

# Mississippi River diversions and phytoplankton dynamics in deltaic Gulf of Mexico estuaries: A review

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## ABSTRACT

River systems worldwide have become substantially influenced by human activities, including land use changes, river diversion operations, and flood control measures. Some of the unambiguous and best studied examples of effects of enhanced eutrophication on biotic resources can be found in Louisiana estuaries at the terminus of the Mississippi-Atchafalaya River system. The Mississippi River delta has experienced large losses of coastal wetlands due to a combination of human impacts and sea-level rise. State and Federal agencies are moving ahead with plans for building large-scale river sediment diversions, which will capture maximum sediment during spring flood pulses and direct a sediment subsidy into the eroding coastal basins. These large-scale river sediment diversions will also substantially increase freshwater and nutrient inputs and are likely to affect algal bloom formation, including harmful cyanobacterial blooms. There are concerns that discharge of river water containing high concentrations of N, P and Si may trigger algal blooms in the coastal receiving basins. River sediment diversions, as any other flood pulsing, will likely be disruptive to the coastal ecology and so balancing the benefits of slowing coastal land loss against potential negative effects on water quality remains a formidable management challenge. We review here the physical, chemical and biological factors affecting primary production in shallow coastal systems and provide known data on ecosystem response to freshwater diversions, large and small. We also discuss potential management approaches to mitigate the negative impacts of the diversions on the health and stability of the coastal food webs.

## 1. Introduction

Estuaries and coastal systems worldwide have become substantially influenced by human activities, including land use changes, eutrophication, river diversion operations, and flood control measures, which affect the composition, diversity, and biomass of organisms at all trophic levels via physical, chemical, and biological mechanisms (Wetzel, 2001). Freshwater discharge and its associated nutrient loading to surface waters is expected to be altered by such forcings as land use changes, climatic variability, increased storm intensity and frequency, and future hydromodifications (e.g., sediment diversions, hydrologic restoration projects, construction/abandonment of levees, etc.).

Sediment diversions are premised on large flow capacities sufficient to move substantial amounts of riverine sediment to build new estuarine wetlands and provide a sediment subsidy to the existing ones (CPRA, 2017; Peyronnin et al., 2017; Rutherford et al., 2018). The diverted riverine freshwater will also contain substantial amounts of dissolved nutrients, which will likewise end up in coastal wetlands and

estuaries. Herein lies one of the controversies associated with sediment diversion projects, as several key uncertainties remain regarding the phytoplankton community responses to altered residence times, salinity, turbidity, and nutrient regimes (Day et al., 2016). Rivers are important sources of nutrients to coastal and estuarine systems, with their nutrient concentrations often directly related to land use activities within their watersheds (Hecky and Kilham, 1988; Cloern, 1996; Rabalais, 2002 and references therein; Dodds and Smith, 2016). Many river-dominated coastal systems have “use impaired” waters as a result of nutrient over-enrichment, which can lead to hypoxia and harmful algal blooms (HABs) (Rabalais et al., 2007; Paerl et al., 2014, Paerl et al., 2018a,b). For example, toxin producing cyanobacteria are commonly found within the fresh and brackish waters of many estuarine systems. Cyanobacteria are particularly successful in such eutrophic estuaries due to their tolerance to large shifts in water chemistry, including pH, salinity, hypoxia, coupled with an ability of some to fix nitrogen (e.g., Dokulil and Teubner, 2000; Paerl et al., 2001; Paerl and Huismann, 2008).

Some of the best-observed effects of river-enhanced eutrophication

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can be found in the northern Gulf of Mexico coastal waters and estuaries at the terminus of the Mississippi-Atchafalaya River system, which serves as a major conduit transporting nonpoint source sediment, nutrients, and pollutants from a watershed encompassing 41% of the contiguous United States (Turner and Rabalais, 1994). Nutrient rich freshwater pulsed into estuaries affects turbidity, water temperature, salinity, and nutrient concentrations and ratios at irregular intervals, creating a highly dynamic habitat (Lane et al., 1999; Day et al., 2009).

Seasonal and inter-annual variability in riverine freshwater and nutrient loads are important factors affecting the dynamics and composition of estuarine and coastal phytoplankton assemblages in the northern Gulf of Mexico (Randall and Day, 1987; Madden, 1992; Lane et al., 2002, 2010; Lohrenz et al., 2008; Lehrter et al., 2009; Turner and Rabalais, 2013; Riekenberg et al., 2015). Algal biomass is also significantly correlated with salinity and turbidity, suggesting that river diversions exert complex and highly variable environmental controls on estuarine phytoplankton. Typically, nutrient-rich Mississippi River achieves peak flow during the spring due to upstream snowmelt and surface runoff (Turner and Rabalais, 1994; Snedden et al., 2007a; Hyfield et al., 2008). As a result, phytoplankton blooms occur in late spring through early fall in the receiving estuaries in response to increased nutrient delivery, along with commonly observed seasonal shifts in phytoplankton community composition (Murrell et al., 2007; Thronson and Quigg, 2008; Costa et al., 2009). Dinoflagellates and “golden algae” (Chrysophyceae) are often found to bloom in response to hydrological changes (floods, droughts) in the freshwater to marine continuum (Paerl et al., 2018b). In Louisiana freshwater and estuarine systems, diatoms and chlorophytes frequently dominate spring blooms, while cyanobacteria typically dominate during summer, although their summertime blooms are found to be less predictable and vary greatly in terms of species dominance and bloom timing (e.g. Riekenberg et al., 2015).

This review compiled and examined the effects of river diversions on phytoplankton dynamics and aquatic primary productivity, with specific examples given from Mississippi River diversions and phytoplankton dynamics in deltaic Gulf of Mexico estuaries. The objectives are four-fold: (1) to review the effects of river diversions on key environmental drivers that regulate phytoplankton dynamics and community composition, (2) to draw generalities from published reports on how the existing smaller-scale (e.g., Caernarvon Diversion) and large-scale freshwater diversions (e.g., Bonnet Carré Spillway) affect phytoplankton dynamics and community composition, (3) to discuss the key uncertainties in our understanding of the potential impacts of proposed large-scale sediment diversions, and, (4) offer recommendations on future research directions. For an overview of nutrient dynamics and associated water quality issues in the Atchafalaya River Delta system, see the article by Twilley et al. (2019) in this special issue.

## 2. Effects of river diversions on key environmental drivers controlling phytoplankton dynamics and community composition

River diversions affect many environmental factors of significance to coastal and estuarine phytoplankton, including nutrient concentrations and ratios, salinity, turbidity, temperature and estuarine residence times (Fig. 1). These factors, in turn, have a controlling influence on phytoplankton dynamics and aquatic primary productivity.

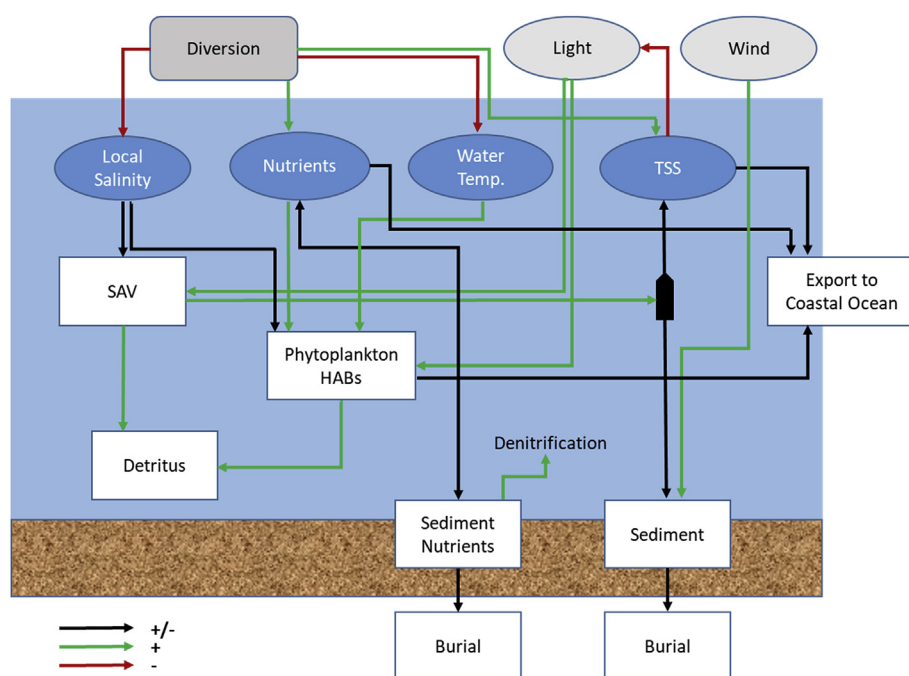
### 2.1. Nutrient concentrations and ratios

