Dissimilatory nitrate reduction to ammonium (DNRA) is marginal relative to denitrification in emerging-eroding wetlands in a subtropical oligohaline and eutrophic coastal delta

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Abstract

Nitrate (NO_3^-) and ammonium (NH_4^+) are reactive nitrogen (N_r) forms that can exacerbate eutrophication in coastal regions. NO_3^- can be lost to the atmosphere as N_2 gas driven by direct denitrification, coupled nitrification-denitrification and annamox or retained within the ecosystems through conversion of NO_3^- to NH_4^+ via dissimilatory nitrate reduction to ammonium (DNRA). Denitrification and DNRA are competitive pathways and hence it is critical to evaluate their functional biogeochemical role. However, there is limited information about the environmental factors driving DNRA in oligohaline habitats, especially within deltaic regions where steep salinity gradients define wetland spatiotemporal distribution. Here we use the Isotope Pairing Technique to evaluate the effect of temperature (10, 20, 30 °C) and *in situ* soil/sediment organic matter (OM%) on total denitrification (Dtotal = direct + coupled nitrification) and DNRA rates in oligohaline forested/marsh wetlands soils and benthic sediment habitats at two sites representing prograding (Wax Lake Delta, WLD) and eroding (Barataria-Lake Cataouatche, BLC) deltaic stages in the Mississippi River Delta Plain (MRDP). Both sites receive MR water with high NO_3^- (>40 µM) concentrations during the year via river diversions. Denitrification rates were significantly higher (range: 18.0 ± 0.4 - 113.0 ± 10.6 µmol m^{-2} h^{-1}) than DNRA rates (range: 0.7 ± 0.2 - 9.2 ± 0.3 µmol m^{-2} h^{-1}). Therefore, DNRA represented on average <10 % of the total NO_3^- reduction (DNRA + Dtotal). Unlike denitrification, DNRA showed no consistent response to temperature. These results indicate that DNRA in wetland soils and benthic sediment is not a major nitrogen transformation in oligohaline regions across the MRDP regardless of wide range of OM% content in these eroding and prograding delta lobes.

1. Introduction

Assessing nitrogen (N) cycling in the coastal zone during the last four decades has shifted —from determining the pace and magnitude of eutrophication—to quantifying the fate and residence time of reactive nitrogen (N_r) and its impact on the interaction between ecosystem productivity and carbon cycling (Martínez-Espinosa et al., 2021; Smith, 2003). This shift is because coastal eutrophication is now recognized as a pervasive and chronic condition at all latitudes due to the intensity and variety of human impacts, especially agriculture, aquaculture, and urban development along watersheds. One of these impacts is reflected in the increasing number of anoxic/hypoxic coastal regions (Gooday et al., 2009; Rabalais, 2011) associated to toxic algae blooms (Bargu et al., 2011; Rabalais et al., 2009) and their threats to human health (Backer et al., 2015; Schmale et al., 2019). Indeed, when considering the degree of human interference with the N cycle, it is acknowledged that at the global scale we have already passed a safe operating boundary (Rockstrom et al., 2009; Steffen et al., 2018).

N_r enters estuarine regions and coastal oceans as nitrate (NO_3^-) and ammonium (NH_4^+) with NO_3^- generally making up >90% of the N_r (Galloway et al., 2003; Galloway and Cowling, 2002; Galloway et al., 2004; Mulholland, 2008; Weller and Jordan, 2020). Both N_r forms are transient in the N cycle and can be lost or retained within the coastal/estuarine water column or wetland soils depending on their source and local environmental conditions (e.g., O_2 availability, temperature, redox gradient, organic carbon concentrations) (Bowen et al., 2020) (**Figure 1**). NO_3^- excess fueling eutrophication, for example, is naturally alleviated by direct denitrification (Burgin and Hamilton, 2007; Mulholland, 2008) which is a dissimilatory N transformation mediated by the microbial community in wetlands soils and benthic sediments; in this path NO_3^- can be quickly transformed to N_2 hence representing a N loss or evasion from the ecosystem (**Figure 1**). In contrast, N_r can be retained by direct plant or microbial assimilation or by the conversion of NO_3^- to NH_4^+ through dissimilatory nitrogen reduction to ammonium (DNRA) (Giblin et al., 2013) by prokaryotic and eukaryotic organisms (Kamp et al., 2011; Kamp et al., 2015) (**Figure 1**), particularly in soils/sediments containing high electron donor: electron acceptor ratios under steep redox gradients (DOC:NO_3; Nikolenko et al., 2018; Tiedje, 1988; Tobias et al., 2001). NH_4^+ can also be lost through denitrification but this requires the conversion of NH_4^+ to NO_3^- via nitrification (coupled nitrification-denitrification), which is regulated by O_2 availability, before denitrification can occur (**Figure 1**). Similar to denitrification, the anaerobic oxidation to NH_4^+ (anammox) also promotes the loss of reactive N via N_2 production and is controlled by the availability of both NH_4^+ and NO_2, however, annamox is generally absent or low in wetlands (Giblin et al., 2013; Li and Tao, 2017; Upreti et al., 2021).

Hence, understanding the relative role and spatiotemporal patterns of these N_r transformations in the context of increasing eutrophication is a coastal management priority, particularly in areas where rivers carrying high N_r concentrations directly discharge into coastal areas (Rosenzweig et al., 2018). Because in organic rich wetland soils, DNRA could potentially become the dominant NO_3^- reduction transformation resulting in the conservation of N within coastal ecosystems, a major priority is to evaluate the local and regional environmental conditions controlling the magnitude and dichotomy between DNRA and denitrification in wetlands (Giblin et al., 2013; Martínez-Espinosa et al., 2021; Palacin-Lizarbe et al., 2019; Rubol et al., 2013).

The Mississippi River delta plain (MRDP) is a subtropical coastal region where human impacts have significantly altered N cycling in the last five decades (Goolsby et al., 2001; McIsaac et al., 2002). This impact is seasonally gauged by the extension and frequency of an increasingly large hypoxic zone in coastal waters that is correlated to the MR annual discharge (7,000–20,000 $m^3\ s^{-1}$) bringing high N_r inputs (1.56×10^6 Mg yr^{-1}) dominated by NO_3^- (Donner et al., 2004; Donner and Scavia, 2007; Goolsby et al., 2001). To ameliorate the impact of this excess N_r, there have been attempts to reduce the use of fertilizer in agriculture throughout the MR watershed by promoting the use of wetlands as N_r sinks (Boesch, 2002; Day et al., 2019; Mitsch et al., 2001) where N_r in highly enriched river waters can be removed via plant uptake (Graham and Mendelssohn, 2016; Poormahdi et al., 2018) and denitrification (Rivera-Monroy et al., 2013). Although the use of wetlands as tertiary treatment to eliminate N_r has been successfully implemented in some locations upstream (Day et al., 2004; Day et al., 2006; Mitsch and Day, 2006; Odum and Odum, 2003)—and across the MR delta plain at smaller scales (e.g., Breaux et al., 1995)— it is unknown how much of the N_r in effluents treated by this type of wetlands is denitrified or maintained within the system via DNRA.

Elucidating the fate of N_r via DNRA in coastal wetlands across the MR wetlands is becoming a pressing management issue due to the apparent conflict between conserving wetlands and managing excess N_r. Because wetland net loss is currently an urgent problem throughout the MR delta plain (Couvillion et al., 2016; Jankowski et al., 2017; Törnqvist et al., 2020), one strategy to restore wetlands at large spatial scales is diverting freshwater from the MR to bring new sediments to promote the establishment and natural succession of wetlands that were previously lost due to erosion (Elsey-Quirk et al., 2019; Xu et al., 2019). It is estimated that ~ 4900 km^2 of wetland area has been lost in coastal Louisiana in the period from 1932-2010, including not only the MRDP but also the Chenier plain (Couvillion et al., 2016; Meckel et al., 2006). Wetland loss has been caused by major changes in hydrology as levees were constructed along the MR and other waterways to protect urban and agriculture areas against flooding. This flooding mitigation strategy initiated in the 1940's (Boesch et al., 1994b), however, has impeded the natural input and redistribution of sediments thus dramatically altering the coastal geomorphology by blocking critical stages in the delta cycle (Bentley et al., 2016; Blum and Roberts, 2009). This unintended negative impact is now compounded by increasing sea level in old interdistributary basins where subsidence rates are also accelerating with further wetland erosion, fragmentation, and vegetation loss (Törnqvist et al., 2021).

Overall, there is a consensus about the benefits of sediment diversions as a management strategy to increase sediment inputs into areas where wetlands are undergoing fragmentation (Allison and Meselhe, 2010; Dean et al., 2014; Kemp et al., 2014; Wang et al., 2018). Yet, there is no agreement about the potential negative consequences of increasing N_r loading into estuarine areas (Day et al., 2019; Kearney et al., 2011; Poormahdi et al., 2018; Turner et al., 2009). One potential negative impact on wetland habitats is that by promoting high NO_3^- availability (as electron acceptor) fueling high heterotrophic denitrification, then organic carbon (an electron donor) demand by microbial activity can also increase leading to higher organic matter (OM) decomposition rates and therefore promoting the consumption of soil organic carbon previously stored in soils and sediments (Bowen et al., 2020; Bulseco et al., 2019; Deegan et al., 2012). If this scenario is plausible, then increasing NO_3^- availability can offset the benefits of river sediment diversions by also promoting the consumption of OM in wetland soils thus causing "peat collapse" (Chambers et al., 2019) and accelerating wetland loss. This pattern, for instance, has been observed in temperate saltmarshes under high N fertilization treatments and in laboratory reactors (e.g., Bowen et al., 2020). Further, excess NO_3^- could also be converted to NH_4^+ via DNRA (**Figure 1**), further enhancing the conservation of N_r (e.g., plan uptake and NH_4^+ adsorption to soil particles) and thus maintaining high eutrophic conditions that could trigger algae blooms in the estuarine/tidal channel water column as NH_4^+ is favored over NO_3^- during plant and phytoplankton uptake (e.g., Ren et al., 2020; Vargas-Lopez et al., 2021).

Therefore, the goal of this study was to experimentally evaluate the relative differences in DNRA magnitude among sites characterized by both different soil OM content and C:N ratios soil content in the MR delta plain impacted by high NO_3^- concentrations (~50 μM). To our knowledge this is the first comparative study assessing differences in the relative role of DNRA vs total denitrification in delta lobes undergoing different stages in the delta cycle (erosional vs progradational) which are dominated by oligohaline conditions. Previously, we showed—using different ^{15}N techniques (i.e., IPT, MIMS/N_2:Ar) —that total denitrification (i.e., Dtotal= direct + coupled; **Figure 1**) and net total denitrification (i.e., total denitrification– N fixation) rates were similar between the Wax Lake Delta (WLD) and upper Barataria Bay (Lake Cataouatche) located in opposite boundaries of the MR delta plain (Upreti et al., 2021). Those study sites are oligohaline (surface and soil pore water salinity <1) and are directly influenced by MR sediment diversions (Elliton et al., 2020; Upreti et al., 2021). We discovered that Dtotal rates varied across different type of wetlands soils (marsh, forested) and benthic sediments where rates were highly correlated with seasonal changes in temperature (spring, summer, winter). The oldest site located in the upper Barataria Bay (>100 years) represent an area where wetlands are eroding (Couvillion et al., 2016; Day et al., 2021) while the WLD is a young (~45 years) prograding delta region where a net wetlands area gain began when it became subaerial in 1973; the delta is gaining land at a rate of ~1-3 km year during the last 30 years (Allen et al., 2012; Meselhe et al., 2021; Shaw et al., 2018).

