mesocosm grazing experiments with samples collected from Lake Okeechobee and found that 'zooplankton grazing is not an important regular of phytoplankton biomass and productivity'. Similar observations have been made for other sub-tropical/tropical lakes around the world (Saunders and Lewis, 1988; Fernando, 1994; Magadza, 1994; Chen et al., 2003). For example, in the case of Lake Taihu, de Kluijver et al. (2012) suggest that cyanobacteria blooms primarily provide carbon to higher tropic levels through bacterial decomposition of senescent bloom biomass, although there is some lower level direct grazing on cyanobacteria which does not significantly impact bloom potential. The basis for the lack of significant control of blooms by direct grazing in Lake Okeechobee may be related to a combination of the character of zooplankton community structure in the lake (Crisman et al., 1995; Havens et al., 1996), and the resistance to grazing exhibited by the dominant bloom-forming cyanobacteria species in the lake, such as *Microcystis aeruginosa*. A number of factors have been linked to the resistance to grazing losses exhibited by bloom-forming cyanobacteria, including the production of toxins and other biologically active compounds, and the morphology of filaments and colonies that represent a physical challenge to grazing capacity (Crisman et al., 1995; Wilson et al., 2006; Yang et al., 2009; Zhu et al., 2013; Vilar et al., 2021). The BLOOM module within Delft3D-WAQ was used to account for the competition among the selected algal functional groups. BLOOM was based on an assumption that each phytoplankton type would try to maximize the total net production of its community in each time step (Deltares, 2019). The mass balance equation for phytoplankton is as follows:

$$\frac{\Delta Phytoplankton}{\Delta t} = loads + transport - settling + resuspension + gross\ primary\ production - respiration - mortality \tag{5}$$

3.5. Sediment settling and resuspension

Vertical fluxes of sediment particles in the lake were modeled since suspended sediments and phytoplankton growth could change turbidity in the lake, resulting in the reduction of light penetration. Sediment was assumed to be presented in the suspended form, as well as high mobility particles of the thixotropic mud layers in the bottom of the lake. The lake sediment zones were defined in SFWMD (2002) and Ji and Jin (2014) to quantify the effect of wind on sediment transport in the lake. An important feature of the mud layer in the deep zone was a 10 cm deep layer of legacy phosphorus accumulating over 50 years, which resulted in a volume of over 30,000 m^3 (Ji and Jin, 2014). Adsorbed phosphate was simulated as a substance besides organic carbon and organic phosphate from detritus decomposition. In summary, sediment cycling includes transport, settling, resuspension, burial and upward transport.

Water quality and biological processes in the lake were not only driven by the aforementioned cycles in the water body, but also atmospheric forcings and other elements. Solar radiation, fraction of cloud coverage, and penetration capacity of sunlight (Secchi depth) were among additional atmospheric variables besides those used in Delft3D-FLOW. In the west and north sides of the lake, the effect of vegetation coverage, which blocked light penetration, was simulated by setting the length of days to 0.1. As electron-acceptors (i.e., O_2, NO_x^-, Fe^{3+}, and SO_4^{2-}) and carbon dioxide (CO_2) were considered, pH might have an important role and was, therefore, also simulated. Finally, silicon (Si), an important nutrient to build skeletal structures of phytoplankton (especially diatoms), was included.

4. Data and scenarios

4.1. Data

Time series data were collected from the DBHYDRO database (available at apps.sfwmd.gov; accessed on March 2022) - an online database maintained by SFWMD [details described in Tarabih and Arias, 2021]. Daily climate forcings (air temperature, wind speed, etc.) were obtained from the same database at four locations (L001, L005, L006, and LZ40). SFWMD calculated flow rates through hydraulic structures from daily water levels, which were measured by using automatic equipment such as solid-state loggers and telemetry (Tarabih and Arias, 2021). Flow rate data from 24 Lake Okeechobee inflow stations were used in the model development. Direct surface runoff beyond these stations was not considered since the dike and hydraulic infrastructure force most of the surface water through one of these stations.

Monitoring data used in the model include: total phosphorus (TP), PO_4^{3-}-P, $NH_4^+ - N$, $NO_x^- - N$, total nitrogen (TN), total Kjeldahl nitrogen (TKN), dissolved oxygen (DO), *Chl-a*, carbon (all forms), turbidity, salinity, Secchi disk depth, Si, Fe^{3+} and SO_4^{2-}. Water quality data were collected monthly or biweekly by using either autosamplers or manual grab. *Chl-a* data were mainly used in this study to calibrate and validate algal production in the lake.