In estuaries and coastal waters, inter-annual and seasonal variations in nutrient concentrations are controlled by a variety of processes including riverine nutrient delivery, atmospheric deposition, nutrient transformation and export (e.g., Goolsby et al., 1999; Paerl and Justic, 2013). Riverine nitrate concentrations, for example, rapidly respond to land use changes and fertilizer use in the watershed (Justic et al., 2003). In contrast to nitrate, phosphate is readily adsorbed onto the surface of

sediments or forms insoluble precipitates and is lost from the water column as sediments are deposited on bay bottoms and surrounding marshes. The retention of phosphorus in soils is more substantial and less reversible under alternating flooding-draining cycles than under conditions of continuous flooding or continuously high soil moisture, primarily due to the mobility of P associated with reduced Fe (Patrick and Khalid, 1974). Phosphate concentrations are modulated by uptake and release of nutrients from intertidal wetlands and bottom sediments of bays and bayous (Childers and Day, 1990; Stern et al., 1991; Day et al., 1995; Perez et al., 2010). As a result, nutrient requirements for phytoplankton growth are rarely balanced by all nutrients supplied in amounts and proportions required for phytoplankton growth (i.e., the Redfield ratio; Redfield et al., 1963). The average molar TN:TP ratios in the Lower Mississippi River, for example, have fluctuated above and below the Redfield ratio of 16:1, from less than 10:1 in the late 1970s to around 40:1 in the 1980s, and then declining to 20:1 by the 2000s (Turner et al., 2007). Since the late 1970s, the rising nitrate concentration in concert with the declining silicate concentration has led to a decline in the silica (Si) to dissolved inorganic nitrogen ratio (Si:DIN) from 4:1 to very near or below the Redfield ratio of 1:1 (Turner et al., 2007). Beginning with the work of Liebig (1840), there has been much discussion of limiting nutrients. Often, one nutrient is present in shortest supply (i.e. limiting), so that its availability determines the phytoplankton community growth rate. Because nutrient delivery to an estuary often occurs in a pulsed manner, the limiting nutrient can switch or several nutrients can simultaneously be close to limiting, creating “co-limited” conditions. While in many estuaries throughout the world nitrogen (N) is the most limiting nutrient (Ryther and Dunstan, 1971; Nixon, 1995; Granéli et al., 1999; Elmgren and Larsson, 2001), N and a phosphorus (P) co-limitation is also commonly observed (Boynton and Kemp, 1985; Malone et al., 1996), especially in the low salinity, upstream segments of estuaries (Fisher et al., 1988; Paerl et al., 1995), and in brackish water deltaic regions where large rivers (e.g., Mississippi) discharge to the coastal ocean (Sylvan et al., 2006). N and P co-limitation as well as more exclusive P limitation are most evident during periods of elevated freshwater runoff, which tend to be N enriched (Fisher et al., 1988; Sylvan et al., 2006; Roy et al., 2013; Leong et al., 2014). Under these conditions, the molar “Redfield ratio” of N:P (16:1) can be greatly exceeded, sometimes reaching 200:1, leading to strong P limitation (Sylvan et al., 2006; Paerl and Justic, 2011).

### 2.2. Salinity

Salinity regimes are important in determining the distributions, abundance, and taxonomic composition of algal functional groups. The freshwater-oriented groups include the chlorophytes, diatoms, and some cyanobacteria. Oligohaline waters (salinity of 2–5) are often dominated by cryptophytes, some dinoflagellate species and cyanobacteria (Paerl and Justic (2011); Hall et al. (2013). Chlorophytes (and sometimes diatoms) can also be big players in oligohaline waters, especially after episodic events such as floods following major storms events. Mesohaline waters (salinity of 5–20) are favorable to diatoms, dinoflagellates, and some cryptophytes (Paerl and Justic, 2013; Paerl et al., 2018b), while euhaline waters (salinity > 20) are preferred by diatoms, some dinoflagellates, picoplanktonic cyanobacteria, and certain chrysophytes (Paerl and Justic, 2013; Paerl et al., 2013). Flushing, or water residence time, strongly interacts with salinity and nutrient supply rates to determine competitive interactions among these groups (Peierls et al., 2012). For example, chlorophytes prefer low salinity and high-nutrient fast-flowing (short residence time) waters, in large part because of their high growth rates (doubling times are short, i.e. < 0.5 day) (Reynolds, 2006; Hall et al., 2013; Paerl et al., 2013). Therefore, periods of high freshwater discharge containing appreciable nutrient loads, such as floodwater discharge following large storms and hurricanes, greatly favor dominance by this group (Pinckney et al., 1999; Peierls et al., 2003; Valdes-Weaver et al., 2006). Conversely, low



**Fig. 1.** Conceptual model of open water processes affected by river diversions (modified from [Justic et al., 2008](#)); Temp. – temperature; TSS – total suspended solids; SAV – submerged aquatic vegetation. Black, green and red arrows denote +/–, + and – effects, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

discharge drought conditions, which lead to high salinity, and low nutrient concentrations, favor certain slow-growing cyanobacterial and “brown tide” assemblages ([Pinckney et al., 1999](#); [Gobler et al., 2002](#); [Paerl et al. 2005, 2013](#)).

### 2.3. Turbidity

Light attenuation depends on key light absorbing and scattering substances in the water column including the water itself, colored dissolved organic matter (CDOM), organic and inorganic suspended particulate material, including inorganic sediments and detrital organic matter, and phytoplankton ([Gallegos et al., 1990](#)). In most estuaries, the value of vertical light attenuation coefficient ( $K_d$ ) ranges from  $< 0.1 \text{ m}^{-1}$  (very clear, oligotrophic) to  $> 4.0 \text{ m}^{-1}$  (highly turbid, eutrophic waters) (e.g., [Gallegos et al., 1990](#)). The relative attenuation attributable to phytoplankton, particulate matter, and CDOM can vary widely, depending on the trophic state, sediment inputs and resuspension, colored organic matter input, and flushing dynamics of any given estuary ([Gallegos et al., 1990](#)).

Light availability is often inversely related to turbidity and is of fundamental importance in controlling the activity, biomass, distribution, and composition of phytoplankton in estuaries. Both the instantaneous flux of light, or irradiance, and the total amount of light available during daylight tend to be excellent predictors of primary production ([Jassby and Platt, 1976](#); [Fee, 1980](#)). For most estuaries, increased freshwater inflow from turbid rivers generally increases light attenuation, which has profound effects on phytoplankton abundance, productivity, and composition ([Harding, 1994](#); [Cloern, 1999, 2001](#); [Valdes-Weaver et al., 2006](#)). Estuarine turbidity and light availability influence timing of winter-spring diatom blooms and late winter dinoflagellate blooms ([Riley, 1967](#); [Hitchcock and Smayda, 1977](#); [Nixon et al., 1979](#); [Litaker et al., 2002](#)).

### 2.4. Temperature

Temperature is an important factor controlling the growth and composition of a phytoplankton community. Laboratory studies suggest that for most phytoplankton species optimum temperatures for growth fall in the range of  $20\text{--}25^\circ\text{C}$  (e.g., [Goldman, 1979](#)). Temperature response curves for phytoplankton growth and photosynthesis are similar

for different algal species, with relatively rapid declines in production at sub-optimal temperatures. In addition to seasonal temperature variations, temperature variability may be due to the influx of colder riverine water. For example, during spring and fall seasons, the temperature of the Mississippi River water is typically  $1\text{--}8^\circ\text{C}$  colder compared to ambient estuarine water temperatures ([White et al., 2009](#); [Roy et al., 2013](#)). The evidence from other estuaries (e.g., [Paerl and Justic, 2011](#)) suggests that temperature exerts a selective force on estuarine phytoplankton species whose temperature optima coincide with local environmental conditions, including nutrient availability, regeneration, and solubility, all of which are indirectly related to temperature. Thus, seasonal succession of estuarine phytoplankton taxa, while affected by temperature (e.g., cyanobacteria, [Paerl and Huisman, 2008](#)), are often co-controlled by additional factors, including freshwater discharge (flushing), light, and nutrients ([Paerl and Justic, 2011](#); [Paerl et al., 2014](#)).

### 2.5. Estuarine residence times

Residence time is the hydraulic replacement time or flushing rate and is calculated using different modeling approaches that include freshwater fraction and tidal prism methods as well as more complex modeling studies involving tracers or Lagrangian particles ([Sheldon and Alber, 2006](#); [Swenson et al., 2006](#); [Das et al., 2010](#); [Huang et al., 2011](#)). Residence time provides a useful metric for making cross-system comparisons and as a correlative index in forecasting how estuarine physical, chemical, and biological processes change under altered basin hydrodynamics. Residence times of the Gulf of Mexico estuaries, for example, range from a few days to about a year ([Solis and Powell, 1999](#); [Huang et al., 2011](#)). Within a given estuary, the residence time is inversely related to the magnitude of freshwater discharge.

Water residence time can also affect the eutrophication process by influencing nutrient availability and uptake, transformations, and sinks as well as the accumulation of phytoplankton biomass and bloom formation ([Peierls et al., 2012](#); [Hall et al., 2013](#)). There is also an inverse relationship between estuarine residence times and nitrogen export to the coastal ocean ([Nixon et al., 1996](#); [Dettmann, 2001](#)). Thus, estuaries with short residence times are generally less susceptible to eutrophication than estuaries with long residence times (months to years) (c.f., [Peierls et al., 2012](#)). Also, because phytoplankton growth rates



rarely exceed 1–2 doublings per day, estuaries with short residence times (hours to days) generally have low phytoplankton biomass with low susceptibility to blooms (Malone, 1977; Cloern et al., 1983).

