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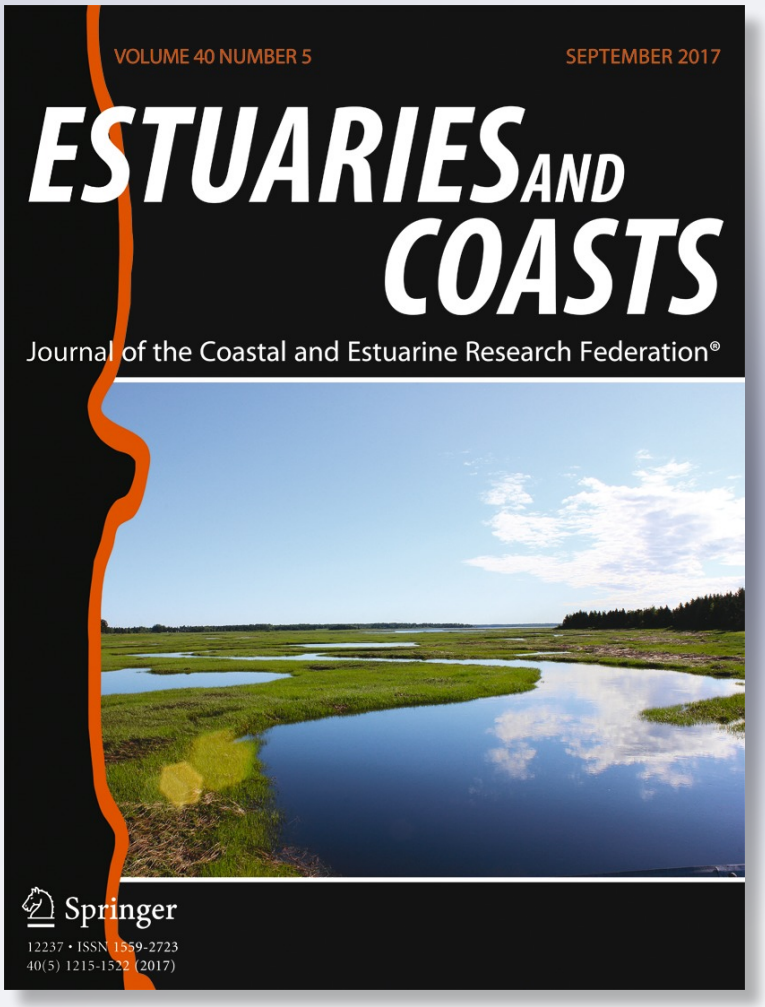

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Spatial and Temporal Patterns in *Thalassia testudinum* Leaf Tissue Nutrients at the Chandeleur Islands, Louisiana, USA

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Abstract Seagrasses are submerged marine plants that are anchored to the substrate and are therefore limited to assimilating nutrients from the surrounding water column or sediment, or by translocating nutrients from adjacent shoots through the belowground rhizome. As a result, seagrasses have been used as reliable ecosystem indicators of surrounding nutrient conditions. The Chandeleur Islands are a chain of barrier islands in the northern Gulf of Mexico that support the only marine seagrass beds in Louisiana, USA, and are the sole location of the seagrass *Thalassia testudinum* across nearly 1000 km of the coastline from west Florida to central Texas. Over the past 150 years, the land area of the Chandeleur Islands has decreased by over half, resulting in a decline of seagrass cover. The goals of this study were to characterize the status of a climax seagrass species at the Chandeleur Islands, *T. testudinum*, in terms of leaf nutrient (nitrogen [N] and phosphorus [P]) changes over time, from 1998 to 2015, and to assess potential drivers of leaf nutrient content. *Thalassia testudinum* leaf nutrients displayed considerable interannual variability in N and P content and molar ratios, which broadly mimicked patterns in annual average dissolved nutrient concentrations in the lower Mississippi River. Hydrological modeling demonstrated the potential for multiple scenarios that would deliver Mississippi River water, and thus nutrients, to *T. testudinum* at the Chandeleur Islands. Although coastal eutrophication is generally accepted as the proximate cause for seagrass loss globally, there is little evidence that nutrient input from the Mississippi River has driven the dramatic declines observed in seagrasses at the Chandeleur Islands. Rather, seagrass cover along the Chandeleur Islands appears to be strongly influenced by island geomorphological processes. Although variable over time, the often elevated nutrient levels of the climax seagrass species, *T. testudinum*, which are potentially driven by river-derived nutrient inputs, raises an important consideration of the potential loss of the ecosystem functions and services associated with these declining seagrass meadows.

