Nutrient and harmful algal bloom (HAB) dynamics in Lake Pontchartrain during a non-spillway opening year

Basic Information

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Publications

1. Roy ED, White JR, Smith EA, Bargu S, Li C. Estuarine ecosystem response to three large-scale Mississippi River flood diversion events. Science of the Total Environment 2013;458-460:374-387.
2. Controls on Microbial Processing of Nitrate in Floodwaters during Large-Scale Diversions of Mississippi River Water. *J.R. White and E. Roy. Invited Oral Presentation at the Annual Meeting of the Society of Wetland Scientists, (June 2-4, 2013) Duluth, MN.
3. Estuarine Ecosystem Response to Three large-scale Mississippi River Flood Diversion Events Roy, E. D., White, J. R., Smith, E., A., Bargu, S., Li, C. Oral Presentation at the ASLO Ocean Sciences Meeting (Feb 2013) New Orleans, LA.
4. Nutrient Dynamics at the Estuarine Sediment-Water Interface during Large Pulses of High Nitrate Mississippi River Water. E.D. Roy and J.R. White. Oral Presentation at the 9th INTECOL International Wetlands Conference (June 2012) Orlando, FL.

Problem and Research Objectives

Phytoplankton are considered to be one of the major primary producers in estuaries that support the diversity and productivity. As estuaries become increasingly subject to higher loads of bioavailable nutrients, eutrophic conditions may become more pronounced shown by high algal production, hypoxia and associated fish kills. During the past five years, the Bonnet Carré spillway has been opened twice (2008, 2011) to mitigate potential flooding to the City of New Orleans and downstream communities. In doing so, a volume of Mississippi River water greater than the volume of the entire lake has been diverted into Lake Pontchartrain along with a very large nutrient load (100s to 10,000s of metric tons of P and N, respectively). In Lake Pontchartrain, both non-toxic and toxic phytoplankton blooms occurred after the 1997 and 2008 Bonnet Carré Spillway openings. Toxic cyanobacteria dominance and their associated toxins were present and varied over time and space threatening the ecosystem (Dortch & Achee, 1998; Bargu et al. 2011).

The effect of these large nutrient and hydraulic fluxes has been studied by the current research team by funding through the National Science Foundation. However, there are no programs/funds available to document the "non-spillway" or background conditions of the lake, especially along the east-west axis of the lake coincident with the salinity gradient. In order to determine the effects of these large nutrient loads on lake water quality, we need to undertake a spatially and temporally explicit field sampling campaign spanning from March – October 2012 to determine water quality including nutrient concentrations, algal toxins and phytoplankton population measures.

The health of Lake Pontchartrain is important to the economy of Louisiana, specifically related to the fisheries. It is imperative to understand the triggers to harmful algal blooms as the associated toxins have the potential to contaminate the entire food web. In order to assess the causes of potential animal mortality and morbidity and its potential link to harmful algal toxins, generating baseline datasets such as the one proposed here is fundamental and necessary as a baseline or point of reference for future research. The findings from this proposal will be shared immediately with the Department of Health & Hospitals – Office of Public Health, and Louisiana Department of Environmental Quality.

The specific objectives include:

(1) Determining baseline dissolved N and P concentrations over time and space
(2) Quantifying cyanotoxin concentration correlated to phytoplankton assemblages over time and space.
(3) Combining data from this effort (non-spillway year) with data from two previous annual sampling campaigns (spillway years) to build a simple ecosystem model on how spillway opening can potentially affect the water quality and health of the fisheries in Lake Pontchartrain.

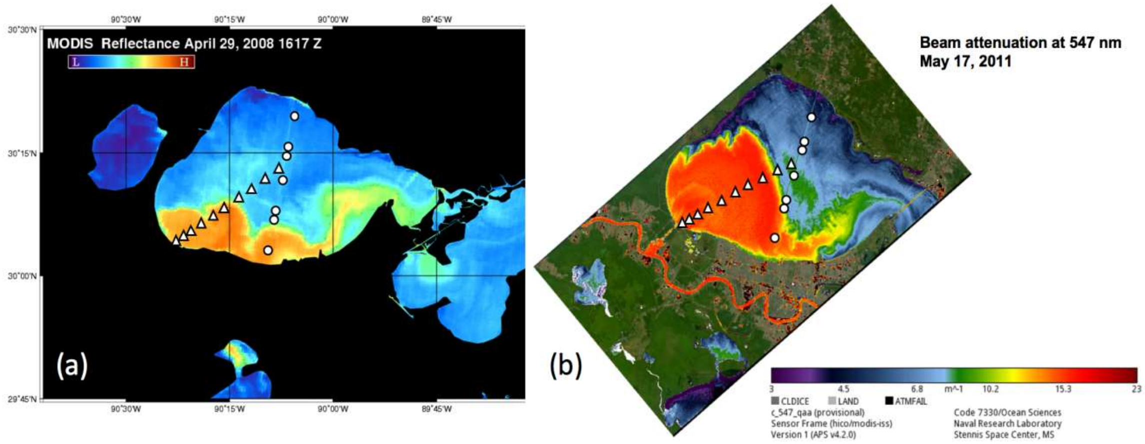

Figure 1. MODIS satellite imagery of Lake Pontchartrain on (a) April 29, 2008 and (b) May 17, 2011 provided by the LSU Earth Scan Laboratory and the US Naval Research Laboratory at the Stennis Space Center in Mississippi, respectively. Orange or red tones depict sediment-laden Mississippi River water (measured as red band reflectance in 2008 and beam attenuation at 547 nm in 2011). Blue tones depict estuarine water and land is colored black and green/brown in the 2008 and 2011 images, respectively. The 10 stations shown as Δ comprise the 30-km transect used in this and past studies (White et al. 2009; Bargu et al. 2011). The 7 stations shown as ○ were sampled by Turner et al. (2004) in 1997.

Methodology

We conducted 7 sampling trips from March to August 2012, focused on the springtime bloom period and the late summer period when HABs have been detected in the Lake Pontchartrain. We sampled three stations spanning in 2012 the length of our previously established a 10-station, 30 km transect in the western portion of the lake during the spillway years (Figure 1). In addition, in 2011, we added stations in the eastern half of the lake including stations at the two outlets to the Gulf of Mexico, The Rigolets and Chef Menteur passes. That sampling schedule gave us excellent spatial coverage along the east-west axis of the lake from the more saline section to the less saline western boundary (Figure 1). In 2012, we focused on the 3 transect stations along with 4 stations in the northwest quadrant of the estuary where cyanobacteria have been previously observed. Additionally, we sampled upstream of the confluences of Pass Manchac, the Tangipahoa River, and the Tchefuncte River with Lake Pontchartrain to help gauge contributions of nutrients and biology from the North Shore.

Water samples were collected at all stations (minimum of 15 spanning the lake) at 10 cm below the surface (to avoid floating debris and hydrophobic films) and at 1 m from the bottom at transect stations. Our experience during the spillway events has shown that other than dissolved oxygen, there were no differences in water quality and water chemistry between the surface and deep stations, primarily due to the turbulence produced by the spillway. However, during the non-spillway years, we will sample both depths to document any stratification. At each station, the secchi disk depth will be recorded, salinity, temperature, DO, and pH will be taken with a YSI handheld meter and turbidity and phycocyanin pigment measurements were taken using a handheld Turner fluorometer. Four discrete water samples were at each depth for each station; 1L sample for total suspended solids (TSS), 125 mL bottle for total nutrients, 30 mL field-filtered sample for dissolved inorganic nutrients, and a 1 L bottle for chlorophyll measurements and characterization of the phytoplankton community. Preliminary examinations of the phytoplankton community revealed species of cyanobacteria capable of producing the cyanotoxins MCs, saxitoxin, anatoxin and cylindrospermopsin in the Lake Pontchartrain (Bargu et al. 2011). MCs are commonly detected toxins in the lake and they can be produced by both *Microcystis* and *Anabaena*, two most common toxic species previously observed in the lake (Bargu et al. 2011).

