

Review

# The Future of Cyanobacteria Toxicity in Estuaries Undergoing Pulsed Nutrient Inputs: A Case Study from Coastal Louisiana

Sibel Bargu <sup>1,2,\*</sup>, Matthew Hiatt <sup>1,2</sup>, Kanchan Maiti <sup>1,2</sup>, Paul Miller <sup>1,2</sup> and John R. White <sup>1,2</sup>

<sup>1</sup> Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, LA 70803, USA; mhiatt1@lsu.edu (M.H.); kmaiti@lsu.edu (K.M.); pmiller1@lsu.edu (P.M.); jrwhite@lsu.edu (J.R.W.)

<sup>2</sup> Coastal Studies Institute, Louisiana State University, Baton Rouge, LA 70803, USA

\* Correspondence: sbargu@lsu.edu

**Abstract:** Harmful cyanobacteria blooms (cyanoHABs) are a global phenomenon, especially in calm, warm, and nutrient-rich freshwater and estuarine systems. These blooms can produce various potent toxins responsible for animal poisoning and human health problems. Nutrient-rich freshwater pulsed into estuaries affects turbidity, water temperature, salinity, and nutrient concentrations and ratios at irregular intervals, creating a highly dynamic habitat. However, the underlying processes that lead to the selective development of cyanoHABs for certain species and the fate of their toxins are still uncertain. This paper draws upon the rich body of research available for one such system, the Lake Pontchartrain Estuary, Louisiana, to generate insights about future research directions in pulsed-nutrient-delivery estuaries. Toxin-producing cyanobacteria blooms in river-dominated Louisiana coastal ecosystems have already been documented at high concentrations, presenting a potential risk to human health as \$2.4 billion worth of Louisiana's fish and shellfish are consumed by millions of people throughout the US every year. Recent studies have shown that the Lake Pontchartrain Estuary, just north of New Orleans, Louisiana has been experiencing cyanoHABs, likely connected to combinations of (a) high interannual variability in nutrient loading associated with seasonal and episodic rainfall, (b) the timing, duration, and magnitude of the flood-stage Mississippi River water diverted into the Lake Pontchartrain Estuary, and (c) saltwater inputs from tropical storms. It is expected that cyanoHABs will become more frequent in Louisiana with a warming climate and changes to the timing and magnitude of river water diverted into the Lake Pontchartrain Estuary, which will play a dominant role in the development of blooms in this region. More studies are needed to focus on the environmental conditions that control the succession or/and co-existence of different cyanobacteria species and their toxins, optimally culminating in a near-term forecasting tool since this information is critical for health agencies to mitigate or to provide early warnings. Toxin forecasts for pulsed-nutrient estuaries, including Lake Pontchartrain, could directly inform state and municipal health agencies on human exposure risks to upcoming cyanobacteria toxicity events by predicting cyanobacteria species shifts, potency, and toxin modality along the freshwater-to-marine continuum while also informing a longer-term projection on how the changing climate will impact the frequency and potency of such blooms.

**Keywords:** harmful algal blooms; cyanobacteria; toxicity; nutrient loading; forecasting; Lake Pontchartrain Estuary



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## 1. Introduction

Phytoplankton blooms are increasing worldwide due to the eutrophication of aquatic environments [1–3]. The anthropogenic nutrient enrichment (both nitrogen and phosphorus) of estuaries directly impacts the phytoplankton species composition and the formation of noxious and toxic blooms, as well as surface scums [4]. Cyanobacteria (also known as blue-green algae) are a global phenomenon, especially in calm, nutrient-rich fresh, and brackish waters, and can produce a variety of potent toxins that are responsible for animal

poisonings and human health problems [2]. Harmful cyanobacteria blooms (cyanoHABs) are expected to pose a serious threat to the use and sustainability of existing freshwater and estuarine resources with climate change drivers increasing the temperature regime of these ecosystems and selecting for more cyanobacteria.

Cyanobacteria species produce diverse types of toxins, including hepatotoxins (microcystins and nodularin), cytotoxins (cylindrospermopsins), neurotoxins (saxitoxins, jamaicamides, anatoxins), and dermatoxins (lyngbyatoxin and aplysiatoxin) [5] that have a broad range of impacts on human and ecosystem health. Microcystins are the most frequently reported algal toxins in freshwater systems, with cylindrospermopsins emerging as an important cyanotoxin [6]. Most cyanobacteria also produce lipopolysaccharides, which are contact irritants and cause allergic, inflammatory, and pyrogenic responses. Moreover, most of the knowledge about cyanotoxin production is traditionally associated with planktonic cyanobacterial blooms. The extent and frequency of toxin production by benthic cyanobacteria in freshwater systems are not well understood despite records of poisonings of animals caused by them [7,8]. Additionally, environmental conditions (especially physical forces, like hurricanes) can affect the modality (extracellular vs. intracellular) of the toxin and therefore determine the fate of the toxin in the water column and, consequently, in the pelagic and benthic food web, which can create different pathways for human contamination.

In recent years it has become increasingly clear that cyanoHABs are formed under a complex interweaving of physical, chemical, and biological processes [9,10]. For example, a massive cyanoHAB in the western basin of Lake Erie in 2011 was brought about by extreme spring precipitation events delivering a large pulse of dissolved reactive phosphorous to Lake Erie, which was experiencing quiescent wind conditions, warm lake waters, and weak circulation that led to anomalously long water residence times [11]; recent studies have found that water transit times (e.g., residence times) are among the strongest predictors cyanoHAB prevalence in coastal environments, e.g., [12,13]. Other studies have also found that submarine groundwater discharge into water bodies can be a significant source of dissolved nutrients that can drive cyanoHABs [14,15]. Accordingly, there is a growing recognition that cyanoHAB prediction and monitoring must account for hydrology, land-use practices, weather, and anthropogenic influences in addition to understanding the chemical and biological conditions that support HABs, especially in the face of climate change [16].