Keywords Seagrass · Louisiana · Chandeleur Islands · Nitrogen · Phosphorus

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Introduction

Seagrasses occur along most temperate and tropical coastlines worldwide and provide many ecosystem services, including provision of essential habitat and contributions to primary production, carbon sequestration, nutrient cycling, and export of organic matter (Larkum et al. 2006; Heck et al. 2008; Fourqurean et al. 2012). Plant growth and distribution are influenced by factors such as light, temperature, salinity, substrate type, water movement, grazing pressure, and nutrient levels (Short et al. 2007). Seagrasses are anchored to the

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substrate and are therefore limited to assimilating nutrients from the surrounding water column or sediment, or translocating nutrients from adjacent shoots through the belowground rhizome (Tomasko and Dawes 1989). As a result, they have been used as reliable ecosystem indicators of surrounding nutrient conditions (Lee et al. 2004).

The northern Gulf of Mexico is dominated by three marine seagrass species: *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii* (Short et al. 2007). Although these species are found in monospecific stands, they often co-occur in mixed beds and may also be intermixed with other less common species such as *Ruppia maritima* and *Halophila* spp. Seagrass cover is declining in the northern Gulf of Mexico; the rate and total amount of loss vary between locations, but can be substantial (Kirschenfeld et al. 2007; Carter et al. 2011). Declines in the northern Gulf are attributed to factors including loss of protective barrier islands, coastal nutrient loading, and anthropogenic development. Such declines are expected to increase with effects of climate change (Handley et al. 2007), which may influence future river discharge nutrient loadings from several large river systems, including the Mississippi, Pearl, Pascagoula, Mobile-Tensaw, Trinity, and Apalachicola Rivers (Britton and Martin 1989).

The Chandeleur Islands, a chain of barrier islands representing remains of the historic St. Bernard Delta of the Mississippi River and located 25 km north of Venice, LA, and 35 km south of Biloxi, MS, are a hotspot for dynamic changes in seagrass cover (Poirrier and Handley 2007; Bethel and Martinez 2008). Although diverse low salinity submerged aquatic vegetation communities grow within the freshwater and brackish water Mississippi Delta, the shoals west of the Chandeleur Islands support a regionally unique suite of marine seagrass species, in waters characterized by high salinity, low nutrients, and relatively low turbidity compared to the rest of the Louisiana coast (Poirrier 2007). All five of the seagrass species occurring in the northern Gulf of Mexico grow along the Chandeleur Islands, representing the only mixed species meadows of *T. testudinum*, *S. filiforme*, and *Halophila engelmannii* between Perdido Bay in Florida and the Texas Coastal Bend, approximately 1000 km apart, and the unique co-occurring assemblage of *T. testudinum* and *R. maritima*. These seagrass beds have historically been considered relatively pristine, because of the inaccessibility of the Islands and lack of direct human impacts such as pollution and coastal nutrient loading (Poirrier and Handley 2007). The Islands were designated a wildlife refuge in 1904 by an executive order of President Theodore Roosevelt, included in the National Wilderness Preservation System in 1975, and were recently identified as a priority site for conservation in the Gulf of Mexico in part due to the ecological importance of the Islands' seagrass beds (Beck et al. 2000).