Laboratory Analyses

Nutrient Analyses. Filtered water samples were analyzed for dissolved Si, NH_4, NO_3 and DRP on a Seal Analytical Discrete Colorimetric analyzer (USEPA, 1993). DOC and DON were analyzed on a Shimadzu TOC/TN analyzer. Unfiltered samples underwent acid digestion and then analyzed for TKN and TP.

Total Suspended Solids: Total Suspended Solids and Total Volatile Solids were determined within 24 hours by filtration through pre-ashed and pre-washed glass fiber filters, dried and weight for TSS. Then samples were ashed at 550 C for 4 hours and reweighed to determine weight percent volatile solids (APHA, 2540 D and E/G).

Chlorophyll a (chl a) and Microscopy Analyses. Chlorophyll *a* were determined for all stations as a measure of phytoplankton biomass using a Turner fluorometer (Model 10-AU) following the protocol from Parsons et al. (1984). Subsamples preserved with 2% gluteraldehyde and kept in a dark, at room temperature were used to determine the species composition of the phytoplankton community using an inverted microscope (Axiovert 135, Zeiss).

Phycotoxin Measurements. Water samples were analyzed for the cyanobacteria toxins, microcystin and cylindrospermopsin, using Enzyme-Linked Immunosorbant Assay (ELISA) with a detection limit of 0.10 $\mu g\ l^{-1}$. Samples were analyzed following the protocols included in the ELISA kits (Abraxis, LLC).

Lake Hydrodynamics

Hydrodynamic and hydrographic data will be used to help the interpretation of the distribution of nutrients and the bio-chemical characteristics of the lake. A long time series of hydrodynamic and hydrographic data has been collected in the lake during several projects funded by NSF after Hurricane Katrina, the 2008 and 2011 flood and Bonnet Carré Spillway opening. These include current velocity profiles, water level, and water temperature and salinity from the tidal channels (Rigolets, Chef, and Industrial Canal). Data from along the causeway also were collected for water level, water temperature, and salinity. Numerous ship based surveys were also conducted in the Lake at various locations and along many transects. These shipboard measurements will be repeated during each sampling cruise.

Principal Findings and Significance

Comparative Analysis of Spillway Openings

This work was compiled into a manuscript, submitted for review, accepted, and published during the funding period (Roy et al. 2013). The two spillway events analyzed were all characterized by the discharge of a volume of Mississippi River water greater than the total volume of Lake Pontchartrain. The 2011 opening had the largest total discharge (21.9 km^3) and occurred later than the events in 2008 (7.5 km^3). Discharges in 2008 and 2011 were equal to 113% and 330% of Lake Pontchartrain's volume, respectively (Table 1).

Table 1. Physical characteristics, nitrate (NO_x-N) plume collapse times, and phytoplankton dynamics in Lake Pontchartrain during the Bonnet Carré Spillway inflow events in 2008 and 2011.

	2008	2011
% of Lake Volume Discharged by Spillway	113[a]	330
Day Spillway Closed	9-May	20-Jun
NO_x-N Plume Collapse Time (d)	21[b]	21
Date of Full NO_x-N Plume Collapse	30-May	11-Jul
Max Chl *a* (µg/L)	58[c]	45
CyanoHAB Observed	Yes[c]	No
Date CyanoHAB Detected	21-May	-

[a]White et al. (2009). [b]Bargu et al. (2011), [*]From surface algal bloom.

The greater discharge in 2011 resulted in a near-linear increase in the sediment-rich freshwater plume area to a maximum of 1241 km^2 14 days post-opening in comparison to the 616 km^2 plume observed by White et al. (2009) in 2008 (Figure 3). The maximum turbid freshwater plume areas in 2008 and 2011 were equal to 38% and 76% of the total surface area of Lake Pontchartrain, respectively. Sediment-rich water was observed exiting Lake Pontchartrain via both of its eastern outlets in satellite imagery on May 23, 2011, indicating that the leading edge of the turbid freshwater plume traveled across the estuary in $\leq$ 14 days in 2011. As in 2008 (White et al., 2009), the leading plume edge in 2011 initially traveled along the southern edge of Lake Pontchartrain (Figure 1).

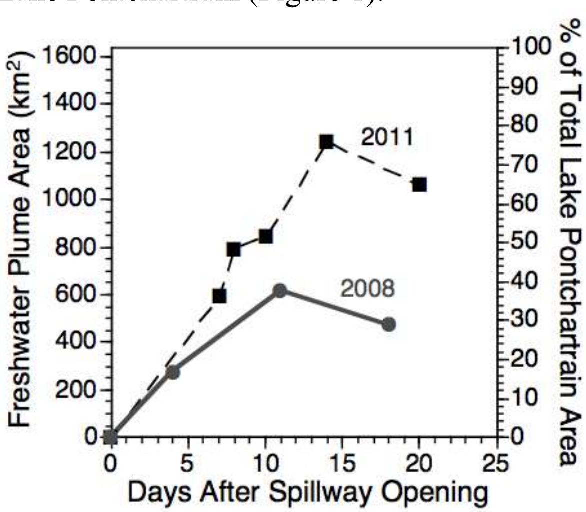

Figure 3. Area of sediment-rich freshwater plume in Lake Pontchartrain as a function of time identified using satellite imagery from the LSU Earth Scan Laboratory during the Bonnet Carré Spillway events in 2008 (White et al. 2009) and 2011 (this study).

Salinity (Figure 4) and surface water temperature (Figure 5) dynamics in 2008 are described in detail in White et al. (2009) and Bargu et al. (2011). In 2011, salinity in Lake Pontchartrain across the sample transect ranged from 2.6-4.9 PSU on May 8th prior to the 2011 spillway opening (Figure 4). Lower salinities at stations closest to the spillway indicated leakage of Mississippi River water through the spillway prior to its opening. Salinity on May 18, 2011 was

≤ 0.15 PSU at all stations except the two furthest from the inflow (0.79-2.72 PSU) during the spillway opening (Figure 4). Fluctuations in salinity occurred at the three stations furthest from the inflow through June 16, 2011. Surface water temperature was > 20.0 ˚C at all stations on May 18, 2011 and increased to > 28.2 ˚C at all stations by June 16, 2011 (Figure 5). Following spillway closure on June 20th, salinity averaged 0.34 PSU across the transect on June 21st and remained below 1.2 PSU at all stations through July 11th during the nitrate collapse period with evidence of slow dilution by estuarine water (Figure 4). Surface water temperatures were > 29.0 ˚C at all stations during the nitrate collapse period in 2011 (Figure 5). On August 10, 2011 salinity remained ≤ 1.2 PSU at all stations, indicating a much slower rate of salinity increase following spillway closure than observed in 2008 by Bargu et al. (2011) (Figure 4). Post-nitrate collapse surface water temperatures in 2011 were > 28.7 ˚C at all stations (Figure 5).

Nutrient loading to Lake Pontchartrain during the three events was correlated to discharge (Table 2). In all two events, the DIN pool in spillway influx was consistently dominated by NO_3^- with total NO_x-N loads of 9714 and 25395 Mg in 2008 and 2011, respectively. In general nutrient loads were 2.6-3.5 times greater in 2011 than in 2008. For both events the DIN:DIP molar ratio of spillway inflow waters (≥ 50:1) was well above the Redfield ratio of 16:1, indicating potential for eventual P limitation of primary production. The DSi:DIN molar ratio of spillway influx was near or greater than 1:1 for all events.

Table 2. Nutrient loads to Lake Pontchartrain from the Bonnet Carré Spillway in 2008 and 2011. The final column shows 2011 loads divided by 2008 loads.

	2008	2011	2011/2008
Nitrate+Nitrite (Mg NO_x-N)	9714[a]	25395	2.6
Ammonia (Mg NH_4-N)	224[a]	690	3.1
DIN (Mg N)	9938[a]	26085	2.6
DIP (Mg P)	400[b]	1122	2.8
DSi (Mg Si)	19347	67319	3.5
DSi:DIN:DIP Inflow Molar Ratio	57:59:1	63:50:1	-

[a]Based on values reported in White et al. (2009). [b]Roy et al. (2012)

Secchi depth in Lake Pontchartrain ranged from 0.8-1.2 m on May 8, 2011 prior to the 2011 spillway opening and decreased to 0.2-0.6 m during the spillway opening (Figure 6). Following spillway closure on June 20, 2011, Secchi depth increased to as high as 3.4 m in July under NO_3^- depleted conditions and remained > 0.76 m at all stations through August with several measurements > 2 m (Figure 6).

