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## RESEARCH ARTICLE

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James P. Geaghan is Deceased

### Key Points:

- Denitrification rates in coastal deltaic wetlands with low carbon availability are high when  $[\text{NO}_3^-] > 30 \mu\text{M}$  and water temperature  $> 10^\circ\text{C}$
- Denitrification rates in wetlands of prograding and degrading delta lobes were linearly correlated with seasonal differences in temperature
- Direct denitrification was higher than coupled denitrification in all seasons and habitats under oligohaline conditions ( $< 1$  ppt)

### Supporting Information:

Supporting Information may be found in the online version of this article.

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## Emerging Wetlands From River Diversions Can Sustain High Denitrification Rates in a Coastal Delta

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**Abstract** It is assumed that to treat excess  $\text{NO}_3^-$  high soil organic matter content (%OM) is required to maintain high denitrification rates in natural or restored wetlands. However, this excess also represents a risk by increasing soil decomposition rates triggering peat collapse and wetland fragmentation. Here, we evaluated the role of %OM and temperature interactions controlling denitrification rates in eroding (Barataria Bay-BLC) and emerging (Wax Lake Delta-WLD) deltaic regions in coastal Louisiana using the isotope pairing (IPT) and  $\text{N}_2:\text{Ar}$  techniques. We also assessed differences between total (direct denitrification + coupled nitrification-denitrification) and net (total denitrification minus nitrogen fixation) denitrification rates in benthic and wetland habitats with contrasting %OM and bulk density (BD). Sediment (benthic) and soil (wetland) cores were collected during summer, spring, and winter (2015–2016) and incubated at close to in-situ temperatures ( $30^\circ\text{C}$ ,  $20^\circ\text{C}$ , and  $10^\circ\text{C}$ , respectively). Denitrification rates were linearly correlated with temperature; maximum mean rates ranged from  $40.1\text{--}124.1 \mu\text{mol m}^{-2} \text{h}^{-1}$  in the summer with lower rates ( $< 26.2 \pm 5.3 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) in the winter seasons. Direct denitrification was higher than coupled denitrification in all seasons. Denitrification rates were higher in WLD despite lower %OM, lower total N concentration, and higher BD in wetland soils. Therefore, in environments with low carbon availability, high denitrification rates can be sustained as long as  $\text{NO}_3^-$  concentrations are high ( $> 30 \mu\text{M}$ ) and water temperature is  $> 10^\circ\text{C}$ . In coastal Louisiana, substrates under these regimes are represented by emergent supra-tidal flats or land created by sediment diversions under oligohaline conditions ( $< 1$  ppt).

## 1. Introduction

Denitrification is a microbial respiration pathway that leads to the loss of nitrogen (N) pool from terrestrial and aquatic ecosystems by converting inorganic N (e.g., nitrate:  $\text{NO}_3^-$ ; nitrite:  $\text{NO}_2^-$ ) to gaseous forms (e.g.,  $\text{N}_2$ ) under near anoxic or anoxic conditions (Burgin & Hamilton, 2007; Canfield, 2006; Hulth et al., 2005). This biochemical transformation can be supported by nitrate diffusion and infiltration into sediment and soils from overlying water (i.e., direct denitrification  $\text{NO}_3^- \rightarrow \text{N}_2$ ) or by  $\text{NO}_3^-$  generated from nitrification within these substrates (coupled nitrification-denitrification:  $\text{NH}_4^+ \rightarrow \text{NO}_3^- \rightarrow \text{N}_2$ ). Because these N transformations can potentially ameliorate eutrophication (i.e., N enrichment) in inland and coastal waters (Allred & Baines, 2016; Mitsch et al., 2005), denitrification is considered a key ecosystem service in coastal zones that are often subjected to high N loads as a result of human impacts (Coleman et al., 1998; Cook et al., 2006; Rosenzweig et al., 2018).

Temperature is one of the critical drivers controlling denitrification due to its regulatory role on other physicochemical processes that modulate not only the denitrification magnitude, but also its spatial distribution at different temporal scales (e.g., seasonal) (Cornwell et al., 1999; Spieles & Mitsch, 1999; Stober et al., 1997; Willers et al., 1993). Thus, the role of denitrification in coastal systems and associated wetlands at different latitudes vary according to seasonal changes in temperature and N availability mediated by the landscape scale interaction between coastal geomorphology and hydrology (Damashek & Francis, 2018; Rosenzweig et al., 2018). This is the case for subtropical coastal regions in northern latitudes where seasonal variation in air and water temperatures is large (e.g., from  $4^\circ\text{C}$  to  $35^\circ\text{C}$ ).

Wetlands are increasingly impacted by human activities that cause a wide range of eutrophic conditions (Rosenzweig et al., 2018; Zhang et al., 2019). Because wetlands can assimilate N under anoxic conditions—

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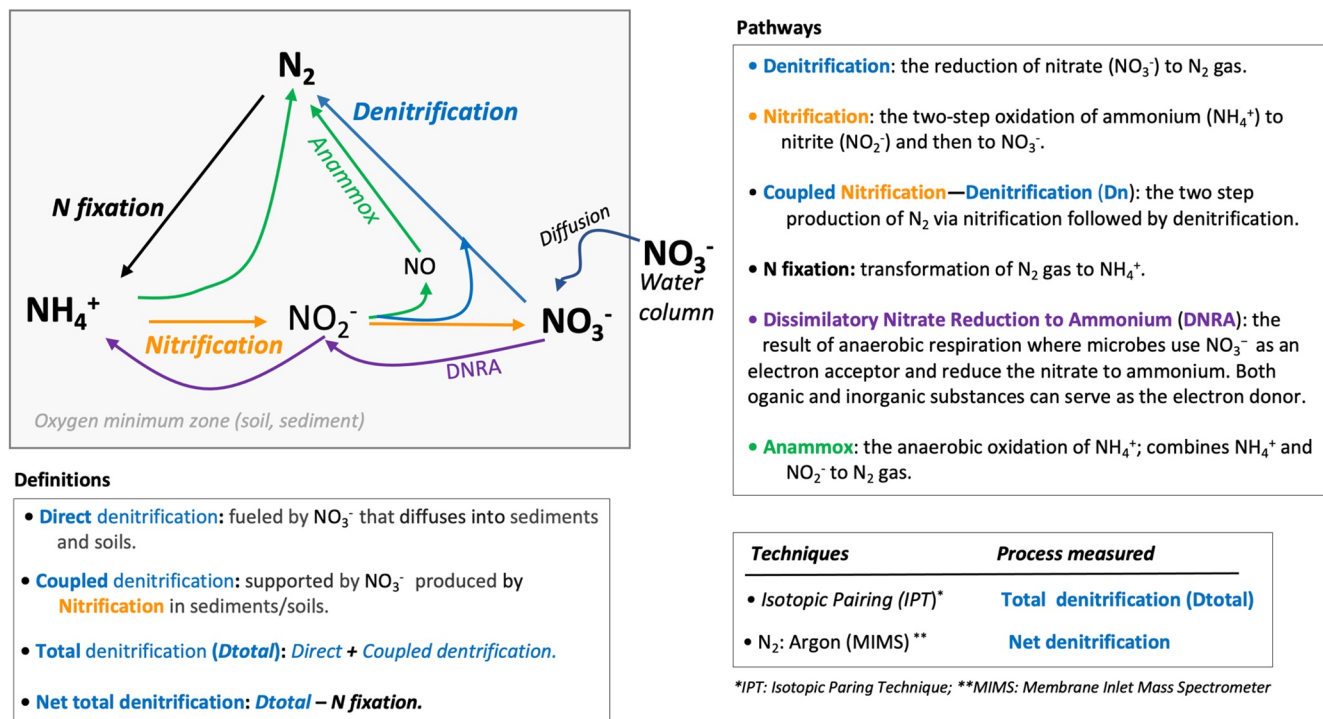
through enhanced denitrification—they are sometimes used to reduce excess N. Unfortunately, there is an increasing loss of wetlands and their ecosystem services (i.e., denitrification) as a result of other human impacts such as major changes in land use/change (e.g., urbanization, agriculture infrastructure construction) and the negative effect of nutrient loading on coastal wetland stability. It has been proposed that high nutrient loading disrupts the stability of wetlands through increased denitrification in wetland soils causing the reduction of both soil OM content and soil bulk density and strength, thus triggering “creek-bank/peat collapse” (Day et al., 2018; Deegan et al., 2012; Turner, 2011).

Direct and indirect measurement of denitrification in wetlands has been extensive (Kadlec, 2016). In natural wetlands, these measurements have advanced our understanding of the relative role of denitrification in the N cycle in coastal wetlands, especially when considering its interaction with other biogeochemical cycles (i.e., carbon and phosphorus) (Burgin & Hamilton, 2007; Giblin et al., 2013). Despite these advances, there is still a lack of data and information to comparatively assess denitrification rates within and across different ecogeomorphic settings in both natural and constructed wetlands (Rosenzweig et al., 2018), especially in cases where landscape-level freshwater diversions deliver high concentrations of mineral sediments and organic/inorganic N to promote sediment accumulation. This sediment input promotes an increase in soil relative elevation and induce vegetation establishment while enhancing N assimilation as both—in situ OM production and allochthonous OM deposition—increase during soil formation and vegetation establishment either by natural succession or direct planting (e.g., Elsey-Quirk et al., 2019; Jafari et al., 2019).

Comparison of rates has also been hindered by the confounding effect of different techniques used to measure denitrification in wetlands with different plant species composition and/or functional vegetation groups (e.g., trees vs. herbaceous; salt vs. freshwater wetlands) (Allred & Baines, 2016). Although direct techniques (e.g., intact soil cores using N<sub>2</sub>:Ar, isotopic pairing technique [IPT], 15NH<sub>4</sub><sup>+</sup>/<sup>15</sup>NO<sub>3</sub><sup>-</sup> additions) (Cornwell et al., 1999; Groffman et al., 2006; Steingruber et al., 2001) are preferred over indirect techniques (e.g., soils/sediment slurries using acetylene reduction, denitrification enzyme activity, DEA; whole system N mass balance), most studies have used the latter (Allred & Baines, 2016; Groffman et al., 2006). This preference—due to their implementation simplicity and cost—limits our understanding to assess the relative importance of direct and coupled nitrification-denitrification as each wetland type can influence the utilization of different inorganic nitrogen species (i.e., NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>) in the water column and/or within soil/sediments during denitrification (Groffman et al., 2006; Lam & Kuypers, 2011; Steingruber et al., 2001). The operational partition among the different types of denitrification is useful to define the functional role of a particular type of wetland as an N transformer, source, or sinks (Mayorga et al., 2010). For instance, the N<sub>2</sub>:Ar technique measures “net total denitrification” since this rate represents the difference between total denitrification (direct + coupled) and N fixation while the IPT differentiates the source of NO<sub>3</sub><sup>-</sup> from the water column (direct) or from nitrification in the soil/sediment (coupled); the N<sub>2</sub>:Ar technique also includes, if present, the contribution of anammox to the N<sub>2</sub> pool (see Figure 1 for definitions; Steingruber et al., 2001). Direct techniques also facilitate the assessment of the role of electron donor presence (e.g., OM) and O<sub>2</sub> availability in regulating the magnitude of denitrification rates.

Regional comparisons to characterize denitrification as a functional trait in either aquatic ecosystems (Lam & Kuypers, 2011; Piña-Ochoa & Álvarez-Cobelas, 2006) or wetlands have been based on annually averaged statistical comparisons (e.g., meta-data analysis; Allred & Baines, 2016). This assessment includes a wide range of wetland types where seasonal and interannual variations in temperature and other environmental drivers regulating denitrification are averaged over time. Yet, our understanding of the specific regulatory effect of seasonal temperature on denitrification in different wetland types under high N enrichment is still limited to be able to mechanistically link functional plant traits to denitrification (Allred & Baines, 2016).

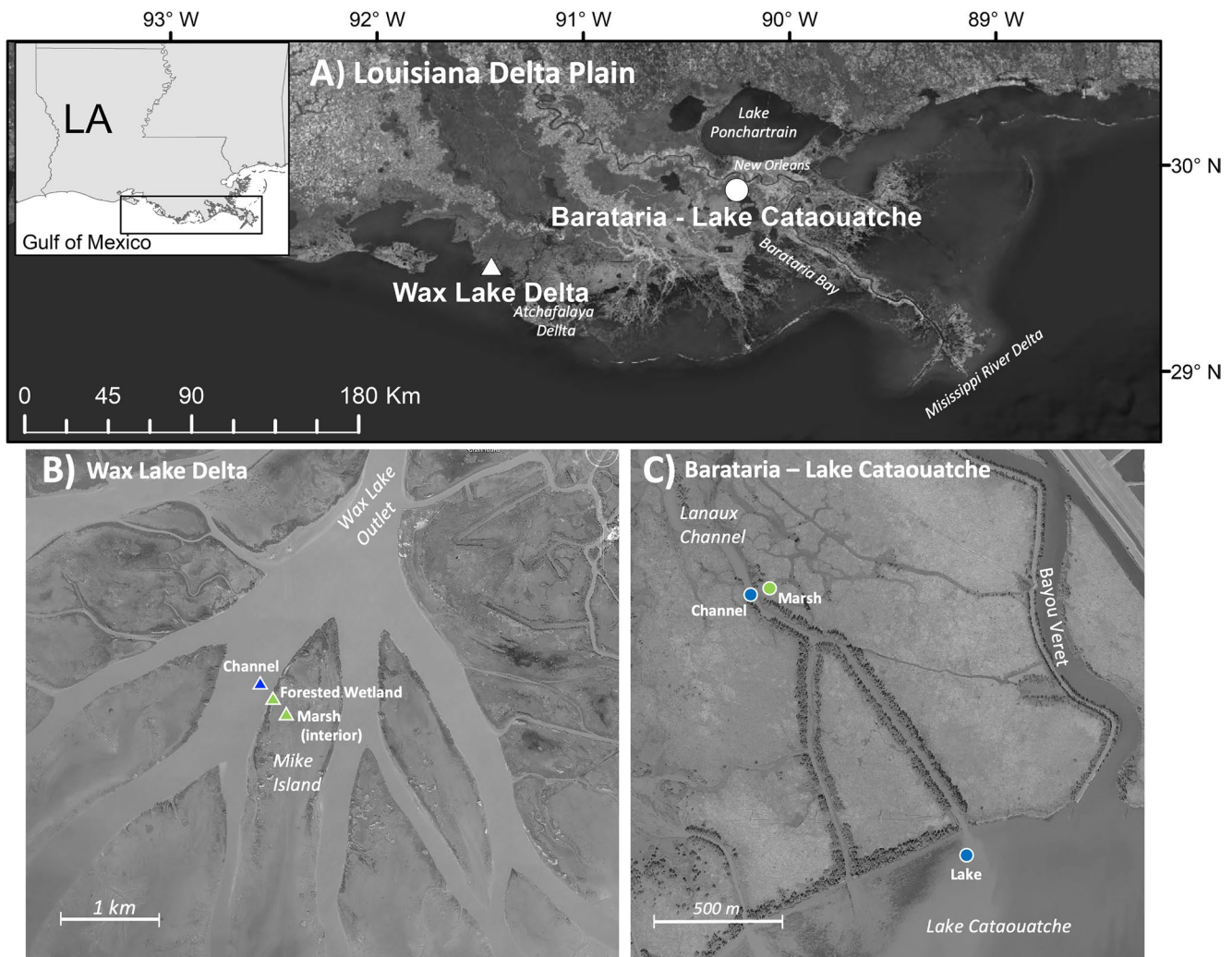
The general objective of this study was to evaluate the relative importance of denitrification in different wetland and open water (i.e., benthic) habitats in a subtropical riverine deltaic setting. We assessed the role of temperature in regulating rates and the partitioning between direct and coupled nitrification-denitrification across different types of wetlands (i.e., freshwater marsh and forested wetland) with different soil OM and mineral content using direct techniques (i.e., N<sub>2</sub>:Ar, IPT). Our study sites are located in the largest wetland area (4,000 km<sup>2</sup>) in the conterminous United States that are part of the Mississippi River (MR) deltaic plain region (12,000 km<sup>2</sup>) in the northern Gulf of Mexico (nGOM). This is a subtropical coastal region where wetland species composition is shifting (e.g., mangrove expansion into salt marshes) partially as a result of