Island geomorphology has been altered substantially with the passage of storms and hurricanes (Williams et al. 1997). Over the past 150 years, land area of the Chandeleur Islands has decreased over 65% (Fig. 1, USGS and EPA 2011); Hurricane Georges, alone, resulted in a 40% reduction in land

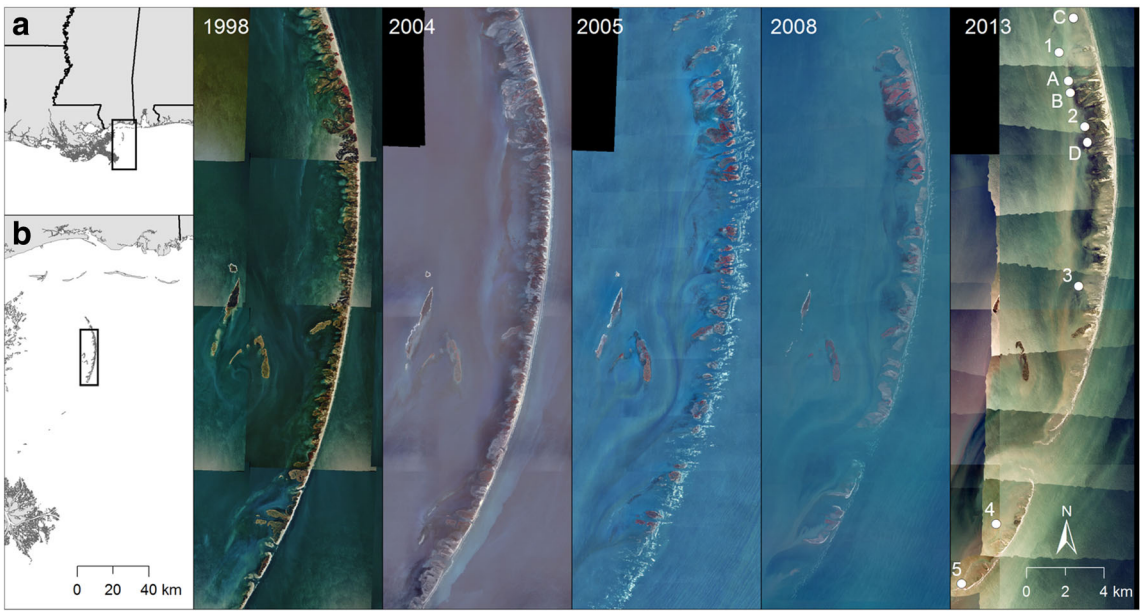

Fig. 1 Location of the Chandeleur Islands relative to the Louisiana coast (*A*), spatial extent of sampling along the Islands (*B*), and orthoimagery of the islands over time (1998–2013). Site locations from the current study are denoted by *white circles* on the 2013 image. Sites 1–3 were sampled in both October 2014 and April 2015, sites 4 and 5 were sampled in April 2015 only, sites A and B were sampled in August 1998 and 1999, April 2006, and September 2011, and sites C and D were sampled in May and September 2003 and 2004. Orthoimagery sources are as follows: 1998, 2004, and 2005: Louisiana Oil Spill Coordinators Office, distributed by "Atlas: The Louisiana Statewide GIS," LSU CADGIS Research Laboratory; 2008: USGS National Wetlands Research Center and Louisiana CWPPRA Task Force; and 2013: USDA National Agriculture Imagery Program

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area in 1998 (Penland et al. 2001), and the impact of Hurricane Katrina (2005) is evident when comparing orthoimagery of the Islands from 2004 and 2005 (Fig. 1), with a reduction of land area from 13.9 to 2.5 km^2, or a loss of over 80% (Sallenger et al. 2009). Storm-related land loss and altered island geomorphology are likely the dominant factors leading to observed seagrass decline, as changes in seagrass cover are strongly related to the loss of protected shallow areas as the islands are degraded by storms (Poirrier and Handley 2007; USGS and EPA 2011). The passage of Hurricane Camille, for example, resulted in a loss of 17.1 km^2 of seagrass cover between April and October 1969 (Poirrier and Handley 2007). Overwash from the islands, burial by sediment deposition, and increased turbidity can lead to short-term seagrass decline, whereas island erosion, transgression, narrowing and disappearance of entire islands, or widening of inlets can lead to long-term decline and seagrass disappearance. Poirrier and Handley (2007) recommended that monitoring aspects of seagrass biology such as seasonal patterns, flowering, and epiphyte growth could provide a standard against which other less pristine areas could be compared. Understanding dynamics of these seagrasses provides information to better identify the ecosystem functions and services they provide to the northern Gulf of Mexico, and in particular, Louisiana.