River systems have become substantially influenced by human activities through land-use changes, river diversion operations, and flood control measures. The estuarine waters of Louisiana are physically and biologically influenced by variability in the Mississippi River discharge and seasonal factors determining which phytoplankton assemblages dominate these systems. The presence of toxin-producing cyanobacteria blooms in several Louisiana estuaries has been documented at relatively high concentrations, including the contamination of blue crab by cyanotoxins called microcystins in Lac Des Allemandes [17], high toxic cyanobacteria abundance in Breton Sound [18], and reoccurring cyanoHABs in the Lake Pontchartrain Estuary (LPE) following openings of a river diversion called the Bonnet Carré Spillway (BCS) [19–23]. These studies have exclusively focused on the identification and monitoring of *Microcystis* and *Dolichospermum*, the two most common cyanobacteria bloom-forming genera and toxin producers. However, other toxic cyanobacteria species, such as *Cylindrospermopsis raciborskii*, *Raphidiopsis curvata*, and *Anabaenopsis* cf. *elenkenii*, have also been observed in Louisiana estuaries, which are associated with either or both hepatotoxin or/and neurotoxin production [17–19,24–28].

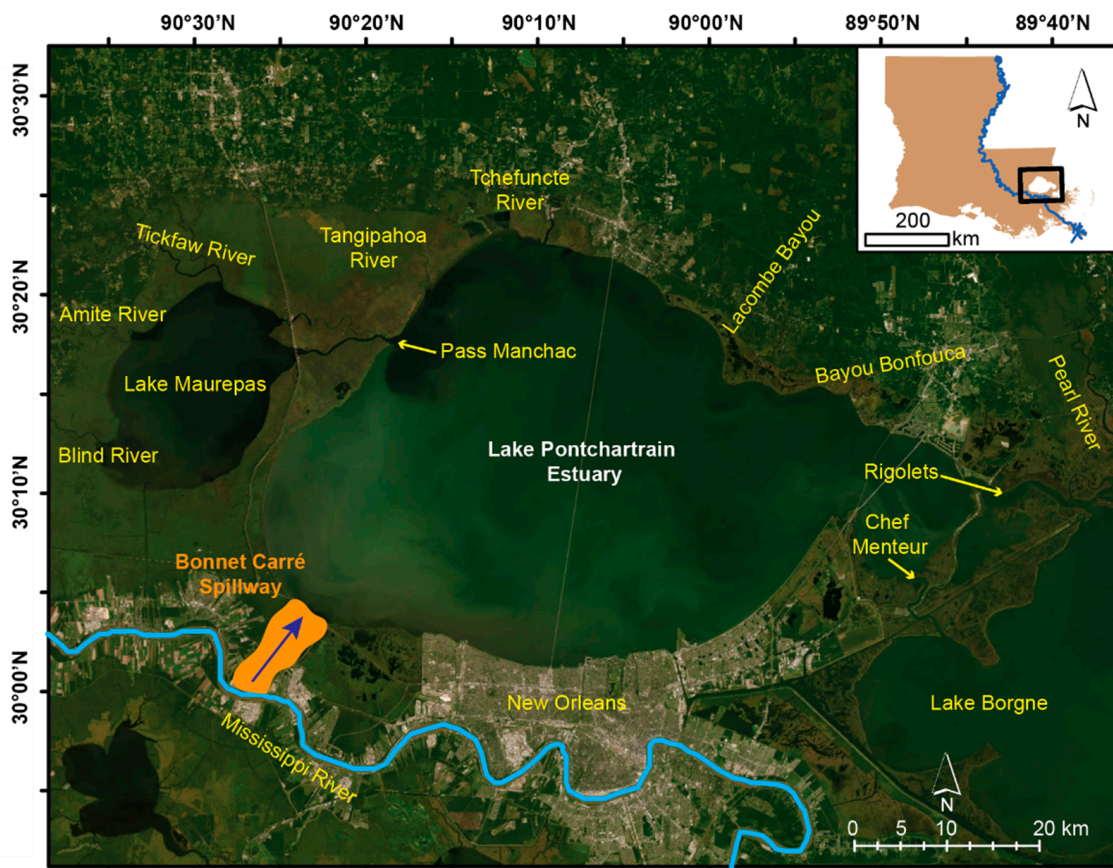
The essential environmental drivers (e.g., dissolved inorganic N (DIN), dissolved inorganic phosphorus (DIP) ratios, temperature, turbulence, light levels, etc.) promoting the blooms of each of these species are likely to be very different. Additional studies are needed to fill the gap in our knowledge of the role of nutrient-loaded freshwater pulses in phytoplankton succession and phycotoxin production during seasonal timescales and varied flow regimes in estuaries, providing essential information for effected restoration

efforts in deltaic systems, like the Mississippi River Delta. Whereas previous synthesis papers have examined estuaries writ large [29–31] or in non-pulsed nutrient delivery settings [32], this review will use the well-studied Lake Pontchartrain Estuary, Louisiana, as the archetype to generate insights about future research directions in pulsed-nutrient-delivery estuaries. The goals of this review include: (1) discussing the environmental and biological drivers supporting the LPE cyanoHABs; (2) describing the nutrient pathways that contribute to the LPE cyanoHABs; and (3) casting a vision for an eventual human exposure forecasting tool based on this information. Current knowledge gaps preventing the progress of the LPE toxin exposure forecasts will also be identified. Systematic, long-term studies of the LPE system, with respect to the variability in sources and magnitude of nutrient inputs, the physical drivers controlling the LPE circulation and water residence time, and the associated cyanoHAB responses, are needed to construct a fundamental understanding for translation into a forecasting model.