Because previous field surveys detected high NH_4^+ concentrations (10-80 μM) in intertidal wetland soil pore waters (5-20 cm depth) in the WLD (Rivera-Monroy et al., unpublished data; Elliton et al., 2020) after the peak river discharge (spring), we aimed to evaluate if these concentrations were the result of DNRA given the high NO_3^- availability under different soil/sediment C:N ratios represented by emerging (~9) and deteriorating (~15) delta lobes where peak summer wetland biomass and productivity is high (Carle and Sasser, 2016; Rivera-Monroy et al., 2019). Thus, we hypothesize that DNRA was a significant N_r transformation and probably more prevalent than D_{total}. The specific objectives of this study were to: 1) evaluate differences in DNRA rates among benthic and wetland habitats in emerging and eroding delta lobes in coastal Louisiana, 2) determine how temperature regulates DNRA rates in these habitats, and 3) analyze the ecological role and management impact of differences between D_{total} and DNRA as two processes representing N removal (Dtotal) and retention (DNRA) in this coastal region with extensive wetland loss.

2. Materials and Methods

2.1 Study area description

This study was performed in soils and sediments obtained in two sites: the WLD and the upper Barataria Bay region (**Figure 2**). These sites have contrasting hydrology and geomorphology and are dominated by oligohaline conditions (annual salinity range: 0.1-0.4 ppt) (Elliton et al., 2020; Upreti et al., 2021). The WLD is located in coastal Louisiana ~20 miles southwest of Morgan City. This delta was recently formed as a result of sediment input through a man-made outlet (Wax Lake Outlet, WLO), which was dredged to divert water from the Atchafalaya River to the Gulf of Mexico thus protecting Morgan city during pulsing high river stages (**Figure 2A, B**) (Hiatt and Passalacqua, 2015; Roberts and Sneider, 2003; Rosen and Xu, 2013) Approximately 30% of the annual average water flow of the Atchafalaya River is diverted through the WLO outlet, which is equivalent to ~10% of the annual average discharge of the Mississippi River (7,000–20,000 m^3 s^{-1}). New land emerged in the WLD above the water line after the extreme flood of 1973 by forming a subaerial delta (Hiatt et al., 2018; Hiatt and Passalacqua, 2015).

The WLD is characterized by a diurnal micro tidal regime (<30 cm), which can be altered by wind-driven effects (Allen et al., 2012; Li et al., 2018). The prograding WLD has a current extension of 65 km^2 and has increased at a rate of 1 km^2 yr^{-1} (1983-2010) (Meselhe et al., 2021; Shaw et al., 2018). This land gain is controlled by a complex network of channels that facilitate sediment and nutrient transport into adjacent coastal waters thus promoting the establishment of distinct marsh and forested wetland vegetation across well defined elevation gradients (Allen et al., 2012; Holm and Sasser, 2001). Our marsh and tidal creek study sites are located in Mike Island, one of the oldest delta lobes (**Figure 2B**) within WLD where herbaceous (e.g., *Sagitaria lancifolia, S. platyphylla,, Colocasia esculenta, Typha dominguensis,*) and forested wetlands (*Salix nigra*) are the dominat vegetation (Paola et al., 2011).

Barataria Bay is an estuarine wetland system located between the Mississippi River and Bayou Lafourche and separated from the Gulf of Mexico by a chain of barrier islands (Day et al., 2021; FitzGerald et al., 2004). The basin is in a degrading delta stage with significant wetland loss at a rate of about 23 km^2 yr^{-1} between 1974 and 1990 (Barras et al., 2003; Coleman et al., 1998; Habib et al., 2008; Stone et al., 1997) (**Figure 2C)**. The basin encompasses a total of approximately 6,000 km^2 of water bodies and wetlands (Das et al., 2012). Wetland loss in this coastal region is attributed to large-scale flood control levees along the MR and continuous deepening and maintenance of navigation channels, which are starving wetlands from seasonal sediment inputs from the river (Boesch, 2006; Boesch et al., 1994a; Wang et al., 2017). Our study sites in Barataria Bay were established in the northern section of Lake Cataouatche proper (henceforth refered as BLC) (i.e., open water-benthic sediment) (**Figure 2C**), a channel influenced by the Davis Pond freshwater diversion during high peak river discharge (Lanaux canal-dreged, **Figure 2C**) and an adjacent wetland dominated by herbaceous marsh vegetation dominated by herbaceous species (e.g, *Sagittaria spp, Typha sp*, *Bidens spp*; **Figure 2C**).

2.2 Field experimental set up and core sampling

Sediment and soil cores were collected from three distinct habitats for both the WLD and northern BLC regions (**Figure 2B-C**). These habitats were selected based on the presence of wetland vegetation (marsh and forested wetland), flooding duration and water depth (channels and open water). Because one of the objectives was to evaluate differences in soil DNRA rates in wetlands, regardless of species composition within each site, we selected marsh sites with herbaceous vegetation in both the WLD and BLC (**Figure 2B, C**). We also selected a forested wetland in the WLD site to assess differences between wetlands at different elevation and succesional stage. In addition to evaluating differences in DNRA and denitrification rates between wetlands soils, sediments were also sampled in adjacent channels (northern BLC and WLD) and open water (BLC) (**Table S1**).

Cores were sampled in triplicate as described in Upreti et al. (2021). Briefly, sediment cores in wetland habitats were collected by placing an acrylic tube (length: 36 cm; internal diameter: 10.1 cm) on the sediment surface and carefully pushing 16 cm into the sediment while avoiding any compaction. Benthic cores in open water and tidal creeks were collected using a suction core sampling device (Hartzell et al., 2010). Sediment cores with overlying water were transported in a cooler to the laboratory within 6 hours of collection. Once in the laboratory, cores were placed at average field temperatures and allowed to equilibrate (see below). Water and soil pore water samples were also collected for nutrient analysis. Salinity, pH, redox, and O_2 concentrations were measured at the time of collection while inorganic N (NH_4^+, NO_2^-, NO_3^-) concentrations were determined after filtration (0.45 µm pore size) in the laboratory (Upreti et al., 2021). DNRA experiments were performed in the laboratory (see below). All cores were collected in the study sites during the summer (2015), winter (2015), and spring (2016) seasons.

2.3 Laboratory Incubation Experiments

2.3.1 Intact Core Incubations

DNRA was measured using intact core incubations enriched with ^{15}N using the isotope pairing technique (Christensen et al., 2000; Marchant et al., 2016a; Steingruber et al., 2001b) application to measure direct and coupled nitrification-denitrification as described in Upreti et al., (2021). This method has been widely used in number of studies to assess DNRA rates in coastal and estuarine environments (Christensen et al., 2000; Koop-Jakobsen and Giblin, 2010; Yin et al., 2015).

Once in the laboratory, the cores were placed in dark conditions and under water bath 2-3 hours prior to the start of the experiment. Temperature was controlled by recirculating water at the temperature corresponding to the average seasonal condition when the cores were sampled i.e., summer, winter, spring (**Table S1**). The overlying water column in each core was replaced with deionized water (DI) to which $^{15}NO_3$ (99.9 atom% KNO_3) and NaCl were added to match both *in situ* surface water nitrate concentrations (~50 µM) and salinity values (0.1-0.3 ppt) (Upreti et al., 2021). Because it is difficult to discern a $^{14}N\text{-}NO_3^-$ signature to detect coupled nitrification/ denitrification at high dissolved NO_3^- concentration (~50 µM), we used DI water amended with 50 µM $^{15}NO_3$ (99.9 atom% KNO_3) (Christensen et al., 2000; Koop-Jakobsen and Giblin, 2010; Yin et al., 2015). The $^{15}NO_3^-$ enriched water was bubbled to oxygen-saturation. Hence, this solution with high $^{15}NO_3^-$ concentration represented the average high $^{14}NO_3$ concentration and salinity values measured *in situ* across all seasons and habitats and fueling comparable ambient total denitrification (see Upreti et al., 2021) and DNRA rates.

To fully capture the seasonal cycle and to facilitate comparisons between sites, cores from both sites were incubated at the same temperature (i.e., summer, 30 °C; winter, 10 °C; spring, 20 °C) (**Table S1**). The overlying water column in each core was replaced with site-specific filtered water that has been bubbled to oxygen saturation. Each core was then capped tightly without any headspace using custom-made PVC caps. The caps were equipped with electronically controlled stirrers to maintain homogeneous water column inside each core. Two independent ports located on the top of each lid allowed simultaneous water sampling and water replacement in the core by a reservoir filled with site specific filtered water.

Dissolved O_2 (DO) concentrations inside the cores were monitored throughout the duration of the experiment using a microelectrode oxygen sensor (Unisense, Inc.) (Upreti et al., 2021). The incubations were terminated when oxygen concentration dropped to ~50% of the initial DO concentrations to avoid artifacts/analytical error associated with O_2 non-linearity (Lunstrum and Aoki, 2016). Samples were collected every 1.5-3 hours depending on DO consumption via the sampling port on the core lid. The total incubation period lasted from 6-18 hours .

Water samples were collected in at each sampling time after discarding the first ~10ml of tube dead volume using 12 mL Labco exetainers vials, allowing water to overflow to minimize air contamination (Burgin et al., 2013b; Kana et al., 1998). Water samples were immediately placed in a container, submerged in water to avoid contamination and stored at 4 ^oC until analysis using MIMS (Hamilton and Ostrom, 2007).

Water samples collected for the determination of direct and coupled denitrification were measured in a mass spectrometer (Pfeiffer Vacuum) using the ^{15}N isotope paring technique (IPT) (Marchant et al., 2016a; Nielsen, 1992). The IPT (Marchant et al., 2016a; Nielsen, 1992) was used to measure direct denitrification fueled by NO_3^- in the water column (Dw, sensu Steingruber et al., 2001a) and coupled nitrification-dentrification maintained by NO_3^- produced within the soil/sediment via nitrification (Dn) (Christensen et al., 2000; Koop-Jakobsen and Giblin, 2010; Yin et al., 2015). Because the $^{15}NO_3^-$ was added to the water column at the same concentration as present in ambient water, Dtot was interpreted as being an actual, rather than a potential rate as explained above.

At the end of the experiment, the intact cores were sliced at 4 cm interval for the analysis of bulk density (BD), total carbon (TC), total nitrogen (TN), and organic matter content (OM%). Although these data are already published (see Upreti et al., 2021 for analytical details), we only include here the first segment 0-4 cm to evaluate the relationship between DNRA and soil physicochemical properties at the interface between the water column and sediment/soil surface. Briefly, BD was determined by dividing the total dried weight of the sediment by the wet soil volume (g cm^{-3}). Before the analysis of OM content, each sample was ground to fine powder using a Straub grinding mill and analyzed using the Loss of Ignition (LOI) method at 550 °C (Hoogsteen et al., 2015). TC and TN were analyzed using an elemental ECS 4010 CHN analyzer (Costech Analytical Technologies, Inc., Valencia, CA). Approximately one-third of the soil/ sediment subsample (length 4 cm, diameter 2.1 cm) was preserved in a freezer for further analysis of ^{15}N-NH$_4^+$ content by mass spectrometry (diffusion/KCl extraction; see below) and determination of DNRA rates (Domangue and Mortazavi, 2018; Koop-Jakobsen and Giblin, 2010).