The goals of this study were to determine the current nutrient status of the climax seagrass species *T. testudinum* at the Chandeleur Islands, in terms of leaf nutrient levels; characterize conditions within seagrass meadows at the Chandeleur Islands by quantifying water column and sediment nutrient levels, water column chlorophyll concentration, benthic microalgae abundance, sediment composition, sediment grain size, and seagrass percent cover and reproductive status; assess *T. testudinum* leaf nutrient levels over time using previously unpublished leaf nutrient data; and investigate potential sources of nutrients for *T. testudinum* at the Chandeleur Islands. Specifically, the following questions were addressed: (1) Have *T. testudinum* tissue nutrient concentrations changed over time? and (2) Are *T. testudinum* leaf nutrient levels linked to Mississippi River outflow?

Methods

Water Quality

Seagrass meadows were sampled at the Chandeleur Islands on October 1, 2014, and April 15, 2015. Three sites were sampled in 2014, and these, plus an additional two sites, were sampled in 2015 to ensure sampling from the northern to southern extent of seagrasses along the Islands. Sampling was concentrated relatively close to the Islands and did not extend across the entire back barrier shelf (Fig. 1). At each site, water depth and Secchi depth were recorded, and a YSI EXO2 Multiparameter datasonde (Yellow Springs, OH, USA) was used to measure water temperature, salinity, and dissolved oxygen approximately 10 cm below the water surface and 10 cm above the sediment. Water column inorganic nutrient levels (ammonium [NH_4^+], phosphate [PO_4^{3-}], and nitrate + nitrite [$NO_3^- + NO_2^-$]) were measured in triplicate water samples collected at each site and filtered using Whatman® GF/F 0.7-μm fiber filters. Water column chlorophyll was also measured with the datasonde in 2015 only.

Sediment Nutrients, Benthic Microalgae, Grain Size, and Composition

At each site, during both sampling events, triplicate sediment core samples (3 cm diameter × 10 cm deep) were collected haphazardly at least 5 m apart to determine grain size and sediment composition. Samples were kept on ice until returned to the laboratory, where they were frozen until processing. Samples were thawed and dried at 60 °C to a constant weight, after which sediment aggregates were broken up and the sample was split into two subsamples for determination of grain size and sediment composition. For grain size analysis, approximately 10 g of sediment was placed in a sieve tower containing the following mesh sizes: 1.0, 0.5, 0.25, 0.125, and 0.063 mm. Samples were shaken on a sieve shaker for 10 min, after which the sediment retained on each sieve was weighed to the nearest 0.0001 g. To determine sediment composition, approximately 5 g of sediment was heated in a muffle furnace for 5 h at 550 °C to remove organics and re-weighed. The sediment sample was again placed in a muffle furnace for 5 h at 950 °C to remove carbonates and re-weighed. Percent composition of the sample as organic, carbonate, and mineral (silica) was then calculated.

A second set of triplicate sediment core samples (3 cm diameter × 10 cm deep) were collected at each site for determination of porewater nutrients. It was not possible to obtain porewater from the sediment through centrifugation; instead, nutrient levels were determined for the sediment itself. Samples were held as described above (on ice, and frozen until processing) and ammonium, nitrate, and nitrite were extracted using a 2 M KCl solution and determined spectrophotometrically using a Flow Solution IV auto-analyzer (OI Analytical, College Station, TX, USA) at the Louisiana State University Wetland Biogeochemistry Analytical Services laboratory.