4.2. Scenarios

We ran the model for the period from January 2016 to December 2018 for calibration and from January 2019 to December 2021 for validation. This period was chosen since algal blooms were prominent and monitoring datasets widely available and complete. We then used the period from January 2016 to December 2018 for a baseline scenario. Besides R^2, the mean absolute error (MAE), which was the average of the absolute difference between the observed and simulated values, was used to evaluate model performance (Eq. (6)).

$$MAE = \frac{1}{N} \times \sum_{i=1}^{N} |y_i - \hat{y}_i| \tag{6}$$

where $\hat{y}_i$ is the simulated daily value and y_i is the observed daily value.

Our simulation scenarios focused on efforts at the watershed scale that directly influence nutrient inflows into the lake. In order to design best management practices for contributing watersheds, it is necessary to study effective nutrient reduction targets. Thus, we ran different combinations of PO_4^{3-} and NO_x^- load reductions (i.e., 25%, 50%, 75%, and 100%). Additionally, we also simulated a nutrient removal scenario as in James and Pollman (2011). They suggested that about 500 $km^2 \times 10$ cm of the offshore mud sediments in the deep zone (Fig. 1) should be dredged. Alternatively, James and Pollman (2011) also evaluated chemical treatment as a solution for nutrient removal. In this study, we considered nutrient removal as a general term, covering the two above approaches without considering their short-term effects.

A fixed computational time step of 10 s (s) was adopted in the water quality model to ensure its stability. The simulation results, however, were exported as hourly averaged time series. Initial conditions were obtained by interpolating data at the six stations (Fig. 1) in the lake using the Inverse Distance Weighting (IDW) method. The list of variables and their values for Delft3D-FLOW and Delft3D-WAQ is available in Supplemental Information Tables S1, S2, and S3. The model was calibrated manually with the trial-and-error method owing to the expensive computational time of a three-dimensional model.

5. Results and discussion

5.1. Model calibration and validation

For hydrodynamic modeling with Delft3D-FLOW, the coefficient of determination (R^2) between gauged and observed water levels at LZ40 was 0.98 (see Section 1 in Supplemental Information for more details). Delft3D-WAQ was calibrated and validated with respect to the concentration of DO, NO_x^-, PO_4^{3-}, and *Chl-a* using data observed at the six sites illustrated in Fig. 1 (grab samples from 0.5 m below the water surface). These six sites are distributed around the lake in locations with different hydrologic and biological characteristics. Calibration/validation results showed that the model could reproduce the main multi-annual and seasonal trends of key variables; Fig. 3 shows results for two stations, L007 and L008, and calibration/validation results for the other stations are included in Supplemental Information Table S4 and Figure S4. Most phytoplankton can use NH_4^+ and NO_x^- as nitrogen sources. However, the concentration of NH_4^+ was low in the lake, in part because nitrification and algal uptake can both occur rapidly (Ambrose et al., 1993; Lee et al., 2015); thus NH_4^+ was excluded in model calibration.

DO is a central component of any water quality model and it is among the most important indicators of the health of aquatic environments (Tang et al., 2016). The Mean Absolute Error (MAE) values of simulated DO concentration were about 0.45 mg/L during the calibration period and these values were from 0.36 to 0.87 mg/L during the validation period. The R^2 values ranged from 0.66 to 0.90 and from 0.67 to 0.88 for the calibration and validation periods, respectively. There was a clear seasonal pattern in DO, which tended to be the opposite of temperature (see Figure S5 in Supplemental Information for correlations among variables); we observed higher DO concentrations in the winter (December–March) and lower concentration in the summer (June–September). This was reasonable since DO depended on water temperature as shown in Eq. (1). In some other case studies [e.g., Bilaletdin et al., 2011], salinity levels affected DO and limited algal growth, but this was not the case for Lake Okeechobee since the concentration