## 2. Focus Region: The Lake Pontchartrain Estuary (LPE)

The LPE (Figure 1) is a large, oligohaline estuary located north of New Orleans, Louisiana with a mean annual water temperature of 22.8 °C, according to observations from New Canal Station between 2007 and 2022. Over the last 15 years, water temperatures have experienced their peak of 30.8 °C in August while cooling to an annual minimum of 12.8 °C in January. The estuarine circulation is dominated by the wind, with a surface area of about 1600 km<sup>2</sup>, an average depth of 3.7 m, a volume of ~6 km<sup>3</sup> [33], and a mean tidal range of about 0.16 m. Freshwater can be introduced into the estuary via the north shore tributaries and overland flow, Lake Maurepas, New Orleans urban runoff, and the Bonnet Carré Spillway (BCS) [34]. The BCS is a flood control structure located in the southwestern region of the estuary (Figure 1) and can temporarily connect the Mississippi River to the estuary during threatening river flood stages. The BCS is made up of 350 bays, which are blocked by vertically placed railroad ties that are manually removed during the flood stage. In the event that all bays are opened, the BCS discharges fresh river water into the LPE at a design rate of ~7000 m<sup>3</sup> s<sup>-1</sup> [23]. The LPE exchanges water with the Gulf of Mexico through two narrow outlets called the Rigolets and the Chef Channel. The water average residence time for the LPE has been estimated at 15–25 days during spillway openings [33,35,36]. Estimates of water residence time vary widely for time periods without spillway openings [37,38]; however, there are no systematic evaluations of residence time using numerical models during quiescent conditions, during which cyanoHABs have been observed [20]. Estimates of estuary-wide residence time obtained using a simple tidal prism model [39] range from about 30 to over 50 days when the spillway is closed, depending on hydrodynamic conditions; however, such estimates do not include the dominant effect of wind on the Lake Pontchartrain estuarine hydrodynamics [40] or consider the geometry of the system. Salinity in the LPE averages ~7 [40,41] but can vary depending on location, tidal conditions, and wind conditions.

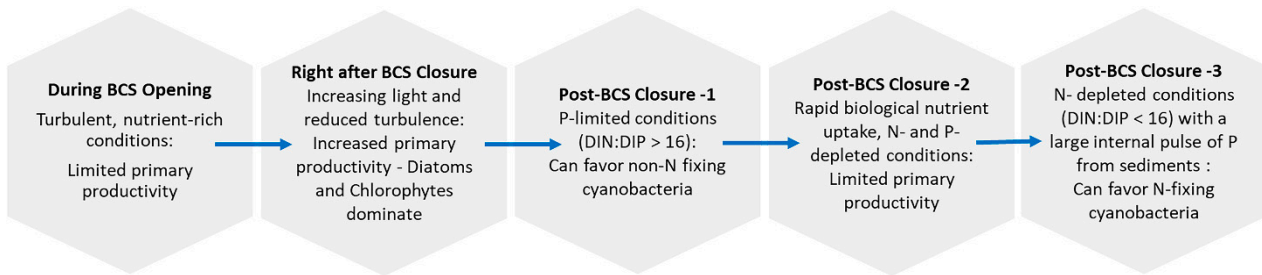
Recent studies have shown that the LPE experiences high interannual variability in nutrients and phytoplankton community dynamics. This is likely due to the effects of seasonal and episodic rainfall; the timing, duration, and magnitude of Mississippi River water being diverted into the estuary; and tributary discharges and saltwater inputs from tropical activity; although, other processes, such as groundwater discharge and the internal loading/benthic flux of nutrients, cannot be ruled out due to a lack of quantitative studies. Historically, the BCS has opened 15 times since its construction in 1931 to protect New Orleans from Mississippi River flooding during the high river stage. However, six of those came in the 2011–2020 decade alone, including two consecutive openings in 2019, as well as the earliest opening on record, 2016. Several previous BCS openings have been associated with cyanoHABs [19,21,23,34] and there is concern that more frequently occurring river discharges due to changes in climate can foster more frequent blooms, especially in shoreline areas utilized by the public, possibly exposing people and/or their pets to harmful levels of cyanobacteria toxins.



**Figure 1.** The Lake Pontchartrain Estuary (LPE) and important hydrological features. The black box in the inset map of Louisiana shows the spatial extents of Lake Pontchartrain Estuary and surrounding features.