**Figure 1.** Diagram of N cycling pathways and relationship to the techniques and types of denitrification mentioned in this study (Figure modified from Giblin et al., 2013).

increasing air temperature induced by climate change (Osland et al., 2020). Further, this deltaic plain is currently undergoing a historical wetland loss (i.e., 28–84 km<sup>2</sup> yr<sup>-1</sup>; Couvillion et al., 2016; Wang et al., 2014) caused by human impacts that continue altering the MR watershed hydrology and sediment transport (Elliton et al., 2020; Jafari et al., 2019). The natural delta cycle in this region (Blum & Roberts, 2012) has been impacted by the significant reduction and redistribution of sediment associated with the annual MR discharge (7,000–20,000 m<sup>3</sup> s<sup>-1</sup>) and high N loading rates (1.56 × 10<sup>6</sup> Mg yr<sup>-1</sup>) that fuel a growing hypoxia zone (~21,000 km<sup>2</sup> (Hyfield et al., 2008; Rabalais et al., 2001, 2002; Scavia et al., 2004; Turner et al., 2012).

Due to the low number of denitrification rates obtained using direct methods in deltaic geomorphic settings (Cornwell et al., 2014; Rivera-Monroy et al., 2013), there are limitations to advance the use of denitrification as a potential wetland functional classification property (Allred & Baines, 2016). Our study contributes to advance this classification by showing not only how denitrification influences N loss and retention under different temperature regimes, but also to determine how these rates vary between areas (i.e., delta lobes) undergoing wetland loss/fragmentation (i.e., erosional stage) and land gains (progradational stage). These processes are part of the natural delta cycle that directly impact regional N budgets in the MR delta plain (Bennett et al., 2014; Rivera-Monroy et al., 2013). Thus, we also aim to determine how denitrification in benthic sediment from open water bodies (e.g., lake, channels) receiving freshwater from the MR—a current management strategy to restore/rehabilitate wetlands in the Louisiana delta plain—reduce N before it is delivered to the nGOM. Because of the acceleration of wetland loss as a result of increasing sea level rise (Blum & Roberts, 2009) and subsidence (Tornqvist et al., 2008) in the MR delta plain, it is not clear how this habitat shifting, that is, from wetlands to open water areas, will reduce or increase N loss via denitrification (Rivera-Monroy et al., 2013). We hypothesized that denitrification rates will increase with temperature, yet, we expect that denitrification rates measured at the same temperature will be significantly higher in wetland soils undergoing a deltaic erosional stage than in an progradational stage due to higher organic matter (%OM) content; especially in the case of benthic sediments where OM% content in channels or open water bodies (i.e., lake) is generally lower than in wetland soils (e.g., freshwater marsh, forested wetland). Specifically, the objectives were to (1) determine the magnitude of denitrification rates associated to low (winter, 10°C), intermediate (spring, 20°C), and high (summer, 30°C) temperatures in each type of substrate



**Figure 2.** (a) Atchafalaya and Mississippi Deltas; (b) Wax Lake Delta (WLD); (c) Upper Barataria-Lake Cataouatche (BLC) Louisiana (LA) regions; sampling sites are located in benthic (Channel, Lake) and wetland (marsh, forested) habitats.

(wetland soil vs. benthic sediment); (2) evaluate differences in denitrification rates in benthic (i.e., channels and open water lake) and wetland habitats (interior/inland freshwater marsh and forested wetland) of prograding and degrading delta lobes with varying soil %OM under high nitrate concentrations; and (3) evaluate the relative importance of specific N transformations such as coupled nitrification-denitrification and N fixation using different denitrification techniques (i.e., IPT and  $N_2:Ar$ ) across temperature representing seasonal differences and habitat types.

## 2. Materials and Methods

### 2.1. Study Area Description

This study was performed using soils and sediments collected in two regions: the Wax Lake Delta (WLD) and the upper Barataria Bay (Figure 2). These regions have contrasting hydrology and geomorphology and are dominated by oligohaline conditions (annual salinity range: 0.1–0.4 ppt) (Upreti et al., 2019). The WLD region is located in coastal Louisiana about 20 miles Southwest of Morgan City. This delta was recently formed (prograding delta stage) as a result of sediment input through a man-made outlet (Wax Lake Outlet), which was dredged to divert water from the Atchafalaya River to the Gulf of Mexico, thus protecting Morgan city during pulsing high river stages (Figures 2a and 2b) (Roberts & Sneider, 2003; Rosen & Xu, 2013).

Approximately 30% of the annual average water flow of the Atchafalaya River is diverted through the WLD outlet which is equivalent to ~10% of the annual average discharge of the MR. New land emerged in the WLD region above the water line after the extreme flood of 1973 by forming a subaerial delta (Hiatt & Passalacqua, 2015; Hiatt et al., 2018).

The WLD region is characterized by a diurnal micro-tidal regime (<30 cm), which can be altered by wind-driven effects (Allen et al., 2012; Bevington et al., 2017; Elliton et al., 2020). Together, the prograding delta lobes have a current extension of 65 km<sup>2</sup>, which has increased at a rate of 1 km<sup>2</sup> yr<sup>-1</sup> (1983–2010). 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 freshwater marsh and forested wetland habitats across well-defined elevation gradients (Allen et al., 2012; Holm & Sasser, 2001). Our study sites in this region consisted of two types of wetlands (interior or inland marsh, and forested wetland) and a tidal creek (henceforth “channel”) located on Mike Island—one of the oldest delta lobes (Figure 2b)—where herbaceous (e.g., *Sagittaria sp.*, *Colocasia esculenta*, *Typha sp.*) and forested wetlands (*Salix nigra*) are the dominant vegetation (Carle et al., 2015).

Barataria Bay is an estuarine wetland system located between the MR and Bayou Lafourche and separated from the Gulf of Mexico by a chain of barrier islands (FitzGerald et al., 2004). The basin is in a degrading delta stage with significant wetland losses at a rate of about 23 km<sup>2</sup> yr<sup>-1</sup> 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<sup>2</sup> 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 inputs of fresh water and sediment from the MR (Boesch, 2006; Boesch et al., 1994; Wang et al., 2017). Our study sites in the Barataria Bay were established in the northern area of Lake Cataouatche (henceforth referred to as BLC region); the wetland site (i.e., interior marsh) was dominated by herbaceous vegetation (e.g., *Sagittaria sp.*, *Typha sp.*, *Bidens sp.*; Figure 2c). A tidal channel (benthic habitat) was located adjacent to the marsh wetland site while another benthic site was established in Lake Cataouatche proper (henceforth “lake”); all sites are influenced by the Davis Pond freshwater diversion during high peak discharge via the Lanaux canal-dredged (Figure 2c).

## 2.2. Field Experimental Set-Up and Core Sampling

Wetland soil and benthic intact sediment cores were collected in both the WLD and northern Barataria Bay-Lake Cataouatche (BLC) regions (Figures 2b and 2c) based on the presence of wetland vegetation (marsh and forested wetland) and flooding duration and water depth (i.e., channels and open water). Because one of the objectives was to evaluate differences in soil denitrification rates in wetlands, regardless of species composition within each site, we selected sites with herbaceous vegetation in both regions (Figures 2b and 2c; “marsh” in BLC and “interior” marsh in WLD). We also selected a forested wetland in the WLD region to assess differences between wetlands at different elevations and vegetation successional stages. The forested wetland—dominated by the tree species *Salix nigra*—is geomorphological older (~45 years) and characterized by a height relative elevation when compared with the interior marsh (Bevington et al., 2017). In addition to evaluating differences in denitrification rates between wetlands soils within the WLD (marsh vs. forested wetland) and among regions (i.e., herbaceous marshes), benthic sediments were also sampled in adjacent channels (northern BLC and WLD) and open water (BLC) (Table 1). No forested wetland was sampled in BLC due to logistical constraints.

During each season, undisturbed soil cores in vegetated wetland habitats were collected by hand insertion of an acrylic tube (length: 36 cm; internal diameter: 10.1 cm) on the soil surface of an open space among either individual herbaceous plants or trees and carefully pushing 16 cm into the sediment while avoiding any compaction (Eriksson et al., 2003; Upreti, 2019). Cores were collected such that no leaves or large stems were present inside the core; lateral roots were carefully cut once the core was inserted to facilitate extraction and avoid disturbing the soil layers. Benthic sediment cores in open water and creeks (no rooted vegetation) were collected using a suction core sampling device operated from a vessel (water depth range: 1–2.5 m depending on tide/river stage) (Hartzell et al., 2010). In situ water temperature was also measured during core samplings (YSI model 35); temperature in the WLD ranged from 12.7°C to 15.2°C in winter,

**Table 1**  
Core Sampling Information Per Site, Habitat, and Experimental Temperature Treatments

Year	Season	Incubation temperature (°C)	Habitat					
			Wetland			Benthic		
			Marsh		Forested	Channel	Lake	Channel
			WLD	BLC	WLD	WLD	BLC	BLC
2015	Winter	10	X	X	X	X	X	X
2016	Spring	20	X	X	X	X	X	X
2016	Summer	30	X	X	X	X	X	X

Note. X:  $N = 3$  cores.

Abbreviations: BLC, Barataria-Lake Cataouatche; WLD, Wax Lake Delta.

23.7°C to 25.9°C in spring, and 26.3°C to 31.7°C in summer. Temperature range in the BLC region was similar to WLD measurements (winter: 12.5°C–14.6°C; spring: 20.5°C–22.4°C; summer 26.5°C–30.2°C). All cores were collected in the study sites during the summer (2015), winter (2015), and spring (2016) seasons (Figures 2b and 2c).

Once collected, all cores with overlying water were transported in a cooler to the laboratory within 6 h of collection. Once in the laboratory, cores were placed at average field temperatures and allowed to equilibrate (see below) before incubation. Water and soil pore-water samples were also collected. Salinity, pH, redox, and O<sub>2</sub> concentrations were measured at the time of collection using a YSI Probe (YSI model 35) while inorganic N (NH<sub>4</sub><sup>+</sup>, NO<sub>2</sub><sup>-</sup>, and NO<sub>3</sub><sup>-</sup>) concentrations were determined after filtration (0.45-μm pore size) in the laboratory using a Flow Solution IV AutoAnalyzer (OI Analytical, College Station, Texas). Denitrification experiments were performed in the laboratory (see below).

### 2.3. Laboratory Incubation Experiments

#### 2.3.1. Net Denitrification

The cores were placed in a water bath 2–3 h before the start of the experiment. Temperature was controlled by recirculating water at the temperature close to the average seasonal condition when the cores were sampled; however, 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), and spring (20°C) (Table 1). 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 a 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 (Upreti, 2019). Dissolved O<sub>2</sub> (DO) concentrations inside the cores were monitored throughout the duration of the experiment using a microelectrode oxygen sensor (Unisense, Inc.). The incubations were terminated when oxygen concentration dropped to ~50% of the initial DO concentrations to avoid artifacts/analytical error associated with O<sub>2</sub> non-linearity (Lunstrum & Aoki, 2016). Because of differences in soil/sediment OM% and incubation temperature, the incubation period was variable; overall, it ranged from 15–18 h with shorter duration during summer (30°C) when incubations lasted from 6 to 7.5 h. Samples were collected every 1.5–3 h depending on DO consumption via the sampling port on the core lid. Because the total incubation period lasted from 6 to 18 h, all incubations were performed in the dark (e.g., Cornwell et al., 2014; Eriksson et al., 2003).