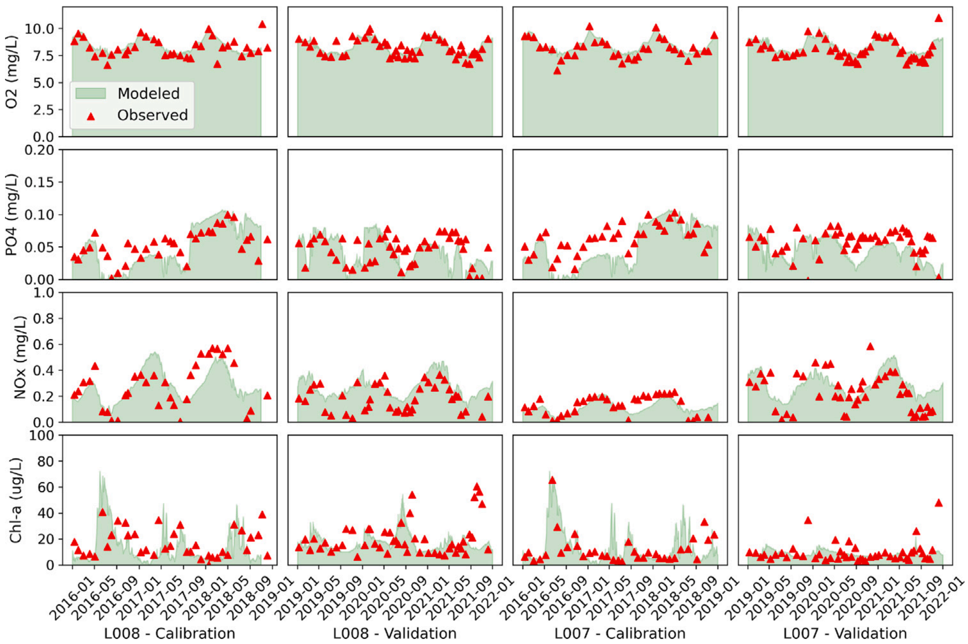

Fig. 3. Calibration (2016–2018) and validation (2019–2021) results of water quality variables (*DO*, PO_4^{3-}, NO_x^-, and *Chl-a*) at L008 and L007.

Table 1
Comparison between Delft3D-FM and other Lake Okeechobee models.

Model	Spatial features	P		NOx		Chl-a		References
		R2	RMSE	R2	RMSE	R2	RMSE	
Delft3D	7,623 FM (6 stations)	0.21–0.55	2.3–2.6	0.28–0.60	2.3–13.9	0.23–0.55	9.5–12.8	This study
LOWQM	Spatially averaged	0.34	2.5	0.37	5.8	0.18	5.4	James et al. (2005)
LOEM	2,121 cells (only L002)	Null	16.16	Null	26.83	Null	24.27	Jin et al. (2007)
EUTRO	Spatially averaged	Null	Null	Null	Null	Null	Null	Jin et al. (1998)
EFDC	625 cells (19 stations)	−0.31 (NSE)	Null	−0.24 (NSE)	Null	−0.56 (NSE)	Null	Shin et al. (2023)

of chloride (Cl^-) was relatively low and stable (< 70 mg/L). *DO* fluctuated slightly when ABs occurred because of the presence of primary producers.

PO_4^{3-} and NO_x^- are important nutrients for the growth of algae if NH_4^+ is limited. For the calibration period, the means of MAE of modeled PO_4^{3-} and NO_x^- were 0.02 mg/L and 0.12 mg/L, respectively. The averaged MAE for the validation periods were 0.02 and 0.11 mg/L for PO_4^{3-} and NO_x^-, respectively. R^2 for PO_4^{3-} calculated for the calibration and validation periods were 0.41 and 0.44, respectively. R^2 for NO_x^- were 0.30, and 0.41 for the calibration and validation periods. In general, the model can capture well the observed PO_4^{3-} data although it missed some peak points, which may have been due to sample heterogeneity caused by local turbulence under external forces (e.g., wind gusts or boat traffic causing random resuspension or consistent wind leading to large waves) in the shallow lake. The MAE values of simulated PO_4^{3-} and NO_x^-, which was approximate 10% and 20% of the maximum concentration (0.11 and 0.59 mg/L), were acceptable, considering the spatial coverage of the large computational domain, and spatial (15–1000 m) and temporal (hourly) resolutions of the model.

We used *Chl-a* as a surrogate for phytoplankton concentrations. The MAE value of modeled *Chl-a* was 8.92 μg/L and 9.10 μg/L for the calibration and validation periods, respectively. The corresponding R^2 values were 0.35 and 0.30. The values of *Chl-a* varied largely every day and had one annual peak in the summer. Observed *Chl-a* at L007 sometimes dropped below 5 μg/L.

Lake Okeechobee has been previously modeled at the same temporal resolution (daily) by using both empirical and process-based models. For example, James et al. (2005) used the Lake Okeechobee Water Quality Model (LOWQM), a deterministic and mass balance model to model P, N, and phytoplankton. Although the model calibration results seem equivalent to this study, LOWQM is unable to provide information on spatial dynamics. Lake Okeechobee Environment Model (LOEM), a 3-D hydrodynamic-water quality model developed by Jin et al. (2007) can provide more values in understanding spatial dynamics of the system, but it was only calibrated for one station and is limited by its rectangular mesh, which is unable to represent the canal rim around the lake and other non-uniform spatial features. An earlier model developed by Jin et al. (1998) for the lake called EUTRO was not calibrated. Environmental Fluid Dynamics Code (EFDC) gave negative NSEs in predicting the water quality variables in Shin et al. (2023). The performance of these models is summarized in Table 1.