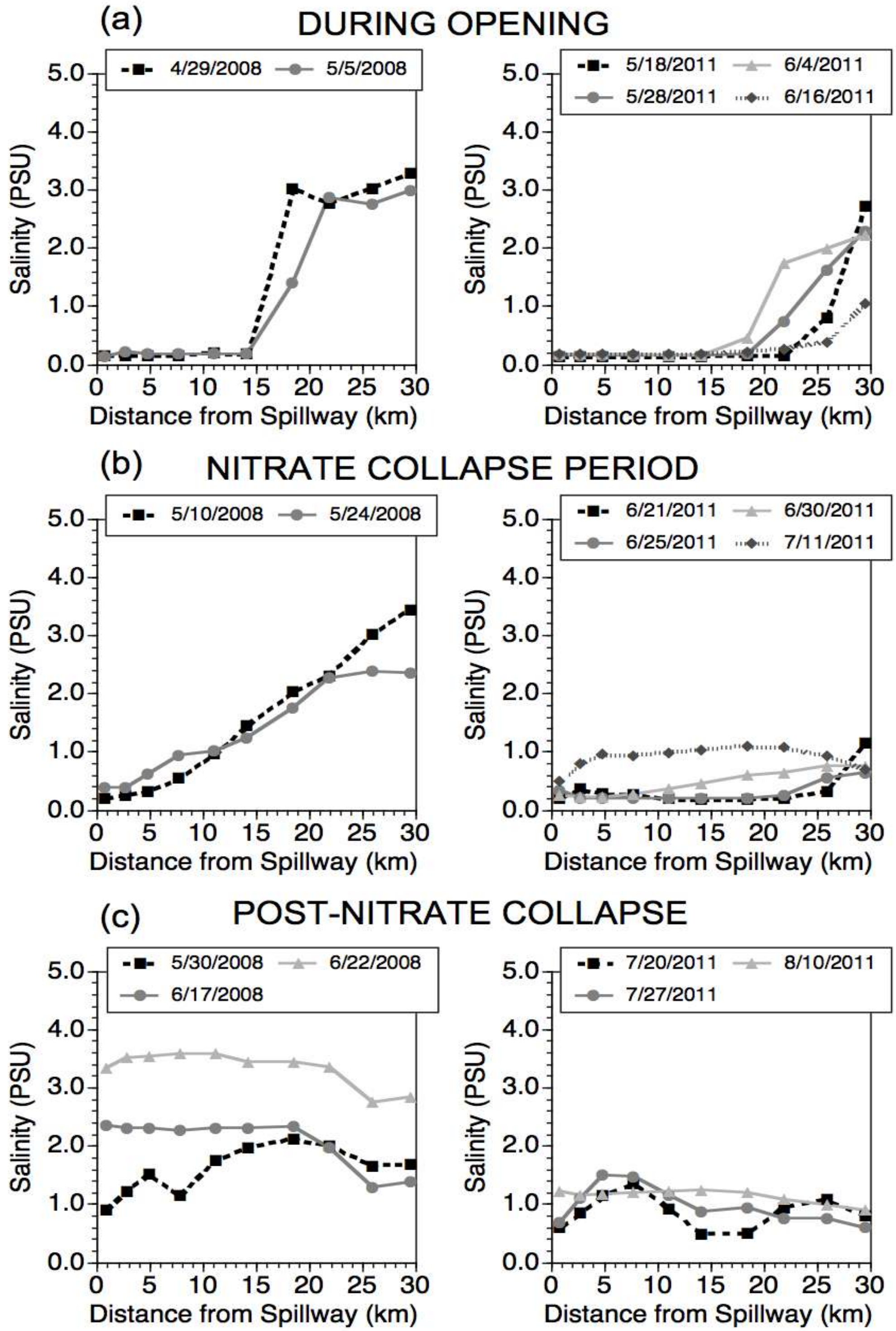

Figure 4. Salinity along the 30-km 10-station study transect (Fig. 1, Δ) during (a) the spillway opening, (b) nitrate collapse, and (c) post-nitrate collapse periods in 2008 (left panel) and 2011 (right panel). 2008 data are from White et al. (2009) and Bargu et al. (2011).

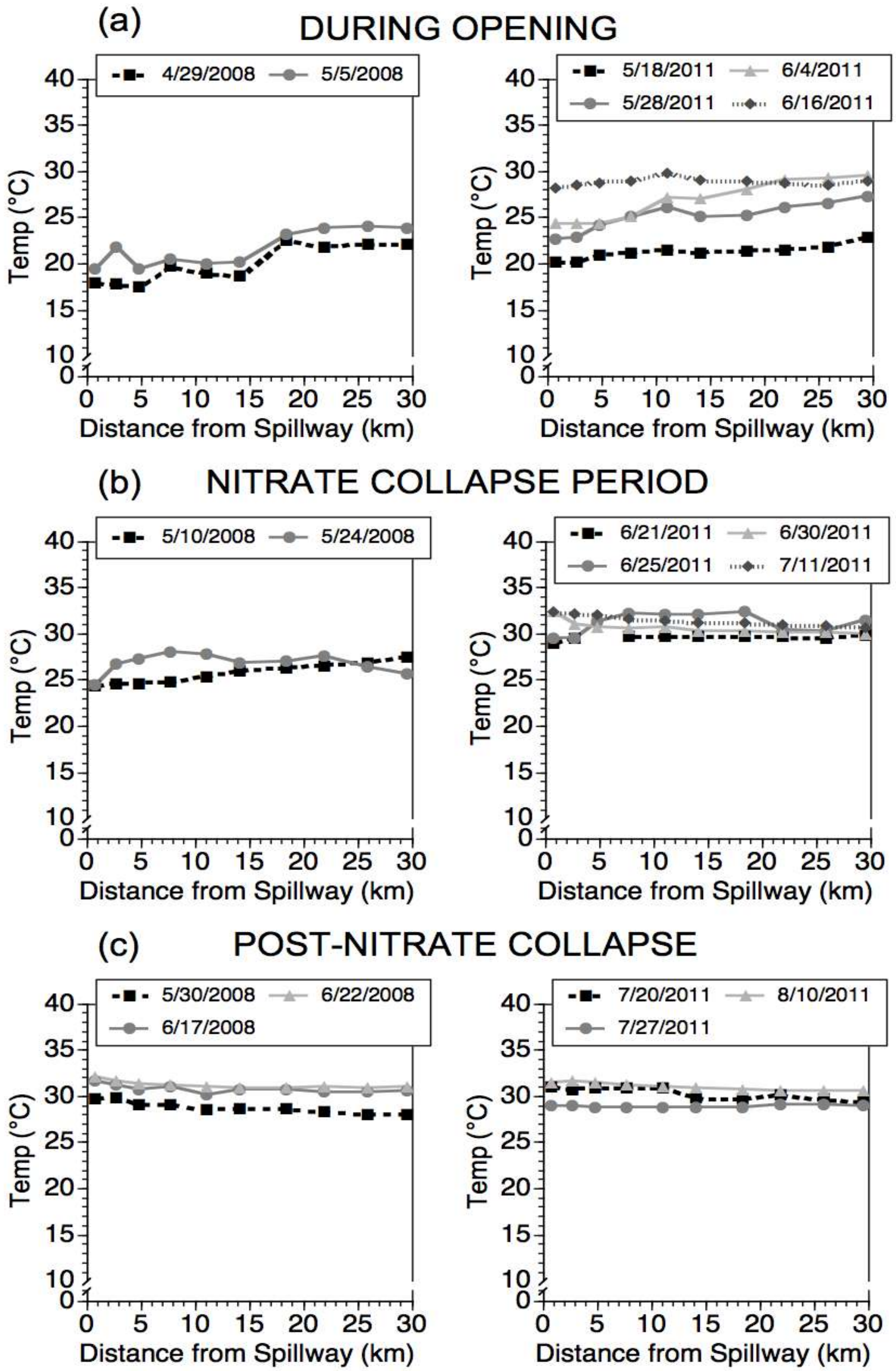

Figure 5. Surface water temperature along the 30-km 10-station study transect (Fig. 1, Δ) during (a) the spillway opening, (b) nitrate collapse, and (c) post-nitrate collapse periods in 2008 (left panel) and 2011 (right panel). 2008 data are from White et al. (2009) and Bargu et al. (2011).