Water samples were collected at each sampling time after discarding the first ~10 ml of tube dead volume. Duplicate water samples used for net denitrification measurement (N<sub>2</sub>:Ar ratio; Eyre et al., 2002; Kana et al., 1998) were collected using 12-ml Labco exetainers vials, allowing water to overflow to minimize air contamination; samples were poisoned with 10 μl of 5% HgCl<sub>2</sub> and immediately placed in a container, submerged in water to avoid atmospheric gas exchange and stored at 4°C until analysis using Mass Inlet Mass

Spectrometry (MIMS) (Burgin, Hamilton, et al., 2013; Burgin, Lazar, et al., 2013; Hamilton & Ostrom, 2007; Kana et al., 1998). Water samples for nutrients were filtered (0.45  $\mu\text{m}$ ) and stored frozen until analyses of  $\text{NO}_2^-$ ,  $\text{NO}_3^-$ , and  $\text{NH}_4^+$ , using a Flow Solution IV AutoAnalyzer (OI Analytical, College Station, Texas). At the end of the incubation period, cores were uncapped, and sediment cores were sliced at 4-cm depth-interval and oven-dried at 60°C for the determination of bulk density (BD), % organic matter (%OM), total carbon (TC), and total N (TN). Organic matter content is defined as a percent of ash-free dry weight, determined by combusting samples in a furnace for 2 h at 550°C (Davies, 1974). TC and TN were determined on two analytical replicates of each core sample with an ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia, CA).

Water samples collected for the determination of net denitrification were measured in a mass spectrometer (MIMS; Pfeiffer Vacuum) using the  $\text{N}_2$ :Ar method (Kana et al., 1994; Koop-Jakobsen & Giblin, 2010). The  $\text{N}_2$  fluxes were calculated from the linear regression plots of  $\text{N}_2$  concentration (corrected for sample volume withdrawn) as a function of time.

### 2.3.2. Direct and Coupled Nitrification-Denitrification

The  $^{15}\text{N}$  isotope pairing technique (Marchant et al., 2016; Nielsen, 1992) was used to measure direct denitrification fueled by  $\text{NO}_3^-$  in the water column ( $D_w$ , sensu Steingruber et al., 2001) and coupled denitrification maintained by  $\text{NO}_3^-$  produced within the soil/sediment by nitrification ( $D_n$ ) (Christensen et al., 2000; Koop-Jakobsen & Giblin, 2010; Yin et al., 2015). Cores were collected and processed following the same protocol as  $\text{N}_2$ :Ar technique but with one modification. In these experiments, we used deionized water to which  $^{15}\text{NO}_3^-$  (99.9 atom %  $\text{KNO}_3$ ) and NaCl were added to match both in situ nitrate concentrations ( $\sim 50 \mu\text{M}$ ) and salinity values (0.1–0.3 ppt) (Koop-Jakobsen & Giblin, 2010). Because it is difficult to discern a  $^{14}\text{N}$ - $\text{NO}_3^-$  signature to detect coupled nitrification/denitrification at high dissolved  $\text{NO}_3^-$  concentration ( $\sim 50 \mu\text{M}$ ), we used DI water amended with  $50 \mu\text{M}$   $^{15}\text{NO}_3^-$  (99.9 atom %  $\text{KNO}_3$ ) (Koop-Jakobsen & Giblin, 2010). We assumed that this solution with a high  $^{15}\text{NO}_3^-$  concentration represented the average high  $^{14}\text{NO}_3^-$  concentrations and salinity values measured in situ across all seasons and habitats and fueling comparable ambient total denitrification rates. Thus, calculation of water column ( $D_w$ ) denitrification was measured as ( $D_{15}$ ), denitrification of added  $^{15}\text{NO}_3^-$  ( $D_w = D_{15}$ ) (Steingruber et al., 2001). At the end of the experiment, core soil was sliced at 4-cm interval and analyzed for bulk density (BD), %OM, TC, and TN.

### 2.4. Statistical Analysis

The relationship between temperature and denitrification rates was first assessed per core using linear regressions. The slope of each linear model per core ( $N = 3$  cores per treatment combination; Table 1) quantitatively defines how denitrification rates varied over a 10°C–30°C temperature range across treatments. This slope value was then used to perform two- and three-way ANOVAs to evaluate the role of each treatment and their interactions, including the type of substrate (i.e., soil vs. sediment representing two different habitats, i.e., benthic vs. wetland), regions (WLD vs. BLC), sites within each region (e.g., marsh, forested wetland, and channel), and denitrification technique (IPT vs.  $\text{N}_2$ :Ar). The data set for BD, %OM, TC, TN collected for each core incubation was used to evaluate if the denitrification treatment had any effect on soil properties within each habitat. All ANOVAs were performed using SAS and JMP-Pro (SAS, 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.

## 3. Results

### 3.1. Field Nutrient Concentrations in Surface and Pore Water

Inorganic nutrient concentration in the WLD and BLC reflect seasonal and hydrological differences within each region (Table S1).  $\text{NO}_3^-$  concentrations in open water (channel) in the WLD did not vary seasonally (range: 50.4–65.7  $\mu\text{mol L}^{-1}$ ) in contrast to BLC where higher concentrations (channel: 82.4  $\mu\text{mol L}^{-1}$ ; lake: 73.9  $\mu\text{mol L}^{-1}$ ) were observed only in the winter season (Table S1) while lower concentrations were measured in both spring (channel: 7.1; lake 10.1  $\mu\text{mol L}^{-1}$ ) and summer (channel: 44.8  $\mu\text{mol L}^{-1}$ ; lake 11.8  $\mu\text{mol L}^{-1}$ ).

$L^{-1}$ ) (Table S1). In contrast,  $NO_2^-$  concentrations were very low at both sites with values ranging from 0.61 to 0.80  $\mu\text{mol L}^{-1}$  and 0.47 to 0.88  $\mu\text{mol L}^{-1}$  in the WLD and BLC regions, respectively.  $NH_4^+$  concentrations in the water column were lower than  $NO_3^-$  concentrations and ranged from 1.2 to 3.1  $\mu\text{mol L}^{-1}$  in WLD, except during the spring, when the highest  $NH_4^+$  concentration reached 11  $\mu\text{mol L}^{-1}$ .  $NH_4^+$  water surface concentrations in BLC were low in all seasons ranging from 0.5 to 2.7  $\mu\text{mol L}^{-1}$ .

High  $NO_3^-$  concentrations were regularly observed in open water in contrast with low values measured in pore water ( $<5 \mu\text{mol L}^{-1}$ ; 20-cm soil depth) across all wetland types and sites, indicating rapid uptake of this nutrient from the water column. Pore water  $NO_3^-$  concentration was consistently  $<1 \mu\text{mol L}^{-1}$  in WLD, whereas in BLC values were  $<1 \mu\text{mol L}^{-1}$  during spring and summer and 1.5  $\mu\text{mol L}^{-1}$  during winter (Table S1). Accordingly,  $NO_2^-$  concentrations were even lower ( $<0.5 \mu\text{mol L}^{-1}$ ) in both WLD and BLC habitats. Pore water  $NH_4^+$  concentrations were high in the WLD interior marsh, where values decreased in summer (9.8  $\mu\text{mol L}^{-1}$ ) compared to concentrations observed in winter (27.1  $\mu\text{mol L}^{-1}$ ) (Table S1). Overall  $NH_4^+$  concentrations were lower across all seasons in BLC (range: 1.6–2.9  $\mu\text{mol L}^{-1}$ ).

### 3.2. Substrate Physicochemical Properties

All substrate properties show significant differences with depth (Figure 3). %OM in sediment/soils were higher in BLC (channel  $24.5 \pm 1.9\%$ , lake  $16.7 \pm 0.7\%$ , and marsh  $42.7 \pm 9.5\%$ ) than in WLD habitats (channel  $7.1 \pm 0.1\%$ , forested wetland  $7.7 \pm 0.1\%$ , and marsh  $17.2 \pm 1.9\%$ ) (Figure 3) as a result of differences in mineral sediment input via direct river discharge and therefore younger in age given the time needed to accumulate OM as observed in BLC (Figure 2). Overall, there was a significant difference in %OM content with depth ( $P < 0.001$ , Table 2). BD was low in habitats with higher %OM content and differed significantly with depth in both WLD and BLC habitats ( $P < 0.001$ , Table 2). In WLD habitats, BD was higher (channel:  $0.82 \pm 0.03 \text{ g cm}^{-3}$ ; forested wetland  $1.09 \pm 0.03 \text{ g cm}^{-3}$ ; marsh  $0.21 \pm 0.01 \text{ g cm}^{-3}$  marsh) (Figure 3). BD values in BLC were  $0.2 \pm 0.03 \text{ g cm}^{-3}$ ,  $0.2 \pm 0.04 \text{ g cm}^{-3}$ , and  $0.41 \pm 0.01 \text{ g cm}^{-3}$  in the channel, lake, and marsh, respectively.

Overall, sediment TN was low in the WLD channel ( $1.0 \pm 0.03 \text{ g cm}^{-3}$ ) and forested wetland ( $1.8 \pm 0.17 \text{ g cm}^{-3}$ ) (Figure 3). TN changed significantly with depth ( $P < 0.0001$ , Table 2), particularly in the WLD interior marsh ( $1.1 \pm 0.09 \text{ g cm}^{-3}$ ). Mean TC values at the top 4 cm in WLD were  $11.9 \pm 2.4 \text{ g cm}^{-3}$  (channel),  $21.5 \pm 1.4 \text{ g cm}^{-3}$  (forested wetland), and  $13.3 \pm 1.05 \text{ g cm}^{-3}$  (marsh). The TC:TN molar ratio in WLD sites were similar (channel:  $12.0 \pm 0.21$ ; forested wetland:  $11.9 \pm 0.4$ ; marsh  $11.8 \pm 0.2$ ); TN values in BLC sites were  $1.5 \pm 0.15 \text{ g cm}^{-3}$  (channel)  $1.3 \pm 0.34 \text{ g cm}^{-3}$ , (lake) and  $5.2 \pm 0.34 \text{ g cm}^{-3}$  (marsh) (Figure 3). Mean soil/sediment TC over depth was  $18.9 \pm 2.5 \text{ g cm}^{-3}$  in the channel,  $65.9 \pm 4.5 \text{ g cm}^{-3}$  in the marsh, and  $17.7 \pm 4.5 \text{ g cm}^{-3}$  in the lake (Figure 3). TC:TN molar ratio in the BLC sites was similar among habitats (channel:  $12.3 \pm 0.3$ ; marsh:  $12.77 \pm 0.1$ ; lake:  $13.3 \pm 0.2$ ) and WLD habitats.

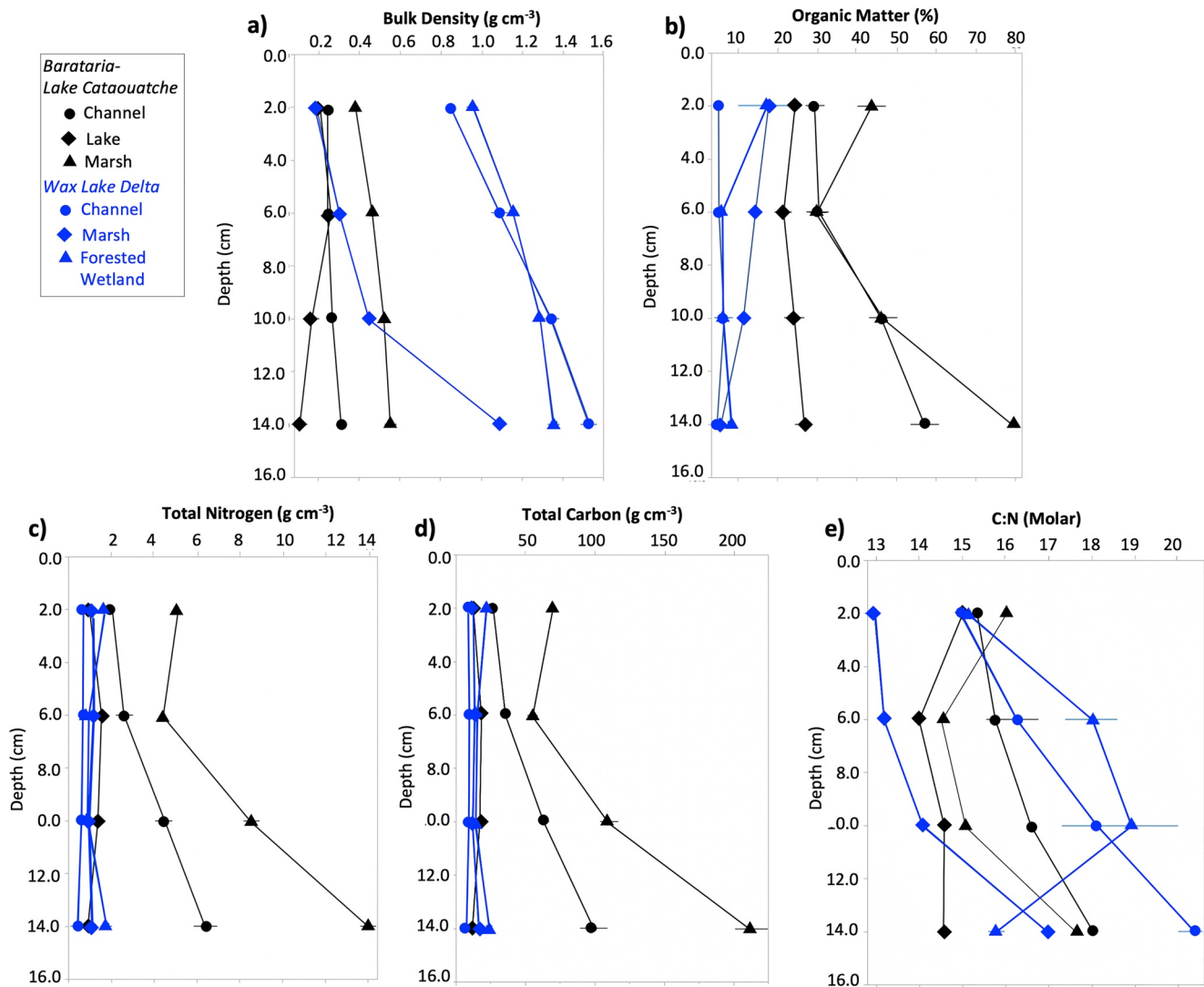
### 3.3. Sediment Dissolved Oxygen Consumption

All sites showed significant DO consumption but the rates varied across habitat depending on organic matter content and temperature (Table S2). The highest DO consumption rate was observed in both wetland soil (forested wetland:  $-1,718 \mu\text{mol m}^{-2} \text{ h}^{-1}$ , interior marsh:  $-1,916 \mu\text{mol m}^{-2} \text{ h}^{-1}$ ; BLC marsh:  $-875 \mu\text{mol m}^{-2} \text{ h}^{-1}$ ) and benthic sediments (WLD channel:  $-1,467 \mu\text{mol m}^{-2} \text{ h}^{-1}$ ; BLC channel:  $-976 \mu\text{mol m}^{-2} \text{ h}^{-1}$ , lake:  $649 \mu\text{mol m}^{-2} \text{ h}^{-1}$ ) at 30°C, while oxygen uptake was lower by up to 25% in benthic sediments at 10°C and 20°C (Figure 6; Tables S2 and S3).