### 3. Influence of Mississippi river diversions on water quality and phytoplankton dynamics and community composition in deltaic Gulf of Mexico estuaries

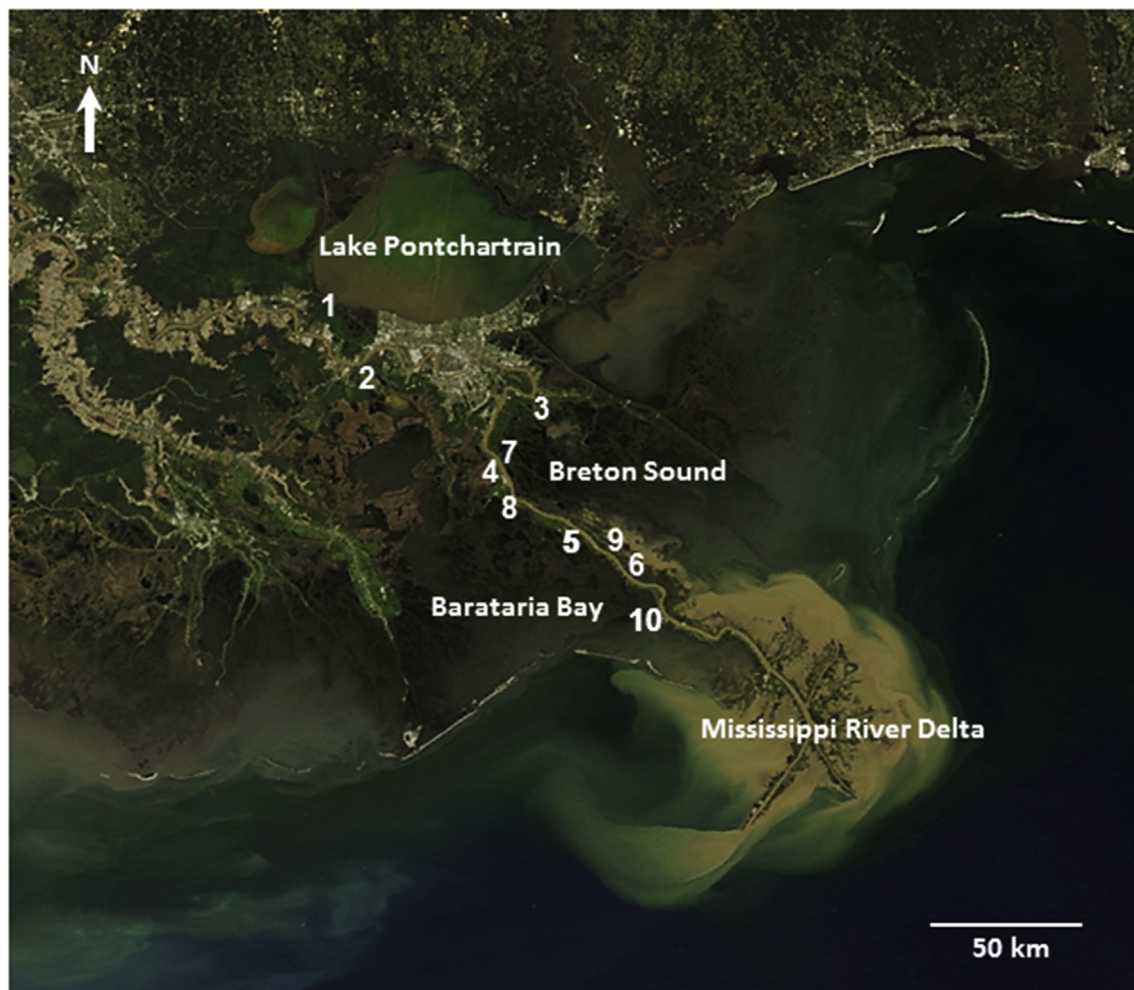
Freshwater diversions on the Lower Mississippi River play a central role in the proposed \$50-billion, 50-year strategy for restoring the Louisiana's coast. The strategy, as outlined in the Louisiana's Comprehensive Master Plan for a Sustainable Coast (CPRA, 2007) and subsequent five-year updates (CPRA, 2012, 2017), includes diversions of Mississippi and Atchafalaya River water, sediments and nutrients into the estuarine basins of the Louisiana Deltaic Plain. The key objective is to mitigate the loss of coastal wetlands and achieve biophysical and socio-economic sustainability of the State's coastal resources. In the past three decades the State, together with its federal and local partners, has constructed and operated two small freshwater river diversions, the Caernarvon Diversion (~maximum flow of 220 m<sup>3</sup>/s) in Breton Sound Estuary and the Davis Pond Diversion (~maximum flow of 300 m<sup>3</sup>/s) in Barataria Estuary, as well as the West Bay Sediment Diversion (~maximum flow of 700 m<sup>3</sup>/s) and several smaller siphons (Fig. 2). Lake Pontchartrain is, on the other hand, a large, oligotrophic estuary in South Louisiana that receives both continuous and episodic

freshwater inputs. Occasionally, episodic freshwater inflows occur in the form of Bonnet Carré Spillway (BCS) openings (~maximum flow of 7000 m<sup>3</sup>/s).

The latest update to the Coastal Master Plan (CPRA, 2017) detailed the construction of four large-scale sediment diversions into the Barataria and Breton Sound estuaries (Fig. 2) whose discharge capacity will be an order of magnitude higher (e.g., ~990–2120 m<sup>3</sup>/s) than the Caernarvon and Davis Pond freshwater Diversions. The following two regional examples provide a review of existing knowledge on algal bloom dynamics in deltaic Louisiana estuaries and discuss the possible outcomes of planned large-scale river diversions.

#### 3.1. Lake Pontchartrain (Bonnet Carré Spillway)

*River Nutrient Loading* - Flood discharge events of Mississippi River water through the Bonnet Carré Spillway into the Lake Pontchartrain have provided an opportunity to examine the processing and ultimate fate of bioavailable N (primarily NO<sub>3</sub><sup>-</sup>) and dissolved inorganic P (DIP). The most studied recent spillway openings occurred in 2008 and 2011. Freshwater inflow during Bonnet Carré Spillway events can approximately equal (2008) or greatly exceed (2011) both the annual input from local tributaries discharging into the estuary and the volume of the estuary itself (Day et al., 2012; Roy et al., 2013). Therefore, these events lead to large N and P loading over a very short period of time (~1 month) (Fig. 3).



**Fig. 2.** Existing and proposed Mississippi River Diversions (CPRA, 2017); 1 – Bonnet Carré Spillway; 2 – Davis Pond Diversion; 3 – Caernarvon Diversion; 4 – Naomi Siphon; 5 – West Pointe à la Hache Siphon; 6 – Bohemia Spillway; 7 – Mid-Breton Sound (proposed); 8 – Mid-Barataria (proposed); 9 – Lower Breton Sound (proposed); 10 – Lower Barataria (proposed). Image: LSU Earth Scan Laboratory.

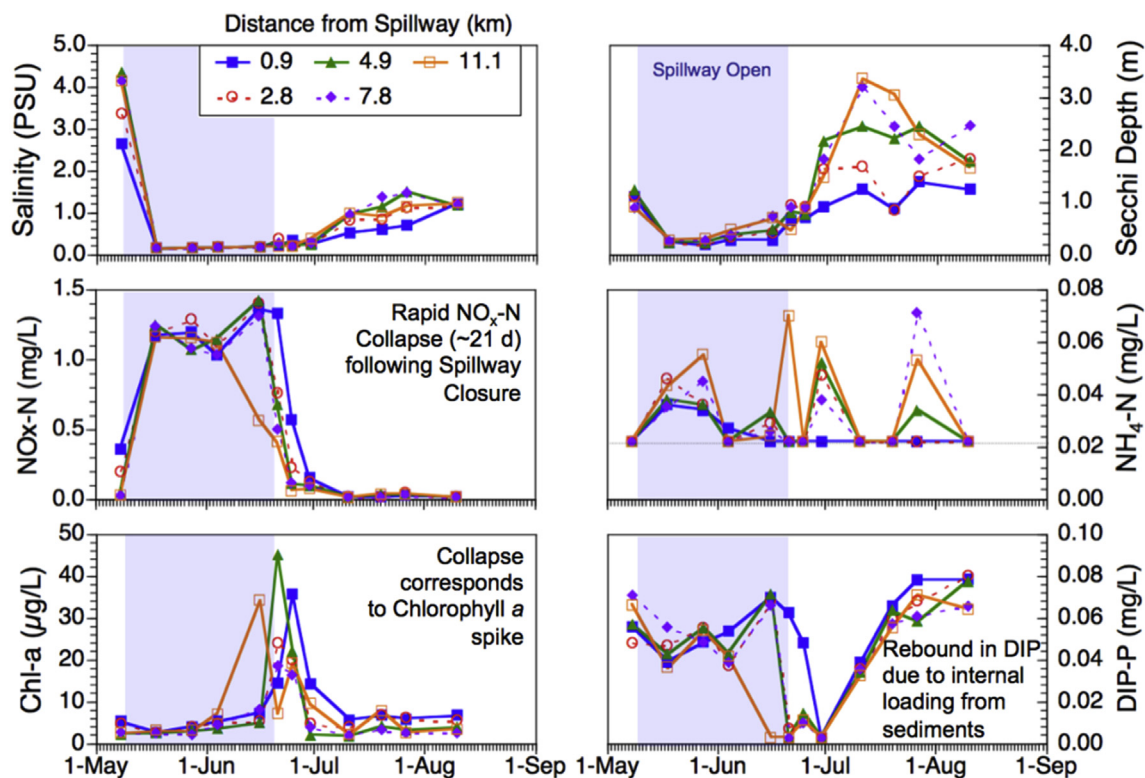


Fig. 3. Salinity, light, nutrient, and phytoplankton dynamics in Lake Pontchartrain in 2011 during the Bonnet Carré Spillway opening (modified from Roy et al., 2013).