### 3. Environmental and Biological Drivers Supporting cyanoHABs

Even small environmental changes can impact the structure and function of phytoplankton assemblages. For instance, seasonal variations are found to be an important factor in determining which phytoplankton assemblage dominates a system, as illustrated by the 2008, 2016, and 2019 BCS openings described below. The flow of nutrient-rich water into the LPE after the 2008 BCS spring opening led to a phytoplankton succession in the estuary, as shown in Figure 2 [19,21]. High turbidity and low light availability limited phytoplankton growth while the diversion was open, despite the nutrient-rich conditions. Right after the diversion was closed, diatoms and chlorophytes dominated the system as sediment settled out and water clarity increased. They were slowly replaced with toxic cyanobacteria species of *Microcystis* when phosphorus-limited conditions occurred. During the post-diversion period, N-fixing *Dolichospermum* became more abundant in July and *Raphidiopsis* and *Cylindrospermopsis* spp. were more frequently observed in August. Different species of cyanobacteria employ different nutrient acquisition strategies to gain competitive advantages, such as nutrient storage (“luxury uptake”), vertical migration, or cyst formation [42]. For example, differences in the timing of occurrence between *Dolichospermum* and *Microcystis* are largely driven by N biogeochemistry [9,43,44]. *Microcystis* spp. depend on DIN in the water column and are typically observed in late spring or early summer when DIN is provided by external inputs. *Dolichospermum* spp., on the contrary, are able to fix atmospheric N and can become the dominant species when water column DIN is depleted and DIP remains available [21].



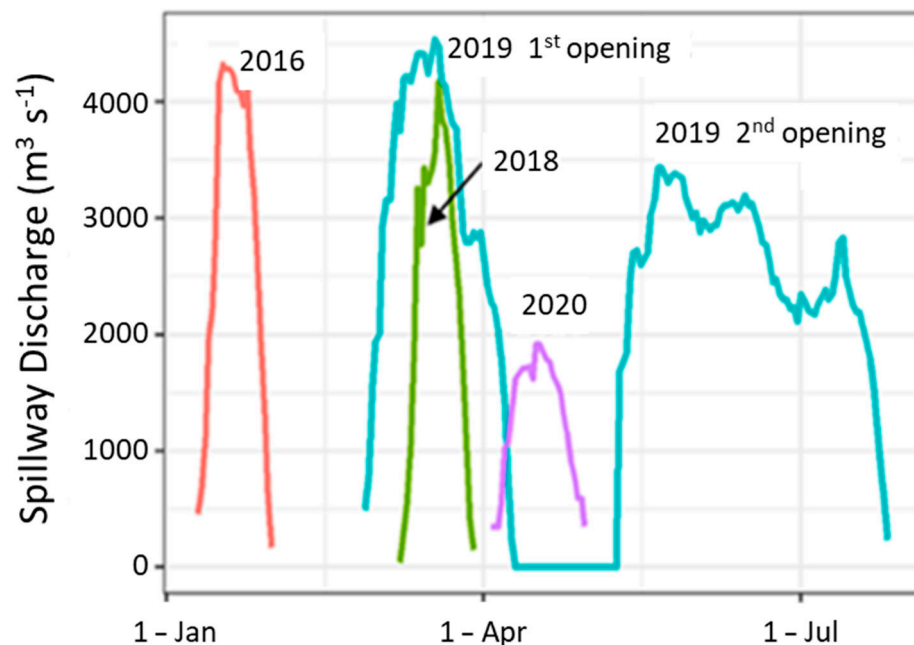
**Figure 2.** Estuarine biogeochemical dynamics and phytoplankton succession during large inflows of nitrate-rich freshwater. The diagram is based on observations in the Lake Pontchartrain Estuary during the 2008 and 2011 Bonnet Carré Spillway (BCS) openings. BCS closure 1–3 indicates that the system can move from P-limitation to N-limitation in <1 month during warm periods (water temperature  $\geq 25$  °C). Modified from [22].

Vegetative cells of some cyanobacteria, like *Dolichospermum*, can also differentiate into heterocysts or akinetes, thick-walled resting cells, allowing blooms to persist during extreme environmental conditions [45]. Differences in nutrient acquisition strategies employed by *Microcystis* and *Dolichospermum* spp. indicate that different environmental factors may control the cyanobacteria community structure and their toxin production [46–48].

In the LPE, residence times are modulated by river discharge, the spillway, tides, and wind. Lagrangian particle tracking in a hydrodynamic model of the LPE showed that residence time during the spillway opening was about 25 days [34]. Simpler models also predict residence times during spillway openings of a similar order at about 15 days [35]. The dominant drivers of residence time and circulation are the spillway discharge and wind conditions [34]. During quiescent conditions, estimates of residence time are available and range widely [32,37]; however, there have been no analyses of residence time using numerical modeling to test the sensitivity of local and system-scale residence to the driving physical factors of tributary discharge, wind, and tides. Such analyses are vital in systems globally to identify conditions that lead to increased residence times and, subsequently, a high potential for algal blooms on both the local and system scales. In general, residence time is inversely correlated with freshwater discharge in coastal environments while tides, wind, and marine influences may have a direct or inverse effect on flushing time, depending on system geometry and the interplay of environmental forces, e.g., [49–51]. Consequently, eutrophication is affected because residence times influence nutrient availability and uptake, transformations, and sinks. Estuaries with short residence times are less vulnerable to the accumulation of phytoplankton biomass and HAB formation [52,53] because freshwater discharge flushes the system relatively quickly, giving little time for phytoplankton growth rates (one to two doublings per day) to develop significant biomass [54]. On the other hand, systems with long residence times (orders of magnitude greater than phytoplankton growth rates) may be especially susceptible to eutrophication and bloom formation [10]. However, even systems with overall short residence times may have zones of more isolated, slower-moving water due to spatial heterogeneity in geometry, vegetation, or the impacts of environmental forcings, e.g., [50,55,56]. For example, the relatively low discharges from LPE northern shore tributaries compared to system-wide circulation may lead to zones of slow flow and increased residence time, exacerbating the prevalence of cyanoHABs in this area of the system. How spatial heterogeneity in residence times impacts phytoplankton community development is an important issue that is understudied worldwide and an increased understanding of this phenomenon will be helpful for identifying ‘hotspots’ of potential HAB development.