### 3.4. Nitrogen Fluxes

Sediments from both WLD and BLC consumed  $NO_3^-$  but rates varied depending on temperature and type of substrate (Tables S2 and S3). Since we used in situ water to perform the experiments, there was an intrinsic natural variability in  $NO_3^-$  concentration among cores used in the  $N_2$ :Ar experiments at the beginning of the incubation; this variation was in part due to differences in habitat (wetland vs. benthic) and season. In contrast, in the case of the IPT experiments, the overlying water was enriched to a constant value of 50  $\mu\text{M}$   $15NO_3$  (99.9 at%  $KNO_3^-$ ). This led to a difference in the percentage in  $NO_3^-$  consumption which ranged





**Figure 3.** Soil profiles (0–16 cm) of variables in sediment and soil cores sampled in different habitats in Barataria-Lake Cataouatche and Wax Lake Delta regions in winter 2016. (a) Bulk density ( $\text{g cm}^{-3}$ ), (b) organic matter (%), (c) total nitrogen, (d) total carbon, and (e) molar C:N ratios. Values are the mean ( $\pm$ SE) depth (cm) value of soil and sediment sampled at four intervals: 0–4, 4–8, 8–12, and 12–16 cm (see methods).

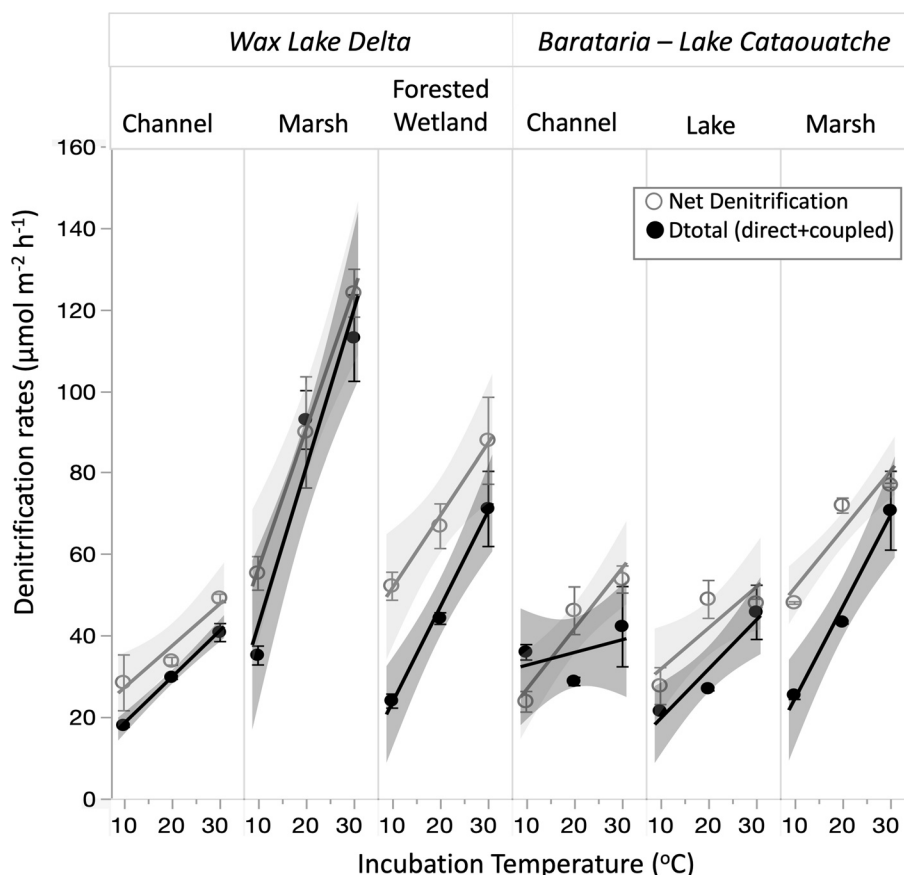
**Table 2**

ANOVA Table Results for Bulk Density ( $\text{g cm}^{-3}$ ), Organic Matter (%), Total Carbon ( $\text{g cm}^{-3}$ ), and Total Nitrogen ( $\text{g cm}^{-3}$ ) in Benthic (Channel, Lake) and Wetland (Marsh, Forested) Habitats in the Upper Barataria Bay (Lake Cataouatche) and the Wax Lake Delta Regions

Variables	Nparm	DF	Bulk density			Organic matter			Total carbon			Total nitrogen		
			Sum squares	F ratio	Prob > F	Sum squares	F ratio	Prob > F	Sum squares	F ratio	Prob > F	Sum squares	F ratio	Prob > F
Site	5	5	72.10	685.43	<0.0001*	59,364.61	125.96	<0.0001*	522829.18	303.41	<0.0001*	2907.54	372.70	<0.0001*
Depth	3	3	7.36	116.62	<0.0001*	4123.07	14.58	<0.0001*	96459.41	85.15	<0.0001*	347.23	74.18	<0.0001*
Site $\times$ depth	15	15	8.38	26.55	<0.0001*	13,956.08	9.87	<0.0001*	229183.87	40.46	<0.0001*	928.60	39.67	<0.0001*

Note. See Figure 1 for site location.

\* statistically significant ( $p < 0.05$ )



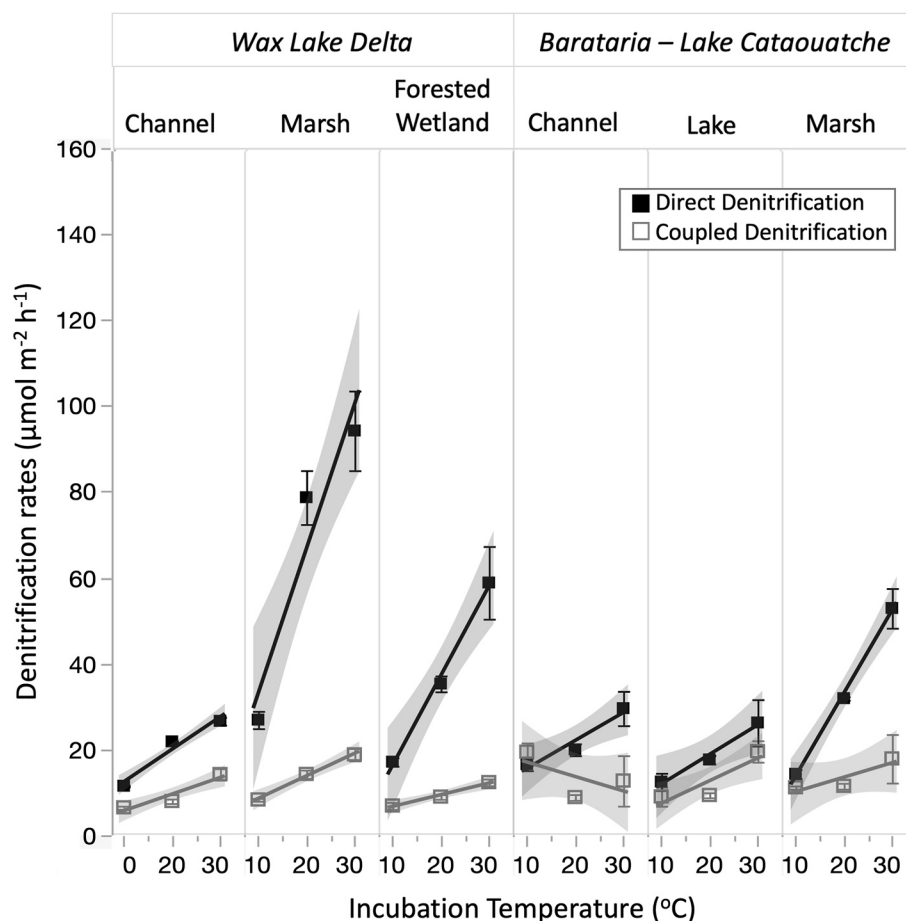
**Figure 4.** Mean ( $\pm$ SE) net denitrification and total denitrification ( $D_{total}$ ) rates in benthic (Channel, Lake) and wetland (marsh, forested wetlands) habitats of Wax Lake Delta (WLD) and Barataria-Lake Cataouatche (BLC) regions.

from 3% to 83% in the cores with ambient nitrate and from 4% to 38% in the incubations when nitrate was added (see methods) (Tables S2 and S3).  $\text{NO}_3^-$  uptake ( $\text{NO}_3^-$  consumption) was highest during summer in both WLD (channel:  $65.9 \mu\text{mol m}^{-2} \text{h}^{-1}$ ; forested wetland:  $167.3 \mu\text{mol m}^{-2} \text{h}^{-1}$ ; marsh:  $433.6 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) and BLC (channel:  $63.5 \mu\text{mol m}^{-2} \text{h}^{-1}$ ; lake:  $92.7 \mu\text{mol m}^{-2} \text{h}^{-1}$ ; marsh:  $139 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) habitats (Figure 7); the concurrent drop in  $\text{NH}_4^+$  concentrations was variable (Tables S2 and S3).

### 3.5. Net, Direct, and Coupled Denitrification Rates

Maximal net denitrification rates obtained using the  $\text{N}_2:\text{Ar}$  technique were highest in wetland sites, during summer with the highest rates found in marsh cores sampled in WLD ( $124.1 \pm 5.8 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) followed by the forested wetland ( $87.9 \pm 10.6 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) and the BLC marsh site ( $77.0 \pm 0.5 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) (Figure 4). The lower rates were observed in benthic sediments: WLD-channel ( $49.3 \pm 1.0 \mu\text{mol m}^{-2} \text{h}^{-1}$ ), BLC-channel ( $53.9 \pm 3.3 \mu\text{mol m}^{-2} \text{h}^{-1}$ ), and BLC-lake ( $48.0 \pm 1.0 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) (Figure 4). Seasonal denitrification rates in marshes were higher than in submerged sites (channels and lake station) and the differences were greater in WLD habitats ( $P < 0.05$ ). There was no significant difference in denitrification rates between BLC habitats (Table 5). Similar trend was observed when denitrification rates were measured using the IPT technique (Figure 5).  $D_{total}$  (direct + coupled) rates were highest in WLD marshes ( $113 \pm 10 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) and BLC marshes ( $70.8 \pm 9 \mu\text{mol m}^{-2} \text{h}^{-1}$ ). The lowest  $d_{total}$  rates were observed in benthic WLD-channel ( $18 \pm 0.4 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) and BLC-channel ( $28.8 \pm 1.0 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) (Figures 4 and 5; Tables 3 and 4).

There were no significant differences in denitrification rates measured using both techniques ( $SS = 0.01$ ;  $F_{1,6} = 0.01$ ;  $\text{Prob} > F = 0.92$ ; Table 6), including similar maximum rates. This similarity in trends and magnitudes was also observed in the case of benthic sediments across sites (Figure 4; Table 5). Denitrification rates



**Figure 5.** Mean ( $\pm$ SE) direct and coupled nitrification-denitrification rates in benthic (sites: Channel, Lake) and wetland (sites: marsh, forested wetlands) habitats across the Wax Lake Delta (WLD) and Barataria-Lake Cataouatche (BLC) regions.

obtained using both the  $N_2:Ar$  and IPT techniques were significantly controlled by temperature ( $p < 0.0001$ ) and followed a positive linear relationship where maximum rates were measured at 30°C treatment in wetland habitats in both WLD and BLC habitats. Temperature represented summer (30°C), spring (20°C), and winter (10°C) environmental conditions in both benthic and wetland sediments across habitats. Maximum net denitrification rates were measured at 30°C treatment in WLD wetlands (marsh, forested) and in the BLC marsh (Figure 4). The net denitrification maximum values for benthic sediments at 30°C were almost 50% lower than those observed in wetlands in both regions (WLD-channel:  $49.3 \pm 1.0$ ; BLC-channel:  $53.9 \pm 3.3$ , BLC-lake:  $48.0 \pm 1.0 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) (Figure 4). Direct and coupled denitrification rates obtained using the IPT followed the same linear pattern (i.e., rates vs. temperature) observed for net denitrification rates ( $N_2:Ar$  technique). The only exception was in the case of coupled denitrification in benthic channel substrates in BLC (Figures 4 and 5). High direct denitrification values were also measured at the wetlands sites in BLC ( $52.9 \pm 4.6 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) and WLD (forested wetland:  $58.9 \pm 8.5 \mu\text{mol m}^{-2} \text{h}^{-1}$ , Figure 5). Maximum  $D_{\text{total}}$  values were also observed at 30°C for benthic sediments; although these values were significantly lower (channel-BLC:  $29.6 \pm 3.9$ ; channel-WLD:  $26.4 \pm 0.9$ ; lake-BLC:  $26.2 \pm 5.3 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) than in wetland soils (Table 3; Figure 4). The rates for coupled denitrification were not significantly different across benthic and wetland habitats (Table 3; Figure 5).