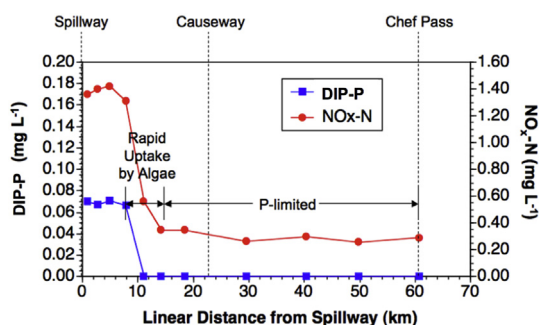


Fig. 4. Changes in nutrient concentrations with distance from Spillway during the 2011 Bonnet Carré opening (modified from Roy et al., 2016).

**Nitrate Dynamics** - Studies illustrate a sequence of estuarine nutrient dynamics in response to large inflows of Mississippi River water, which is likely related to the relatively high DIN:DIP molar ratio of inflowing freshwater ( $\geq 50$ ). Bargu et al. (2011) and Roy et al. (2013) indicate that  $\text{NO}_3^-$ -concentrations can decrease rapidly to below detection in approximately three weeks following spillway closure when water temperature is  $\geq 25^\circ\text{C}$  (Fig. 3), coincident with a spike in chlorophyll *a*, a result of phytoplankton uptake and growth. However, phytoplankton uptake is controlled by both water clarity and ambient temperature. Diatoms, chlorophytes, and cryptophytes often do well during early spring, cooler periods, but in the absence of these groups, cold temperatures of the river during the active diversion period can limit algal nitrogen uptake leading to a greater nitrogen export from the lake. Otherwise, low-turbidity plumes, post diversion, are likely to undergo continual  $\text{NO}_3^-$ -removal as long as temperatures remain favorable.

The potential for additional  $\text{NO}_3^-$ -removal through microbially-mediated denitrification in open water, estuarine and shallow lake systems has been examined by a number of studies. Denitrification, where  $\text{NO}_3^-$  is reduced to  $\text{N}_2$  gas and is effectively removed from the

aquatic system, optimally occurs under conditions of low  $\text{O}_2$ , such as can be found in flooded muddy sediments and requires bio-reactive DOC (Marks et al., 2016). Due to the relatively high concentration of organic matter in flooded soils, denitrification is most often limited by  $\text{NO}_3^-$ -concentration (Gardner and White, 2010). These conditions are generally met in the sediments of estuaries and shallow lakes; however, little overall denitrification was found to occur in Lake Pontchartrain estuarine sediments (Roy and White, 2012). For example, during the 2008 spillway opening, only 3% of the  $\text{NO}_3^-$ -load amounting to 309 Mg of  $\text{NO}_3^-$  N was removed by this microbial process in the sediments (Roy and White, 2012). This low denitrification potential may be indicative of a temperature or carbon limitation. At Breton Sound, there was a 10-fold increase in denitrification rate of vegetated marsh soils compared to bayou sediments. This suggests that the microbial denitrifying pool is generally low in open water sediments since the organic matter content of both the wetland soil and bayou sediment was greater than 10% (VanZomerem et al., 2013). Consequently, the reduction of externally-supplied  $\text{NO}_3^-$  is generally limited to assimilation by phytoplankton or export to the coastal ocean when significant discharge volumes into shallow, open-water systems occurs controlled by residence time.

**Phosphorus Dynamics** - Mississippi River water is generally low in bioavailable P. The aforementioned high DIN:DIP molar ratio of inflowing freshwater ( $\geq 50$ ) leads to P-limitation in Lake Pontchartrain during algal growth (Mize and Demcheck, 2009). Due to this limitation, the percentage load of DIP is more rapidly assimilated than DIN and this limitation can halt further algal uptake, once DIP concentrations are diminished (Fig. 4). In order to remove additional N, an internal source of DIP is required through mineralization/decomposition of organic matter and/or release of DIP due to Fe reduction in the sediments. Following the depletion of both water column DIP and DIN in 2011, the rapid rebound of DIP concentrations observed occurred by internal loading from sediments as there was no significant external source of DIP. Roy et al. (2012) showed that internal P loading from Lake Pontchartrain estuarine sediments occurs regardless of bottom water

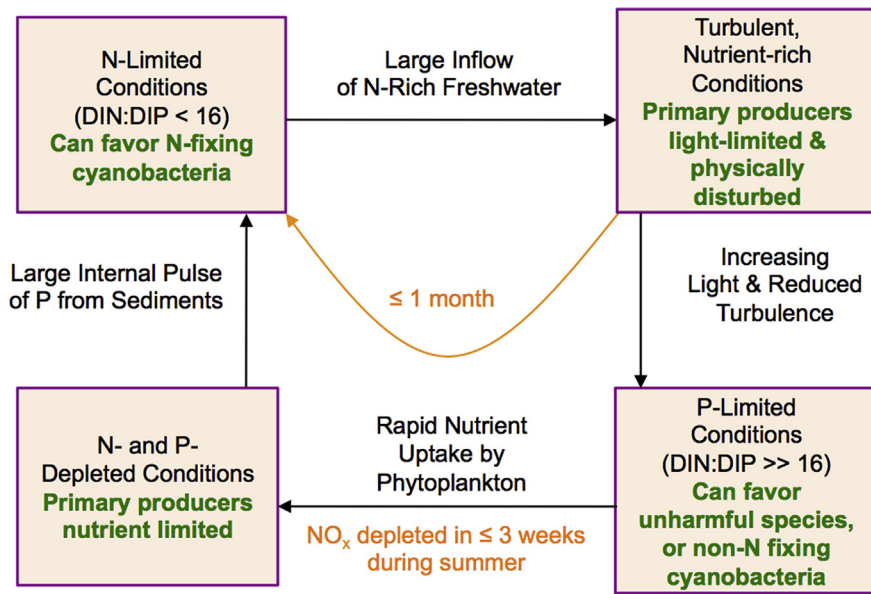


Fig. 5. Lake Pontchartrain ecosystem response to Bonnet Carré diversions (modified from Roy et al., 2013).