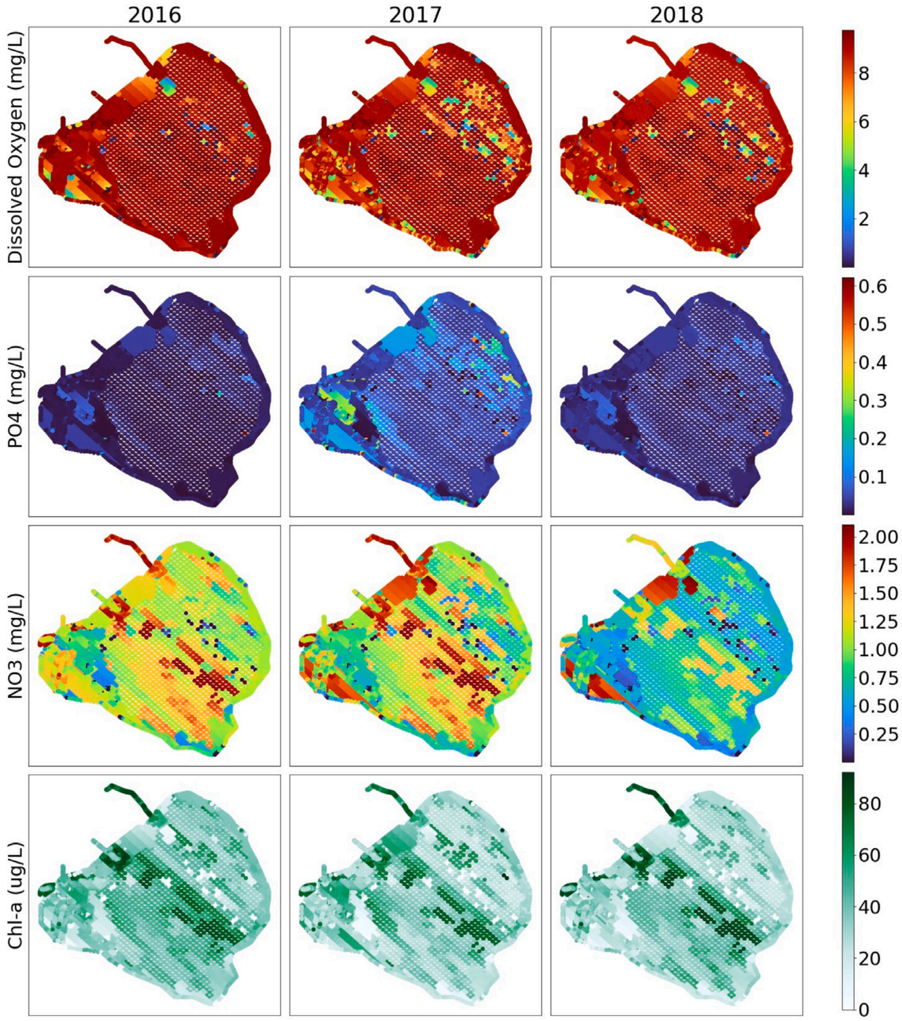

Fig. 4. Spatial variation of *DO*, PO_4^{3-}, NO_x^-, and *Chl-a* annual average in Lake Okeechobee from 2016 to 2018. The unit of *DO*, PO_4^{3-} and NO_x^- is mg/L and of *Chl-a* is μg/L.

5.2. Temporal and spatial variations and drivers of algal blooms

In this study, we reported the temporal and spatial variations of ABs over the period of three simulation years. We performed the non-parametric Mann–Kendall Trend Test and found no statistically significant trend (p-value = 0.35) in algal concentrations in the lake during the period 2016–2021, which is consistent with trend analyses based on observations (Tarabih and Arias, 2021). Before 2001, the total phosphorus concentration in the lake increased rapidly from 40 to 120 μg/L, which drove the Florida Department of Environmental Protection (FDEP) to establish a total maximum daily load (TMDL) of 140 metric tons total phosphorus per year for the lake (FDEP, 2001). This might result in the reduction of *Chl-a* concentrations after that, and the trend during 2016–2021 became unclear. Fig. 4 shows the annual average of *DO*, PO_4^{3-}, NO_x^- and *Chl-a* in each year for the period 2016–2018. *DO* was low at the mouth of the Kissimmee River and the SW bay, whereas *DO* was quite high in the center of the lake. This phenomenon might be a result of high COD near the canal mouths, noting that the Kissimmee River is the source of approximately 75% of organic matter into the lake (Phlips et al., 2020; Tarabih and Arias, 2021). Meanwhile, low *DO* in the southwest of the lake may be caused by nearby agricultural activities. The concentrations of PO_4^{3-}, NO_x^- and *Chl-a* tended to be higher in the center, northwest, and southeast of the lake. Phlips et al. (1994) and James et al. (2009) explained that phosphorus concentrations in the central region was high because of soft phosphorus-rich sediments. However, we found high concentrations in the central lake likely reflected wind-facilitated transport of blooms emanating from other regions, rather than autochthonous production. James et al. (2009) found higher *Chl-a* in the western and northern nearshore regions of Lake Okeechobee compared to the central region. These observations suggest the importance of nutrient inputs from tributaries in the north and west for AB formation, as well as the shallower depths in these regions compared to the center of the lake, which enhance light availability for photosynthesis.