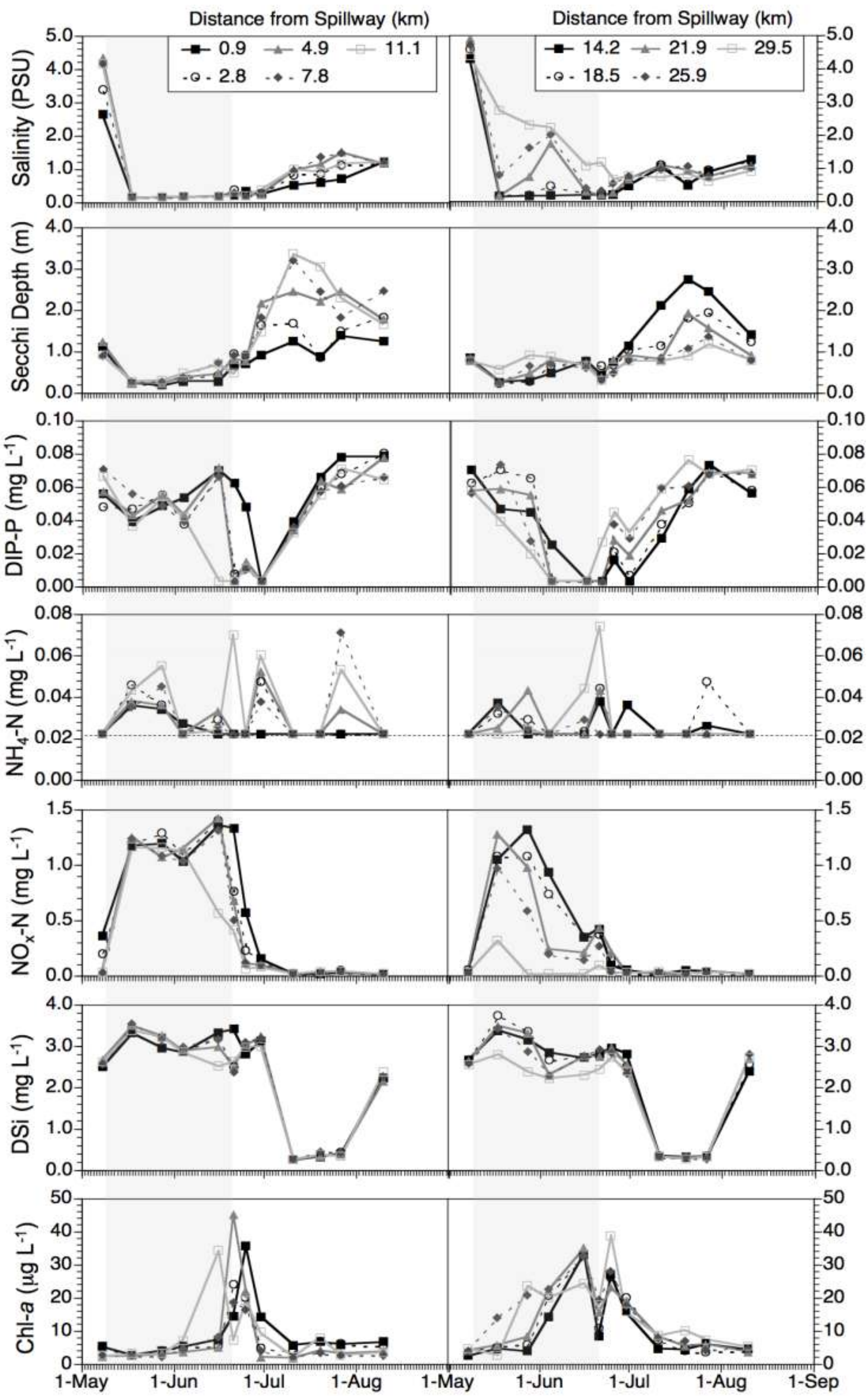

Figure 6. Salinity (PSU), Secchi depth (m), dissolved inorganic phosphorus (mg DIP-P L^{-1}), ammonium (mg NH_4-N L^{-1}), nitrate (mg NO_x-N L^{-1}), dissolved silica (mg DSi L^{-1}) and chlorophyll-*a* (µg L^{-1}) across the 30-km 10 station transect in Lake Pontchartrain extending from the Bonnet Carré Spillway inflow (0.9 km) to the lake center (29.5 km) (Fig. 1, Δ). The left and right panels show stations 0.9-11.1 km and 14.2-29.5 km from the spillway inflow, respectively. The shaded regions indicate the period during which the spillway was open (May 9 – June 20). Dotted lines in the NH_4-N plots indicate the detection limit.

Nitrate concentrations on May 18, 2011 in the Mississippi River plume ranged from 1.04-1.27 mg NO_x-N L^{-1} (Figure 6). During this time, NO_3^- concentrations remained $\geq$ 1 mg NO_x-N L^{-1} at stations with salinity $\leq$ 0.2 PSU except on June 16th when concentrations began to decline. Nitrate concentrations decreased rapidly following spillway closure and by July 11th, NO_x-N concentrations were below detection (detection limit = 0.016 mg L^{-1}) at all stations except the two furthest from the spillway inflow (0.03-0.04 mg L^{-1}) (Figure 6), indicating a NO_3^- plume collapse time of 21 days (Table 1). Nitrate concentrations largely remained below 0.04 mg NO_x-N L^{-1} at all stations through August. NH_4-N concentrations were often below detection (< 0.022 mg L^{-1}) and never increased above 0.07 mg L^{-1} throughout the spillway opening and post-closure period (Figure 6).

The mean measured DIP-P concentration was 0.054 mg L^{-1} in spillway inflow waters. Water column DIP concentrations decreased rapidly in Lake Pontchartrain between June 4th and June 30th with depletion occurring earlier with increased distance from the spillway due partially to dilution (Figure 6). Following DIP depletion across the entire transect post-spillway closure, concentrations rebounded at all sites and by July 27th were greater than the concentration of loaded Mississippi River water at all stations.

Water column DSi concentrations were near or above 3 mg L^{-1} within the Mississippi River plume during the opening, before rapidly decreasing below 0.5 mg L^{-1} between June 30th and July 11th (Figure 6). DSi concentrations remained low before increasing rapidly between July 27th and August 10th to > 2 mg L^{-1}.

On May 8, 2011, Chl *a* values were relatively low (2.32-10.26 µg L^{-1}) and then increased during the spillway opening at the outer most stations (5.67- 34.13 µg L^{-1}) (Figure 6). Results indicate that low light availability (measured as Secchi disk depth) corresponded to low phytoplankton biomass (measured as Chl *a*) within the sediment-rich Mississippi River plume near the spillway inflow despite available nutrients. Immediately following spillway closure, the Chl *a* concentration reached a maximum of 45.09 µg L^{-1} on June 21st at 4.9 km from the spillway inflow. Chlorophyll peaks corresponded to depletion of NO_3^- and DIP of Mississippi River origin (Figure 6). Chlorophytes were the dominant phytoplankton group at the time and location of maximum Chl *a* and accounted for a spatial average of 52-76% of the phytoplankton group composition during the period of greatest Chl *a* (June 16th, 21st, and 25th) (Figure 7). Cyanobacteria accounted for a spatial average of 7-22% of the group composition during this period. Phytoplankton biomass declined after June 25th and by July 11th Chl *a* concentrations were < 8.55 µg L^{-1} at all sites. No increases in biomass were observed from this time through the final sampling on August 10th (Figure 6).