2.3.2 KCL extraction

KCl extraction was performed using ~ 50 g of wet homogenized soil/sediment subsamples from the core top 4 cm. The sample was then placed inside an Erlenmeyer flask and 250 ml of 2M KCl was added. The flask was then placed on an orbital shaker (VWR Standard Orbital Shaker, Model 5000) and shaken for about 15 minutes at 200 rpm for 1 hour. The suspension was then filtered through 185 mm Whatman filter paper and collected in a glass flask. The filtered solution was transferred into two 50 mL centrifuge tubes and one 20 mL plastic scintillation vials. The scintillation vials were analyzed in the autoanalyzer to determine the initial NO$_3^-$ and NH$_4^+$ concentrations. The filtered solution was used to determine DNRA rates using the diffusion technique (see below). Centrifuge tubes and vials were stored in a freezer until further analysis.

2.3.3. ^{15}N-NH$_4^+$ Diffusion

The ^{15}N-NH$_4^+$ abundance to determine DNRA rates were obtained using the diffusion technique (Brooks et al., 1989; Herman et al., 1995) followed by isotope ratio mass spectrometer (IRMS) analysis (Koop-Jakobsen and Giblin, 2010) This technique collects nitrogen by the diffusion of NH$_4^+$ dissolved in soil KCl extracts into an acidified glass microfiber filter (Whatman GF/C) disk, which was enclosed in a Teflon Millipore membrane envelope (Brooks et al., 1989; Herman et al., 1995; Holmes et al., 1998).

Filter packs were prepared with ~7 mm GF/C filter disks acidified with 10 µL 2.5 M KHSO$_4$, sandwiched between two 2.5 cm diameter 10 µm pore-size Teflon membranes (Millipore LCWP 02500) after combusting them at 400°C for 4 hrs. To test the diffusion efficiency, fresh ^{15}N standards (20, 40, 60, 80, 100, and 120 µM) were prepared on the day of incubation in 100 mL solutions using 10 mM ^{15}N-NO_3+^{15}N-NH_4 stock solution and 2 M KCl. After diffusion, filter packs were dried for 1-2 days in a vacuum desiccator containing silica gel and 30-50 mL concentrated sulfuric acid. After drying, the filters were packed in a tin capsule and stored in a microtiter plate and placed in a desiccator (Koop-Jakobsen and Giblin, 2010). The ^{15}N-NH_4^+ content on the filters was measured using a Europa ANCA-SL elemental analyzer–gas chromatograph preparation system attached to a continuous flow Europa 20-20 gas source IRMS (Stable Isotope Laboratory, the Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts).

2.4. Statistical Analysis

The relationship betweeen temperature and DNRA rates was first assessed per core/ treatment using linear regressions. The slope of each linear model (N=2-3 cores per site and temperature treatment, **Table S1**) defines how DNRA rates varied over the three temperature treatments (10, 20, 30 °C). Depending on the linear regressions significance, either the slope or the DNRA rates per site/temperature combination were used to evalute differences among factors using a three way ANOVA: substrate (benthic, wetland), habitat (marsh, forested wetland) and region (WLD, BLC). The dataset for BD, OM%, TC, and TN collected for each core incubation was used to evaluate if the DNRA treatment had any effect on soil properties within each habitat (Upreti et al., 2021). All ANOVAs and regression analysis was perfomed using SAS and JMP-Pro (SAS institute 2012). Pairwise comparisons among treatments were assessed with both Tukey's HSD (honest significant difference) test and Least Square Means (LSM) for *post hoc* pairwise comparisons for significant interactions and main effects. To estimate the relative contribution of DNRA to the total NO_3^- reduction in this study, DNRA values were divided by the sum of DNRA and total denitrification (D_{Total}) and expressed as percentage (%DNRA = DNRA/ [DNRA + D_{Total}]) (Nikolenko et al., 2018).

3. Results

3.1 Field Nutrient concentrations in surface and pore water

Inorganic nutrient concentration in WLD and BLC reflect seasonal and hydrological differences among sites. NO_3^- concentrations in open water (channel) in the WLD did not vary seasonally (range: 50.4-65.7 µmol L^{-1}) in contrast to BLC where higher concentrations (channel: 82.4 µmol L^{-1}; lake: 73.9 µmol L^{-1}) were observed only in the winter season (see **Table S1** in Upreti et al. 2021) while lower concentrations were measured in both spring (channel: 7.1 µmol L^{-1}; lake 10.1 µmol L^{-1}) and summer (channel: 44.8 µmol L^{-1}; lake 11.8 µmol L^{-1}) (see Table S1 in Upreti et al. 2021). In contrast, NO_2^- concentrations were very low at both sites (< 1 µmol L^{-1}) with values ranging from 0.61-0.80 µmol L^{-1} and from 0.47-0.88 µmol L^{-1} in the WLD and BLC, respectively. NH_4^+ concentrations in the water column were lower than NO_3^- concentrations and ranged from 1.2-3.1 µmol L^{-1} in WLD, except during the spring, when the highest NH_4^+ concentration reached 11 µmol L^{-1}. NH_4^+ water surface concentrations in BLC were low in all seasons ranging from 0.5-2.7 µmol L^{-1}.

High surface NO_3^- concentrations were regularly observed in open water in contrast with low values measured in pore water (<5 µmol L^{-1}; 20 cm soil depth) across all wetland types and sites during the study; this indicates a rapid uptake from the water column. Porewater NO_3^- concentration were consistenly <1 µmol L^{-1} in WLD whereas in BLC values were <1 µmol L^{-1} during spring and summer and 1.58 µmol L^{-1} during winter (see **Table S1** in Upreti et al. 2021). Accordingly, NO_2^- concentration were even lower (<0.5 µmol L^{-1}) in both WLD and BLC habitats. Porewater NH_4^+ concentrations were high in WLD marshes where values decreased in summer (9.8 µmol L^{-1}) compared to concentrations observed in winter (27.1 µmol L^{-1}). Overall NH_4^+ concentrations were lower across all seasons in BLC (range: 1.6-2.9 µmol L^{-1}) (see **Table S1** in Upreti et al. 2021)**.**

3.2. Controls on Dissimilatory Nitrate Reduction to Ammonium (DNRA)

There was not a significant linear relationship between temperature and DNRA rates across regions, habitats, and type of substrate (**Table S2**); the only exception was observed in the WLD benthic channel where this relationship was negative, yet the rates were very low, <3 µmol m^{-2} h^{-1} (**Figure 3**). Therefore, the ANOVAs were performed using the DNRA rates proper to assess differences among regions, habitats, and type of substrate. Despite the low DNRA values, there was a significant interaction between regions and type of substrate (**Table 1**); the highest mean rate was measured in the BLC wetland habitat (marsh; 7.7 ± 0.91 µmol m^{-2} h^{-1}). This rate was significantly different when compared with the benthic substrates in the same region (i.e., Lake and Channel; mean 3.01 ±0.51) and the other habitats in the WLD (mean range: 1.76 – 1.94

μmol m^{-2} h^{-1}; **Table 1**; **Figure 3)**. Overall DNRA rates were much lower than for denitrification (Dtotal) rates for all habitat and temperature treatments (**Figure 4**). While the percentage of the total nitrate reduction (Dtot+DNRA) that is made up as DNRA decreased with temperature, this is solely due to the increase in denitrification with temperature. As reported in Upreti et al. (2021), on average, Dtotal (direct + coupled) rates were highest in WLD marshes (113 ± 10 μmol m^{-2} h^{-1}); this site had the lowest percentage of nitrate reduction being due to DNRA (**Figure 4**) compared to other habitats although overall we did not see a correlation between denitrification and DNRA.

3.3 Substrate physicochemical properties

There was a significant positive linear relationship between soil/sediment BD and TN in the BLC (R^2= 0.84; F(1,52); RMSE: 0.73; p<0.0001) but not in the WLD (R^2= 0.02; F(1,52); RMSE: 0.92; p=0.34) (**Figure 5**). The BLC site has a wider TN range (0.2-6.1 mg cm^{-3}) in contrast to BD (0.1-0.5 g cm^{-3}); this pattern was opposite in the case of the WLD (BD: 0.1-1.2 g cm^{-3}; TN: 0-2.5 mg cm^{-3}) due to differences in mineral sediment input via direct river discharge and therefore younger delta lobe formation. Thus, the higherst TN values were registered in the BLC marsh (**Figure 5**).

Although there was a significant inverse linear relationship bewteen BD and OM% in both benthic and wetland soil substrates, the R^2 was only 0.12 (RMSE: 16.6; $F_{1,16}$: 47.9, Pvalue =<0.0001) due to major the differences in OM% and BLD across the different type of wetlands (**Figure 6**). The BLC marsh had the highest values and wider OM% range (26.5-60) when compared to the WLD forested wetland (6.7-12.3) (**Figure 6**). The higher C:N value was registered in the BLC marsh (13.7± 0.4). There were not significant differences in C:N ratio among benthic and wetland types (range: 12.4-13.7), except in the WLD marsh (11.1) (ANOVA; $F_{(5, 100)}$: 4.7; MSE: 2.9, Pvalue=0.0006).

4. Discussion

4.1. DNRA spatiotemporal patterns associated to temperature and soil/sediment C:N ratios in the Louisiana delta plain

Our study revealed that DNRA rates were significantly lower (range: 0.7 ±0.2 - 9.2 ±0.3 μmol m^{-2} h^{-1}; **Figure 3**) than direct and coupled nitrification-denitrification rates (18.0 ±0.4 -

113.0 ±10.6 µmol m^{-2} h^{-1}; Upreti et al 2021) under oligohaline conditions in both the WLD and the BB throughout the year (**Figure 4**). This pattern was observed despite differences in the type of habitat (benthic vs wetland) and between marsh and forested wetlands.

Although in a previous study we showed that denitrification rates follow a positive linear relationship at different temperatures in the same sites (Upreti et al., 2021), DNRA rates were lower and not related to temperature across all wetland types, particularly in the WLD (**Figure 3; Table 1**). This demonstrates that the low conversion of NO_3^- to NH_4^+ is not widespread and does not reflect differences due to changes in temperature (**Figure 3**); thus, most of the NO_3^- (>95 %) entering both deltaic stages are not retained in the soil and hence lost from the system as N_2 gas (**Figure 1**) This is underscored by the total NO_3^- reduction ratio (i.e., %DNRA= DNRA/ [Dtotal + DNRA]; Nikolenko et al., 2018) ranging from 2-13 in the WLD and from 3-25 % in the BLC (**Table 2**).