However, the opening of the BCS is not fixed in time and is solely dependent on the predicted flood stage of the Mississippi River. In contrast to the spring 2008 opening, the BCS has recently been operated at seasonally atypical timeframes. For instance, the Mississippi flood pulse in January 2016 required the early opening of the BCS flood release structure to prevent flooding in New Orleans (Figure 3). This is the earliest opening date

in the 80+ years of operating the BCS, suggesting climate change impacts on watershed hydrology are already occurring and the peak river discharge period could shift earlier from the current normal spring flood period of April/May in the future [57]. The BCS was later closed on 1 February, totaling 23 days of diverted Mississippi River freshwater entering into the LPE. Limited phytoplankton biomass (chlorophyll a concentration) was associated with this opening due to the cold-water temperatures associated with the early BCS opening, limiting the growth of phytoplankton in the estuary [57]. In 2019, the BCS was operated twice in the same year for the first time in history for a record total of 123 days, diverting 28.7 km<sup>3</sup> of Mississippi River water into the LPE in the spring and summer months to release pressure on levees downstream and protecting New Orleans from catastrophic flooding [58] (Figure 3). This resulted in reoccurring cyanoHABs that caused concerns for the public and public health officials and resulted in the Louisiana Department of Health and Mississippi Department of Environmental Quality issuing beach advisories or closures. Satellite images [18] showed that the influx of a high volume of river water from the LPE to connected waters during the 2019 BCS openings created a fresh and nutrient-rich habitat for cyanobacteria to easily proliferate further out into coastal areas of Lake Borgne and coastal Mississippi and increased the complexity of the bloom-related problems [19]. The reduced salinity due to river input appears to be one of the important factors driving the cyanobacteria's success and the persistence of their toxicity in these coastal areas [59]. CyanoHABs also occurred in the LPE several times during the second BCS opening (10 May–27 July 2019); however, they were patchy and variable in their location and intensity. A large cyanoHAB quickly formed at the northern part of the LPE, right after the second BCS closure (27 July 2019), and the bloom expanded to the southeast in August. Interestingly, the co-dominance of both *Microcystis* and *Dolichospermum* was observed due to long-term external nitrogen input to the estuary from early spring to late summer [19,36].



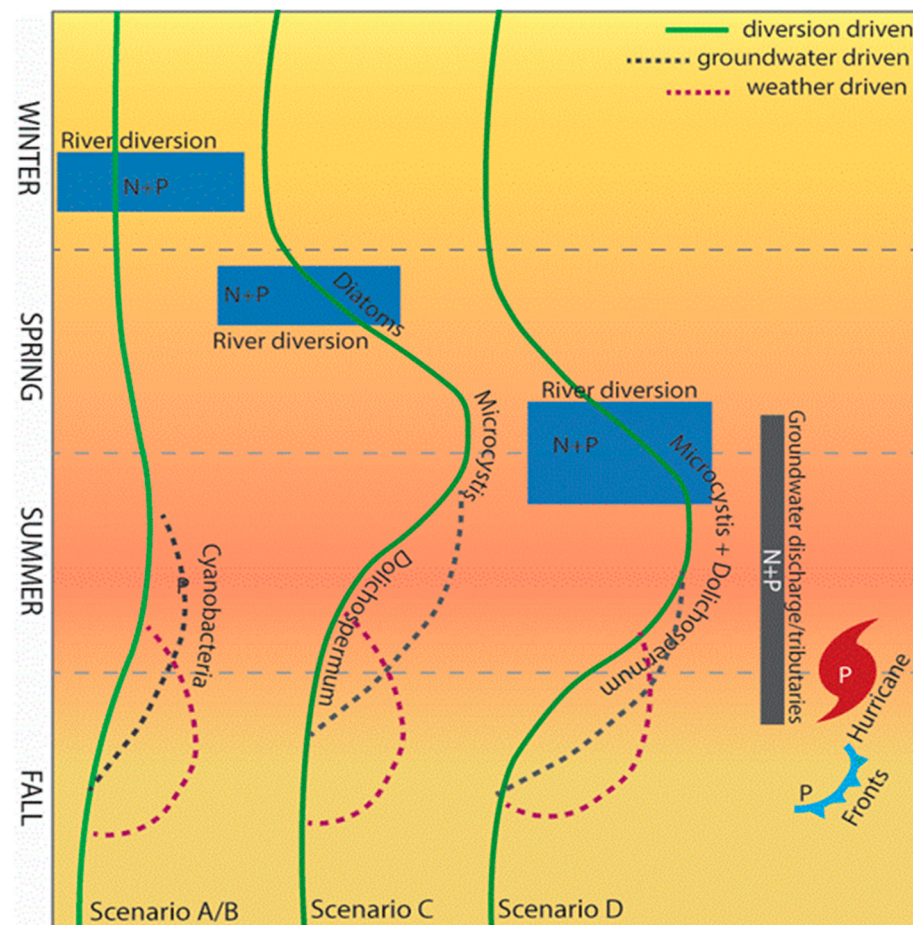
**Figure 3.** Timing, rate, and total magnitude of Bonnet Carré Spillway discharge in 2016 (red), 2018 (green), 2019 (turquoise), and 2020 (purple). Data courtesy of the United States Army Corps of Engineers.