The observed times for NO_3^- plume collapse following spillway closure were identical in 2008 and 2011 at 21 days (Table 1).

Dominance of the phytoplankton community by CyanoHAB species was observed in 2008 (May 21st, Bargu et al., 2011) following closure of the spillway, but not in 2011 (Figure 7). Maximum Chl *a* concentrations were 58 and 45 µg L^{-1} for 2008 and 2011, respectively. The 2008 CyanoHAB occurred within 2 weeks of closure (Table 1).

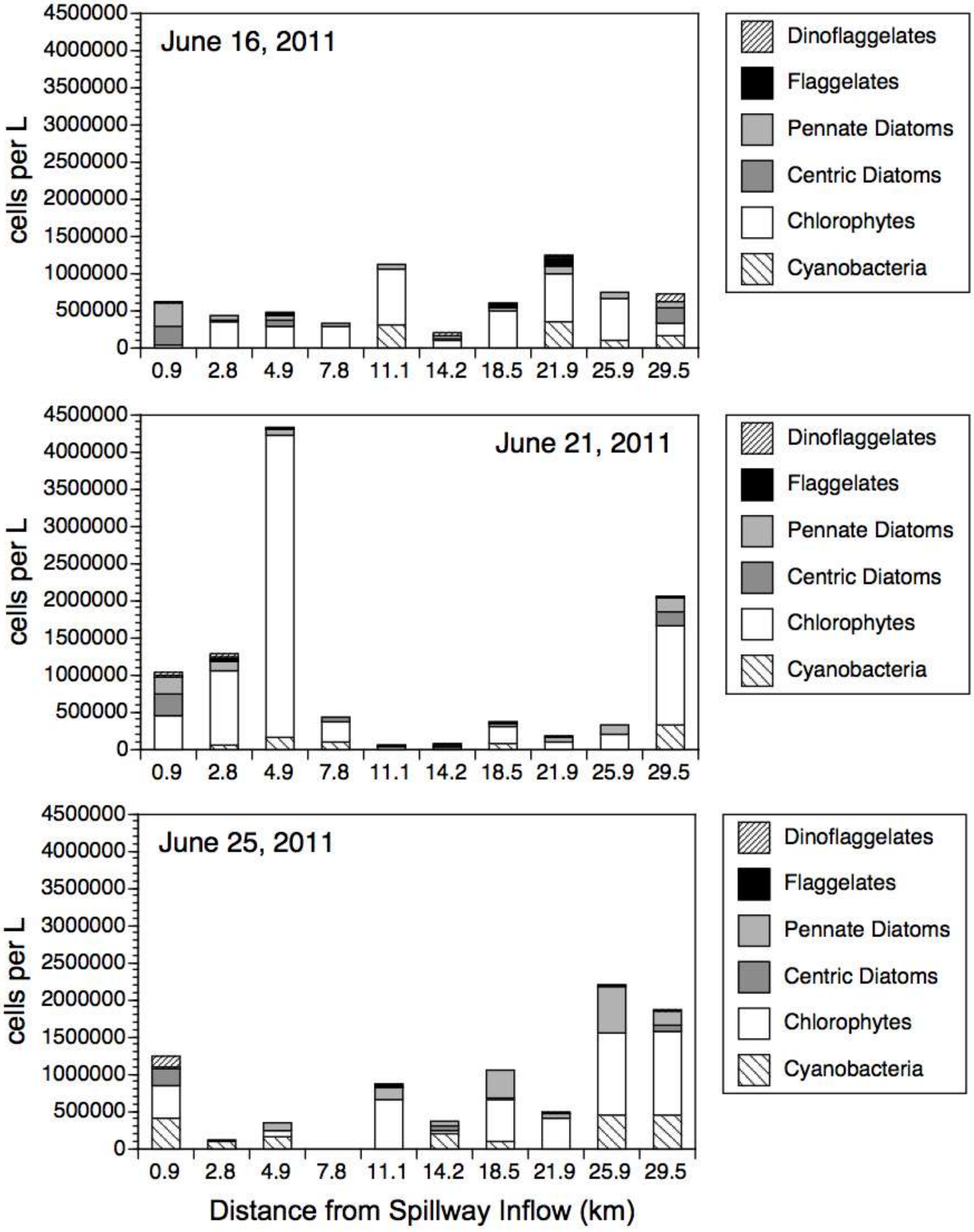

Figure 7. Phytoplankton group composition across the 30 km transect extending northeast from the Bonnet Carré Spillway inflow (Fig. 1, Δ) during the period of increased Chl *a* observed following the 2011 opening.

The Bonnet Carré Spillway events analyzed here had closures in May (2008) and June (2011) (Figure 2). The 30-d time period following closure in 2011 was characterized by significantly ($P < 0.01$) lower daily mean wind speed and significantly ($P < 0.01$) higher daily mean air temperature than those in 2008 (Table 3).

Table 3. Weather and Lake Pontchartrain surface water characteristics during the period following the closure of the Bonnet Carré Spillway in 2008 and 2011. Weather data is from the National Climatic Data Center (Louis Armstrong New Orleans Int'l Airport). Letters indicate significant differences (P<0.01) in weather characteristics for different time periods.

Year	2008	2011
Days After Spillway Closure	1 - 30	1 - 30
Daily Mean Wind Speed ($m\ s^{-1}$)	3.6 ± 1.1^{b}	2.9 ± 1.1^{c}
Daily Mean Air Temp. (°C)	26.0 ± 2.2^{a}	28.9 ± 1.2^{b}

*From Bargu et al. (2011).

The immense rate of freshwater discharge through the Bonnet Carré Spillway during diversions (up to nearly 9000 $m^3\ s^{-1}$ in 2011, Figure 2) results in a relatively rapid expansion of a freshwater plume that can impact a significant portion of Lake Pontchartrain (Figures 3 and 4). The plume is characterized horizontally by a narrow (<10 km) edge of mixed fresh and estuarine water (Figure 4) and is vertically well mixed (White et al., 2009). Essentially, the plume behaves as a river flowing through the shallow estuary during the inflow event. The tendency for the plume waters to travel along the southern rim of the estuary is driven by the Coriolis effect, but can also be impacted by wind (White et al., 2009). Plume waters near the spillway during the opening are characterized by high suspended sediments (White et al., 2009) and low Secchi depth (Figure 6). Phytoplankton biomass (represented here as Chl *a*) in this region of the freshwater plume is therefore limited by light availability despite readily available nutrients (Figures 6 and 8). The high discharge rate creates a turbulent, horizontally dynamic, and vertically well-mixed environment in the region near the spillway, likely also depressing primary productivity (Figure 8).

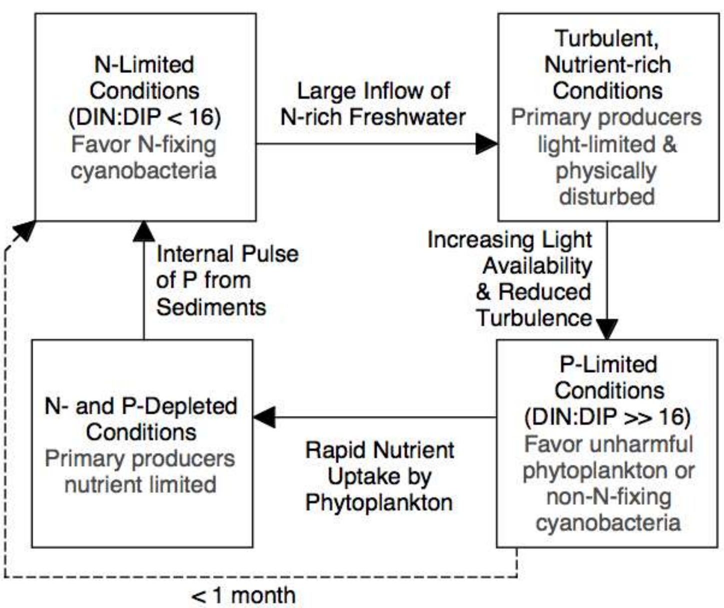

Figure 9. Estuarine biogeochemical dynamics during large inflows of nitrate-rich freshwater. Diagram is based on observations in Lake Pontchartrain during the 2008 and 2011 Bonnet Carré Spillway openings. Dotted line indicates that the system can move from P-limitation to N-limitation in < 1 month.