Denitrification (i.e., NO_3^- loss) has also been reported to be dominant over DNRA (i.e., NO_3^- retention) in a range of soil OM% representing a delta island age chronosequence (from ~45 years to < 20 years) along the WLD (Li and Twilley, 2021) (**Table 2**). In this experimental study using intact soil cores and a flow-thru system, DNRA values ranged from 0-65 µmol m^{-2} h^{-1} in wetland soils with low OM% values (9-11; **Table 2**); comparatively, that study also reported DNRA rates lower than our maximum value thus representing 0-27% of the total NO_3^- reduction and where denitrification rates ranged from 4-276 µmol m^{-2} h^{-1}. Interestingly, the higher mean DNRA rate (32 ± 6 µmol m^{-2} h^{-1}) in that experiment, which used higher experimental NO_3^- enrichment (100 µM), occurred in cores with soil OM% values ranging from 17-25%. This range is approximately half the highest OM% value measured in our experiment where DNRA rates ranged from 5.1 (±1.5) - 9.2 (±0.3) µmol m^{-2} h^{-1} in the BLC marsh soil (26-59) (**Figure 3**). Despite this difference in soil OM%, the DNRA rate overall still represented comparatively <14% of the denitrification rate (Li and Twilley, 2021), which was also measured using the IPT (Steingruber et al., 2001b). Thus, these DNRA rates—independently obtained across the WLD using intact soil/sediment cores subjected to different experimental enrichment conditions (5, 50, 100 µM), —highlight the low activity of this N transformation pathway in oligohaline areas in a eutrophic coastal delta plain regardless of seasonal temperature and organic matter differences.

4.2. Comparative DNRA activity in oligohaline benthic sediment and wetland soils

The number of DNRA estimates in wetland soils and benthic sediments in delta dominated coastal environments and riparian ecosystems using ^{15}N techniques and intact sediment cores is limited (**Table 2**). The DNRA rates reported in our study are similar to rates reported for freshwater and oligohaline systems where the contribution of DNRA to total NO_3^- reduction was low (%DNRA column **Table 2**). It is proposed that DNRA rates in oligohaline benthic sediments appears to be low relative to denitrification when compared to brackish/saline environments (Scott et al., 2008; Zhang et al., 2019). For example, potential DNRA rates in Lake Waco Texas, ranged from 1.3 - 33 µmol m^{-2} h^{-1} (i.e., %DNRA: 3-11; **Table 2**) and were lower than denitrification rates (50-270 µmol m^{-2} h^{-1}: Scott et al., 2008). Studies in oligohaline constructed wetlands reported denitrification to be dominant removing >70% of the NO_3^- loadings while DNRA was negatively affected by a high NO_3^- concentrations under a range of C/N ratios (0.7-1.7) (Hernández-Del Amo and Bañeras, 2021). Interestingly, in warmer productive freshwater lakes benthic habitats, DNRA is dominant in lower sediment layers while denitrification is more common in the upper layers (Palacin-Lizarbe et al., 2019). This shift in the N_r fate was explained by a corresponding shift in microbial genetic potential from DNRA promoting internal N accumulation to losses via denitrification. DNRA dominance has been attributed, for example, to low oxygen availability and low redox potentials in groundwater under constructed wetlands characterized by high C concentrations and TC:NO_3^- ratios (Algar and Vallino, 2014; Jahangir et al., 2017); those results follow the general observation that DNRA activity in wetlands is enhanced in sites under limited N sources but sufficient carbon sources (Pan et al., 2020). Other oligotrophic environments showing low %DNRA values include Lakes Ca' Stanga (1-5) and Verde (3-7), Italy (Nizzoli et al., 2010) and freshwater treatment wetlands in Melbourne, Australia (2-59; Rahman et al., 2019) (**Table 2**).

In contrast, %DNRA values —the relative contribution of DNRA to total NO_3^- reduction—increase in brackish/saline benthic areas where DNRA can become potentially dominant (**Table 2**) (Santoro, 2010). This general pattern could be attributed to the fact that in saline systems autotrophic DNRA, sulfide oxidation —coupled with nitrate reduction—is more likely (Burgin et al., 2013a; Giblin et al., 2013). This is apparent in coastal Alabama, USA (98; Domangue and Mortazavi, 2018), Gulf of Thailand (74; Dong et al., 2011), Java north coast, Indonesia (75; Dong et al., 2011), Vunidawa-Rewa, Fiji (68; Dong et al., 2011), and Wallis Lake, Australia (99; Erler et al., 2017) and in hypohaline areas as Laguna Madre and Baffin Bay

(82; An and Gardner, 2002) (**Table 2**). In other mid to high salinity coastal areas denitrification and DNRA have relatively similar values as is the case in Little Lagoon, Alabama, USA (30-84; Bernard et al., 2015), Laguna Madre, Texas, USA (45-60; Gardner et al., 2006), Sweeney and West Creeks, Plum Island Sound Estuary, Massachusetts, USA (31-69; Koop-Jakobsen and Giblin, 2010) and estuaries in Southern Australia (7-75; Kessler et al., 2018) where the prevalence of denitrification or DNRA can shift seasonally.

This shift in dominance by DNRA over denitrification between freshwater/riparian and coastal sites has been partially explained by the negative impact of high H_2S concentrations usually found in coastal environments on denitrification where sulfate reduction rates are generally higher than in freshwater systems (Gardner et al., 2006; Rysgaard et al., 1996; Tiedje, 1988). As DNRA is apparently favored in organic rich and sulfidic sediments with high ratios of labile organic carbon to nitrate and/or with low NO_3^- availability (Nizzoli et al., 2010), these conditions partially explain our results in both the WLD and BLC where H_2S concentration is low (Rivera-Monroy, personal observation); these conditions appear to favor bacteria carrying out DNRA (Nizzoli et al., 2010).

Our findings in the WLD where denitrification is high but both OM% and C are low suggests that other electron donors, besides C might be involved (Nogaro and Burgin, 2014) (Kraft et al., 2014; Salk et al., 2017). Fe (III) oxides availability associated to riverine discharge, for example, might be important in the WLD where soils are rich in iron. Under anaerobic conditions iron oxides are reduced thus increasing Fe^{+2} availability as an electron donor for nitrate reduction thus fueling denitrification as suggested by other studies (Bonaglia et al., 2016; Rahman et al., 2019; Roberts et al., 2014). A previous study in the WLD reported a close interaction between PO_4^{-3} availability and iron reduction depending on the OM:Fe ratio, which controls PO_4^{-3} release that is mediated by the Fe reducing bacteria *Shewanella putrefaciens* (Upreti et al., 2019). Hence, this mechanism might play a role in maintaining high denitrification rates in this area throughout the year. However, further studies evaluating the dependence of denitrification (autotrophic and heterotrophic) and DNRA on different electron donors are needed to discern these potential mechanisms controlling both DNRA and denitrification in the absence of higher labile carbon concentrations (e.g., Kraft et al., 2014; Su et al., 2017).

4.3. Methodological considerations when interpreting the interaction between DNRA rates

and N_r availability

Assessing the dichotomy between DNRA and denitrification in coastal sediments and wetlands soils requires considerations about the experimental and methodological approaches (Burgin et al., 2013a; Giblin et al., 2013; Zhang et al., 2019). This is because depending on the type of substrate used in incubations (e.g., packed sieved substrate, slurries, intact sediments cores), technique (e.g., ^{15}N tracer, mass balance, acetylene reduction) and experimental set up, the interpretation of denitrification and DNRA rates might vary when identifying the actual in *situ* environmental factors controlling the prevalence of each N pathways under natural conditions and when attempting to extrapolate those rates at the landscape level (e.g., Rivera-Monroy et al., 2013). This is one of the reasons why we compared our values to other sites that used both intact sediment cores and the IPT.

The use of intact soil cores (e.g., Upreti et al., 2021) vs slurries (e.g., Rahman et al., 2019) can influence the DNRA relative magnitude and functional role (Rivera-Monroy et al., 2010) depending on the spatiotemporal diversity and abundance of archaea/bacteria from the soil surface to deeper layers. A study, for instance, simultaneously comparing DNRA and denitrification rates using both intact cores and slurries from shelf benthic sediments off the MRDP showed how the availability of NO_3^- through advection can overestimate DNRA (Behrendt et al., 2013). When slurries from deeper sediment layers were exposed directly to high NO_3^-, DNRA was higher than denitrification as NO_3^-limitation was released. This was in contrast to the use of intact core sediments where NO_3^- diffuses from the water column into the soil and could be assimilated or dissimilated (**Figure 1**) in the top sediment layers (e.g., 0-5 cm) thus limiting NO_3^-availability in deeper layers where anoxic conditions can potentially enhance DNRA (Behrendt et al., 2013; Kraft et al., 2014).

This vertical zonation is functionally relevant since it is at deeper soil layers where OC accumulates over time; if OC is exposed to high NO_3^-, then it can be used in denitrification respiration (Behrendt et al., 2014). Since temperature, OC availability, and type of N_r available are major drivers of both DNRA and denitrification across soil/sediment horizontal gradients, it is expected that the presence and dominance of either biogeochemical transformation will vary depending on substrate depth. This has been reported in the case of soils along riparian ecosystems and adjacent to groundwater sources where carbon availability and anoxic/hypoxic conditions are dominant and impacted by excess N_r from agriculture (Kelso et al 1997;

McPhillips 2015; Dhondt 2003; McPhillips 2015; Nikolenco 2018; Lutz et al., 2020; Weitzamn et al 2020).

Additionally, these methodological differences can also affect the role of different type of bacteria/archaea performing dual roles regulating DNRA and Dtotal in different type of substrates and soil depths (Kraft et al., 2014; Zhang et al., 2019). Due to advances in genomics (Bu et al., 2017; Bulseco et al., 2020; Yin et al., 2002), in combination with slurry experiments and the use of reactors, studies show how differences in NH_4^+ or NO_3^- availability can trigger DNRA activity when none was initially observed (Behrendt et al., 2013). Thus, given the dynamic change in environmental variables controlling NO_3^- transformation by Dtotal and DNRA across the BLC and WLD, genomic studies are urgently needed in estuarine habitats throughout the Louisiana delta plain (Coles and Hood, 2016; Engel et al., 2017; Jackson and Vallaire, 2009; Lamendella et al., 2014). Genomic, transcriptomic, and proteomic data and information are required to understand how the microbial community taxonomic composition, functional diversity, and regulatory capacity could shift from DNRA to denitrification (e.g., Shu et al., 2015; Yin et al., 2002; Yoon et al., 2015), as OC availability is controlled by seasonal wetland productivity but under a steady supply of NO_3^- (Zhang et al., 2019). It is also necessary to evaluate how a major shift between NO_3^- diffusion and advection in the soil could potentially affect OM decomposition rates by different microbial groups (Bowen et al., 2020; Damashek and Francis, 2018). Of particular interest is to determine at what soil/sediment depth denitrification could potentially become detrimental to carbon storage as different forms of organic matter are used in the long term under different NO_3^- enrichment treatments (Palacin-Lizarbe et al., 2019). Our results show that at least under the current environmental conditions (e.g., soil C:N ratios, OM%) in the WLD and BB regions, Dtotal respiration dominates over DNRA decreasing N retention in the long term.

One of the sources of high soil OC in the WLD is the accumulation of dead aboveground vegetation (e.g., herbaceous) after a high peak production during summer (Carle and Sasser, 2016; Carle et al., 2015 ; Carle et al., 2014; Elliton et al., 2020). It is worth noting that despite persistent high NO_3^- loads over >35 years into these highly productivity wetlands, and high denitrification rates, OC is still stored along hydrological gradients in old and young delta lobes (Hiatt and Passalacqua, 2015; Shields et al., 2017). This may be due in part due to the fact that this material can be rapidly buried by new sediment deposited during high river discharge and frequent storms (i.e., cold fronts and hurricanes; Bevington et al., 2017; Elliton et al., 2020; Hiatt et al., 2019; Li et al., 2011; Xing et al., 2017). It is estimated that storms and pulsing high river discharge can deposit up to 2-5 cm of sediment contributing to high burial rates as reflected by the relatively rapid delta expansion (Bevington et al., 2017; Hiatt and Passalacqua, 2017; Shaw et al., 2018).