**Table 3**  
Mean ( $\pm$ SE) Net and  $D_{total}$  (Direct + Coupled) Denitrification Rates at Different Incubation Temperatures in the Upper Barataria-Lake Cataouatche and the Wax Lake Delta Regions

Region	Site	Habitat	Incubation ( $^{\circ}$ C)	( $\mu\text{mol m}^{-2} \text{h}^{-1}$ )	Direct ( $\mu\text{mol m}^{-2} \text{h}^{-1}$ )	Coupled ( $\mu\text{mol m}^{-2} \text{h}^{-1}$ )	$D_{total}$ ( $\mu\text{mol m}^{-2} \text{h}^{-1}$ )
Barataria-Lake Cataouatche	Channel	Benthic	10	23.9 $\pm$ 2.5	16.5 $\pm$ 1.5	19.4 $\pm$ 2.1	36.06 $\pm$ 1.9
			20	46.3 $\pm$ 5.8	19.9 $\pm$ 1.4	8.9 $\pm$ 0.7	28.89 $\pm$ 1.0
			30	53.9 $\pm$ 3.3	29.6 $\pm$ 4.0	12.7 $\pm$ 5.9	42.3 $\pm$ 9.8
	Lake	Benthic	10	27.8 $\pm$ 4.5	12.5 $\pm$ 2.0	9.0 $\pm$ 2.2	21.5 $\pm$ 0.4
			20	49.0 $\pm$ 4.7	17.6 $\pm$ 1.0	9.4 $\pm$ 0.6	27 $\pm$ 0.4
			30	48.1 $\pm$ 1.0	26.2 $\pm$ 5.4	19.6 $\pm$ 2.5	45.8 $\pm$ 6.7
	Marsh	Wetland	10	48.2 $\pm$ 0.3	14.3 $\pm$ 1.0	11.1 $\pm$ 0.4	25.5 $\pm$ 1.0
			20	72.1 $\pm$ 1.8	31.9 $\pm$ 0.4	11.5 $\pm$ 0.7	43.4 $\pm$ 0.4
			30	77.1 $\pm$ 0.5	52.9 $\pm$ 4.6	17.8 $\pm$ 5.7	70.8 $\pm$ 9.7
Wax Lake Delta	Channel	Benthic	10	28.6 $\pm$ 6.8	11.5 $\pm$ 0.2	6.5 $\pm$ 0.4	18 $\pm$ 0.4
			20	33.9 $\pm$ 0.9	21.8 $\pm$ 0.2	8.0 $\pm$ 0.5	29.8 $\pm$ 0.4
			30	49.3 $\pm$ 1.0	26.6 $\pm$ 0.9	14.2 $\pm$ 1.3	40.9 $\pm$ 2.2
	Forested	Wetland	10	52.3 $\pm$ 3.4	17.1 $\pm$ 1.0	6.9 $\pm$ 0.8	24.08 $\pm$ 1.7
			20	67.0 $\pm$ 5.5	35.3 $\pm$ 1.9	9.0 $\pm$ 0.6	44.3 $\pm$ 1.4
			30	87.9 $\pm$ 10.6	58.8 $\pm$ 8.5	12.3 $\pm$ 0.8	71.2 $\pm$ 9.2
	Marsh	Wetland	10	55.4 $\pm$ 4.1	26.9 $\pm$ 2.0	8.3 $\pm$ 0.3	35.2 $\pm$ 2.3
			20	90.0 $\pm$ 13.6	78.7 $\pm$ 6.3	14.2 $\pm$ 1.0	93.0 $\pm$ 7.2
			30	124.1 $\pm$ 5.9	94.2 $\pm$ 9.3	18.8 $\pm$ 1.4	113.0 $\pm$ 10.6

#### 4. Discussion

Our results revealed that denitrification rates were high in wetland and benthic habitats and that wetland sites were also more responsive to temperature. Denitrification rates in benthic habitats were similar between WLD and BLC, although the marsh site at WLD showed higher denitrification rates than in the BLC

**Table 4**  
Regression Results of Site and Habitat Interactions Effect on Direct and Coupled Denitrification Rates

Type of denitrification	Region	Site	Habitat	Estimate	$p > [t]$	Least sq. mean	DF	Sum of squares	Mean square	F-value	p-value
Direct	Barataria-Lake Cataouatche	Channel	Benthic	-0.928	0.013*	0.650 <sup>B</sup>	5	17.72	3.544	9.566	0.0007*
		Lake	Benthic	-0.891	0.016*	0.688 <sup>B</sup>					
		Marsh	Wetland	0.35	0.296	1.929 <sup>AB</sup>					
	Wax Lake Delta	Channel	Benthic	-0.823	0.024*	0.755 <sup>B</sup>					
		Forested	Wetland	0.506	0.14	2.086 <sup>AB</sup>					
		Marsh		1.786	0.0001*	3.366 <sup>A</sup>					
Coupled	Barataria-Lake Cataouatche	Channel	Benthic	-0.621	0.009*	-0.336 <sup>A</sup>	5	1.546	0.309	2.136	0.13
		Lake	Benthic	0.241	0.251	0.527 <sup>A</sup>					
		Marsh	Wetland	0.05	0.804	0.336 <sup>A</sup>					
	Wax Lake Delta	Channel	Benthic	0.101	0.62	0.387 <sup>A</sup>					
		Forested	Wetland	-0.012	0.95	0.272 <sup>A</sup>					
		Marsh	Wetland	0.239	0.254	0.525 <sup>A</sup>					

Notes. See Figure 1 for definitions of the different types of denitrification. Least square mean values with different letter (A, B) are significantly different (\*,  $p < 0.05$ ).

**Table 5**  
Regression Results of Site and Habitat Interactions Effect on Net and  $D_{total}$  Denitrification Rates

Type of denitrification	Region	Site	Habitat	Estimate	p > [t]	Least sq. mean	DF	Sum of squares	Mean square	F-value	P-value
Net	Barataria-Lake Cataouatche	Channel	Benthic	-0.201	0.586	1.500 <sup>B</sup>	5	12.09	2.418	5.147	0.009*
		Lake	Benthic	-0.686	0.081	1.015 <sup>B</sup>					
		Marsh	Wetland	-0.257	0.489	1.444 <sup>B</sup>					
	Wax Lake Delta	Channel	Benthic	-0.666	0.089	1.036 <sup>B</sup>					
		Forested	Wetland	0.08	0.827	1.783 <sup>AB</sup>					
		Marsh	Wetland	1.732	0.0004*	3.434 <sup>A</sup>					
$D_{total}$ (Direct + Coupled)	Barataria-Lake Cataouatche	Channel	Benthic	-1.339	0.024*	0.314 <sup>B</sup>	5	15.894	3.178	3.248	0.043*
		Lake	Benthic	-0.438	0.416	1.215 <sup>AB</sup>					
		Marsh	Wetland	-0.014	0.978	1.638 <sup>AB</sup>					
	Wax Lake Delta	Channel	Benthic	-0.51	0.346	1.142 <sup>AB</sup>					
		Forested	Wetland	0.704	0.201	2.358 <sup>AB</sup>					
		Marsh	Wetland	1.598	0.009*	3.251 <sup>A</sup>					

Notes. See Figure 1 for definitions of the different types of denitrification. Least square mean values with different letter (A, B) are significantly different (\*,  $p < 0.05$ ).

site in spite of having lower concentrations of organic matter. We also found a significant linear relationship between denitrification rates and temperature regardless of sediment/soil composition (i.e., OM, C:N ratio, and BD) across all habitats in erosional (BLC) and progradational (WLD) delta lobes in the Mississippi River delta plain.

Although the initial  $\text{NO}_3^-$  concentrations in the IPT ( $\sim 50 \mu\text{M}$ ) and  $\text{N}_2:\text{Ar}$  ( $44.8 \pm 21.7$ ) core incubations were slightly different, the similarity in the rates by both methods indicates that N fixation is low and not a major N input into these wetland ecosystems. This is expected given the generally high ( $>40 \mu\text{M}$ ) inorganic N availability in the water column (i.e.,  $\text{NO}_3^-$ ; Table S1) and sediment ( $\text{NH}_4^+$  plus  $\text{NO}_3^-$ ; Elliton et al., 2020; Li et al., 2020) in both the Barataria Bay and WLD regions throughout the year. Overall, N fixation in wetlands and benthic sediments is generally low when other sources of N are available due to the high energetic cost of fixing atmospheric  $\text{N}_2$  by the microbial community (Andersson et al., 2014; Foster & Fulweiler, 2014) (see Figure 1).

When partitioning the total denitrification ( $D_{total}$ ) into direct and coupled nitrification-denitrification (i.e.,  $D_{total}$ ; see Figure 1), our results showed that direct denitrification was the dominant pathway for  $\text{N}_2$  production over coupled nitrification-denitrification in all habitats and seasons (i.e., spring, summer, and fall). This result underscores the importance of high  $\text{NO}_3^-$  concentrations during river discharge, which drives N transformations on seasonal and annual basis in the Louisiana delta plain. There was a higher denitrification response to temperature changes in the marsh than in the forested wetland in the WLD. Denitrification response to temperature in marshes from both regions was higher in the WLD marsh than in the marsh located in the northern Barataria Bay (BLC). Conversely, the denitrification rates in benthic sediments (i.e.,

**Table 6**  
Summary Results of ANOVAs Comparing Rates of Different Types of Denitrification, That Is, Net ( $\text{N}_2:\text{Ar}$ ) Versus  $D_{total}$  Rates and Direct Versus Coupled Denitrification Rates in the Barataria-Lake Cataouatche and Wax Lake Delta Regions; See Figure 1 for Definitions of the Different Types of Denitrification

Variables	Nparm	DF	Net versus $D_{total}$ denitrification			Direct versus coupled denitrification		
			Sum of squares	F ratio	Prob > F	Sum of squares	F ratio	Prob > F
Type of denitrification	1	1	0.01	0.01	0.9213	9.40	36.14	<0.0001*
Site	6	6	26.09	5.81	0.0009*	12.12	7.77	<0.0001*
Type of denitrification $\times$ site	6	6	2.81	0.63	0.7068	4.88	4.88	<0.0026*

tidal channels and northern Lake Cataouctache) were approximately the same across all sites (Figures 4 and 5), indicating the role of temperature in controlling denitrification rates, but not at the same rate as in the case of wetland soils.

In the following sections, we discuss specific processes regulating denitrification in comparison to other coastal regions and the use of denitrification as a functional ecosystem property. This includes management implications of denitrification in wetlands and coastal restoration/tertiary treatment programs.

#### 4.1. Denitrification Response to Temperature

To determine temperature responses, we collected intact cores during winter, spring, and summer and incubated them at temperatures close to the measured in situ temperature at the time of collection. We use this approach to assure that the microbial consortium will not be exposed to an extreme difference (Lee & Francis, 2017; Nair et al., 2007). Temperature is reported to influence the metabolic activity, community diversity, biomass, and spatial distribution of nitrifying and denitrifying archaea/bacteria in both natural and constructed wetlands (Phipps & Crumpton, 1994; Reddy et al., 1980; Spieles & Mitsch, 1999; Willers et al., 1993); thus, we hypothesized that denitrification rates would be highest during summer and lowest during winter seasons at both study sites (Canion et al., 2014; Cornwell et al., 1999; Rivera-Monroy et al., 2013). Our results show that during winter (10°C), denitrification activity is reduced by 17%–55% in BLC and 47%–66% in WLD when compared to ambient late spring/early summer temperature (20°C). This variable response to temperature has management implications given the maximum river discharge in this region occurs during late winter/early spring when air and water temperature are low (<15°C). Because the current freshwater diversions used to create/restore wetlands are generally operational during spring when the MR is at a high stage to facilitate the pumping of riverine water and sediments into the restored estuarine areas, it is expected that during low river discharge in the summer,  $\text{NO}_3^-$  concentrations become a limiting factor for extensive denitrification at the landscape level (see Section 4.4).

To our knowledge, there are no studies determining denitrification rates simultaneously using direct techniques under different temperature regimes in other subtropical wetlands within deltaic environments (Table 7) (Adame et al., 2019; Pérez-Villalona et al., 2015; Piña-Ochoa & Álvarez-Cobelas, 2006) (Table 7). Yet, selected studies using either technique in natural areas, including upper watersheds, coastal regions, and treatment wetlands, show ranges that are similar to our denitrification estimates (Table 7). For example, previous studies show a rapid increase in denitrification activity ( $77.2 \mu\text{mol N m}^{-2} \text{h}^{-1}$  at 8°C to  $289.6 \mu\text{mol N m}^{-2} \text{h}^{-1}$  at 30°C) in wetlands sediments collected within the Atchafalaya River basin when the temperature was experimentally increased from 8°C to 22°C–30°C (Lindau et al., 2011). The only study reporting denitrification rates using direct techniques in a deltaic coastal system was performed in the San Francisco Bay delta, where benthic sediments were sampled along a salinity (0.1–10.2) gradient where denitrification rates ranged from  $25\text{--}41.7 \mu\text{mol m}^{-2} \text{h}^{-1}$  (Cornwell et al., 2014). Similar to the MR delta region, the San Francisco Bay is also undergoing eutrophication as a result of high dissolved inorganic N loading rates ( $27, 717 \text{ Mt yr}^{-1}$ ) due to agriculture and urban development (Beck et al., 2018). One study assessing denitrification in benthic sediments showed similar values from both techniques (IPT,  $8\text{--}30 \mu\text{mol m}^{-2} \text{h}^{-1}$ ;  $\text{N}_2:\text{Ar}$ ,  $20\text{--}60 \mu\text{mol m}^{-2} \text{h}^{-1}$ ; Moreton Bay, Australia) (Ferguson Angus & Eyre, 2007).

Selected studies in both natural and treatment wetlands using either the  $\text{N}_2:\text{Ar}$  or IPT techniques show similar or higher rates at temperatures  $>20^\circ\text{C}$  in diverse types of wetlands (Table 7). One study performed using the IPT in different wetlands habitats found that mean rates at high temperature ( $29^\circ\text{C}\text{--}31^\circ\text{C}$ ) were  $507 \pm 25$  (freshwater),  $236 \pm 36$  (saltmarsh), and  $107 \pm 32 \mu\text{mol m}^{-2} \text{h}^{-1}$  (mangrove); these values were higher than our maximum values in the marsh ( $70.8\text{--}113.1 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) and forested wetland habitats ( $71.2 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) (Table 7).

In contrast, other studies show rates similar to our values at spring and summer temperatures (i.e.,  $91 \mu\text{mol m}^{-2} \text{h}^{-1}$ , Great Sippewissett Marsh/Estuary; Kaplan et al., 1979) ( $214 \mu\text{mol m}^{-2} \text{h}^{-1}$ , Dyke Marsh Preserve; Hopfensperger et al., 2009) and in other natural wetlands (Table 7). Still, the highest denitrification values are observed in constructed wetlands (range:  $290\text{--}965.9 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) under high N loads at relatively low ( $14^\circ\text{C}$ ) to high temperatures ( $18^\circ\text{C}\text{--}28^\circ\text{C}$ ) (Table 7).