As light limitation is alleviated and physical disturbance decreases, either in regions more distant from the spillway during the opening or following spillway closure, phytoplankton rapidly compete for a one-time N-rich nutrient-boon (Figures 6 and 8). Continued freshwater inflow causes continued horizontal displacement of water in regions further from the spillway despite less turbulent and turbid conditions, resulting in outflow to the coastal ocean (Figure 1). Previous research has shown that cyanobacteria exhibit greater relative biomass when flushing is minimal (i.e., less horizontal displacement of the water column) (Paerl, 2006). Therefore, the river-like nature of the flowing freshwater plume during spillway events likely provides a competitive advantage for diatoms and chlorophytes.

Temperature and wind are two physical factors that may influence phytoplankton community composition during the period of rapid nutrient assimilation and peak phytoplankton biomass. Cyanobacteria generally exhibit greater growth rates at high surface water temperatures (> 25˚C) than diatoms, although chlorophytes also achieve maximum growth rates at > 25˚C (Paerl et al., 2011). Diverted Mississippi River water that is cooler than resident estuarine water quickly warms in the estuary as air temperatures increase (Figure 5). Not surprisingly, diversion timing impacts temperature dynamics. The earlier diversion period in 2008 resulted in surface water temperatures of 24-28˚C during the nitrate collapse period in comparison to 28-32˚C in 2011 (Figure 5).

Lake Pontchartrain is an exposed, wind-dominated estuary and wind-induced turbulence and turbidity can limit cyanobacterial success in estuaries due to disruption of vertical stratification and surface bloom formation (Paerl, 2006). However, our results showing that daily mean wind speeds were significantly lower for the 30 days following spillway closure in 2011 in comparison to periods in 2008 when CyanoHABs were observed (Table 3) suggest that wind-wave action was not the dominant factor responsible for the absence of cyanobacterial dominance in 2011 (Table 3).

Following spillway closure, mixing of estuarine water with the freshwater plume occurs at a pace and areal extent depending on the magnitude of the diversion (Figure 4). Salinity in Lake Pontchartrain is always low enough (< 15 PSU) to not limit N-fixing *Anabaena* sp. In 2011, salinity remained below 2 PSU on August 10th, indicating that salinity did not likely limit *Microcystis* sp. either. Salinity increased above 2 PSU following nitrate collapse in 2008 (Bargu et al., 2011; Figure 4), however at this time *Microcystis* sp. growth was likely restricted by lack of available DIN.

Our results illustrate a sequence of estuarine nutrient dynamics in response to large inflows of Mississippi River water (Figure 8): (1) high nutrient bioavailability in turbulent, sediment-rich conditions with a DIN:DIP molar ratio >>16, (2) rapid assimilation of DIP and NO_3^- during periods of increased light availability and reduced turbulence, (3) P-limitation of primary productivity, (4) nutrient-depleted conditions, and finally (5) a return to pre-inflow N-limitation following a rebound in DIP availability. Findings in 2008 (Bargu et al., 2011) and 2011 (this study) indicate that NO_3^- concentrations decrease rapidly to below detection in approximately three weeks following spillway closure (Table 2). Only a small percentage of incoming NO_3^- is removed via denitrification in sediments (e.g., 3% in 2008) due to the immense NO_3^- loading rate during spillway openings (Roy et al., 2012). Therefore, the vast majority of loaded NO_3^- is either assimilated by phytoplankton or transported to the coastal ocean. The combination in 2011 of rapid NO_3^- decline and slow influx of higher salinity dilution water to the transect region (Figure 6) suggests that phytoplankton assimilation could possibly account for the majority of DIN-depletion that year. Further research is needed to make mass balance estimates of nitrate assimilated versus loaded to the coastal ocean. Nitrate remained the dominant form of DIN throughout the study period in 2011. Oscillations in NH_4-N at low concentrations (Figure 6) were likely a result of mineralization processes, phytoplankton assimilation, and release from sediments due to concentration gradients (Wawrik et al., 2004; Roy et al., 2012).

Phosphorus bioavailability in Lake Pontchartrain during and after spillway events likely plays an important role in phytoplankton community response. The high DIN:DIP molar ratio of inflowing freshwater (≥ 50, Table 2) leads to eventual P-limitation during the nitrate collapse period (Mize and Demcheck, 2009). Once loaded DIP is rapidly assimilated during this period, further primary production relies on internal sources of DIP including mineralization and internal loading from sediments. These P-limited conditions put N-fixing cyanobacteria (*Anabaena* sp.) at a competitive disadvantage (Paerl, 1988). Following the depletion of both water column DIP and DIN in 2011, the rapid rebound in DIP concentrations observed (Figure 6) could only occur by internal loading from sediments because northern tributaries were in drought conditions and there was no significant external source of DIP. Roy et al. (2012) show that internal P loading from Lake Pontchartrain sediments occurs regardless of bottom water oxygen availability and estimate that internal DIP loading by diffusion alone has the potential to regenerate water column DIP concentrations from below detection to the Mississippi River concentration during the 2011 event (0.05 mg P L^{-1}) in < 60 days. Our field observations (Figure 6) suggest that this internal pulse of P from sediments can return the system to pre-inflow N-limitation conditions even faster (< 1 month following spillway closure), perhaps due to additional advective flux. High Secchi disk transparency and low chlorophyll *a* measurements following July 11, 2011 (Figure 6) indicate that primary productivity was limited by N at this time. The dynamic interaction between high external N loading during inflows and subsequent internal P loading and return to N-limitation observed here (Figure 8) has rarely been documented in estuaries (Cook et al., 2010). Further research is needed to determine the impact of spillway openings on the potentially bioavailable phosphorus pool in Lake Pontchartrain sediments.

Si bioavailability is also a factor that can determine phytoplankton community response to inflows by influencing diatom success (Turner, 2002). The DSi:DIN molar ratio in Mississippi River water is near or above 1:1 during diversion periods (Table 2), indicating nutrient conditions favorable for diatom growth (Redfield et al., 1963; Officer and Ryther, 1980; Lane et al., 2001). Following nitrate collapse in 2011, DSi concentrations plummeted, potentially indicating diatom uptake, before rebounding a few weeks later (Figure 6). The observed rebound was likely due to the dissolution of diatom silica and resultant internal loading from sediments (Conley et al., 1988).

The Lake Pontchartrain environment is physically and chemically dynamic during and after spillway events, leading to dynamic biological response. The spatiotemporal dynamics of cyanobacteria in 2008 illustrate a sequence of interrelated nutrient depletion and species appearance (Bargu et al., 2011). At stations directly influenced by the spillway plume, *Microcystis* sp. was the first cyanobacterium observed as NO_3^- depletion progressed (centric diatoms and chlorophytes were dominant), while *Anabaena* sp. was initially observed at low abundance in waters outside of the spillway plume influence where nutrient concentrations were low. Following depletion of spillway-loaded NO_3^-, there was a shift to cyanobacterial dominance by N-fixing *Anabaena* sp. It is likely that P release from sediments contributed to this bloom of N-fixers (Roy et al., 2012), as observed in other systems including the Baltic Sea (Vahtera et al., 2007). In contrast, cyanobacteria never achieved dominance following the 2011 closure (Figure 7).

The ecosystem dynamics in Lake Pontchartrain following freshwater inflow events that we have described (Figure 8) coupled with observations in 2008 lead to two questions about phytoplankton response in 2011. First, why wasn't there a bloom of *Microcystis* sp. immediately following the closure of the spillway when both DIN and DIP were readily available? Second, why wasn't there a bloom of N-fixing *Anabaena* sp. after spillway DIN was depleted, sediments provided an internal source of DIP, and N-limited conditions were restored?