Overall, our results show that at least under the current environmental conditions (e.g., C:N ratios, OM%) in the WLD and BB regions, Denitrification dominates over DNRA decreasing N retention in the long term. The balance between NO_3^-, advection and diffusion and the predominance of denitrification over DNRA in these wetland soils and benthic/sediments also applies to O_2 availability controlling horizontal and vertical redox potential gradients. These are widely altered in surficial substrate layers by the presence of vegetation (Vila-Costa et al., 2016; Zhang et al., 2017) and degree of wetland erosion and fragmentation allowing O_2 lateral advection; moreover in wetlands areas undergoing fragmentation across the MRDP (Mariotti, 2020; Turner and Rao, 1990). Because wetland vegetation regulates O_2 diffusion throughout stems/roots depending on its density and spatial distribution, plants can create a soil/sediment oxic/suboxic zones (e.g., minimum oxygen zone; Koop-Jakobsen and Giblin, 2010; Upreti et al., 2021) within the same soil depth. O_2 availability can promote nitrification inducing the dominance of both direct and coupled nitrification-denitrification over DNRA, especially within the soil top 5 cm (Palacin-Lizarbe et al., 2019; Verhoeven et al., 2018; Vila-Costa et al., 2016) as reported in riparian soils and sediments with presence/absence of vascular plants (Matheson et al., 2002; Ruiz-Rueda et al., 2009).

Our experiment did not directly evaluate the role of the rhizosphere in regulating O_2 availability or the role of root exudates potentially favoring DNRA, due to our experimental set up (see methods), thus it is not possible to evaluate the role of vegetation in mediating DNRA and denitrification. We note that at the WLD site during peak vegetation productivity in the summer both water river discharge and flooding duration are at minimum (Carle and Sasser, 2016; Elliton et al., 2020) extensive high-intertidal and supratidal zones are exposed and O_2 can diffuse into the first 2-5 cm soil layer (**Figure 6**). This aeration in turn can enhance coupled nitrification-denitrification (Davidsson et al., 1997; Marchant et al., 2016b; Patrick and Reddy, 1976; Verhoeven et al., 2018) and the loss of any residual NO_3^- trapped in soil pore water as indicated by the generally low NO_3^- concentrations in the soil pore waters at soil depths >5 cm

(Elliton et al., 2020; Knights et al., 2020; Upreti et al., 2021). Thus, denitrification may prevail over DNRA under conditions of high O_2 diffusion conditions into the soils and sediments. This may become more significant as NO_3^- concentrations are maintained over the year, or even increased in oligohaline environments undergoing eutrophication (e.g., Nogaro and Burgin, 2014).

5. Summary and Conclusions

This is the first study evaluating the magnitude of dissimilatory NO_3^- reduction to NH_4^+ (DNRA) rates in both oligohaline marsh/forested wetlands soils and benthic sediment habitats under different temperature regimes (10, 20, 30 ºC) in two regions representing progradational (Wax Lake Delta, WLD) and erosional (Barataria- Lake Cataouatche, BLC) deltaic stages in the Mississippi River Delta plain (MRDP). Both sites receive MR water with high NO_3^- concentrations throughout the year (>40 µM) via river diversions to mitigate flooding and directly/indirectly induce sediment inputs to promote accretion and wetland succession in wetland restoration programs. Using the isotope pairing technique we found that in contrast to total denitrification (direct + coupled nitrification-denitrification; range: 18.0 ±0.4 - 113.0 ±10.6), DNRA rates were low (range: 0.7 ±0.2 - 9.2 ±0.3) and represented on average <10 % of the total NO_3^- consumption (DNRA + Dtotal) indicating that DNRA in wetland soils and benthic sediment is not a major nitrogen transformation in oligohaline regions across the MRDP; this is regardless of low (2-20) and high (26-61) OM% values in soil/sediments in progradational and erosional delta lobes, respectively.

Because high NO_3^-availability (as electron acceptor) fuels high heterotrophic denitrification rates, there is a potential risk as carbon (an electron donor) demand by microbial activity can also increase organic matter decomposition rates and cause the consumption of soil organic carbon previously stored in soils and sediments. Our study shows that in oligohaline wetlands and benthic sediments across the MRDP, there is a net C storage despite high NO_3^- concentrations. However, more comparative large-scale studies among different type of wetlands and latitudes are necessary—particularly in deltaic systems— to further advance our understanding of the role of DNRA in N retention and organic matter decomposition in coastal ecosystems; moreover, in areas undergoing large-scale wetland restoration and rehabilitation under increasing eutrophic conditions.

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LIST OF FIGURES

Figure 1. Conceptual model showing the fate of Dissolved Inorganic Nitrogen (DIN; NO_3^- and NH_4+) from river discharge and/or river diversions into wetlands and estuarine/coastal areas. This model emphasizes the potential dominance of either DNRA (assimilation) or denitrification (dissimilation) representing DIN permanent loss or retention within the system (*Modified from Bowen et al., 2020*). DNRA = Dissimilatory Nitrogen Reduction to Ammonium.

Figure 2. A) Louisiana Delta plain (inset) indicating location of the Atchafalaya and Mississippi river deltas; B) Wax Lake Delta (WLD); C) upper Barataria-Lake Cataouatche (BLC) regions; sampling sites are located in benthic (Channel, Lake) and wetland (marsh, forested) habitats.

Figure 3. Dissimilatory nitrate reduction to ammonium (DNRA) rates in the Wax Lake Delta (WLD) and Barataria-Lake Cataouatche (BLC). *** = significantly different $p<0.001$; see **Table 2** for interaction statistics. Figure 2 shows study site locations, regions and habitats.

Figure 4. Total denitrification (Dtotal; µmol m^{-2} h^{-1}) and dissimilatory nitrate reduction to ammonium (DNRA; µmol m^{-2} h^{-1}) in the Wax Lake Delta (WLD) and Barataria-Lake Cataouatche (BLC). The percentage value within each bar is the total NO3 reduction ratio (%) (i.e. [%DNRA] / [DNRA + Dotal]; Nikolenko et al., 2018) attributed to DNRA; see Table 2 for corresponding %Dtotal values. Dtotal = direct denitrification + couple nitrification; see methods section for definitions. Site locations is in Figure 2. Denitrification rates are from Upreti et al., (2021).

Figure 5 Linear regressions between bulk density (g cm^{-3}) and total nitrogen (mg cm^{-3}) in substrates (wetland soil and benthic sediments) in Barataria-Lake Cataouatche (BLC) and Wax Lake Delta (WLD) areas; sampling sites are located in benthic (Channel, Lake) and wetland (marsh, forested) habitats. See Figure 2 for habitat location.

Figure 6. Linear regressions between bulk density (g cm^{-3}) and organic matter (%) in substrates (wetland soil and benthic sediments) from the upper Barataria-Lake Cataouatche (BLC) and Wax Lake Delta (WLD) areas; sampling sites are located in benthic (Channel, Lake) and wetland (marsh, forested) habitats. See Figure 2 for habitat location.

FIGURE 1

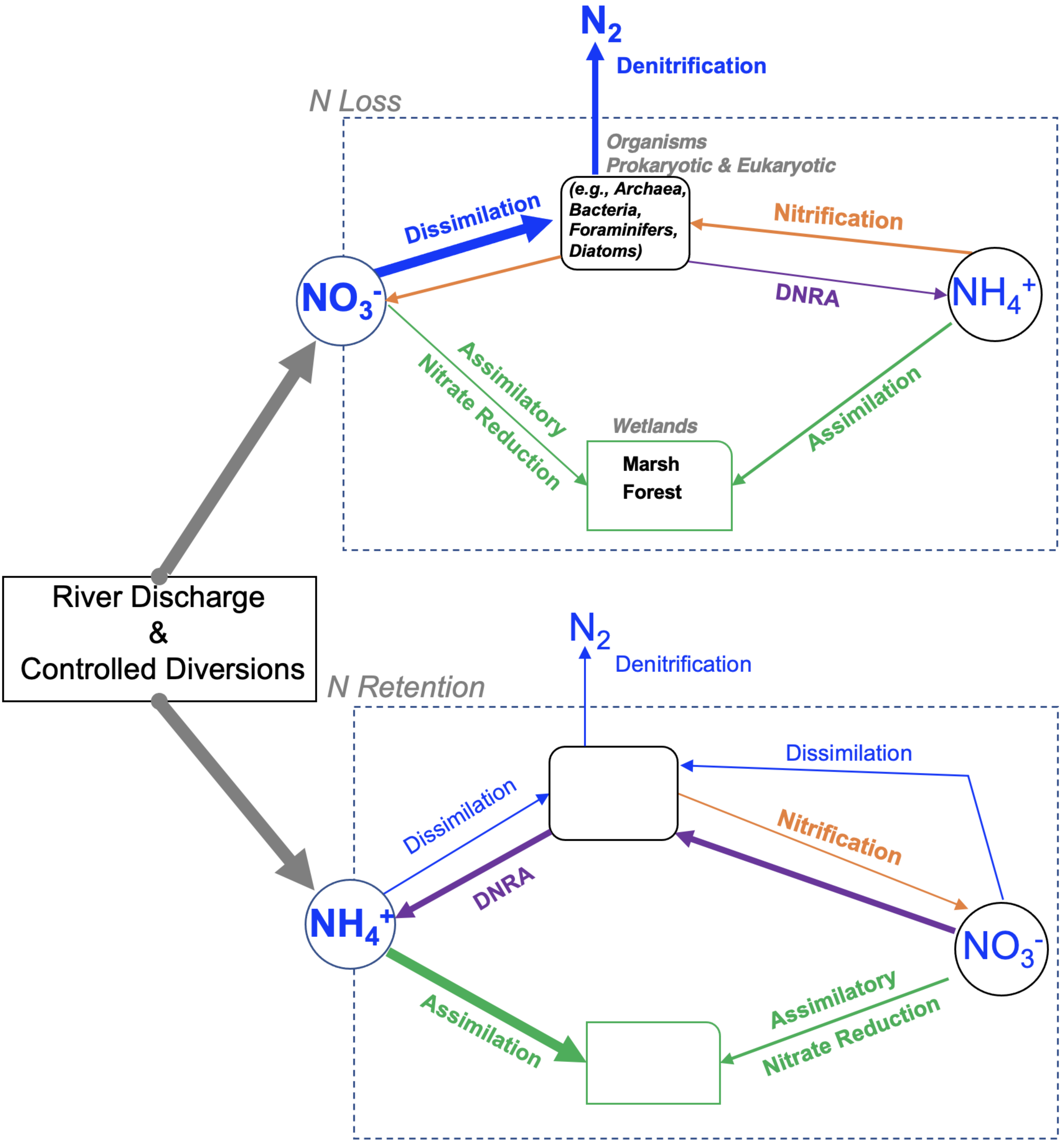

N_2
Denitrification
N Loss
Organisms
Prokaryotic & Eukaryotic
(e.g., Archaea, Bacteria, Foraminifers, Diatoms)
Dissimilation
Nitrification
DNRA
NO_3^-
NH_4^+
Assimilatory Nitrate Reduction
Assimilation
Wetlands
Marsh
Forest
River Discharge & Controlled Diversions
N_2
Denitrification
N Retention
Dissimilation
Dissimilation
Nitrification
DNRA
NH_4^+
NO_3^-
Assimilation
Assimilatory Nitrate Reduction