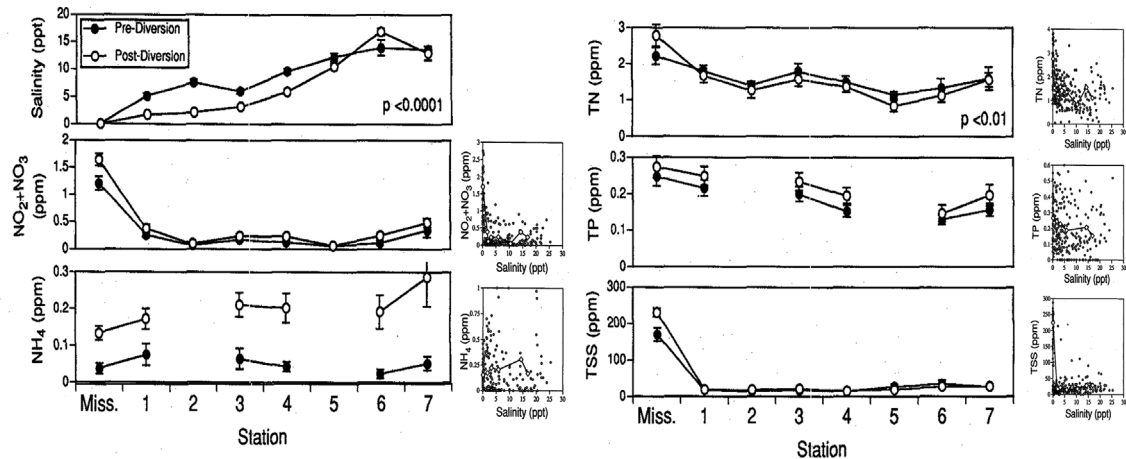


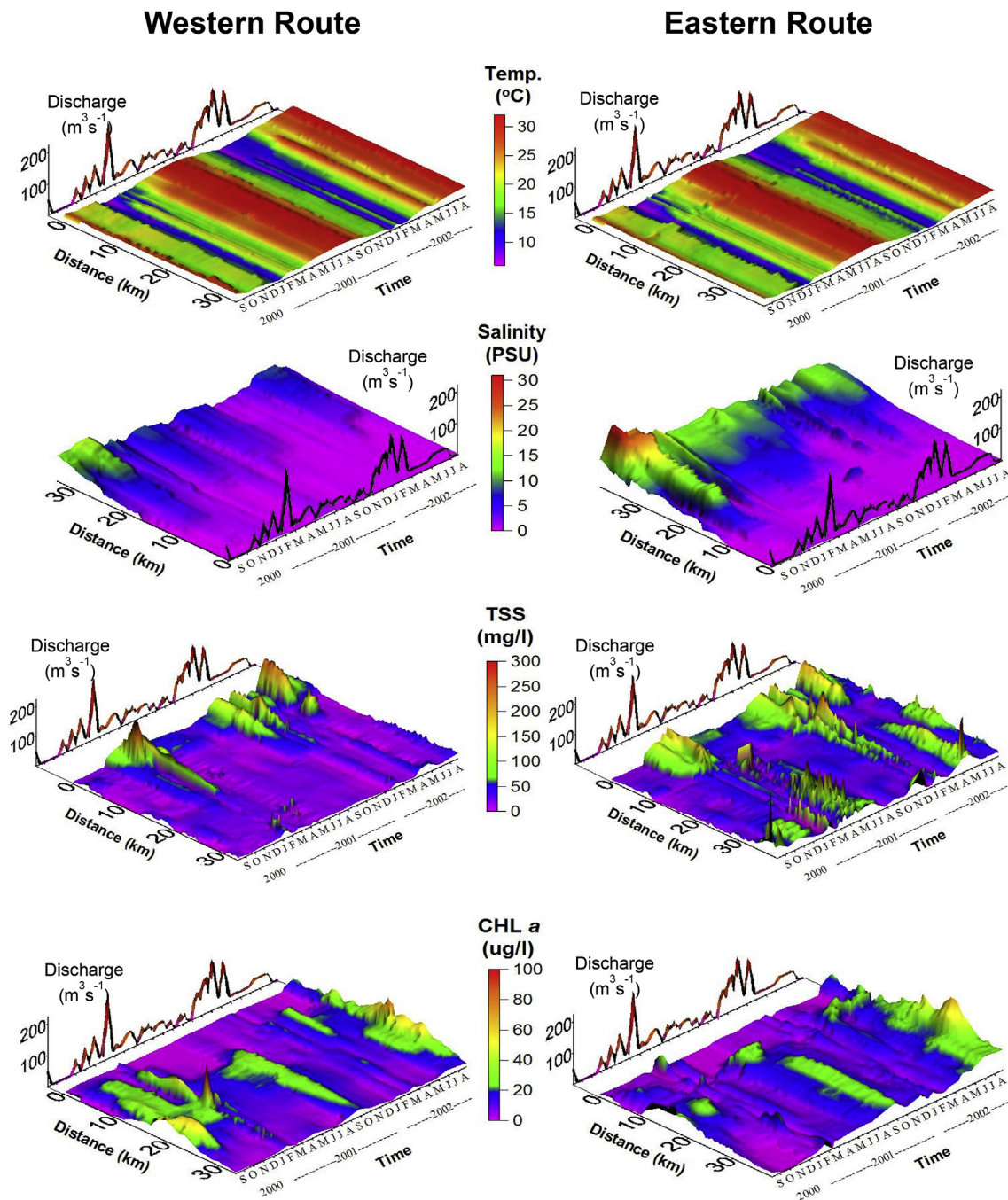
Fig. 6. Pre- and post-diversion (i.e., 1991) water quality station annual means ( $\pm 1$  standard error) for salinity, NO<sub>x</sub>, NH<sub>4</sub>, TN, TP, and TSS, and post-diversion salinity mixing diagrams (modified from Lane et al., 1999).

oxygen availability and estimated that diffusive flux can regenerate water column DIP concentrations from below detection to Mississippi River concentration ( $0.05 \text{ mg P L}^{-1}$ ) in  $< 60$  days. Field observations suggest that this internal load of P from sediments can return the DIP concentrations back to the previous levels in  $< 1$  month (Roy et al., 2013). The dynamic interaction between high external N loading during river inflows and the subsequent internal sediment P loading and re-establishment of N-limitation observed in the Lake Pontchartrain has not commonly been documented in other estuaries (Cook et al., 2010). It has been shown that diverted Mississippi River water can also be a source of sediment-bound P, which once deposited, can be a significant source of DIP under reduced sediment conditions in both estuarine and coastal shelf settings (Zhang et al., 2012; Adhikari et al., 2015).

**Phytoplankton and Aquatic Primary Productivity** - Recent studies have shown that the Lake Pontchartrain experiences high interannual variability in nutrients and cyanobacterial bloom dynamics, mainly due to the effects of seasonal and episodic rainfall on hydrology and Mississippi River diversions that cause variability in the timing and magnitude of the freshwater discharge to the lake (Turner et al., 2004; Bargu et al., 2011; Roy et al., 2016). Bargu et al. (2011) and Roy et al.

(2013, 2016) examined environmental variables and phytoplankton community dynamics in the Lake Pontchartrain during two spring-summer periods when the system received massive inflows of diverted Mississippi River water via the Bonnet Carré Spillway, and then in a year when the Spillway was closed (Fig. 5). Freshwater diatoms and chlorophytes dominated the system during the Spillway opening. After the Spillway was closed, these were slowly replaced with toxic cyanobacteria species of *Microcystis*. During the post-Spillway period, nitrogen-fixing *Anabaena* became more abundant in July, and *Raphidiopsis* and *Cylindrospermopsis* spp. were more frequently observed in August. Observations indicate that northern tributaries of the lake can serve as a source of nutrients and may play a role in transporting cyanobacteria to the fresher northern region of Lake Pontchartrain. An unresolved question is whether increase in discharge from northern tributaries during late spring and summer can promote cyanobacteria bloom formation and associated toxin production in the northern regions of Lake Pontchartrain. Internal P loading by regeneration, wind mixing and sediment resuspension has the potential to regenerate P in P-depleted waters. Internal phosphorus loading may be an important factor for promoting blooms of nitrogen-fixing harmful algae under summertime low-nutrient conditions (Fig. 5).

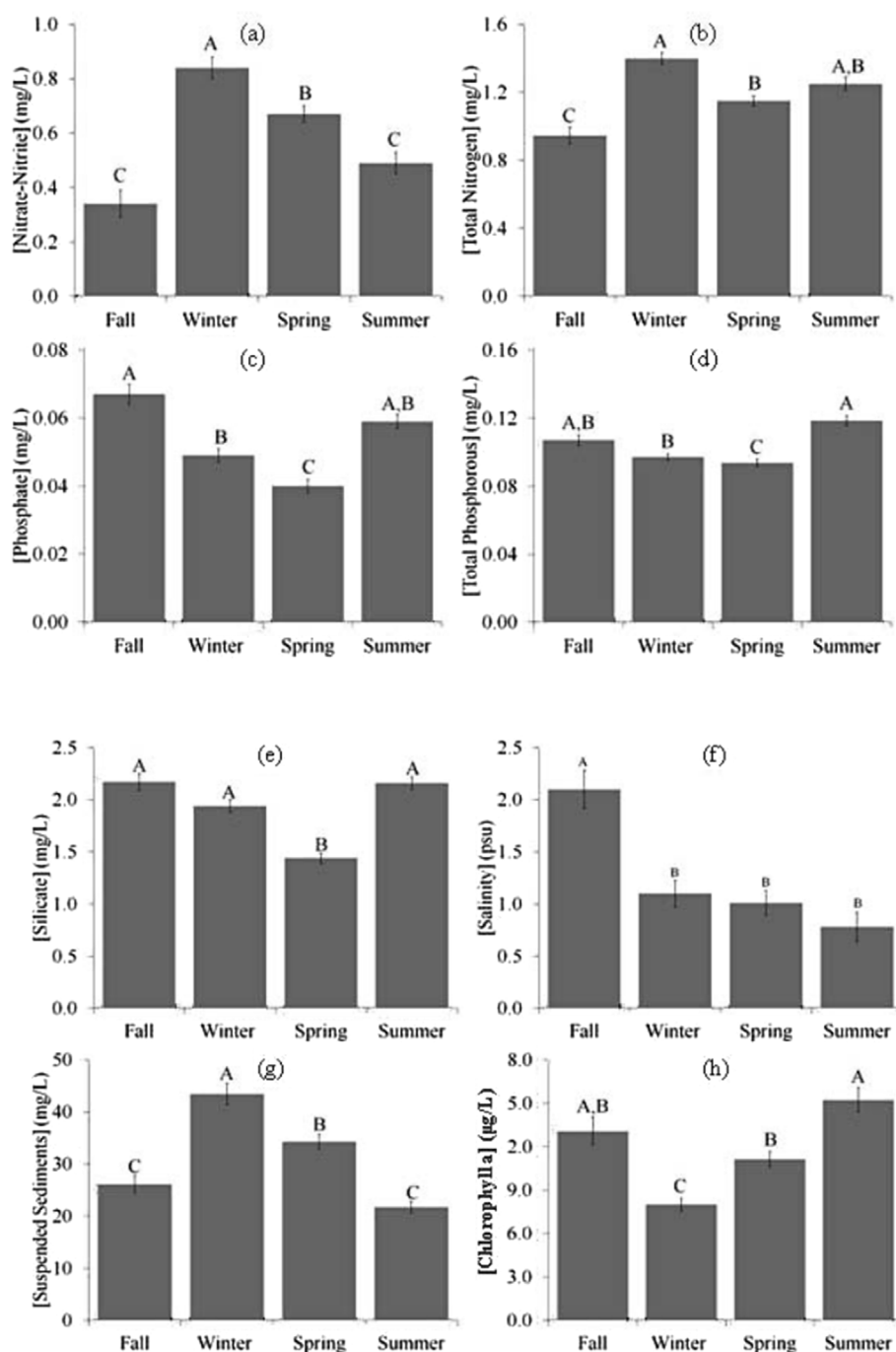




**Fig. 7.** Spatial-temporal graphs of temperature, salinity, total suspended sediment (TSS) and chlorophyll *a* (CHL *a*) in the Breton Sound estuary. Time is shown on the x-axis and distance from the Caernarvon diversion structure on the y-axis. Discharge from the Caernarvon diversion is indicated by the red line superimposed on the x-axis. Note that for clarity the distance axis for salinity is reversed with respect to other parameters (modified from Lane et al., 2007). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