There are two factors that may help answer the first question: water column physical disturbance and the form of DIN present. Surface water temperatures of 30°C likely enabled maximum growth rates for both chlorophytes and cyanobacteria upon spillway closure in 2011 (Paerl et al., 2011). The dominance of chlorophytes during the period of maximum phytoplankton biomass in 2011 (Figure 7), the absence of *Microcystis* sp. dominance in 2008, and previous observations of chlorophytes and diatoms outcompeting cyanobacteria during high inflow events in temperate estuaries (Paerl, 2006) all suggest that physical disturbance of the water column during spillway events may give chlorophytes or diatoms the competitive edge during the nutrient collapse period as light increases and horizontal displacement (i.e., flushing) continues. Whether diatoms or chlorophytes dominate is likely a function of temperature and therefore diversion timing, with higher temperatures similar to those observed in 2011 favoring chlorophytes. Another possible factor is the dominance of the DIN pool by NO_3^-. Blomqvist et al. (1994) suggest that high NO_3^- concentrations favor eukaryotic phytoplankton, while non-N-fixing cyanobacteria (*Microcystis* sp.) are more competitive at low NO_3^- concentrations with sufficient NH_4^+. Observations by Jacoby et al. (2000) support this notion.

We hypothesize that the greater freshwater discharge, greater plume areal extent, and later diversion timing in 2011 compared to 2008 (Figures 2 and 3) all played important roles in limiting the success of N-fixing *Anabaena* sp. during the late summer period of N-limitation in 2011. The 2011 diversion occurred during the time period when CyanoHABs were observed in 2008 (Table 1). Hydraulic alteration to increase turbulence and flushing has been found to prevent or terminate *Anabaena* sp. blooms in river systems (Mitrovic et al., 2011). The spillway diversion may have essentially achieved the same function on a massive scale in Lake Pontchartrain in 2011, eliminating the *Anabaena* sp. seed population necessary for bloom formation.

The variability in Lake Pontchartrain ecosystem response to Bonnet Carré Spillway openings suggests that there is not a simple stimulus-response relationship between N loading and estuarine CyanoHAB formation during large freshwater inflows. Nutrient loading during spillway openings consistently produces relatively high chlorophyll levels, however dominance of the phytoplankton community by CyanoHAB species is not guaranteed. A complex set of parameters including N loading, timing, diversion magnitude, plume hydrodynamics, nutrient molar ratios, internal P loading, weather, and northern tributary discharge can all play a role in ecosystem response. Our work provides a framework for understanding the relationships among large inflows of nitrate-rich freshwater to estuaries, internal nutrient dynamics, and factors determining cyanobacteria success (Figure 9). Physical disturbance of the water column associated with plume hydrodynamics and NO_3^- dominance of the DIN pool likely favor nonharmful phytoplankton species over non-N-fixing cyanobacteria during spillway openings and immediately following spillway closure when loaded nutrients are rapidly assimilated. Our results suggest that the magnitude and timing of hydraulic flushing in 2011 may have been responsible for the paucity of N-fixing cyanobacteria observed.

2012 Field Sampling

Nutrient Dynamics

Field data collected in 2012 indicates that northern tributaries to Lake Pontchartrain are a source of DIP and DIN during spring and summer (Figures 10 and 11). Mean DIP concentrations over the entire sampling period for Pass Manchac, the Tangipahoa River, and the Tchefuncte River were 0.065, 0.047, and 0.089 mg P L^{-1}, respectively. Mean DIN concentrations over the entire sampling period for Pass Manchac, the Tangipahoa River, and the Tchefuncte River were 0.046, 0.108, and 0.113 mg P L^{-1}, respectively. The DIN:DIP molar ratio at tributary sites varied between 0.9 and 12.3, always below the Redfield Ratio of 16, indicating that primary production in tributary waters was N-limited (Figure 12). Nutrient data collected in Lake Pontchartrain indicates that received DIN is rapidly assimilated resulting in DIN measurements rarely above the detection limit of 0.036 mg N L^{-1} (Figure 11) and creating conditions where N-limitation of primary productivity persists at the both the transect stations and northwest corner stations throughout the spring and summer (Figure 12). At these times, DIP is available (Figure 10), most likely due to continued internal loading of P from sediments (Roy et al. 2012, Roy et al. 2013). These conditions are identical to conditions in Lake Pontchartrain prior to the spillway opening in 2011 and correspond to the state described in the upper left-hand corner of Figure 9 where N-limitation and available P favors N-fixing cyanobacteria.

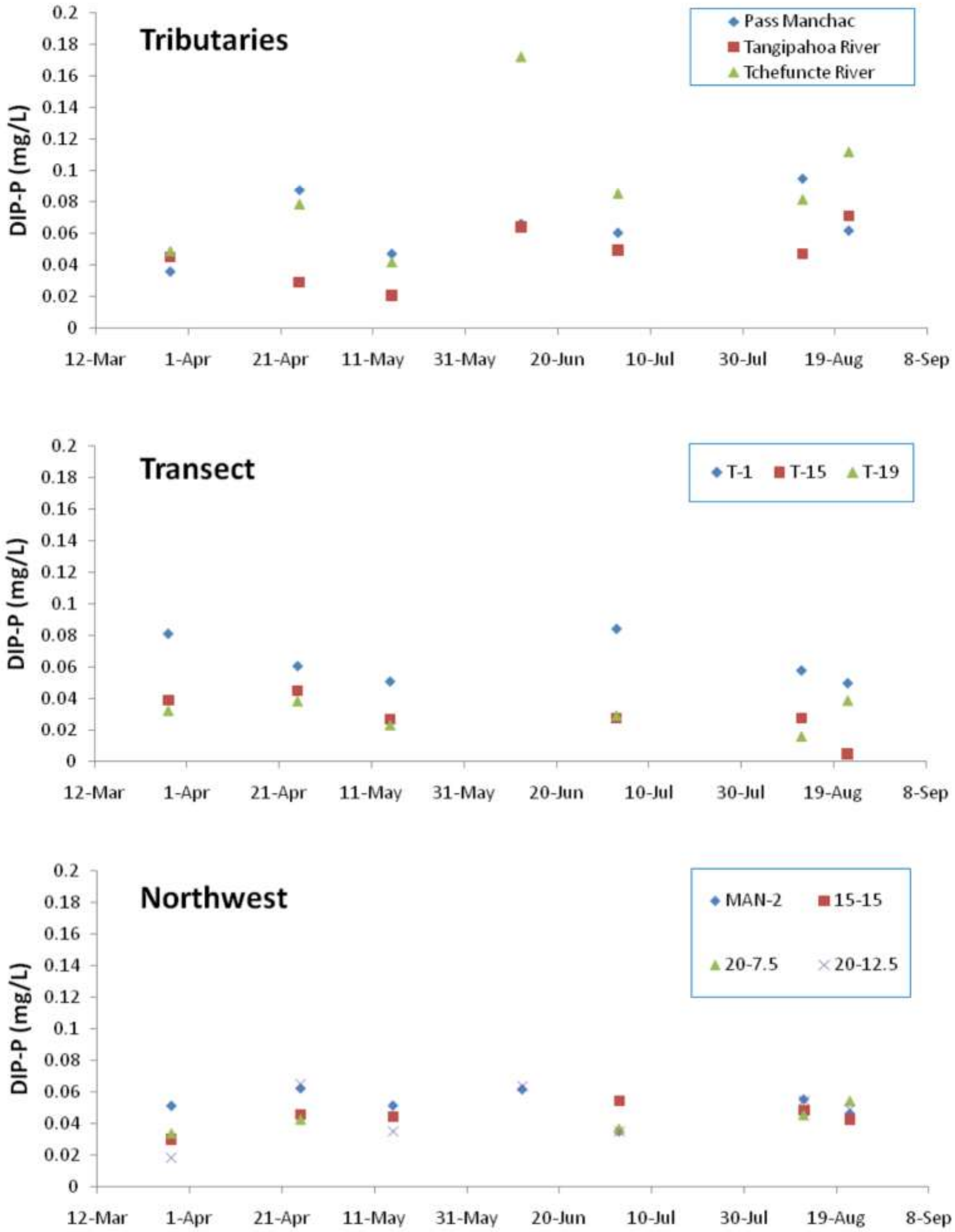

Figure 10. Dissolved inorganic phosphorus (DIP) concentrations in 2012 at tributary, transect, and northwest stations.