FIGURE 1

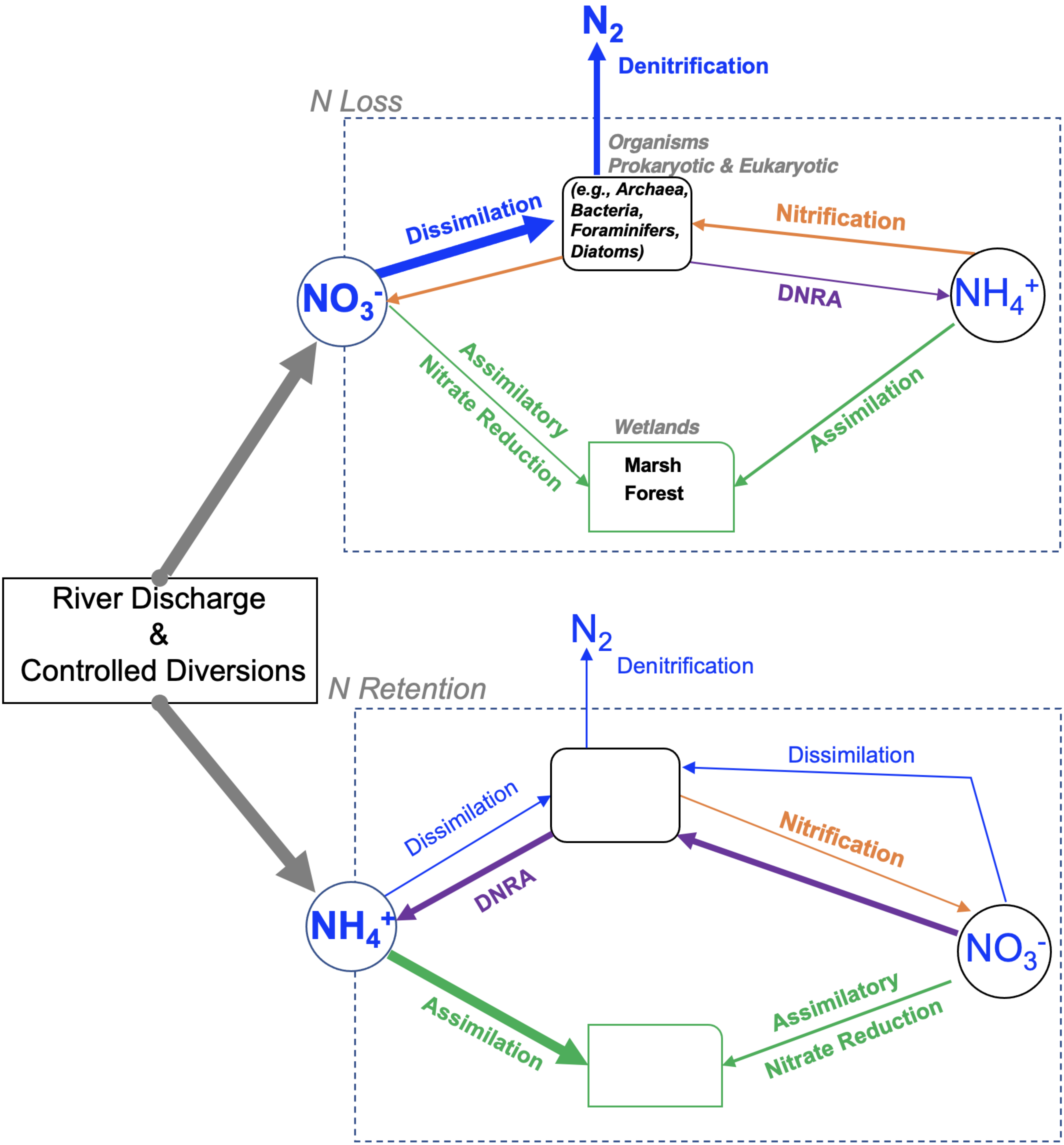
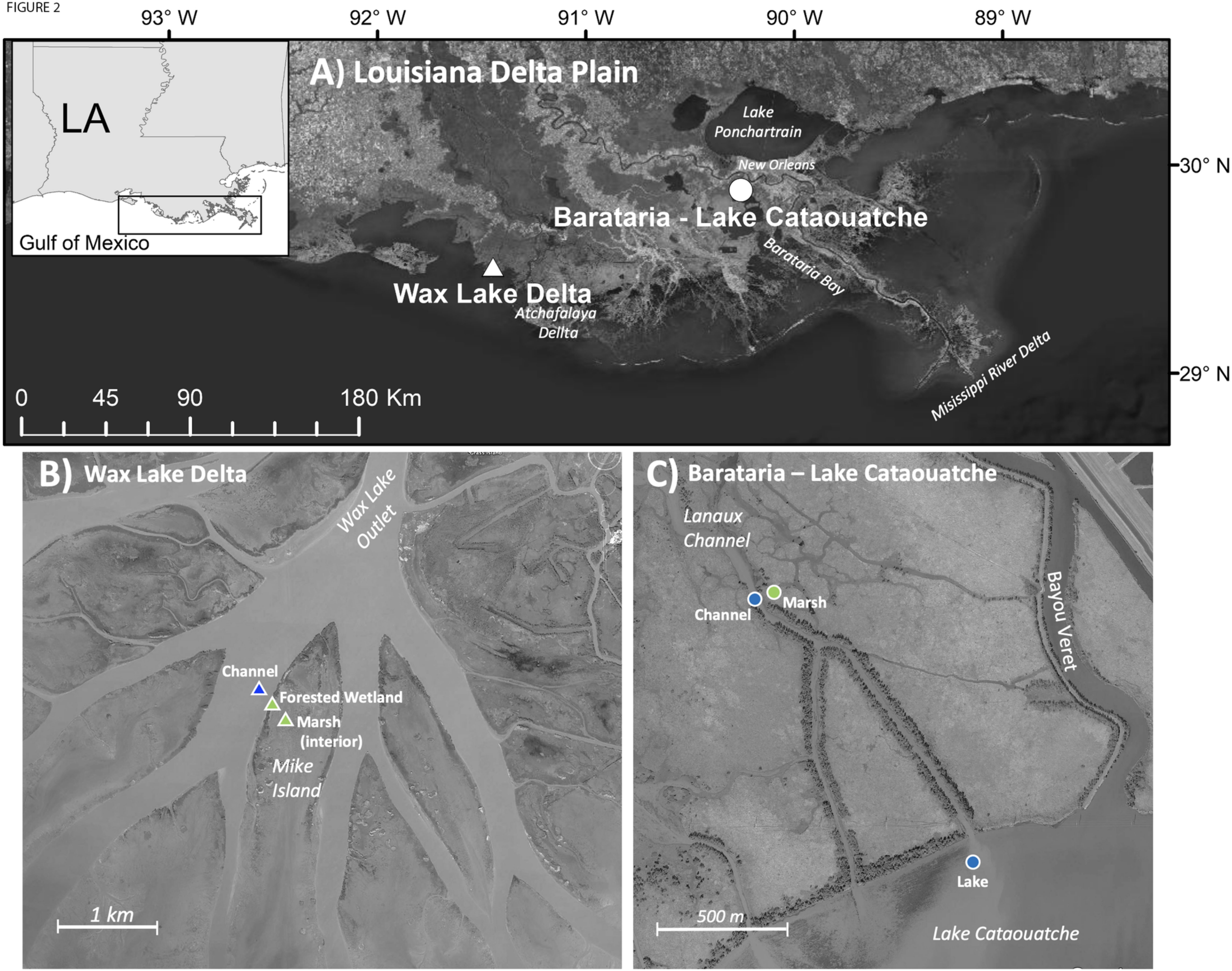

N₂
Denitrification
N Loss
Organisms
Prokaryotic & Eukaryotic
(e.g., Archaea, Bacteria, Foraminifers, Diatoms)
Dissimilation
Nitrification
NO₃⁻
DNRA
NH₄⁺
Assimilatory Nitrate Reduction
Assimilation
Wetlands
Marsh
Forest
River Discharge & Controlled Diversions
N₂
Denitrification
N Retention
Dissimilation
Dissimilation
Nitrification
DNRA
NH₄⁺
NO₃⁻
Assimilation
Assimilatory Nitrate Reduction

FIGURE 2


93° W
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89° W
30° N
29° N
LA
Gulf of Mexico
A) Louisiana Delta Plain
Lake Ponchartrain
New Orleans
Barataria - Lake Cataouatche
Barataria Bay
Wax Lake Delta
Atchafalaya Dellta
Mississippi River Delta
0
45
90
180 Km
B) Wax Lake Delta
Wax Lake Outlet
Channel
Forested Wetland
Marsh (interior)
Mike Island
1 km
C) Barataria – Lake Cataouatche
Lanaux Channel
Marsh
Channel
Bayou Veret
Lake
500 m
Lake Cataouatche