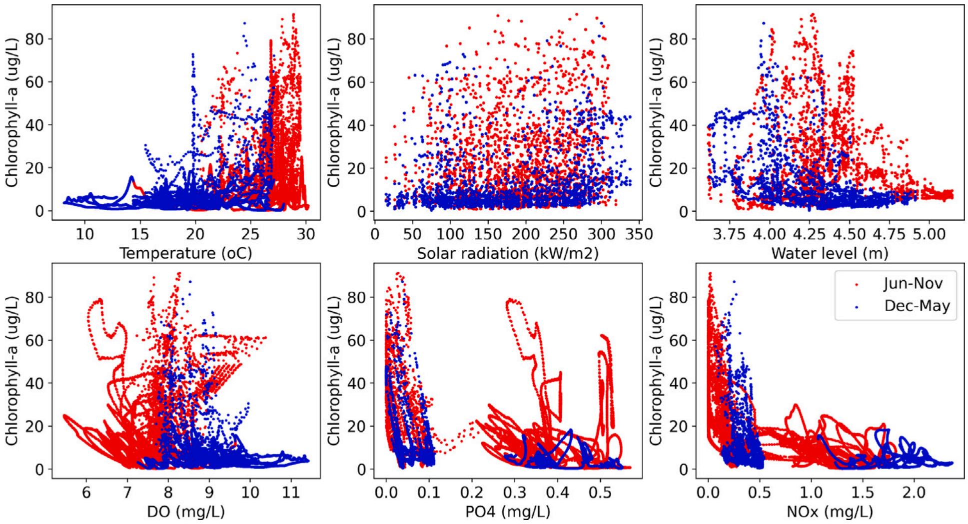

Fig. 5. Relationships between simulated hourly *Chl-a* and physical–chemical variables (Temperature, Solar radiation, Water level, *DO*, PO_4^{3-}, and NO_x^-) in Lake Okeechobee for the period from 2016 to 2018.

There were several physical factors limiting algal growth in the model, water temperature likely being the most important (see Fig. 5). The principal bloom-forming algae in Lake Okeechobee are cyanobacteria, and it is widely recognized that many of these species favor temperatures above 25 °C (Paerl and Hussmann, 2008; Nelson et al., 2018). High temperature and solar radiation in the summer clearly favor AB formation (also, see Figure S5 for correlations between variables). *DO* had a high inverse correlation with water temperature. In this study, we found that the relationship between water level and *Chl-a* was unclear because of the interplay effect of water level, light availability in the water column, wind, turbidity, and microbial processes (Phlips et al., 1997; James et al., 2009). For example, if water levels increase because of inflows and precipitation, water transparency will reduce because inflows bring nutrients and organic and inorganic materials.

In the case of Lake Okeechobee, both observed data and simulation results showed a high concentration of phosphorus and nitrogen in the lake. We observed an increase of *Chl-a* concentrations associated with the decrease of NO_x^-. This is likely a result of large NO_x^- utilization by ABs, which is supported by *in situ* data analysis with phosphorus, nitrogen and *Chl-a* that revealed high turbidity and nitrogen limited algal primary production (Aldridge, 1995; Phlips et al., 1995; Hansen et al., 1997; Havens and East, 1997). Adequate phosphorus supply throughout the years due to both canal inputs and legacy phosphorus might have resulted in the effective use of nitrogen in the form of NO_x^- in water. For example, almost all the points in which *Chl-a* values were above 40 μg/L, NO_x^- dropped below 0.2 mg/L. The concentration of PO_4^{3-} was sometimes below 0.02 mg/L, indicating seasonal minima in phosphorus and inorganic nitrogen were the limiting factors of ABs (Aldridge, 1995; Schelske, 1989). ABs often occurred during the hurricane season when sediment was resuspended owing to high wind speed, but there was a lag between an actual hurricane and an AB event. This lag time could be dependent on physical conditions (e.g., water temperature and solar radiation) and existing conditions of the lake. The summer season, with increased rainfall and tropical hurricanes (e.g. Irma in September 2017) and increased water levels in the lake, tended to dilute nutrients in a very short period since rainfall was among the main sources of water in the lake. Nonetheless, both phosphorus and nitrogen concentrations increased again together with the increased turbidity. Jin et al. (2011) and Phlips et al. (2020) suggested that high rainfall triggered by hurricanes might bring nutrient-rich water to the lake from its watersheds. Despite the nutrient-rich environment, we did not observe major responses of the algal community because high turbidity in water prevented light penetration, which was also mentioned in Phlips et al. (2020). The long residence time of water (average turnover of 3.5 years according to James and Pollman, 2011) then partially aided high potential of algal blooms in the later periods or the next summer, depending on how the lake is managed after the storms.