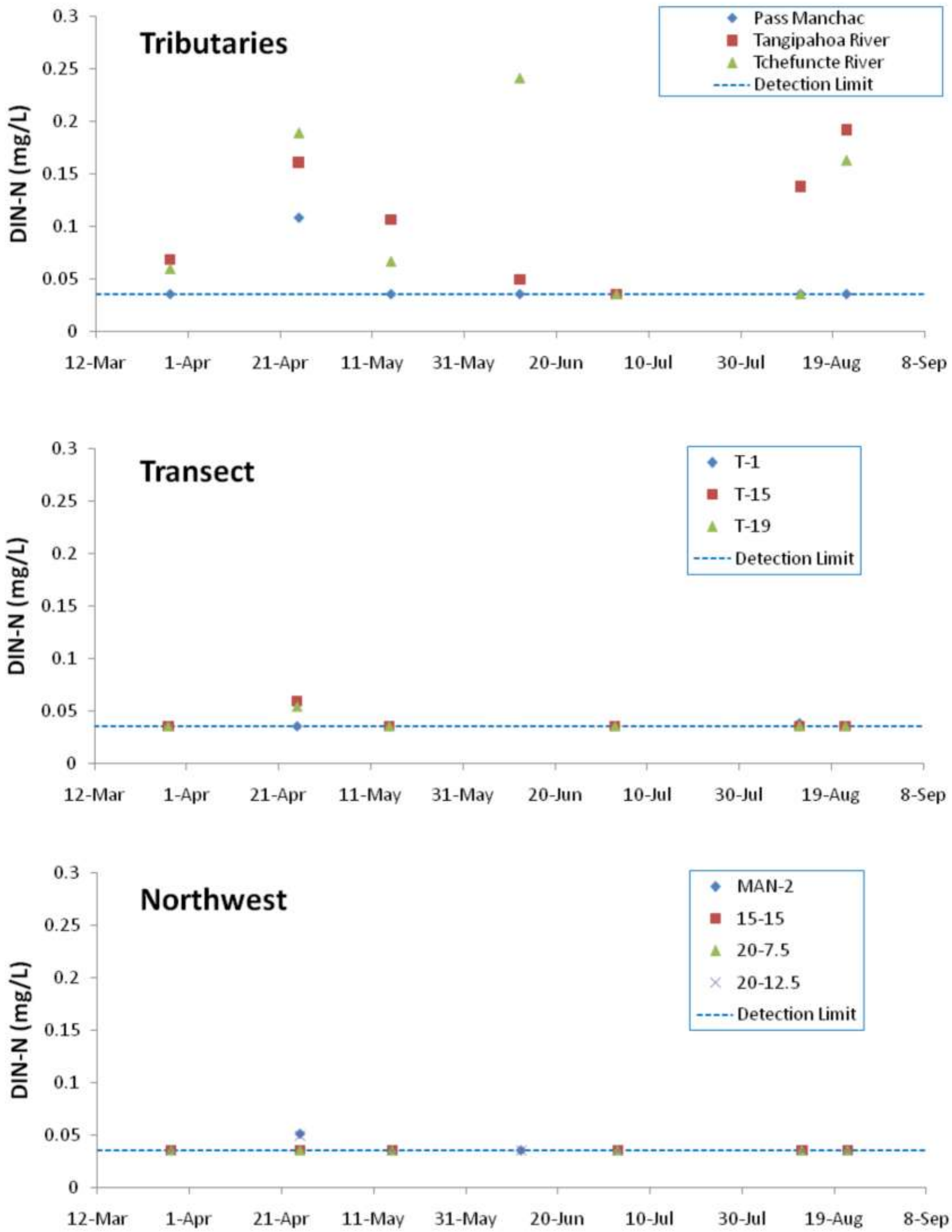

Figure 11. Dissolved inorganic nitrogen (DIN) concentrations in 2012 at tributary, transect, and northwest stations. Detection limit is 0.036 mg N L^{-1}.

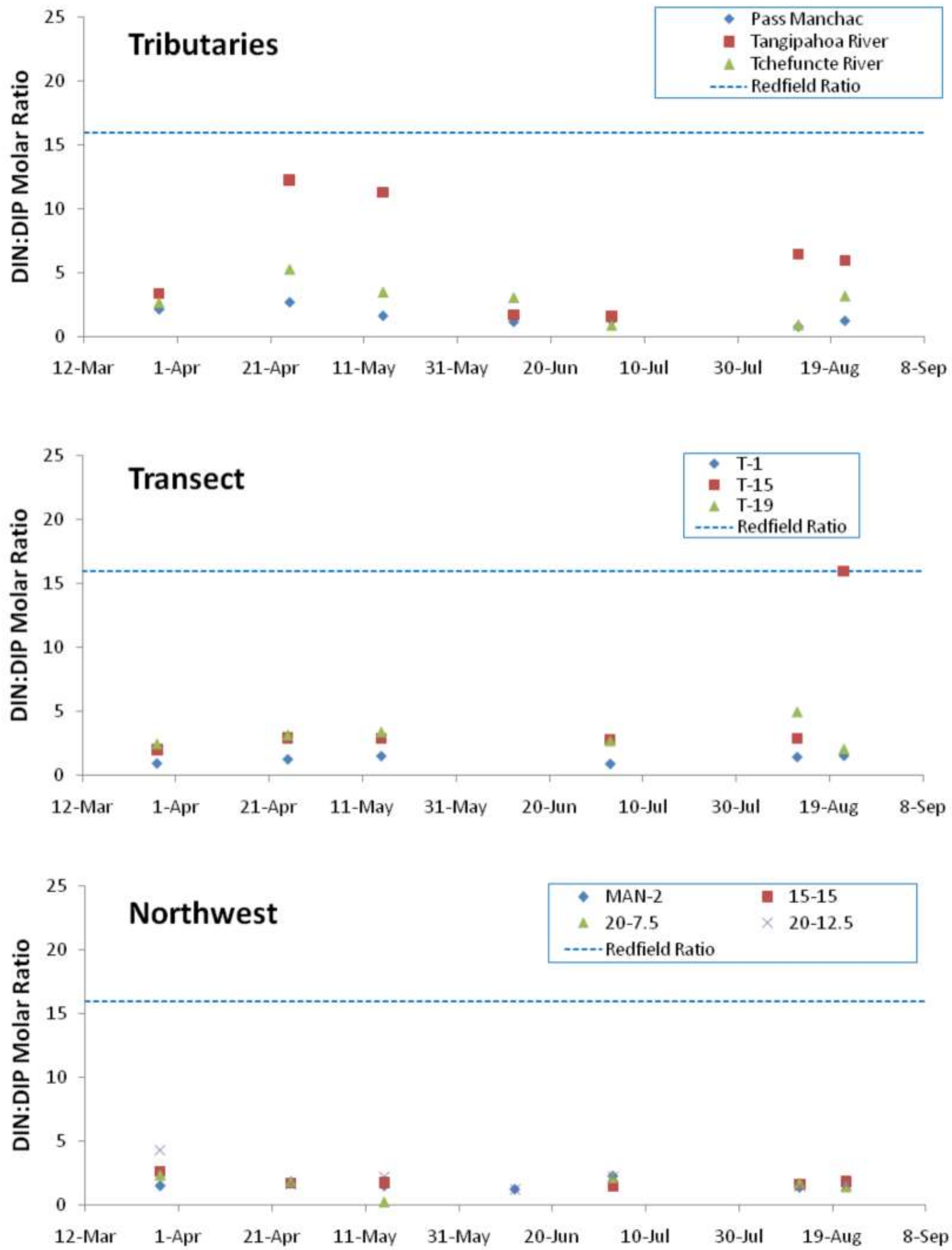

Figure 12. DIN:DIP molar ratios in 2012 at tributary, transect, and northwest stations. The Redfield Ratio (16) is shown. DIN:DIP > 16 indicates P limitation of primary productivity, whereas DIN:DIP < 16 indicates N limitation of primary productivity.

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