FIGURE 3

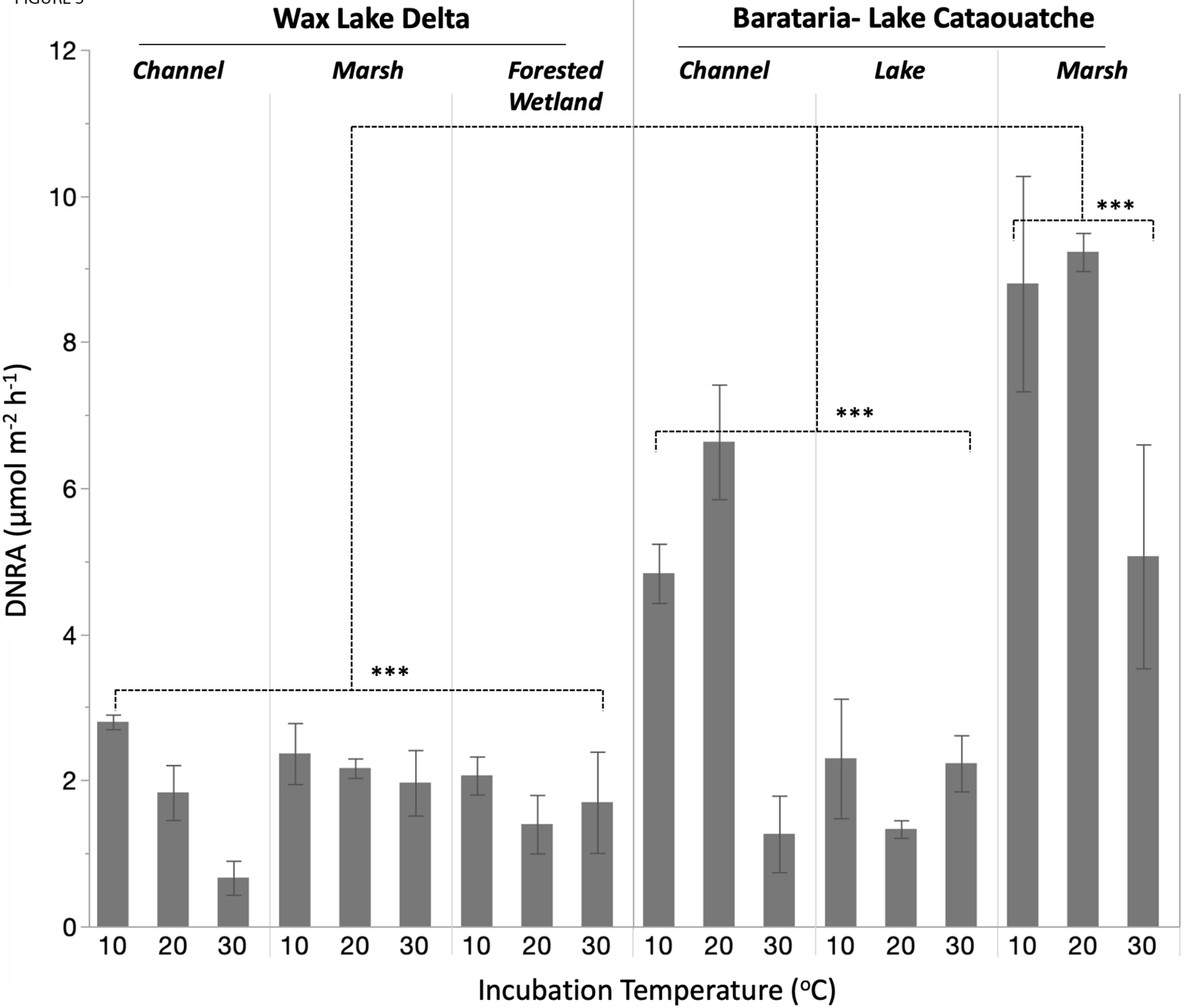

Wax Lake Delta
Barataria- Lake Cataouatche
Channel
Marsh
Forested Wetland
Channel
Lake
Marsh
***
***
***
DNRA (µmol m-2 h-1)
0
2
4
6
8
10
12
10
20
30
10
20
30
10
20
30
10
20
30
10
20
30
10
20
30
Incubation Temperature (oC)

FIGURE 4

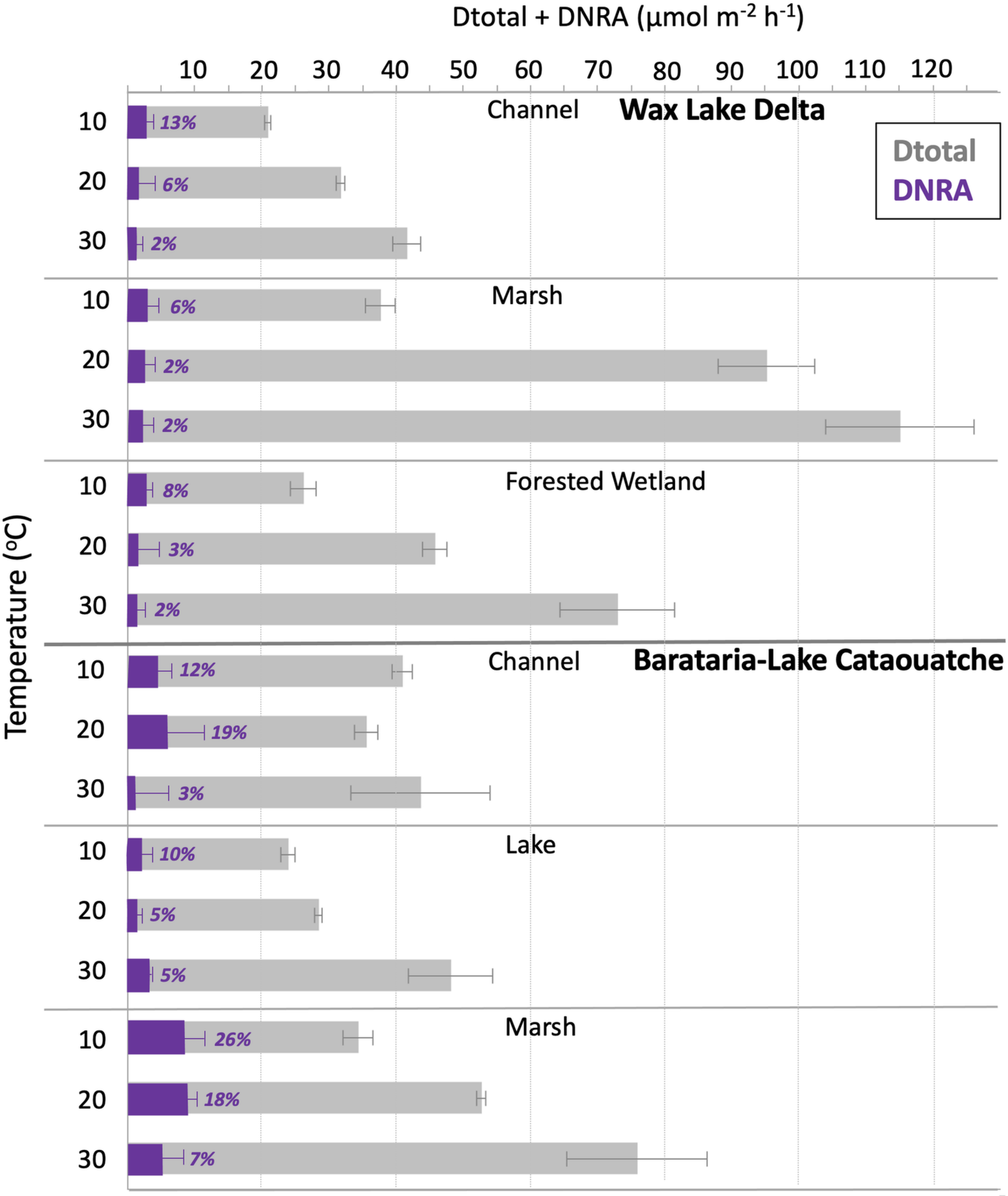

Dtotal + DNRA (µmol m-2 h-1)
10
20
30
40
50
60
70
80
90
100
110
120
Temperature (oC)
Wax Lake Delta
Dtotal
DNRA
Channel
10
13%
20
6%
30
2%
Marsh
10
6%
20
2%
30
2%
Forested Wetland
10
8%
20
3%
30
2%
Barataria-Lake Cataouatche
Channel
10
12%
20
19%
30
3%
Lake
10
10%
20
5%
30
5%
Marsh
10
26%
20
18%
30
7%

FIGURE 5

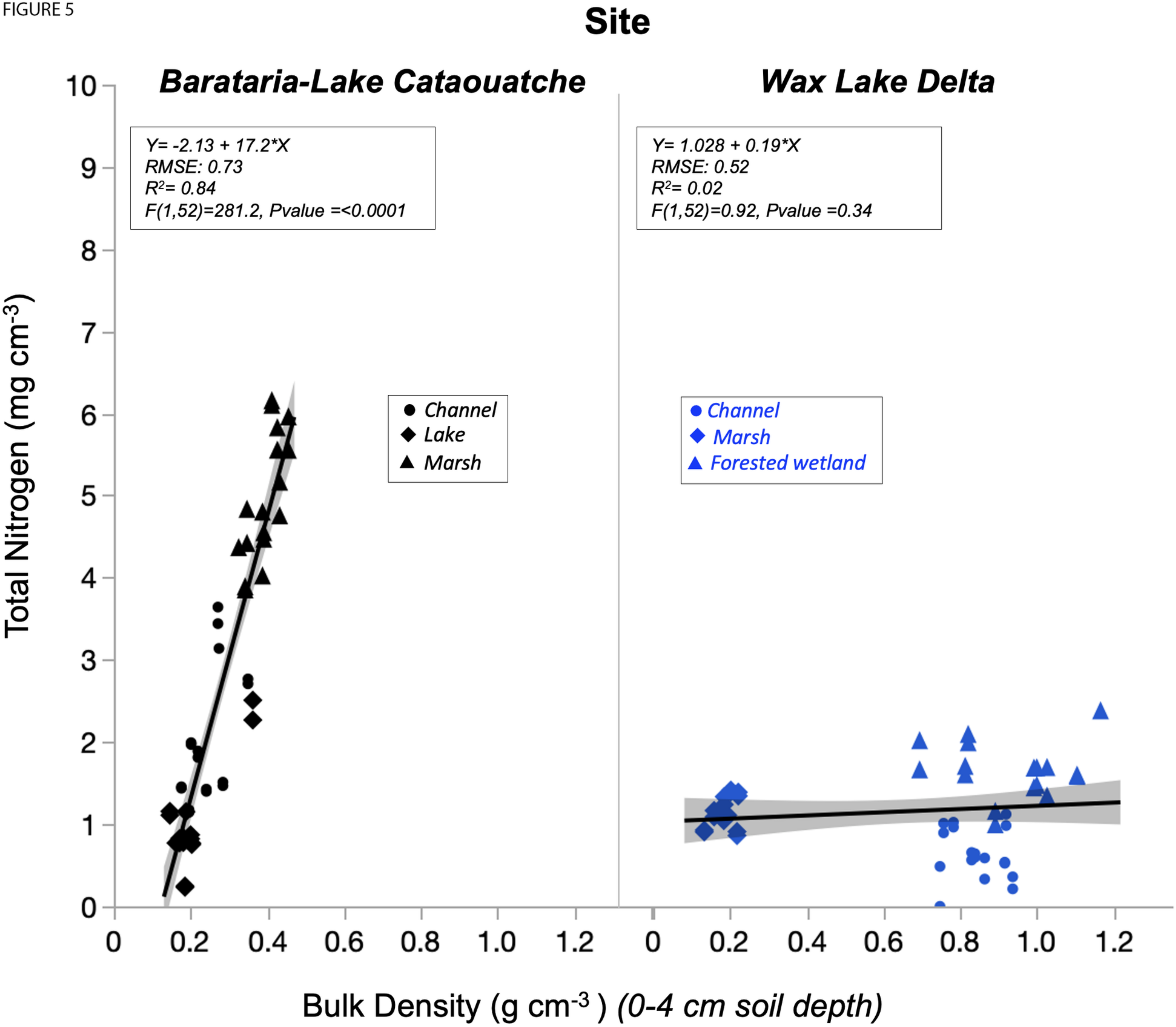
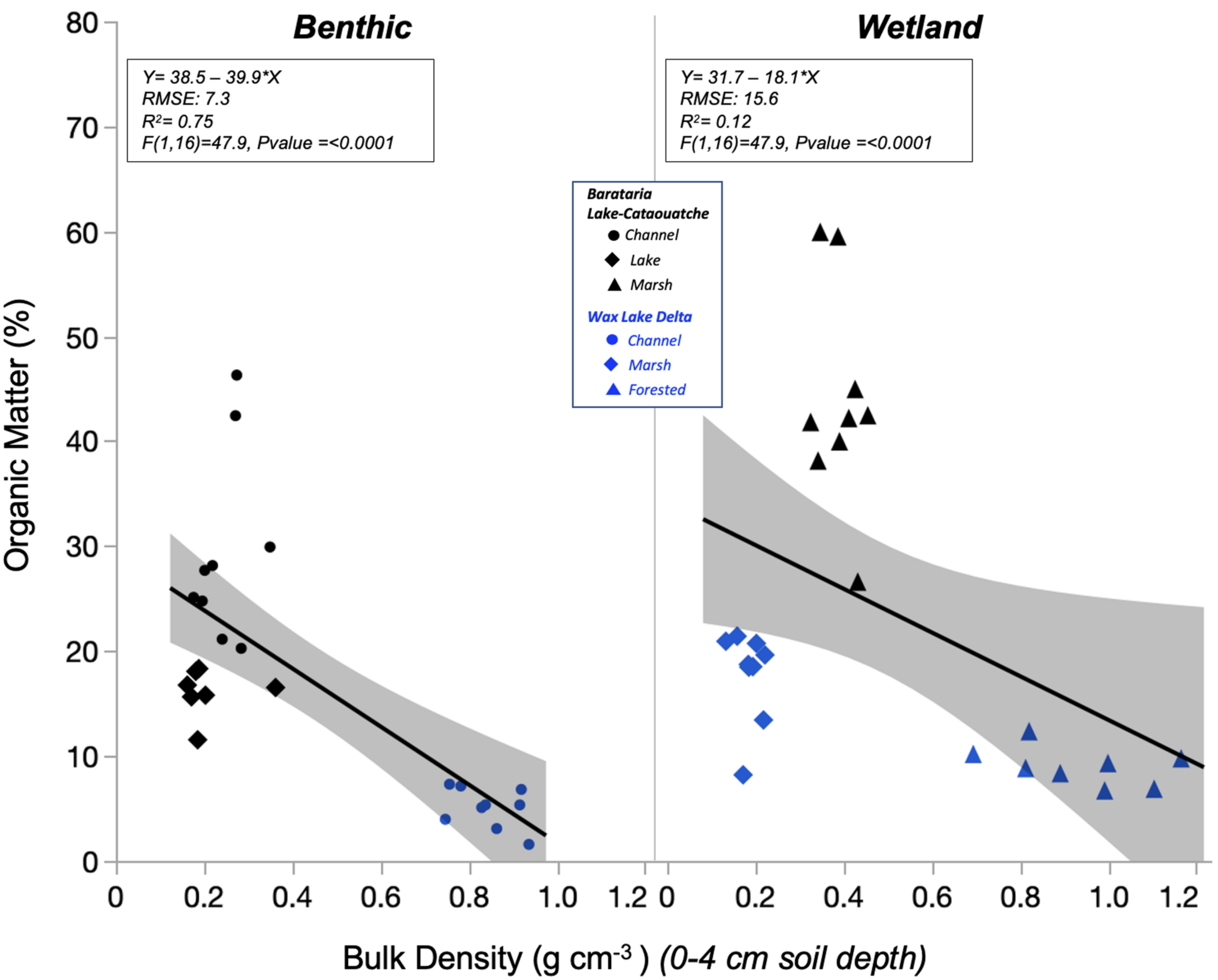