While anecdotal evidence exists to indicate that the shifts in hydrological regimes associated with climate change combined with extensive engineered alterations of the Mississippi River system in Louisiana can strongly influence the occurrence of cyanoHABs, their intensity, spatial distribution, and species selectivity, there exists no systematic study

that has taken a holistic approach to determine how the difference in the timing and magnitude of various sources of nutrients to the LPE can impact future cyanoHABs. For example, alterations to the hydrological inputs and potentially increased water transport time scales may lead to increased productivity for HABs. However, the effects of freshwater releases on residence times in shallow, coastal receiving waters are understudied as an impact of hydrologic restoration [60]. Some studies exist linking changes in phytoplankton dynamics to restoration activities, such as submerged aquatic vegetation planting [61], bivalve restoration and management [62,63], nutrient reduction measures [64], and freshwater diversions [18,36,65,66]. However, a significant advancement in our ability to predict HABs would be to understand the sensitivity of phytoplankton community adaptation to large-scale river diversions and environmental stressors that bring pulsed nutrient loads to coastal environments. Recent work [67] has identified the importance of freshwater diversions to phytoplankton diversity and the origin of the community, which alters water quality for downstream municipalities. The proximity of the LPE to the city of New Orleans and the presence of extensive oyster harvesting grounds downstream of the LPE make cyanoHABs a pressing human health issue that needs to be studied more intensively.

It is imperative that we better understand how phytoplankton succession or co-existence can occur under different timing of BCS openings, nutrient availability, and sources, as well as weather conditions (Figure 4), to determine how it might change in the future. Variability in species dominance or co-existence under changing environmental conditions can further support the variability of the toxins detected. However, both the succession amongst different cyanobacteria species and their toxins remain poorly understood. It is known that cyanobacteria genera can contain one or more species that can produce the same toxin, like microcystin being produced by both *Microcystis* and *Dolichospermum* or one or more species that can produce multiple toxins, like *Dolichospermum* [68,69]. Alternatively, environmental conditions can support the growth of non-toxic strains of the same species or cause variability in cellular toxin levels. Ceballos-Laita et al. [70] have shown that the presence of metal ions can induce the formation of microcystin strains. Vezie et al. [71] found that non-toxic strains are more likely present under low nutrient status; however, toxic strains dominate at high nutrient levels. Additionally, nutrient stoichiometry can play a significant role in toxin diversity since some of these toxins are nitrogen-rich toxins, such as microcystin and saxitoxin, and some are nitrogen-poor toxins, such as anatoxin.

Toxin monitoring was only limited to cyanotoxin “microcystin” in the studies mentioned above [19,72]. Microcystin was detected in each of the cyanobacteria bloom studied but the levels of toxin were not linearly correlated with the levels of cyanobacteria biomass, indicating that the cellular toxin production and/or modality of the toxin (intra- and extra-cellular) can also be affected by changes in environmental conditions, such as temperature, light and nutrient availability, and nutrient ratios [71,73]. However, such studies may be revisited and expanded with the emergence of additional toxin-monitoring technologies [74–76]. Clearly, conditions that could favor species producing certain types of toxins or more toxin-producing species over other phytoplankton species would increase human health risks. Another aspect that would make a difference in terms of the human exposure to these toxins is the modality of the toxin. That is, whether the toxin remains inside the cell (when the cells are healthy) or is excreted outside of the cell (when the cells are stressed), which occurs due to physical disturbance or is lysed when blooms are aging. When the toxin is intact inside the cells, human toxin exposure would likely occur via direct contact during recreational activities or via contaminated fish consumption. On the other hand, when the toxin is outside of the cell in its dissolved form, it can potentially bind to dissolved organic matter, sink to the bottom, and become a health exposure risk via contaminated benthic organisms (such as clams, oysters, and crabs) that can concentrate the toxin and can then be consumed by humans.



**Figure 4.** HAB community responses to variability in nutrient input due to climate and anthropogenic forcing. Scenario A/B represents an early winter river-diversion or no-river-diversion year. Scenario C represents an early spring river diversion resulting in an input of excess N and P. Scenario D represents a late spring or early summer river diversion. The green line represents the plankton community's response to increased N and P from the river diversion and species succession. The dotted gray line represents the plankton response sustained by an additional input of N and P from groundwater discharge and surrounding tributaries. The dotted red line represents a response to the internal input of predominately P through weather-driven resuspension events.

Fortunately, our ability to reliably predict upcoming weather conditions has improved dramatically over the last two decades. Numerous publicly accessible weather models are run multiple times daily and predict the types of meteorological and hydrological conditions that are believed to contribute to the development and spread of cyanoHABs. However, the advancement of cyanoHAB forecasting to include species and toxicity is currently limited due to our lack of understanding regarding the exact physical and chemical conditions that determine species succession, toxin type, and modality.

#### 4. Pathways for Nutrient Transport into Systems of Interest

Nutrient dynamics play an important role in cyanobacteria presence and success. In general, phytoplankton, including cyanobacteria, thrive in aquatic environments receiving excessive inputs of nitrogen (N) and phosphorus (P) [77]. Anthropogenic sources of N and P transported by tributaries include agricultural and urban stormwater runoff, groundwater discharge, and centralized and decentralized (on-site) wastewater treatment discharges [77]. As mentioned above, different environmental factors may control the cyanobacteria community structure and their toxin production; therefore, it is critical to identify and estimate the various nutrient inputs in the LPE that can significantly impact

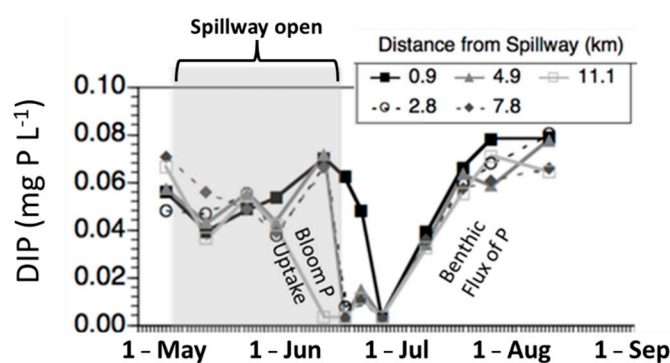


the phytoplankton species. The four predominant pathways for dissolved and particulate nutrients to enter the LPE beyond the BCS opening are (i) submarine groundwater discharge, (ii) leakage through the river spillway structure (BCS), (iii) tributaries, and (iv) the internal loading of nutrients via benthic fluxes. While data are available for tributary and river flood discharges, both submarine groundwater discharge and internal loading from sediments (benthic flux) are not typically measured.