ABs tend to start at the near-shore areas near the outlet of Taylor Creek, Kissimmee River, Indian Prairies Canal, Harney Pond Canal, and Miami Canal (locations in Fig. 1). This can be explained by two phenomena. First, the zones near these points are quite shallow with high water transparency that warms up quickly. This conclusion supported what Phlips et al. (1995) found by using observed data analysis. Second, these rivers and canals drain large agricultural areas. In this study, we found that, besides the bay in the western and southern sites of the lake, ABs also occurred near the outlet of the Kissimmee River and the Taylor Creek, which provide nutrient inputs from their watersheds that help drive cyanobacteria blooms. ABs originating in these nearshore regions can then spread and expand to other regions of the lake by wind-driven circulation (Fig. 6; Figure S3 in Supplemental Information shows changes in current velocity and direction owing to wind). The importance of wind in defining the distribution of ABs has also been highlighted in other studies of Lake Okeechobee (Shin et al., 2023) and other lakes subject to cyanobacteria blooms around the world, such as Lake Taihu in China (Wu et al., 2013; Zhang et al., 2021).

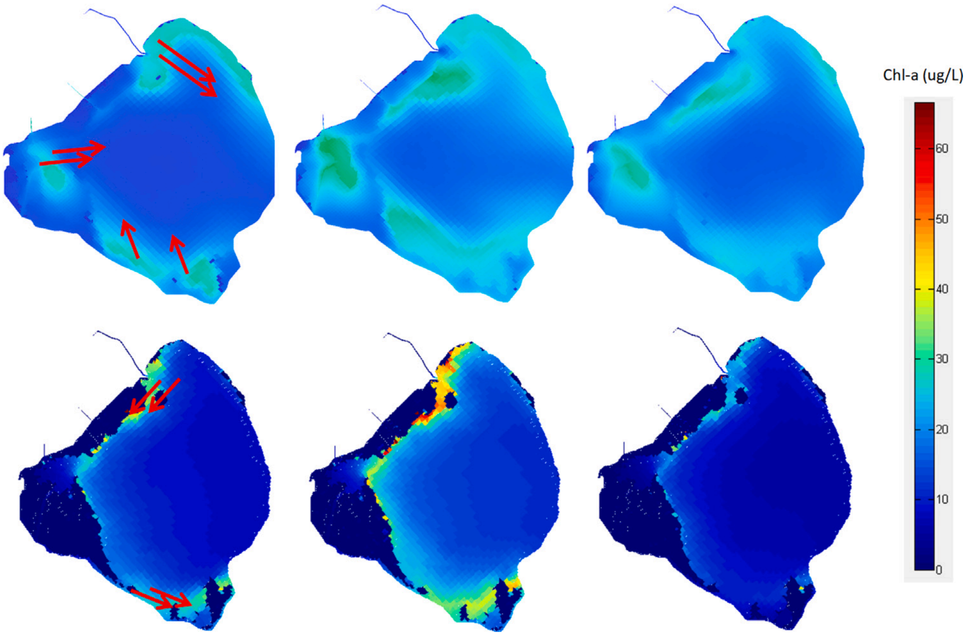

Fig. 6. Upper panel: Spreading of ABs from Fisheating Creek Bay and Taylor Creek over the whole lake. Lower panel: Formation of algal blooms near the mouth of the Kissimmee River and Miami Canal.