**Table 7**  
Selected Denitrification Studies Using Direct Techniques in Coastal Louisiana and Other Coastal Regions and Treatment Wetlands

Region	Location	Habitat (type of substrate)	Incubation temperature (°C)	Method	<sup>15</sup> NO <sub>3</sub> enrichment (μmol L <sup>-1</sup> )	Mean rate range and/or mean ± SE (μmol m <sup>-2</sup> h <sup>-1</sup> )	References	
Coastal Louisiana, USA	Wax Lake Delta	Freshwater Marsh	12, 25	N <sub>2</sub> :Ar (MIMS) <sup>a</sup>	NA	−74.5 to 157.5	Henry and Twilley (2013)	
	Wax Lake Delta	Freshwater Marsh	11–13	N <sub>2</sub> :Ar (MIMS)	NA	34.8–296.2	Li et al. (2020)	
			22	N <sub>2</sub> :Ar (MIMS)	NA	315.2–734.4		
	Continental Shelf River Plume	Benthic sediment	20–30	N <sub>2</sub> :Ar (MIMS)	NA	58.3	Lehrter et al. (2012)	
	Vegetated brackish marsh; Breton Sound	Marsh soil	20–25	NO <sub>3</sub> measurement	32	496.7–568.1	VanZomeran et al. (2012)	
	Salt marsh Barataria Bay	Marsh soil	25	NO <sub>3</sub> depletion measurements	NA	56.5 ± 5.3	Levine et al. (2017)	
	Brackish Marsh Delacroix St. Bernard Parish	Marsh soil	25	NO <sub>3</sub> and NH <sub>4</sub> measurement	32	18.7–24	VanZomeran et al. (2013)	
	Wax Lake Delta	Benthic (Channel)	10, 20, 30	N <sub>2</sub> :Ar (MIMS)	NA	28.57–53.0	This study	
			Forested wetland	10, 20, 30	N <sub>2</sub> :Ar (MIMS)	NA		52.3–87.9
			Freshwater wetland	10, 20, 30	N <sub>2</sub> :Ar (MIMS)	NA		55.4–124.1
	Freshwater; Lake Cataouatche, Upper Barataria Bay	Benthic (Channel)	10, 20, 30	N <sub>2</sub> :Ar (MIMS)	NA	23.9.—53.9	This study	
			Benthic (Lake)	10, 20, 30	N <sub>2</sub> :Ar (MIMS)	NA		27.8–48.1
			Freshwater wetland	10, 20, 30	N <sub>2</sub> :Ar (MIMS)	NA		48.2–77.0
	Freshwater; Wax Lake Delta	Benthic (Channel)	10, 20, 30	IPT <sup>b</sup>	55	18.0–40.1	This study	
			Forested wetland	10, 20, 30	IPT	55		24.1–71.2
			Marsh	10, 20, 30	10, 20, 30	55		35.3–113.1
	Freshwater Lake Cataouatche, Upper Barataria Bay	Benthic (Channel)	10, 20, 30	IPT	55	36.1–42.3	This study	
			Benthic (Lake)	10, 20, 30	IPT	55		21.6.—45.9
			Marsh	10, 20, 30	IPT	55		25.5–70.8
Coastal (Canada)	Lower St. Lawrence Estuary, Quebec	Benthic sediment	4	IPT	100	11.3	Crowe et al. (2012)	
Shelf (US, Denmark and Spitsbergen)	George Island, Hausstrand Sylt; Spitsbergen Ymerbukta	Near shore sediment	−1 to 42	IPT	100	0.08–14.96	Canion et al. (2014)	
Coastal (Australia)	Deception Bay, Brisbane	Muddy sediments	9.4–29.2	IPT	100	8–30	Ferguson Angus and Eyre (2007)	
Coastal (Denmark)	Aarhus Bay and Norsminde Fjord	Benthic		IPT	5, 10, 25, 45, 100	32–124	Eyre et al. (2002)	
Coastal (USA)	Oyster farm, Chesapeake Bay	Oyster farm	20–30	IPT	30	5–19	Lunstrum and Aoki (2016)	
Coastal (Australia)	Deception Bay, Brisbane	Muddy sediments	9.4–29.2	N <sub>2</sub> :Ar (MIMS)	N <sub>2</sub> :Ar (MIMS)	20–60	Ferguson Angus and Eyre (2007)	

**Table 7**  
*Continued*

Region	Location	Habitat (type of substrate)	Incubation temperature (°C)	Method	<sup>15</sup> NO <sub>3</sub> enrichment (μmol L <sup>-1</sup> )	Mean rate range and/or mean ± SE (μmol m <sup>-2</sup> h <sup>-1</sup> )	References
Coastal (Denmark)	Aarhus Bay, Norsminde Fjord	Benthic	10–14	N <sub>2</sub> :Ar (MIMS)	NA	19–99	Eyre et al. (2002)
South Atlantic Bight	Continental Shelf sands	Benthic	22	N <sub>2</sub> :Ar (MIMS)	20	10.6–60.9	Rao et al. (2007)
Coastal (Australia)	Tulley-Murray Rivers/Estuary	Freshwater marsh	29–31	IPT	1.5–40	507 ± 257	Adame et al. (2019)
		Saltmarsh	29–31		1.5–40	236 ± 36	
		Mangroves	29–31		1.5–40	107 ± 32	
		Lake	29–31		1.5–40	6.3–10.8	
Coastal (Venice, Italy)	Coastal Lagoon	Saltmarsh	15	IPT	71	135.7 ± 2.9	Eriksson et al. (2003)
			20			17.9 ± 0.6	
			25			11.4 ± 0.4	
			24			3.6 ± 0.1	
			25			35.7 ± 04	
			25			271.4 ± 28	
		Benthic (creek)	15			150 ± 7.1	
			20			71.4 ± 13	
			25			10.7	
			24			12.9	
			25			53.6 ± 3.6	
			25			285.7 ± 43	
19	155.7 ± 39						
Coastal Lagoon, Puerto Rico	San Jose	Benthic	28.3–30.7	MIMS	NA	329 ± 34218.4–937	Perez-Villalona et al. (2015)

Region	Treatment Wetlands	Habitat (type of substrate)	Incubation temperature (°C)	Method	<sup>15</sup> NO <sub>3</sub> enrichment (μmol L <sup>-1</sup> )	Mean rate range and/or mean ± SE (μmol m <sup>-2</sup> h <sup>-1</sup> )	References
Falmouth, MA, USA	Great Sippewissett Marsh/ Estuary	Saltmarsh	5–35	N <sub>2</sub> :Ar (MIMS) <sup>c</sup>	NA	79.2 ± 12.7	Kaplan et al. (1979)
Chesapeake Bay, Potomac River, USA	Dyke Marsh Preserve	Freshwater Marsh Tidal	13.7	N <sub>2</sub> :Ar (MIMS)	NA	56–214	Hopfensperger et al. (2009)
Neuse River Estuary, North Carolina, USA	Constructed wetland	Emergent marsh/ open water	10–28	N <sub>2</sub> :Ar (MIMS)	NA	59.3–290.4	Poe et al. (2003)
Riverside County, California, USA	Hemet/San Jacinto Multipurpose Demonstration Wetland	Marsh-Pond	15–18	N <sub>2</sub> :Ar (MIMS)	NA	63–2,455	Smith et al. (2000)
Coastal (Australia)	Surface Flow Constructed Wetland New South Wales	Marsh	24	Gas Chromatograph/ Isotope Ratio Mass Spectrometer	100	651.5–965.9	Erlor et al. (2008)

<sup>a</sup>Membrane Inlet Mass Spectrometer (MIMS): N<sub>2</sub>: Argon technique. <sup>b</sup>IPT, Isotopic Pairing Technique. <sup>c</sup>Jar technique; field measurements; NA, do not apply; ND, no data.



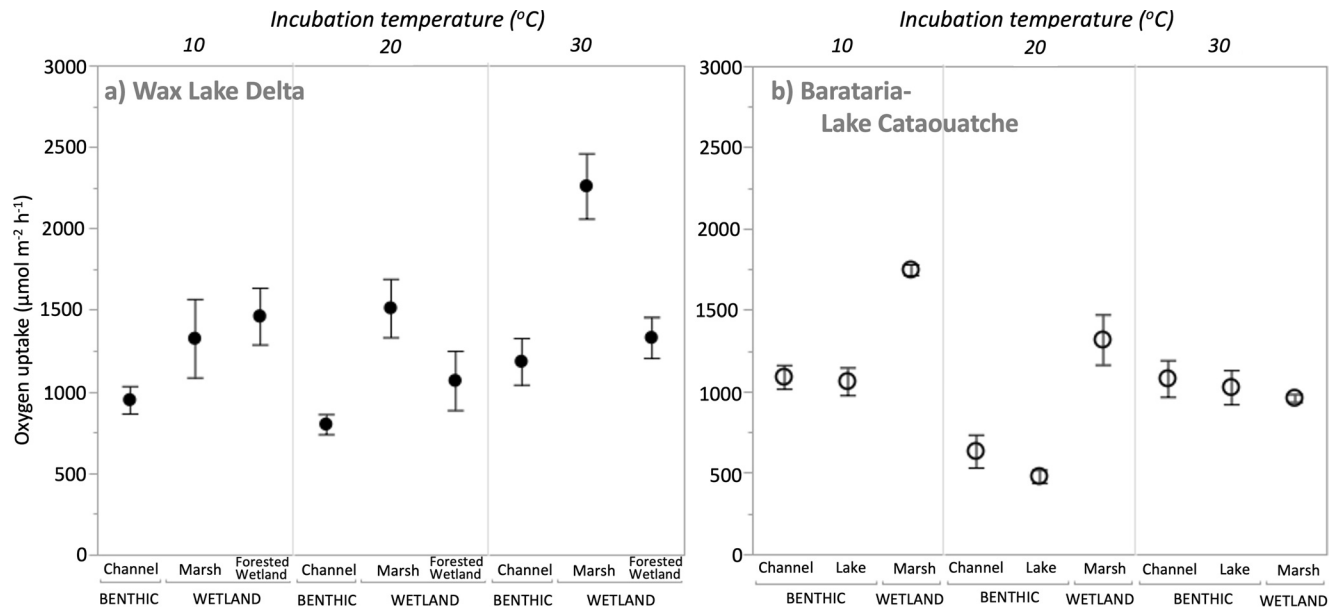
Overall, low benthic denitrification rates were measured in most studies (Table 7). For instance, total denitrification values (IPT) in benthic sediments from a freshwater lake in a subtropical watershed show low values ( $6.3\text{--}10.8\ \mu\text{mol m}^{-2}\ \text{h}^{-1}$ ) (Adame et al., 2019) even when incubated at high temperature range ( $29^\circ\text{C}\text{--}31^\circ\text{C}$ ). Interestingly, another study performed in a tropical climate at high incubation temperatures ( $28^\circ\text{C}\text{--}31^\circ\text{C}$ ) obtained higher rates in experimental incubations of benthic cores sampled in the San Jose Lagoon, Puerto Rico; the mean denitrification rate ( $329 \pm 342\ \mu\text{mol N m}^{-2}\ \text{h}^{-1}$ ) here was among the highest for benthic sediments (Table 7). This result was explained as the interaction between high temperature and high  $\text{NO}_3^-$  availability. Indeed, the San Jose Lagoon is considered a hyper-eutrophic system given the high nutrient loading rates into the lagoon (Perez-Villalona et al., 2015).

Denitrification studies using direct techniques such as the  $\text{N}_2:\text{Ar}$  ratio and IP techniques are scarce in coastal Louisiana. An assessment of previous denitrification studies in this region (1981–2008) showed that the acetylene inhibition (Yoshinari & Knowles, 1976) and  $15\text{N}$  flux (e.g., DeLaune et al., 1998) were the preferred techniques (95%), with most of these studies using sediment slurries rather than intact sediment cores (Rivera-Monroy et al., 2010). Most studies used indirect techniques to assess rates in different wetland habitats along salinity and hydrological gradients. Experimental work (acetylene reduction technique) using soil collected in the Atchafalaya River basin showed a rapid increase in potential denitrification activity from  $77\ \mu\text{mol N m}^{-2}\ \text{h}^{-1}$  at  $8^\circ\text{C}$  to  $290\ \mu\text{mol N m}^{-2}\ \text{h}^{-1}$  at  $30^\circ\text{C}$  (Lindau et al., 2008). The three most recent studies assessing denitrification using the  $\text{N}_2:\text{Ar}$  technique in coastal Louisiana were performed in the WLD wetland habitats (range:  $-74.5\text{--}157.5\ \mu\text{mol m}^{-2}\ \text{h}^{-1}$ ; Henry & Twilley, 2014) (mean seasonal range:  $100\text{--}397\ \mu\text{mol N m}^{-2}\ \text{h}^{-1}$ ; Li et al., 2020) and the Louisiana Continental Shelf ( $58.3\ \mu\text{mol m}^{-2}\ \text{h}^{-1}$ ; Lehrter et al., 2012) (Table 7). The highest mean denitrification rate ( $734\ \mu\text{mol m}^{-2}\ \text{h}^{-1}$ ) was measured in a supratidal area in Mike Island, which is similar to our forested wetland study site, under experimental conditions of high  $\text{NO}_3^-$  ( $\sim 100\ \mu\text{M}$ ) and soil temperature of  $22^\circ\text{C}$ . Another study (VanZomerem et al., 2012) where vegetated plugs from a brackish marsh (*Spartina patens* under flooded conditions) were incubated at fall/summer temperatures ( $20^\circ\text{C}\text{--}25^\circ\text{C}$ ) and enriched with  $32\ \mu\text{M}$   $15\text{N}\text{--}\text{NO}_3^-$  also showed maximum denitrification rates ranging from  $496.7$  to  $568.1\ \mu\text{mol m}^{-2}\ \text{h}^{-1}$  obtained using a mass balance approach (Table 7). These rates are four times of our maximum observed denitrification rates (Figures 4 and 5) and underscore the relative role of  $\text{NO}_3^-$  concentrations partially regulating the slope of the relationship between temperature and denitrification rates as described in other N removal studies in treatment wetlands (Bachand & Horne, 1999; Lu et al., 2009; Spieles & Mitsch, 1999; Stober et al., 1997; Willers et al., 1993).