Submarine groundwater discharge (SGD) is the advection of fresh groundwater or recirculated brackish through sediment and into the water column and is an often-overlooked pathway of nutrient delivery. The rates of SGD are thought to be substantial; estimates suggest that SGD is 300–400% of the total global riverine discharge rates into the ocean [78]. The chemical constituents of SGD can alter the contents of the estuarine water it is discharged into and can have a strong influence on nutrient regimes, with SGD altering concentrations of inorganic nitrogen, phosphate, methane, dissolved inorganic carbon (DIC), and dissolved organic carbon (DOC) [79–81]. A recent study in Mobile Bay, AL reported that SGD comprised up to 37% of the total water inputs during the dry season, coinciding with the time of the year when Jubilees and HABs occur [82]. Similarly, another study from West Florida showed the importance of SGD nutrient contribution to the development of nearshore blooms of *Karenia brevis* [15]. The impact of SGD on the coastal Louisiana nutrient budget is currently undocumented; however, a study in nearby Mississippi Bight, adjacent to the LPE, indicates SDG seepage rates of  $0.055 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ , representing 10–20% of the bottom water input and a substantial impact on the bottom water hypoxia in this region [83]. Thus, SGD can contribute significantly to the LPE nutrient budget and influence cyanoHAB development during late summer and fall when the freshwater discharge into the lake is lowest and the BCS opening is less frequent. It is likely that tropical storms and depressions during this time period would further increase the SGD contribution as storm-driven increases in SGD and nutrient fluxes are well documented in other regions [14]. While direct estimates of SGD from coastal/estuarine Louisiana are limited, modeled results for SGD input for the contiguous United States, based on historical climate records and high-resolution hydrographic data, indicate rates between 100 and  $500 \text{ m}^2 \text{ y}^{-1}$  for coastal Louisiana [84]. Thus, the contribution of SDG to the nutrient budget and cyanoHAB formation may be currently overlooked.

A consequence of river discharge into the estuary is an increase in sediment total P load [85]. For example, a river discharge event to the LPE in 2011 found the total P of the top 5 cm of sediment increased by 36% from  $509 \text{ mg P kg}^{-1}$  to  $692 \text{ mg P kg}^{-1}$  after a one-month diversion opening [86]. There is a high proportion of Fe-bound P in the Mississippi River sediment and once deposited, reduction of the Fe leads to an increase in soluble P (Figure 5). This consequent release can then drive the internal benthic flux supporting N-fixing cyanoHABs. It is thus anticipated that the internal loading of nutrients, especially the benthic flux of P, can also play an important role in sustaining cyanoHABs, which can vary over time based on biological uptake in the water column and other environmental factors, such as wind-driven resuspension events. Previous studies have shown that once the water clarity increases and the spillway closes, the initial diatom bloom consumes most of the DIN and all available DIP over a short period of time due to a high N:P ratio of dissolved nutrients in the discharged river water [22,87]. During the ensuing month, the sediments restore the water column SRP concentration through benthic flux to produce a condition where N is very low but DIP is present, flipping the N:P stoichiometry imparted by the river water, allowing N-fixing cyanoHAB species to proliferate (Figure 5). A limited spatial study has extrapolated this annual diffusive benthic DIP flux in the LPE to be in the range of 227–517 metric tons of P per year [87]. However, storm events in shallow aquatic systems can substantially increase DIP flux. In July 2019, due to the physical disturbance of Category-1 Hurricane Barry crossing the LPE, the DIP concentrations increased up to five times in some areas while DIN concentrations did not [36]. This increase occurred over a 30 km transect, suggesting the release of P from the sediments due to bedload shear in this shallow estuary. For Lake Okeechobee, FL, which also has reported cyanoHABs, the

internal loading of DIP (benthic flux) was found to be equal to or exceeding the tributary loading to the lake [88].