5.3. Potential management solutions

We evaluated the reduction of both phosphorus and nitrogen inputs into the lake model by different proportions to test how incoming nutrients influence ABs in the lake. ANOVA test showed significant differences ($p < 0.01$) among the simulated results for all the scenarios. The *Chl-a* threshold of 40 μg/L was chosen as an indicator of AB events as in Havens and Walker Jr. (2002) and Tarabih and Arias (2021). Simulations showed that either limiting phosphorus or nitrogen individually could have an effect, but to a limited extent. If nitrogen concentrations were reduced, yielding TN:TP ratios below 22:1 by mass, N-fixing cyanobacteria (e.g., Dolichospermum spp., Aphanizomenon spp.) would increase [see Smith, 1995 and Tarabih and Arias, 2021], potentially providing some nitrogen for non-N-fixing species (e.g. *Microcystis aeruginosa*). If phosphorus concentrations were reduced, the loss of phosphorus inflows might be compensated for legacy phosphorus, so reducing phosphorus inflows to the lake would not prevent ABs without addressing legacy loads. A similar conclusion was made for Lake Taihu in China, for which the authors concluded that a significant reduction of nitrogen and phosphorus of up to 80% and 30%, respectively, was required to reduce *Chl-a* by approximately 24%–38% (Tang et al., 2016). Hellweger et al. (2022) developed an agent-based model to simulate *Microcystis* growth in Lake Erie and concluded that nutrient control must include both phosphorus and nitrogen. In this study, we found that by reducing 75% of phosphorus and 75% of nitrogen, the maximum *Chl-a* concentration would be halved (Fig. 7). More importantly, the number of hours in which *Chl-a* exceeded 40 μg/L was reduced to 0 (see Fig. 7). The simultaneous reduction of phosphorus and nitrogen inputs seems the most rigorous solution for Lake Okeechobee in the long term, a statement in agreement with the call for a paradigm shift in lake nutrient management outlined in Paerl et al. (2016). In the short term, however, it is difficult to apply a systematic approach to achieve such targets; thus, optimizing the location of existing and emerging nutrient management practices for upstream catchments should be an immediate action. Riparian buffers or filter strips may be attractive solutions due to their low establishment costs (Hashemi et al., 2016). Since nitrogen is more often the limited nutrient for phytoplankton production in Lake Okeechobee (Aldridge, 1995), an initial focus on targeting reductions in nitrogen loads from local watersheds may help to reduce the intensity of blooms of non-nitrogen-fixing species of cyanobacteria, such as *Microcystis aeruginosa*, which is currently viewed as the most prevalent toxin threat in the lake (Rosen et al., 2017; Paerl et al., 2020; Phlips et al., 2020).

Lake nutrient removal has been proposed as an alternative to reduce ABs. Using model-derived estimates, James and Pollman (2011) suggested removing 51,458 ha or 70% of accessible phosphorus-laden mud sediment over 15 years at a cost of $3 billion USD. These estimates were derived from the Internal Loading Phosphorus Model (ILPM) and Lake Okeechobee Water Quality Model (LOWQM) lumped models, which did not take into account spatial distribution of sediment when dredging was applied. In this study, we tested the case of removing lake (legacy) nutrients in combination with reducing input nutrients (phosphorus and nitrogen) up to 50%. We found that there was a significant difference between scenarios with and without removing lake nutrients, the difference in the mean *Chl-a* of the two time series datasets was only around 5.62 μg/L, suggesting that nutrients from both canals and lakes are important nutrient sources that fueled ABs. Indeed, *Chl-a* dropped to almost 0 μg/L when lake legacy nutrients were removed. Model simulations still showed some comparatively small blooms. In these events, nitrogen inflows originated from atmospheric deposition may benefit *Microcystis aeruginosa* (Paerl et al., 2020). Our model experiment revealed that reducing all phosphorus and