#### 4.2. Denitrification Pathway and Magnitude

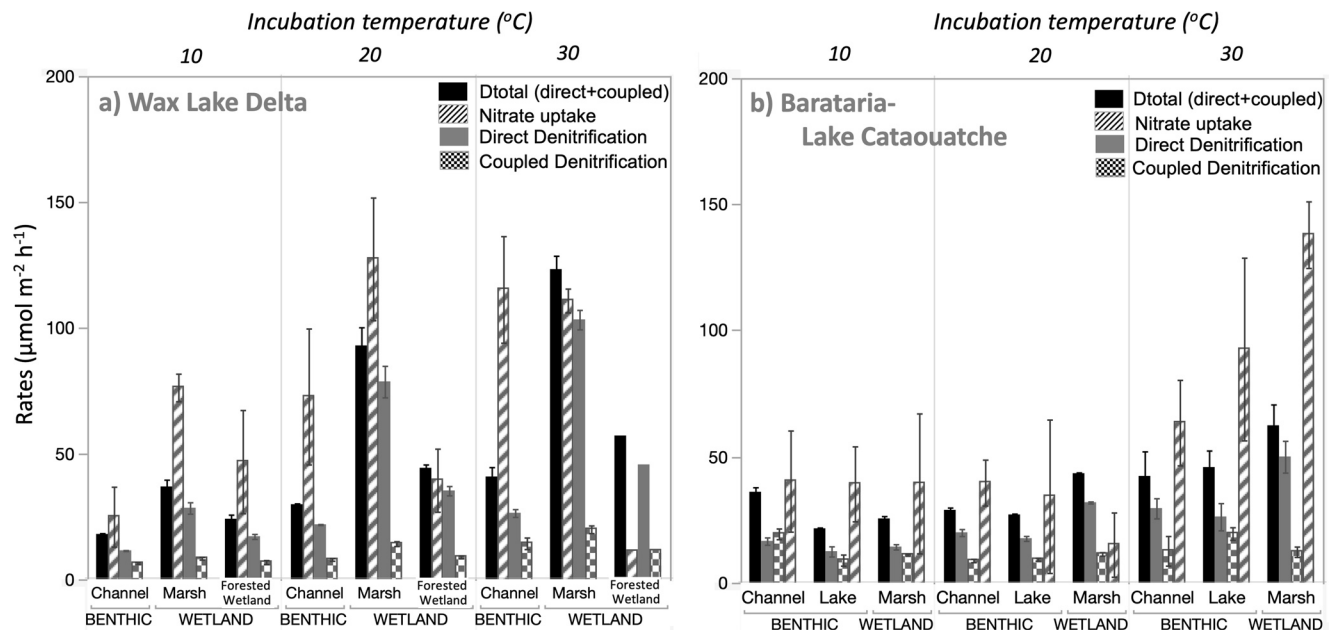
The use of different techniques to measure denitrification, despite different assumptions and interpretations of the  $\text{N}_2$  flux source, allowed the evaluation of the relative importance of specific N transformations such as coupled nitrification-denitrification (IPT) and N fixation ( $\text{N}_2:\text{Ar}$ ) (Figure 4). Our experiments showed that although coupled denitrification occurred in sediments from both sites, its contribution was generally very low, even at high-temperature treatments (Figure 5) and from sites with high  $\text{NH}_4^+$  concentrations in pore water (Table S1). Direct denitrification, for example, measured in marsh cores from both BLC and WLD and incubated at  $30^\circ\text{C}$  was  $52.9 \pm 4.6$  and  $94.2 \pm 9.3\ \mu\text{mol m}^{-2}\ \text{h}^{-1}$ , respectively. In this case, coupled denitrification rates in both sites were significantly lower ( $17.9 \pm 5.6$  and  $18.8 \pm 1.4\ \mu\text{mol m}^{-2}\ \text{h}^{-1}$ ) representing on average  $<20\%$  of the total denitrification rate. Overall, our results suggest that direct denitrification is the dominant microbial respiration in all types of substrates under high  $\text{NO}_3^-$  availability. Although denitrification was apparently supported by  $\text{NO}_3^-$  from nitrification, these rates were lower (Figure 5). These  $\text{NO}_3^-$  production/consumption and net nitrate reduction values indicate a rapid nitrification and denitrification interactions in coastal Louisiana. Indeed, the net denitrification rates observed in the WLD are comparable to other studies in the same area (range:  $\sim 50\text{--}300\ \mu\text{mol m}^{-2}\ \text{h}^{-1}$  (Henry & Twilley, 2014) (Table 7). It is assumed that in the absence of N fixation, net denitrification equals  $D_{\text{total}}$  denitrification since this balance could be offset by the presence of N fixation (An et al., 2001; Foster & Fulweiler, 2014) (see Figure 1).

As mentioned, the two most recent studies assessing denitrification using the  $\text{N}_2:\text{Ar}$  technique in coastal Louisiana were performed in wetland habitats across the WLD (range:  $-74.5\text{--}157.5\ \mu\text{mol m}^{-2}\ \text{h}^{-1}$ , Henry & Twilley, 2014; mean range:  $100$  (Spring) $\text{--}397$  (Summer)  $\mu\text{mol m}^{-2}\ \text{h}^{-1}$ , Li et al., 2020). Given the range of  $\text{NO}_3^-$  enrichments and temperature treatments used to estimate denitrification in those studies and our



**Figure 6.** Mean ( $\pm$ SE) oxygen uptake rates in (a) Wax Lake Delta (WLD), and (b) Barataria-Lake Cataouatche (BLC) regions during isotope pairing technique experiments.

results, it is apparent that direct denitrification is the dominant transformation in the WLD. In the case of the BLC, one experimental study using the  $^{15}\text{N}\text{-NO}_3$  mass balance approach sampled cores in benthic and freshwater/brackish marshes close to the MR and reported high denitrification rates at  $25^\circ\text{C}$  (e.g.,  $496.7 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) (VanZomerem et al., 2012, 2013) (Table 7). This study suggested, that  $\text{NH}_4^+$  production in both benthic sediments and marsh soil could be a source of  $\text{NO}_3^-$  through coupled N mineralization and nitrification, thus decreasing potential  $\text{NO}_3^-$  removal capacity by denitrification. However, our results show that in both, the WLD and BLC oligohaline habitats, coupled nitrification-denitrification rates were significantly lower than direct denitrification at low ( $10^\circ\text{C}$ ) and high temperatures ( $30^\circ\text{C}$ ). In the case of WLD wetland habitats,



**Figure 7.** Mean ( $\pm$ SE) nitrate uptake and total denitrification (direct + coupled) rates in (a) Wax Lake Delta (WLD), and (b) Barataria-Lake Cataouatche (BLC) habitats during isotope pairing technique (IPT) experiments.

$D_{\text{total}}$  was higher than  $\text{NO}_3^-$  uptake (Figure 7), especially during summer when denitrification supported by  $\text{NO}_3^-$  from nitrification process was low (Figure 5). Because of the experimental constraints to include most of the key environmental conditions controlling N transformation when performing soil core incubations (Groffman et al., 2006), we recommend to pair direct and indirect techniques when discerning, for instance, the relative importance between denitrification and anammox or fermentative-DNRA versus Fe-driven denitrification (e.g., Hinshaw et al., 2017) (see Figure 1 for definitions). The  $\text{N}_2:\text{Ar}$  technique, for instance, theoretically included the measurement of  $\text{N}_2$  contribution by anammox to the total  $\text{N}_2$  pool measured in our experiments and was not directly evaluated. Anammox, if present, would also cause us to overestimate denitrification using the IPT. Based on the similarity of our IPT and  $\text{N}_2:\text{Ar}$  results, we believe that anammox is very low or absent as generally observed in other wetlands habitats (e.g., Koop-Jakobsen & Giblin, 2009; Lu et al., 2009). We acknowledge that recent findings in seagrass sediments show that anammox exceeds denitrification accounting for 64%–84% of N loss, particularly when labile carbon concentrations are high (Salk et al., 2017); thus, this interaction should be further investigated. Similarly, Fe-driven denitrification (e.g., Bryce et al., 2018; Garcia-Gil & Golterman, 1993) needs to be evaluated, especially in the WLD, given the high concentrations of Fe bound  $\text{PO}_4^{3-}$  in riverine water and the release of  $\text{PO}_4^{3-}$  during bacterial mediated redox reaction in wetland soils impacted by pulsing sediment deposition (Elliton et al., 2020; Upreti et al., 2019).

### 4.3. Differences in Denitrification as an Ecosystem Service

The highest denitrification rates were measured in the WLD soil and sediments characterized by the higher BD and lower TN values. This shows that emerging/supratidal oligohaline coastal areas rich in mineral sediment composition and low %OM content can sustain high denitrification rates. These rates are maintained as long as inorganic N concentrations are high ( $\text{NO}_3^- > 40 \mu\text{M}$ ) and water temperature is mostly  $>10^\circ\text{C}$ , which is the case during summer and early fall in coastal Louisiana. These high rates also suggest that microbial denitrifiers in Louisiana oligohaline soil/sediments are highly responsive to both  $\text{NO}_3^-$  inputs and wide seasonal fluctuation in water temperature as reported by other studies using indirect techniques (e.g., Boustany et al., 1997; Scaroni et al., 2010; Scaroni et al., 2011).

Comparatively, we found that denitrification rates in marsh soils were higher in the WLD marsh than in BLC across all temperatures (Figure 4). Further, when assessing differences within the WLD, we also found significant differences between the forested wetland and the marsh habitat (Table 3; Figure 4). Unfortunately, due to sampling constraints, we did not sample a forested wetland in the BLC resulting in an unbalance comparison. Nevertheless, our analysis showed a significant interaction between denitrification rates and the type of wetland habitat in each region. This might be due to differences in sediment deposition dynamics, substrate age, and vegetation development stage (Carle & Sasser, 2016; DeLaune et al., 2016; Li et al., 2020). In our experimental design, we established two types of habitats, that is, wetlands and benthic sediments in open water, to evaluate if denitrification rates were different between the WLD and BLC regions. The emerging WLD wetlands are younger (<43 years) (Paola et al., 2011; Shaw & Mohrig, 2014; Shaw et al., 2013) with respect to soil formation and lobe formation and OM/carbon accumulation when compared to the older, but degrading, wetland soil in BLC (Day et al., 2000). Therefore, it was unexpected to find higher denitrification rates in WLD habitats since OM% and total N were consistently lower in these substrates (<25%) than in BLC (>40%) (Figure 3). This finding contrast with the relationship obtained from a past study in the WLD where higher denitrification was associated with higher soil %OM, especially during summer/fall when above ground vegetation biomass is present and temperature is high ( $>28^\circ\text{C}$ ) (e.g., Henry & Twilley, 2014). The oldest sites selected in WLD by Henry and Twilley (2014) and Li et al. (2020) were only 30–35 years old, which can be considered the approximate age of our sites in contrast to our site in the BLC where sediment accumulation might be  $\sim 100$  s of years old. It is possible that carbon storage in the BLC sites is very old and metabolically not that active (i.e., recalcitrant) as suggested by the lower oxygen uptake in BLC habitats (Figure 6) during summer ( $30^\circ\text{C}$ ) despite higher % OM content (>40%). Another explanation is that since BLC sites are degrading, metabolic activity in soils is not as efficient as in the younger WLD sites, and therefore plant productivity and degradations rates do not provide enough new labile carbon in both BLC marshes and submerged sites compared to WLD habitats (e.g., Hinshaw et al., 2017). In this site, it is expected that peak summer vegetation productivity (Carle et al., 2015) and direct input of DOC and DOM throughout the Wax Lake outlet maintains high concentrations of labile C (e.g., Trefry et al., 1994). Thus, the age of the deltaic lobe and both seasonal flood-pulse effects of vegetation and flooding frequency—a typical regime in the case

of the WLD (Elliton et al., 2020)—represent temporal dimensions that might contribute to maintaining high denitrification rates along elevation gradients and inundation frequency (Li et al., 2020).

Vegetation can enhance denitrification rates by 55% on an average by increasing labile organic carbon (e.g., Bachand & Horne, 1999; Hinshaw et al., 2017; Jiang et al., 2017) or decreasing flow velocities and trapping of suspended sediments, especially during the time of the year when they receive most water as in the case of the WLD (Elliton et al., 2020). Because carbon availability (e.g., labile) depends on the source of in situ OM sources, then wetland species composition might also have a role in controlling denitrification (Bastviken et al., 2005; Payne et al., 2014; Roley et al., 2018). For example, the marsh in the WLD is dominated by a mix of herbaceous species, including *Nelumbo lutera*, *Polygonum* spp., and *Sagittaria* sp, while the marsh in BLC is dominated by *Sagittaria* sp., *Typha* sp., and *Bidens* sp. In the case of the forested wetland in the WLD, the dominant species is the tree *Salix nigra* with *Colocasia esculenta* (herbaceous) dominating the understory, especially during the peak biomass/productivity in the summer season (Carle & Sasser, 2016; Rivera-Monroy et al., 2019). Previous studies have attempted to establish a direct relationship between denitrification and wetland vegetation plant assemblages and/or individual plant species traits (e.g., Allred & Baines, 2016) given the wetland environment characterized by low redox and lack of electron acceptors (Pan et al., 2019). Since denitrification is a complex biogeochemical transformation, there is a direct benefit in determining if specific plant assemblages can maximize denitrification, particularly when wetlands are either constructed (“treatment wetlands”; Liu et al., 2009) for secondary treatment of excess N or when used naturally as “assimilation” wetlands” (i.e., non-constructed; Day et al., 2019). For example, a meta-analysis study of 419 published denitrification rates in several wetland communities, including treatment wetlands, showed that denitrification rates in wetlands with plants of different species reported denitrification rates that on average was 55% higher (Allred & Baines, 2016). This difference (%) is similar to our benthic versus wetland habitat denitrification rates, even when considering the regulatory effect of temperature (Figure 4).