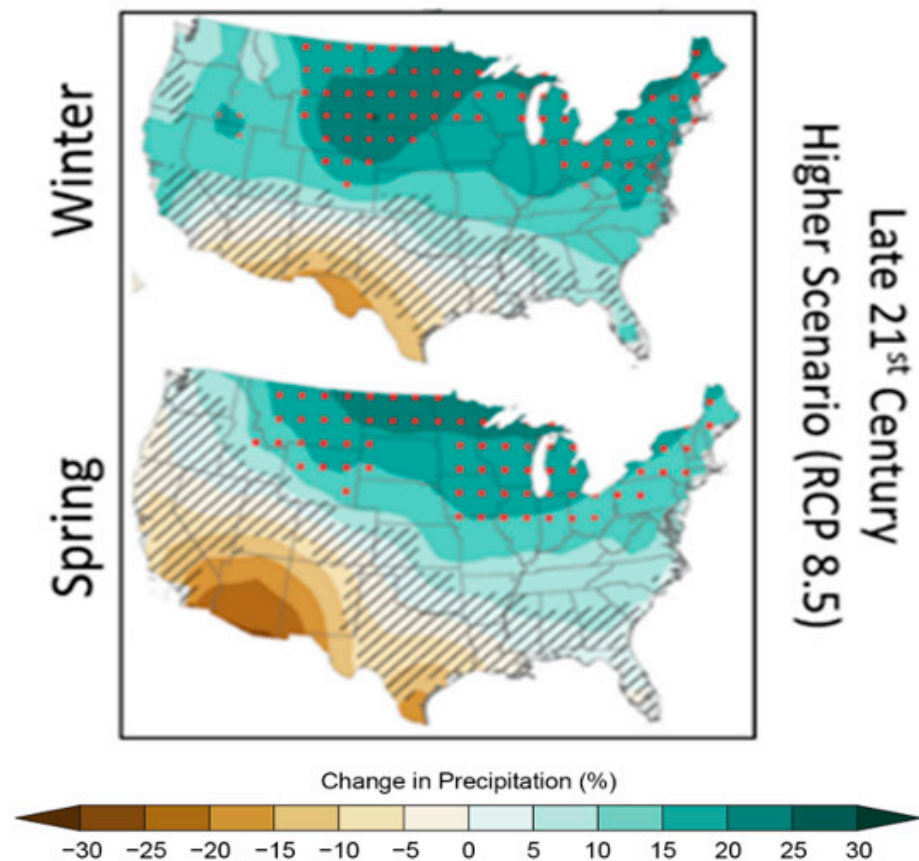
**Figure 5.** The water column DIP concentrations in the Lake Pontchartrain Estuary are first elevated at several stations due to the river discharge period (shaded area); then, a diatom bloom consumes all available P because of a high N:P ratio of surface water in 2011. Then, there is a sediment DIP benthic flux that reinstates the water column P but not the N (Figure modified from [21]).

Leakage through the BCS occurs when the river stage is high enough to contact the wooden piers that block the majority of flow. Only when the wooden piers are lifted, does the BCS discharge up to  $7080 \text{ m}^3 \text{ s}^{-1}$  ( $250,000 \text{ ft}^3 \text{ s}^{-1}$ ) into the LPE. However, since the wooden piers have small spaces between them, there can be significant discharge even when the piers are in place at between  $50$  and  $200 \text{ m}^3 \text{ s}^{-1}$  [35].

### 5. Forecasting to Anticipate Human Exposure: Variations in Cyanobacteria Species, Toxin Type, and Modality as Functions of Growth Stimuli

Efforts to model the cyanoHAB growth stimuli that drive species dominance, toxin type, and modality are motivated by climate change projections for the remainder of the 21st century, which are likely to promote favorable cyanoHAB conditions. Studies have examined how climate warming in air and water temperatures may affect cyanobacteria growth rates, e.g., [89,90]. Future climate projections predict continued wetting over the upper Mississippi River basin during winter and spring (Figure 6), the time of year that generally leads to flooding along the lower Mississippi River and BCS discharges into the LPE. Meanwhile, the same climate simulations also project late-21st century temperatures over the northern Gulf Coast to warm by  $1.6$ – $2.2 \text{ }^\circ\text{C}$  in a lower emission scenario and  $3.3$ – $3.9 \text{ }^\circ\text{C}$  in a higher emission case [91]. Together these outcomes hint at a greater frequency of BCS openings whereby nutrient-rich river water enters a warmer LPE that can support higher cyanoHAB growth rates.

While changes in mean climate variables, such as the ones described above, are well communicated [91], changes to the combinations and sequences of meteorological and hydrological conditions are impossible to infer from their mean changes alone. This motivates the need to develop improved near-term HAB forecasting techniques that leverage recent advances in numerical weather prediction (NWP). While attempts to forecast HAB development in the last decade have been numerous, e.g., [92–94], few methods integrate HAB growth with NWP forecasts from operational weather models, e.g., [95]. The National Centers for Environmental Prediction runs dozens of weather models daily, which can be used in combination with antecedent meteorological conditions to anticipate the near-term growth of cyanobacteria species and their toxicity. The potential for more frequent HABs in the coming decades behooves the development of NWP-enabled HAB, species, and toxicity forecasts for the LPE to anticipate heightened risk for human exposure.



**Figure 6.** Projected precipitation changes over the continental U.S. by the end of the 21st century (high-emission case). Red dots (diagonal hash marks) indicate locations where projected changes are large (small) compared to historical variability. Adapted from the National Climate Assessment Report [91].

## 6. Summary and Conclusions

The global input of freshwater into the coastal ocean and estuaries is currently changing in both seasonality and magnitude, which makes it critical to identify the role of various nutrient inputs in driving HAB toxicity on an annual scale. Using the Lake Pontchartrain Estuary, Louisiana, as an archetype for pulsed-nutrient-delivery systems, it is indicated that cyanohABs produce a variety of potent toxins in response to complex and nonlinear environmental interactions that are currently not well understood. This knowledge gap makes it challenging to forecast HAB occurrence in the near future, thus falling short of connecting such occurrences to human health risks. We recommend that future research should focus on (i) quantifying various sources of external and internal nutrient fluxes into estuaries, such as groundwater, benthic fluxes, and resuspension from the passage of weather fronts; (ii) characterizing the cyanobacteria species composition and toxin production under time-varying nutrient inputs from these varied sources; and (iii) developing forecast succession and toxin dynamics using state-of-the-art weather and climate models.

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