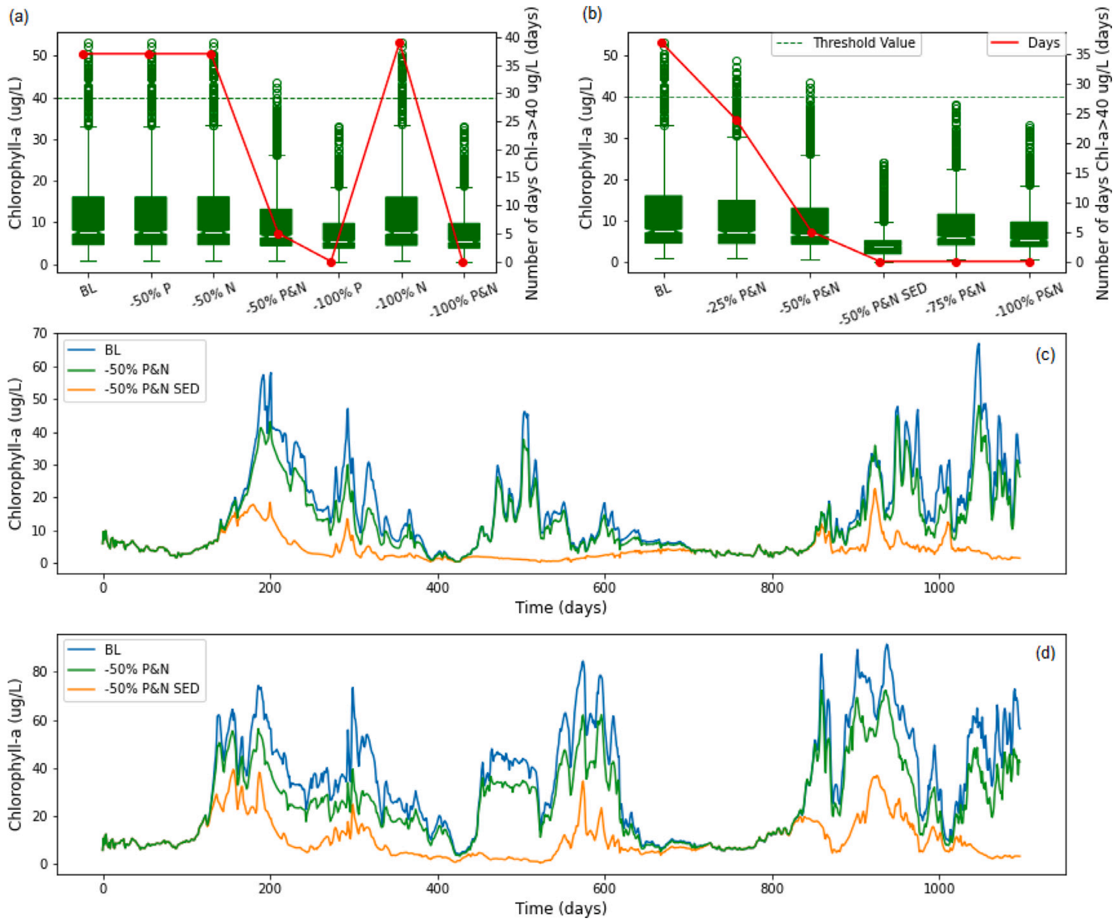

Fig. 7. a and b: Changes in *Chl-a* concentration in Lake Okeechobee regarding engineering and management solutions (Mean of the six locations). *BL* - Baseline; -X% P - reduce phosphorus by X%; -X% *N* - reduce nitrogen by X%; -X% P & *N* - reduce both phosphorus and nitrogen by X%; SED - Removing bottom sediment (in addition); c and d: Time series of *Chl-a* for the period 2016–2018 at L007 and L008.

nitrogen from the watershed cannot completely eliminate AB formation because the effects of the legacy nutrients and atmospheric deposition. Legacy phosphorus, for example, can maintain phosphorus concentrations in the lake to a certain level for over 50 to 75 years (Paerl et al., 2020). Overall, long-term modeling efforts with this high-spatial resolution 3D model demonstrate the need for a portfolio approach to AB prevention in Lake Okeechobee and other eutrophic lakes.

In this study, we did not include the effects of submerged vegetation on the biochemical model developed for Lake Okeechobee. This limitation was due to the lack of current available data on submerged vegetation, but it provides the opportunity to focus on specific aspects of interest (i.e., ABs) and reduced the model's complexity. Future studies may consider incorporating submerged vegetation to further enhance the model's ecological representation as suggested in Zhang et al. (2015).

6. Conclusions

In summary, warm water temperature and a nutrient-rich (phosphorus and nitrogen) environment favor frequent and persistent ABs in Lake Okeechobee. AB limiting factors depend on both temporal and spatial patterns. From May to November, high water temperature and solar radiation triggers AB events. AB events tend to start in shallow regions, especially near tributary inflows which are the source of nutrient loads for phytoplankton growth. Shallow nearshore regions are also characterized by high average light availability in the mixed-layer, which enhance rates of net photosynthesis in the water column, compared to the deeper region of the lake. ABs which form in nearshore regions can then spread to other parts of the lake through wind-driven circulation.

Our simulations indicate, however, that it would be highly unlikely to prevent the occurrence of ABs by reducing nitrogen or phosphorus alone. Instead, due to the presence of legacy nutrients and the different algae functional groups, reducing both phosphorus and nitrogen by a similar mass proportion could be more effective. Since excess nutrients mainly come from inflows of new nutrients from canals, upstream watershed management plans are necessary to improve water quality and mitigate the AB problem in the lake, and receiving canals and estuaries. It is important to simulate different best management practices and technological options to reduce both nitrogen and phosphorus inflows to the lake. Lake Okeechobee is an iconic example where ABs are driven by complex physical and biogeochemical factors; yet, this study can provide useful insights and lessons for the increasing number of lakes and waterways worldwide facing severe ABs.

CRediT authorship contribution statement

Thanh Duc Dang: Conceived and designed the research, Performed the experiments, Analyzed the data, Writing – original draft, Revised the manuscript. **Mauricio E. Arias:** Conceived and designed the research, Secured funding, Writing – original draft, Revised the manuscript. **Osama Tarabih:** Analyzed the data, Revised the manuscript. **Edward J. Phlips:** Writing – original draft, Revised the manuscript. **Sarina J. Ergas:** Secured funding, Revised the manuscript. **Mark C. Rains:** Conceived and designed the research, Secured funding, Revised the manuscript. **Qiong Zhang:** Conceived and designed the research, Secured funding, Revised the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ejrh.2023.101441.

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