Site
Barataria-Lake Cataouatche
Wax Lake Delta
Y= -2.13 + 17.2*X
RMSE: 0.73
R2= 0.84
F(1,52)=281.2, Pvalue =<0.0001
Y= 1.028 + 0.19*X
RMSE: 0.52
R2= 0.02
F(1,52)=0.92, Pvalue =0.34
● Channel
◆ Lake
▲ Marsh
● Channel
◆ Marsh
▲ Forested wetland
Total Nitrogen (mg cm-3)
0
1
2
3
4
5
6
7
8
9
10
0
0.2
0.4
0.6
0.8
1.0
1.2
0
0.2
0.4
0.6
0.8
1.0
1.2
Bulk Density (g cm-3) (0-4 cm soil depth)

FIGURE 6

Substrate



Benthic

Wetland

Table 1. Summary of ANOVA results showing the interaction between region and type of substrate. BLC = Barataria Lake Cataoutche; WLD = Wax Lake Delta. Levels not connected by same letter are significantly different.

Source	**DF**	**Sum of Squares**	**F**	**Prob>F**	**LSM (±SE)**
Region	1	102.23	18.63	0.0001	
BLC					4.64 (0.61)
WLD					1.89 (0.15)
Substrate	1	19.8	2.79	0.1	
Benthic					2.66 (3.85)
Wetland					3.86 (10.29)
Interaction					
*Region*Substrate*	3	229.99	24.32	0.0001	
Tukey HSD					
Level					
BLC, Wetland				*A*	7.71 (0.91)
BLC, Benthic				*B*	3.1 (0.51)
WLD, Wetland				*B*	1.94 (0.16)
WLD, Benthic				*B*	1.76 0.33)

Table 2. Selected dissimilatory nitrate reduction to ammonium (DNRA) and denitrification studies using intact soil/sediments cores and the isotopic pairing technique in different benthic and wetland habitats in coastal regions. %DNRA = DNRA/ [DNRA + DTotal] (Nikolenko et al., 2018); *NI=No included.*

Coastal Region /Country	Latitudinal Zone	Salinity Classification	Salinity	Location	Habitat (type of substrate)	Core Incubation Method	Ambient [NO3] uM	15NO3 enrichment (uM)	15N rates measurment technique	Incubation Temperature	OM (%)	Substrate C:N ratio	DNRA Mean range and/or mean ± SE (μmol m−2 h−1)	Total Dentrification (Dtotal) Mean range and/or mean ± SE (μmol m−2 h−1)	% DNRA	References
Delta Plain **Coastal Louisana, USA**	Subtropical	Oligohaline	<1	Wax Lake Delta	Benthic (Channel)	Batch/Stirring	109.1-114.9	~50	IPT	10, 20, 30	2–7	11	0.7 (±0.2) - 2.8 (±0.1)	18.0 ±0.4 - 40.9 ±2.2	2–13	**This study**
					Freshwater Marsh		3.8-34.4			10, 20, 30	8–21	10	1.2 (±0.4) - 2.4 (±0.4)	35.2 ±2.3 - 113.0 ±10.6	2–6	
					Forested Wetland		0.1-1.7			10, 20, 30	6–20	11	1.4 (±0.4) - 2.1 (±0.3)	24.08 ±1.7 -71.2 ±9.2	2–8	
		Oligohaline	<1	Barataria -Lake Cataouatche	Benthic (Channel)	Batch/Stirring	38.3-113.9	~50	IPT	10, 20, 30	20-46	11 –12	1.2 (±0.52) - 6.6 (±0.8)	28.9 ±1.0 - 42.3 ±9.8	3–19	**This study**
					Benthic (Lake)		78.5-118.5			10, 20, 30	11–61	12	1.3 (±0.12)- 2.3 (±0.8)	27.0 ±0.4 - 45.8 ±6.7	5–10	
					Freshwater Marsh		0.29-60.5			10, 20, 30	26–59	13–15	5.1 (±1.5)- 9.2 (±0.3)	25.5 ±1.0 - 70.8 ±9.7	7–26	
			<1	Wax Lake Delta	Freshwater Marsh /Forested Wetland	Continous flow through /Stirring	13-93	5, 100	IPT	19-24	2–24	9–11	0-65	4-276	0-27	Lee and Twilley (2021)
Po River, Northern Italy	Temperate	Freshwater	<0.5	Lake Ca' Stanga	Benthic	Batch/Stirring	76-259	9-400	IPT	5–7	*NI*	4	1–9	138 ± 11 - 171 ± 27	1–5	Nizzoli et al. (2010)
				Lake Verde			<1 -200			5–13			1–9	31 ± 8 - 125 ± 22	3–7	
Melbourne, Australia		Freshwater	<0.5		Urban Treatment Wetlands	Batch/Stirring	0.2-147	*NI*	IPT	12–28	*NI*	7–17	1.8 (± 1.3) - 200 (± 50)	8.5 ± 0.4 - 140 ± 40	2–59	Rahman et al. (2019)
Waco, Texas, USA,	Subtropical	Freshwater	<0.5	Lake Waco Wetland - North Bosque River	Treatment Wetlands	Continous flow through /Stirring	0.04-36.8	40	IPT	21-26	*NI*	NI	1.3 - 33	50-270	3–11	Scott et al. (2008)
Texas, USA	Subtropical	Hypohaline	19-35	Laguna Madre and Baffin Bay	Benthic	Continous flow through /Stirring	0.1-22.4	~100	MIMS, N2:Argon; high performance liquid chromatography	15	*NI*	*NI*	50	11	82	An and Gardner (2002)
										31			69	55-69	53	
Alabama, USA	Subtropical	Saline	23-34	Little Lagoon	Benthic	Continous flow through /Stirring	0.1-1.2	~100	MIMS; IPT	14-33	*NI*	*NI*	0.1-236	0.1-54.8	30-84	Bernard et al. (2015)
Alabama, USA	Subtropical	Euhaline-Saline	>2–23	Weeks Bay National Estuarine Research Reserve	Benthic	Continous flow through	0.1-20	~100		16-28	*NI*	12–21	44.4 ± 5	0.9 ±2.3	98	Domague et al. (2018)

Table 2. (Cont.)

Thailand, Gulf of Thailand;	Tropical	Freshwater-Euhaline	0-35	Mae Klong	Benthic	Batch/Stirring	0.3-18.0	~50	IPT	24-33	*NI*	5.7	0.23-22.8	0-7.4	74	Dong et al. (2011)
Indonesia, north coast of Java,		Freshwater-Euhaline	0-35	Cisadane	Benthic		0.4-312.0	~50		24-33		8.1	1-1137	0.0-103	75	
Fiji		Freshwater-Euhaline	0-35	Vunidawa-Rewa	Benthic		0.7-12.1	~50		24-33		6.5	0.2-10.2	0.0-2.6	68	
South east coast, Australia	Subtropical	Polyhaline	15-29	Wallis Lake	Benthic	Batch/Stirring	0-12	30	IPT	20	1.3-1.6	1.35	83.8 ± 28.2	1.3 ± 0.5	99	Erler et al.(2017)
South coast, Australia	Temperate	Freshwater-Polyhaline	1–36	Rivers: Hopkins, Curdies, Aire, Yarra, Peterson; Lakes: Wellington, King; Inlets: Tamboon, Wingan, Mallacoota	Benthic	Batch/Stirring	3–49	50	IPT	*NI*	*NI*	*NI*	2–30	4–35	7–75	Kessler et al. (2018)
				Werribee River	Benthic	Batch/Stirring	3–49	50	IPT	*NI*	*NI*	*NI*	19	150	11	Kessler et al. (2018)
Texas Coast, USA	Subtropical	Euhaline-Hypohaline	40-60	Laguna Madre	Benthic	Batch/Stirring	0.4-1.8	~100	MIMS, N2:Argon; high performance liquid chromatography	15.-30	*NI*	*NI*	49.5 ± 18	33.5 ± 7.5	60	Gardener et al. (2006)
			40-60	Bafin Bay	Benthic		0.7-1.2			15.-30		*NI*	23.5 ± 3.9	29.0 ± 3.5	45	
Plum Island Sound Estuary, Massachusetts. USA	Temperate	Polyhaline	28	Sweeney Creek Marsh (Fertilized)	Marsh	Batch/Stirring	4.4	~70-150	MIMS; IPT	22-24	*NI*	*NI*	24.4 ± 3.8	54.1 ± 9.2	31	Koop-Jakobsen and Giblin (2010)
			25		Tidal Creek		6.7			22-24			307.3 ± 82.1	294.9 ± 64.7	51	
			28	West Creek (Reference)	Marsh		4.4			22-24	*NI*	*NI*	3.9 ± 1.1	2.8 ± 6 0.5	58	
			25		Tidal Creek		6.7			22-24			21.7 ± 3.1	9.6 ± 6 0.8	69	