In estuaries worldwide, nutrient dynamics play an important role in cyanobacteria presence and success. Phytoplankton in general, including cyanobacteria, thrive in aquatic environments receiving excessive inputs of nitrogen (N) and phosphorus (P) (Carpenter et al., 1998). Different species of cyanobacteria employ a range of nutrient acquisition strategies to gain a competitive advantage, including nutrient storage (“luxury uptake”),  $N_2$  fixation, vertical migration, or cyst formation (Carey et al., 2012). For example, differences in the timing of occurrence between *Anabaena* and *Microcystis* are largely driven by temperature and N biogeochemistry (Bouvy et al., 1999; Paerl et al., 2001; Paerl and Huisman, 2008; Paerl and Otten, 2016). *Microcystis* spp. depend on dissolved inorganic N (DIN) in the water column and

are typically observed in late spring or early summer when DIN is provided by external inputs. In contrast, *Anabaena* spp., are able to fix atmospheric N, and can become the dominant species when water column DIN is depleted and dissolved inorganic P (DIP) remains available (Roy et al., 2016). Vegetative cells of some cyanobacteria, like *Anabaena*, can often differentiate into heterocysts or akinetes, thick-walled resting cells, allowing blooms to persist during extreme environmental conditions (Dokulil and Teubner, 2000). Differences in nutrient acquisition strategies employed by *Microcystis* and *Anabaena* spp. indicate that different environmental factors likely control cyanobacteria community structure and their toxin production. It has been shown that high pH's from cyanobacteria blooms ( $> 9$ ) release Fe-



**Fig. 8.** Mean seasonal concentrations of nitrate-nitrite, phosphate, silicate and suspended sediments in the Breton Sound estuary (modified from Lundberg et al., 2014).

bound P and hinder microbial nitrification/denitrification and it also helps maintain a single species bloom (Seitzinger, 1991; Gao et al., 2012).

**Sediment Dynamics** - During the Bonnet Carré Spillway openings in April 2008 and May 2011, the freshwater plume that formed in Lake Pontchartrain limited mixing within the rest of the lake (Bargu et al., 2011; Roy et al., 2013). River water with a highly visible sediment plume moved along the south shore of Lake Pontchartrain during the peak flow, and did not fully mix with water in the north-central portion of the estuary. Phytoplankton productivity is generally stimulated by elevated levels of nutrients, however in this case, it is hypothesized that the colder water temperature and the high total suspended solids concentration (turbidity) in the river water muted phytoplankton growth

within the plume (White et al., 2009; Roy et al., 2013).

### 3.2. Breton Sound (Caernarvon Diversion)

A number of studies of water column nutrient dynamics have been carried out as river water diverted through the Caernarvon structure and flowed through the Breton Sound estuary (Lane et al., 1999, 2004; 2007; Wheelock, 2003; Swenson et al., 2006; Snedden et al., 2007b, 2015; Hyfield et al., 2008; Day et al., 2009; Lundberg et al., 2014). Hydrographic transects showed strong seasonal and spatial patterns in nutrient concentration and hydrographic parameters (Lane et al., 1999, 2004, 2007). In general, salinity and  $\text{NH}_4$  increase with distance from the diversion structure while  $\text{NO}_x$ , TN, TP, and TSS decrease with



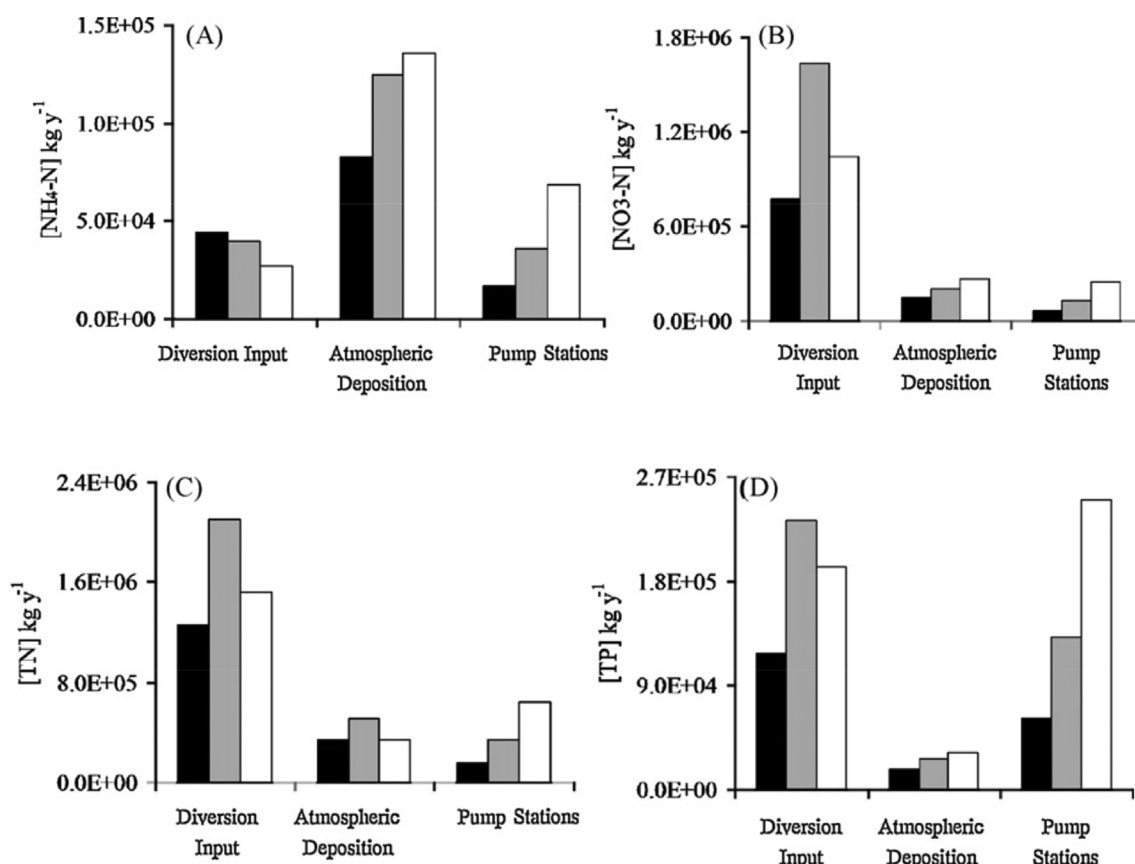


Fig. 9. Nutrient sources to the Breton Sound Estuary for 2000 (black bars), 2001 (gray bars), and 2002 (white bars) for (A) NH<sub>4</sub>, (B) NO<sub>x</sub>, (C) TN, and (D) TP (modified from Hyfield et al., 2008).

distance (Lane et al., 1999, 2004, Figs. 6 and 7); however, TSS can increase in the lower estuary due to resuspension events. Salinity mixing diagrams indicate strong non-conservative uptake of NO<sub>3</sub><sup>-</sup>, TN, and TSS (Figs. 6 and 7). The non-conservative behavior of TN is driven primarily by NO<sub>3</sub><sup>-</sup>, which makes up about half of the TN concentration in river water. Lane et al. (2007) found cold river water permeated through the Breton Sound estuary during high discharges, but generally, temperature gradients diminish quickly with distance from diversion inflow sites due to mixing and heat transfer from the atmosphere.