It is difficult, however, to identify how diverse ecophysiological plant species-specific traits (e.g., aerenchyma, root porosity/radial oxygen loss, and leaf gas films; Pan et al., 2019) in wetland communities integrated by a combination of trees, shrubs, and herbaceous vegetation regulate or impact denitrification rates; especially under a wetland environment characterized by mix of stressful conditions for plant grow (Lam & Kuypers, 2011; Magonigal et al., 2003). Although, for example, a bimodal relationship between the magnitude of denitrification rates and herbaceous plants shoot heights has been suggested (order Poales; e.g., grasses, sedges), further work is needed to identify specific plant species role (Allred & Baines, 2016). The rationale to explain this relationship is that diel sediment oxygenation/diffusion throughout the stem aerenchyma tissue controls oxygen concentration in the soil, thus driving denitrification (Lam & Kuypers, 2011). It is proposed that herbaceous plants with short stems are not as efficient in conducting oxygen to the soil/sediment, thus limiting denitrification since not enough nitrification occurs to drive couple of nitrification-denitrification ( $\text{NH}_4 \rightarrow \text{NO}_3^-$ ; see Figure 1). Our results do not follow this mechanism since direct denitrification, driven by excessive  $\text{NO}_3^-$  (Table 3), is the dominant transformation. This is the case even in habitats with low stature vegetation in the WLD marsh, where denitrification rates were the highest at both low and high temperatures (Table 7).

Another aspect to consider when assessing this functional interaction to draw general patterns is that wetland denitrification studies generally use small intact sediment cores to evaluate denitrification rates, which might be incubated under light or dark treatments or a combination (Cornwell et al., 1999; Damashek & Francis, 2018; Groffman et al., 2006). This contrasts with the low number of experiments using mesocosm where the individual plants can be included in experimental systems, which is a challenging approach when considering forested wetlands as functional groups (e.g., freshwater swamps, mangroves), as is the case in the WLD region. This methodological limitation is further compounded using different denitrification techniques, given that specific assumptions are made for their utilization (Groffman et al., 2006). Our study, for instance, found that denitrification rates using the IPT and the  $\text{N}_2:\text{Ar}$  techniques were relatively similar, allowing us to differentiate specific transformations (e.g., direct denitrification vs. N fixation) in wetland integrated by different species across regions undergoing different sediment deposition/sedimentation processes (deltaic erosional vs. progradational stages).

Further, our experiments also allowed us to establish the relative contribution between different types of denitrification (e.g., direct vs. coupled) since our sites are exposed to yearlong high  $\text{NO}_3^-$  loading rates (Hiatt

& Passalacqua, 2015; Loken et al., 2018; Rabalais et al., 2001). Nevertheless, this N cycling pathway partitioning among different types of denitrification is rarely performed when comparing ecosystems/communities (e.g., Alldred & Baines, 2016; Koop-Jakobsen & Giblin, 2009; Zhang et al., 2019) due to experimental/methodological limitations that include logistical constraints and costs (Rivera-Monroy et al., 2010). Our denitrification rates, for example, were obtained using dark core incubations and might represent an overestimation since denitrification under light diel conditions might influence the integrated daily denitrification rates (see methods section). Still, synthesis and comparative analyses aiming to discern the specific role of vegetation diversity are needed when identifying mechanisms that link functional plant traits to denitrification rates when implementing nitrogen mitigation measures in coastal regions (Damashek & Francis, 2018). Our results advance this analysis, especially under a range of temperatures in deltaic geomorphic settings, where denitrification studies are limited (Alldred & Baines, 2016; Rivera-Monroy et al., 2010).

#### 4.4. Denitrification and N Removal in the Louisiana Delta Plain and Coastal Systems: Management Implications

The linear relationship between denitrification rates and temperature in benthic sediments and wetland soils from progradating (WLD) and eroding (BLC) deltaic lobes in the MR delta plain have significant management implications when assessing the use of wetlands for excess N treatment and wetland rehabilitation/restoration programs in coastal areas. Indeed, our observed seasonal denitrification rates in both deltaic lobes with different OM compositions underscores the need to examine the role of bacteria and archaea in controlling key carbon and nutrient transformations when evaluating excess  $\text{NO}_3^-$  fate in areas where wetland creation/restoration is a priority. Overall, it is assumed that  $\text{NO}_3^-$  in wetlands soils/sediments is either taken up through biomass assimilation or removed by microbial respiratory denitrification coupled to carbon (C) oxidation (e.g., Bachand & Horne, 1999; Burgin & Hamilton, 2007; Burgin, Hamilton, et al., 2013; Burgin, Lazar, et al., 2013; Jiang et al., 2017). In the case of the latter path, it has been proposed that high %OM content is needed to maintain high denitrification rates in natural, created, or restored wetlands to treat this excess N. However, an increase in both denitrification respiration linked to decomposition rates of plant material and soil OM could potentially cause OM loss.

This OM consumption can negatively impact the net accumulation of OM and sediment accretion in the long term (Day et al., 2018; Deegan et al., 2012) causing wetland destabilization followed up by peat collapse and wetland fragmentation. These outcomes have been observed in different salt marshes characterized by organic rich soils located along tidal creeks in temperate estuarine settings (Deegan et al., 2012; Swarzenski et al., 2008; Turner, 2011). This peat collapse mechanism initiated by high denitrification respiration rates might theoretically occur in the Louisiana delta plain or other coastal regions, yet there is no direct experimental evidence. For instance, initial studies underscoring this process of OM consumption via denitrification have been based on the use of indirect techniques (e.g., soil slurries and DEA; Deegan et al., 2012) or stoichiometric calculations (Day et al., 2019; VanZomerem et al., 2012). In fact, recently published stoichiometric calculations to theoretically estimate how much soil OM decomposition could be accounted for by denitrification respiration suggest that only under extremely high N loading rates (i.e.,  $100 \text{ g m}^{-2} \text{ yr}^{-1}$ ) could denitrification account for significant soil OM decomposition (Day et al., 2018). However, these high loading rates are much higher than observed rates ( $<25 \text{ g/m}^2 \text{ yr}^{-1}$ ; Alldred & Baines, 2016) in natural and constructed wetlands (Kadlec & Wallace, 2009).

One of the proposed mechanisms linking wetland soil loss with excess N inputs and denitrification respiration is related to the reduction in root growth that partially controls OM accumulation as a result of high nutrient availability. In this scenario, direct in situ N and P fertilization in saltmarshes can increase high nutrient availability that decreases the need for root foraging activity by wetland plants and reduce belowground standing stocks and OM accumulation in the long term (Darby & Turner, 2008; Deegan et al., 2012; Swarzenski et al., 2008). Thus, it is hypothesized that, if denitrification is a dominant respiration pathway, then it could accelerate wetland loss by consuming OM stored in the soil in both constructed wetland and natural wetlands (Day et al., 2018; Turner et al., 2018). However, our findings indicate that high soil OM is not a condition to fuel high denitrification rates as vegetations can enhance denitrification rates by 55% on an average by increasing labile organic carbon (e.g., Bachand & Horne, 2000; Jian et al., 2017) and not necessarily by the presence of recalcitrant organic material (e.g., Rybczyk et al., 1998).

as indicated by our low %OM values (Figure 3). It is plausible that labile C availability was higher during the summer when the peak vegetation biomass/production occurs across coastal Louisiana (Rivera-Monroy et al., 2019), especially in the WLD (Cale et al., 2015; Elliton et al., 2020). Unfortunately, we did not measure labile C concentrations in the soil/sediments to determine the interaction among carbon availability and temperature.

Indeed, further studies are needed to evaluate the effect of the soil labile C concentrations in the observed linear relationship between denitrification and temperature; for example, by spiking different concentrations of labile C in sediments cores from benthic habitats characterized by the lowest OM value. Additionally, stoichiometric properties of both soil and organic material (Pina-Ochoa & Alvarez-Cobelas, 2006) and  $\text{NO}_3^-$  residence time associated with river discharge and tidal exchange (Day et al., 2019; Hiatt & Passalacqua, 2015; Rivera-Monroy et al., 2010) should be closely considered when spatially scaling up the consequences of enhanced denitrification microbial respiration. Especially, when there are other dissimilatory pathways influencing N removal (e.g., anammox, sulfur-driven nitrate reduction, iron-driven denitrification) (Burgin & Hamilton, 2007; Pina-Ochoa & Alvarez-Cobelas, 2006).

Therefore, to implement and expand freshwater diversions as a wetland restoration strategy, it is critical to advance our understanding of how all environmental drivers (e.g., water level, elevation, temperature, vegetation presence/biomass) interact to influence nitrogen cycling processes collectively across different spatial scales. Most of the studies, for instance, assessing the N removal efficiency in wetlands in general (Rosenzweig et al., 2018), and in coastal Louisiana in particular (Day et al., 2019), show that even after long term operation (26–70 years), treatment wetlands continue to be nutrient sinks (Day et al., 2018). The direct attribution to denitrification is variable since most studies assessing wetland treatment efficiencies consider several processes (e.g., plant uptake, soil N accumulation), yet denitrification is one critical process that can explain significant N removal (Aldred & Baines, 2016).

Most of these treatment wetlands are established in estuarine and inland water bodies at locations close to agriculture fields and waterways (e.g., Woltemade, 2000). Louisiana delta plain is comparatively a unique case because of the large spatial scale (100's  $\text{km}^2$ ; e.g., Caernarvon; Lane et al., 2006) involved in the implementing of a two-fold management goal, that is, to create/restore wetlands and reduce N loading into the coastal ocean. Indeed, given the extension of current and project wetland losses and proposed areas to be restored, the Louisiana delta plain is both the largest restoration project, globally, and the largest in the United States, followed by the Everglades (NASEM, 2016) and San Joaquin Delta (Cornwell et al., 2014) restoration projects. Thus, the potential role of denitrification as a major cause of wetland loss, even when the main objective is to build land throughout sediment deposition/accretion (Else-Quirk et al., 2019), has major economic and management implications that highlight the complex interaction between high loads of inorganic nutrients and sediment input into the Mississippi delta plain. Our study allows the future inclusion of coupled denitrification in landscape-level estimations to further advance the validation and calibration of landscape-level models, including the Integrated Compartment Model (ICM) framework developed for the state of Louisiana's Coastal Master Plan (CPRA, 2017; Haase, 2017; Peyronnin et al., 2013).

The apparent dichotomy about the positive impact of sediments for land building versus denitrification as an “ecosystem service” (N removal; Burgin, Hamilton, et al., 2013; Burgin, Lazar, et al., 2013; Sousa et al., 2012) versus a “ecosystem disservice” (Turner, 2011) (i.e., peat collapse; production of  $\text{N}_2\text{O}$  as greenhouse gas) needs continuous assessment of the net water/sediment discharge from freshwater diversions under different environmental conditions and management scenarios, including the location of these diversions across the landscape (Day et al., 2019; Rivera-Monroy et al., 2019; White et al., 2019). The high denitrification rates in coastal Louisiana deltaic lobes—especially in habitats when soil OM content is low (aggrading)—supports the recommendation of using denitrification respiration to ameliorate the increasing N loading rate into the adjacent coastal ocean that currently fuels the largest hypoxia zone in the Gulf of Mexico and without negatively affecting wetland sustainability in the long term. If seasonal temperature gradually increases as a result of climate change, then impacts on ecosystem functions are expected, including an increase in denitrification rates in the long term as coastal Louisiana undergoes tropicalization (Scheffell et al., 2018).

## 5. Conclusions

Our experiments revealed that sediments from wetlands and benthic habitats in a deltaic setting maintain high denitrification rates in summer and early fall, when exposed to high inorganic N concentrations ( $\text{NO}_3^- > 30 \mu\text{M}$ ). Denitrification rates estimated using both the isotope pairing (IPT) and  $\text{N}_2:\text{Ar}$  techniques were positively associated and linearly controlled by seasonal differences in temperature (spring:  $20^\circ\text{C}$ , summer:  $30^\circ\text{C}$ ; winter:  $10^\circ\text{C}$ ) in the two coastal regions undergoing prograding (WLD) and degrading (BLC) stages in the delta cycle. Maximum mean denitrification rates ranging from  $40.1$  to  $124.1 \mu\text{mol m}^{-2} \text{h}^{-1}$  were measured in the summer while lower rates ( $< 26.2 \pm 5.3 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) were observed in the winter in both regions. These rates followed the same pattern across regions (prograding vs. eroding), habitats (marsh, forested wetland, benthic), and temperature. Overall, both techniques produced similar rates across habitats and temperature ranges. Denitrification rates in wetland sediments were higher ( $> 50\%$ ) than in benthic sediments, especially at  $20^\circ\text{C}$  and  $30^\circ\text{C}$ . The use of different denitrification techniques permitted the evaluation of the relative importance of specific N transformations, such as coupled nitrification-denitrification (IPT) and N fixation ( $\text{N}_2:\text{Ar}$ ). Despite coupled denitrification occurring in substrates from both sites, its contribution was generally low, even at high temperatures. Thus, direct denitrification was the dominant microbial respiration in all types of substrates under high  $\text{NO}_3^-$  availability ( $50 \mu\text{M}$ ). N fixation was found to have a minor role in  $\text{N}_2$  flux gas exchange in both prograding and degrading sites. In general, denitrification rates were higher in the younger WLD ( $< 43$  years) with respect to soil formation and OM/carbon accumulation when compared to older degrading matured BLC habitats ( $\sim 100$  years) despite consistently lower organic matter content and total N. Thus, newly formed wetlands can provide a very valuable ecosystem service, such as denitrification, in the short term. Our findings support the recommendation of using denitrification respiration occurring in both, constructed wetlands and natural wetland formation during river diversions, in coastal Louisiana as a strategy to ameliorate the negative impacts (e.g., hypoxia) of excess reactive N into coastal waters without negatively affecting wetland sustainability in the long term.

## Data Availability Statement

Data sets used in this study are available via Mendeley Data repository in the citation references: Rivera-Monroy, Victor (2020), “Upreti et al. (2020),” Mendeley Data, V1, <https://doi.org/10.17632/7cfnfk63b7.1>

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