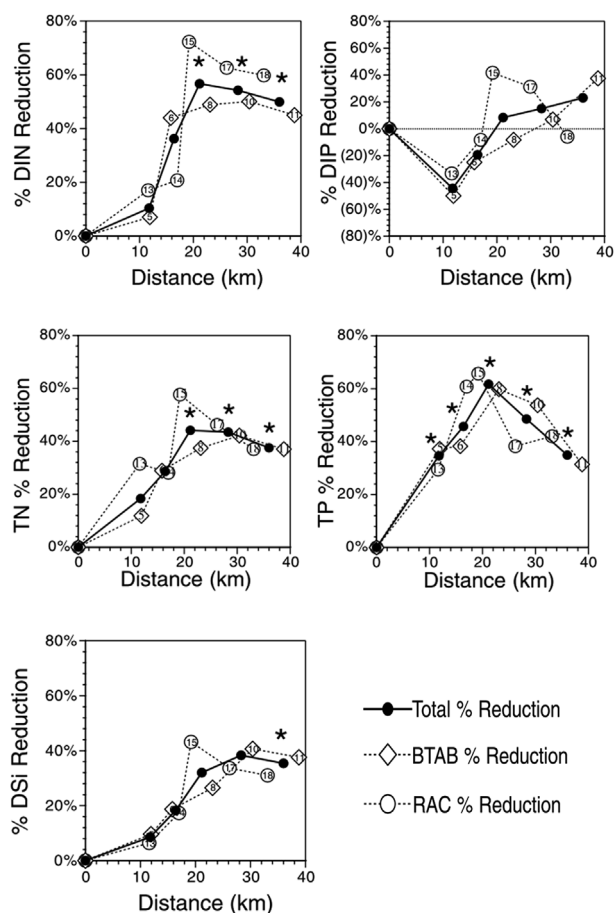
**Nitrate Dynamics** - Nitrate + nitrite (NO<sub>x</sub>) comprises ~90% of dissolved inorganic nitrogen (DIN) input from the diversion, with incoming river water concentrations as high as 3.3 mg L<sup>-1</sup>, and large fluxes entering the basin during the winter and the lowest during summer and fall (Lundberg et al., 2014, Fig. 8). Consistent decreases in NO<sub>x</sub> concentrations occurred along both the eastern and western routes, and salinity-mixing diagrams indicate strong non-conservative uptake of NO<sub>x</sub> and that the estuary acts as a sink for NO<sub>x</sub> (Lane et al., 1999, 2004). There was low loading (< 10 g N m<sup>-2</sup> y<sup>-1</sup>), and potential for high DIN uptake (Hyfield et al., 2008; Lane et al., 1999, 2004). Atmospheric deposition is the largest contributor of NH<sub>4</sub> to the estuary, accounting for 57–62% of the total NH<sub>4</sub> input to the estuary, with the Caernarvon diversion accounting for only 12–31% (Hyfield et al., 2008) (Fig. 9). Basin wide, ammonium concentrations range from below detection limit (0.02 mg L<sup>-1</sup>) to 0.7 mg L<sup>-1</sup> with very little seasonal variability (Lundberg et al., 2014). Salinity mixing diagrams indicate the estuary acts as a source for NH<sub>4</sub>, with ammonium levels initially increasing with distance from the diversion structure, and then stabilizing farther into the estuary (Lane et al., 1999; Lundberg et al., 2014). The estuary acts as a net sink for TN, with concentrations lowest during the fall and highest during the winter, ranging from 0.02 to 4.2 mg L<sup>-1</sup>

(Lane et al., 2004; Lundberg et al., 2014). Loading rates of NO<sub>x</sub> ranged from 5.6 to 13.4 g m<sup>-2</sup> yr<sup>-1</sup>, and total nitrogen from 8.9 to 23.4 g m<sup>-2</sup> yr<sup>-1</sup>, and had removal efficiencies of 88–97% for NO<sub>x</sub>, and 32–67% for TN (Lane et al., 1999).

**Phosphorus Dynamics** - Phosphate concentrations in the Breton Sound estuary range from below detection limit to 0.2 mg L<sup>-1</sup>, are generally lowest during the spring and greatest during the fall, and decrease with increasing distance from the diversion structure (Lundberg et al., 2014, Fig. 8). Analysis of salinity mixing diagrams indicates that the estuary generally acts as a source of PO<sub>4</sub> during the fall and summer months and as a sink during winter and springtime. However, during the 2001 experimental spring pulse from the Caernarvon diversion, Lane et al. (2004) found PO<sub>4</sub> concentrations actually increased with distance from the diversion, peaking 11 km from the diversion structure (Fig. 10, DIP). This P increase is indicative of internal PO<sub>4</sub> flux from the wetland soil and submerged sediments (Reddy et al., 2011). Total phosphorus concentrations showed the same range as PO<sub>4</sub>, with highest levels during the summer and fall when the estuary acts as a source, and lowest during the winter and spring when the estuary acts as a sink (Lundberg et al., 2014, Fig. 8). Loading rates of total phosphorus ranged from 0.9 to 2.0 g m<sup>-2</sup> yr<sup>-1</sup>, with removal efficiencies of < 0–46% for TP (Lane et al., 1999).

**Silicate Dynamics** - Silicate concentrations in Breton Sound estuary range from below detection limit to 5.2 mg L<sup>-1</sup>, are correlated with discharge from diversion, and decrease with distance from the structure (Lundberg et al., 2014, Fig. 8). Lane et al. (2004) found strong reductions in Si as diverted river water flowed through the estuary during the spring flood of 2001 (Fig. 10), Lundberg et al. (2014) reported the estuary to be a Si sink during winter/spring but a source during the fall.

Freshwater diversions can significantly alter riverine nutrient concentrations and ratios as diverted river water passed through estuaries.

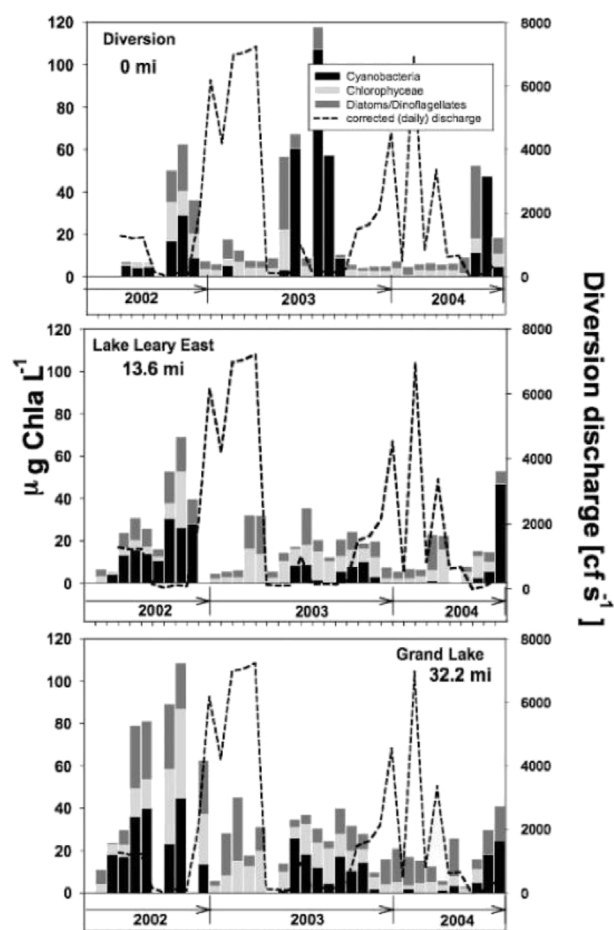


**Fig. 10.** Changes in observed concentrations of water quality parameters versus distance from the Caernarvon diversion during an experimental opening of the Caernarvon structure in March 2001. Dissolved inorganic nitrogen (DIN) and phosphorus (DIP), total nitrogen (TN) and phosphorus (TP), dissolved inorganic silicon (DSi). BTAB and RAC denote the Bayou Terre Aux Boeufs and River Aux Chenes transects, respectively. The symbol (\*) indicates statistically significant differences between the paired stations and Mississippi River water (modified from Lane et al., 2004).

Lane et al. (2004) reported an increase in Si:DIN ratio from 0.9 at the Caernarvon diversion to 2.6 at the marsh end member stations, while the DIN:DIP ratio fell from 107 to 26 at the same stations. Alteration of stoichiometric ratios at which dissolved nutrients are delivered to the coastal ocean can have a significant influence on phytoplankton community composition and hypoxia development.

**Phytoplankton and Aquatic Primary Productivity** - In the Breton Sound estuary, salinity decreases in the upper estuary due to high river input, while total suspended solids (TSS) and nutrients increase adjacent to the Caernarvon Diversion structure (Lane et al., 2007). Water residence times also decrease with high river input, while turbulence and water column mixing increase (Hyfield et al., 2008; Day et al., 2009). During warmer months (May to October), when river water levels decrease, salinity, TSS, nutrients, water residence time, and turbulence exhibit the opposite trends.

Chlorophyll *a* concentrations range from 0.4 to 127.0  $\mu\text{g L}^{-1}$ , with concentrations being greatest during summer and fall and lowest during winter (Lundberg et al., 2014, Fig. 8). Concentrations are generally less than 10  $\mu\text{g L}^{-1}$  in the upper estuary, and rising in the mid-estuary to 20–30  $\mu\text{g L}^{-1}$  during late summer and fall, and decreasing in the lower estuary (Lane et al., 2007). Lane et al. (2007) reported several periods when there were high chlorophyll *a* concentrations, peaking at 38  $\mu\text{g L}^{-1}$  in 2001 and > 60  $\mu\text{g L}^{-1}$  in 2002, and also during the fall of 2000 and early winter of 2001, with peak concentrations ranging from



**Fig. 11.** Temporal and spatial patterns of phytoplankton dynamics in the Breton Sound estuary (modified from Day et al., 2009).

40 to 56  $\mu\text{g L}^{-1}$  (Fig. 7). The highest chlorophyll *a* levels occurred during periods of low or no discharge from the Caernarvon structure, in low salinity (1–5) waters located mid-estuary with TSS concentrations less than 75  $\text{mg L}^{-1}$ . These high chlorophyll *a* concentrations are most likely caused by interactions among water residence time, turbidity, nutrients, and temperature. Water residence time is reduced during periods of high discharge, leading to increased flushing of phytoplankton biomass out of the estuary, and increased turbidity (Fig. 7). Conversely, as discharge decreases, turbidity decreases and water residence time increases, allowing the buildup of phytoplankton biomass and leading to increased chlorophyll *a* concentrations. This increased biomass is most likely supported by an increase in benthic regeneration of nutrients associated with higher summer water temperatures (Kemp and Boynton, 1984). Such seasonal decoupling between riverine nutrient input during spring and peak phytoplankton productivity during summer has been observed in many other estuaries (Boynton et al., 1982; Madden et al., 1988; Peierls et al., 2012).

Recently, Day et al. (2009) and Riekenberg et al. (2015) noted that a decrease in seasonal flow rate and nutrient concentrations within Breton Sound estuary caused a shift in phytoplankton community assemblages from chlorophytes and centric diatoms to groups containing more potentially toxic species of cyanobacteria (Figs. 11 and 12). Riekenberg et al. (2015) explore the shift in the plankton community during a dry year (few flushing events). However, we lack an understanding of community shifts under varying environmental conditions. Potentially-toxic cyanobacteria have been frequently observed in Louisiana estuaries (e.g. Dortch et al., 1999; Garcia et al., 2010; Bargu et al., 2011; Riekenberg et al., 2015). In the Breton Sound estuary, cyanobacteria have been observed (Day et al., 2009, Fig. 11), but

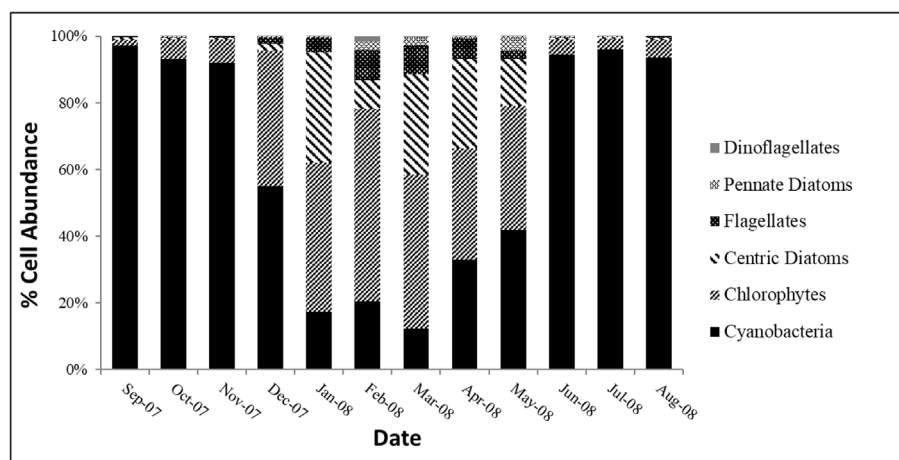


Fig. 12. Percent abundance of individual phytoplankton groups in the Breton Sound estuary (modified from Riekenberg et al., 2015).

specific toxic genera and toxin measurements are limited to few studies. Riekenberg et al. (2015) analyzed monthly water samples from the Breton Sound estuary from September 2007 to August 2008 and found several potentially toxin-producing genera within the Breton Sound estuary, comprising five genera of cyanobacteria and four genera of dinoflagellates. In this study, individual chlorophyll *a* measurements varied from 5.5 to 242.5  $\mu\text{g L}^{-1}$  over the year while monthly mean chlorophyll *a* values fluctuated between 27.9 and 106.7  $\mu\text{g L}^{-1}$ . Chlorophyll *a* was lowest in Lake Leary toward the upper estuary, while the highest average annual value was detected in the lower mid-estuary. The phytoplankton community shifted from cyanobacteria dominating during the majority of the year to chlorophytes becoming dominant during the cool high flow months (Fig. 12). The ability of some cyanobacterial species to fix N and/or store P likely enabled them to outcompete other groups during warmer months with low river input and toward the lower estuary where nutrient concentrations decreased.

**Sediment Dynamics** - The Caernarvon Freshwater Diversion is currently the primary sediment source to the upper estuary, while the lower estuary receives sediments from the river and resuspended during storms (Fig. 2). Once river-derived sediment enters the basin through the diversion, sediment transport is distributed in the estuary primarily down the two main flow routes (i.e., Bayou Terre aux Boeufs and Manuel's Canal/River aux Chenes), unless water levels are high enough to reach the marsh surface and cause sheet flow (Lane et al., 2004, 2007). Lane et al. (2007) found river water entering the estuary had TSS concentrations ranging from 40 to 252  $\text{mg L}^{-1}$ , with an average of 118  $\text{mg L}^{-1}$ . Wind-induced resuspension and transport of sediments stored in channels, lakes (i.e., Big Mar, Lake Leary, and Breton Sound), and ponds are major processes impacting the delivery of sediment to the marsh surface as well as the transport of diverted river sediment farther south into the estuary (Fig. 7) (Moeller et al., 1993; Perez et al., 2000; Lane et al., 2007).

#### 4. Summary and next steps

River diversions affect many environmental factors of significance to coastal and estuarine ecosystems, including salinity, turbidity, residence times, stratification, and nutrient loads, concentrations and ratios. These factors, in turn, have a controlling influence on phytoplankton biomass and composition and aquatic primary productivity. Fluctuations in phytoplankton biomass and community composition in portions of the estuaries adjacent to the diversion structures are strongly related to variation in river flow, nutrient input, and turbidity (Reynolds, 2006; Jöhnk et al., 2008; Day et al., 2009; Paerl and Justic, 2011). The responses of phytoplankton to diverted freshwater inflows, however, appear system-specific. Numerous co-occurring physical,

chemical, and biological processes act on phytoplankton at different spatial and temporal scales, and determine phytoplankton abundance and composition (Platt and Denman, 1980; Gilbert et al., 2005). For example, physiological tolerances to salinity restrict certain phytoplankton taxa to specific environmental ranges, thereby influencing community composition in different regions of the estuaries. Also, although decreases light availability (due mainly to high TSS), determined by vertical mixing and overall depth, during high diversion discharge are disadvantageous for most phytoplankton groups. The resulting stronger turbulence favors phytoplankton groups that are prone to sinking, such as diatoms and chlorophytes, by redistributing them throughout the photic zone (Harris and Baxter, 1996; Visser et al., 1996). The proposed large-scale Mississippi River diversions will substantially increase freshwater, sediment and nutrient inputs to deltaic estuarine basins, which can profoundly influence estuarine aquatic primary productivity and phytoplankton community composition. Due to the pervasive influence of the Mississippi River plume on the continental shelf of the northern Gulf of Mexico (Wang and Justic, 2009; Justic and Wang, 2014), deltaic Louisiana estuaries receive substantial nutrient subsidies from the adjacent coastal waters (Das et al., 2010). Large scale sediment diversions will likely lead to stronger estuarine outwelling of freshwater and nutrients, accompanied by decreased estuarine residence times (Peyronnin et al., 2017).

During the low river input summer months, elevated temperatures, along with water column stability and increased water residence time support the proliferation of potentially toxin-producing cyanobacteria. The ability of certain cyanobacterial species to compete effectively for reduced N ( $\text{NH}_4$ ), fix nitrogen and/or store P (Thompson et al., 1994; Dignum et al., 2005) enable them to outcompete other groups under these conditions. Increased riverine nutrient inputs have been also associated with cyanobacterial HABs in Louisiana coastal waters (Turner et al., 2004; Garcia et al., 2010; Bargu et al., 2011; Riekenberg et al., 2015). Likewise, the presence of cyanobacteria and the associated toxins in several Louisiana estuaries has already been documented at high levels including: blue crab contamination in Lac Des Allemands (Garcia et al., 2010); high levels of cyanobacteria abundance in Breton Sound (Riekenberg et al., 2015); and cyanobacterial HABs in Lake Pontchartrain following Bonnet Carré spillway openings (Turner et al., 2002; Bargu et al., 2011; Roy et al., 2013). Stronger estuarine outwelling could increase the transport of toxin-producing freshwater cyanobacteria into brackish coastal waters thus increasing the possibility of contamination to oyster beds (Smith, 2014; Riekenberg et al., 2015). Evidence suggests that potentially toxin-producing cyanobacteria can grow along the entire range from fresh to oligohaline- (0.5–5) to mesohaline (5–18) waters. Tonk et al. (2007) observed that salinity fluctuations in brackish water favored microcystin-producing species over



other freshwater phytoplankton species, but also resulted in increased dissolved microcystin concentrations measured in waters with salinity greater than 10 possibly due to increased cell lysis. There is a pressing need for more information on how cyanobacteria and their toxins, including microcystins, make their way from the fresh upper estuary to lower, brackish estuary, and to what extent primary and secondary consumers would be exposed to these toxins. Some of these uncertainties will only be fully informed by monitoring before and after diversion structures begin operations. Restoration trajectories can be difficult to predict, but a robust, statistically sound monitoring program is critical to understanding potential shifts in ecosystem dynamics.

To a certain degree, manipulating diversions could be used to mediate water quality, both inshore and offshore. Increasing residence times of water in the estuary can help to maximize denitrification and nutrient uptake by marsh vegetation during the warmer months when concentrations of nutrients in the Mississippi River typically are the highest. One strategy of operating the diversion could be to decrease the flow gradually to prevent nutrient-laden water from becoming stagnant and maintain some residual flow to reduce the probability of algal bloom formation (Peyronnin et al., 2017). Another strategy would be to utilize large river diversions every few years, as in the case of Bonnet Carré Spillway (Day et al., 2016; Rutherford et al., 2018). Management strategies that include dual nutrient input reduction strategies will likely be more successful in reducing and/or reversing eutrophication and minimizing the risk of harmful algal bloom proliferations (Paerl et al., 2014; Paerl and Otten, 2016). However, far-field effects associated with the enhanced delivery of estuarine nutrients and other materials to the near shore environments remain poorly understood and merit further investigation.

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