In addition, during the 2015 sampling event, six replicate sediment cores (2.4 cm diameter × 5 cm deep) were haphazardly collected at least 5 m apart at each site to quantify chlorophyll attributed to benthic microalgae (Grinham et al. 2007). Samples were immediately placed in the dark, kept on ice, and frozen until processing. Chlorophyll *a* concentrations were determined with acetone extraction and a Genesys 20 visible spectrophotometer (Thermo Scientific, St. Martinville, LA, USA) following methods outlined in Grinham et al. (2007)

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using the spectrophotometric equations within and those of Lorenzen (1967).

Seagrass Percent Cover, Reproductive History, and Leaf Nutrient Content

Seagrass percent cover by species was quantified within a 0.25 m^2 quadrat at each site and sampling event. Additionally, at least nine *T. testudinum* shoots were collected at each site (where present) and the number of leaf and flower scars on the short shoots was counted to reconstruct plant reproductive history (van Tussenbroek 1994). Further, observations of plant reproductive status were recorded (e.g., flowering or not flowering) for all seagrass species at each site. During the 2015 sampling event only, evidence of fish grazing on seagrass leaf tissue, as indicated by the presence of distinctive bite marks, was also noted.

At each site in both 2014 and 2015, at least three *T. testudinum* shoots were collected to determine leaf tissue carbon, nitrogen, and phosphorus content. Shoots were placed on ice upon collection and frozen until analysis. Thawed shoots were rinsed, scraped free of epiphytes, and dried at 60 °C to a constant weight before being ground to a fine powder using a Wig-L-Bug (Dentsply Rinn, PA, USA) grinding mill. Ground tissue was analyzed for carbon and nitrogen at the Louisiana State University Wetland Biogeochemistry Analytical Services laboratory using a Costech 1040 CHN Elemental Combustion System (Costech Analytical Technologies, Inc., Valencia, CA, USA). Ground tissue was analyzed for total phosphorus on a Genesys 20 visible spectrophotometer (Thermo Scientific, St. Martinville, LA, USA) following a modified protocol from Chapman and Pratt (1961). Carbon (C), nitrogen (N), and phosphorus (P) data were used to calculate %C, %N, and %P and molar C/N/P ratios.

Leaf Nutrient Changes over Time

To assess changes over time, leaf nutrient contents of *T. testudinum* from October 2014 and April 2015 were compared to unpublished data on *T. testudinum* leaf tissue samples collected from along the northern Chandeleur Islands in August 1998 and 1999, May and September 2003, May 2004, April 2006, and September 2011. *T. testudinum* leaf tissue samples from 1998 to 2011 were collected either by hand or using a benthic corer, with collection methods outlined in Michot et al. (2004) for years 2003 and 2004, and Moncreiff et al. (1999) for years 1998, 1999, 2006, and 2011 (Fig. 1). All *T. testudinum* samples were processed soon after collection, using methods similar to those for samples collected in 2014 and 2015. Carbon and nitrogen levels were measured on *T. testudinum* leaf tissue from all sampling events, and phosphorus levels were measured in leaf tissue from a subset of the sampling events (2006, 2011, 2014, 2015). Living tissue was used for all analyses, and epiphytes were scraped from leaf tissue prior to grinding. Leaf tissue samples collected in 1998, 1999, 2006, and 2011 were ground using a Wiley Mill 3375-E10 Series (Thomas Scientific, Swedesboro, NJ, USA). Samples collected in 1998 and 1999 were analyzed for carbon and nitrogen at the Environmental Isotope Laboratory at the University of Waterloo, Canada. Samples collected in 2006 and 2011 were analyzed for carbon and nitrogen on a Costech 4010 CHN (Costech Analytical Technologies, Inc., Valencia, CA, USA) and analyzed for phosphorus using the colorimetric methods described above. Leaf samples collected in 2003 and 2004 were ground by hand and, similar to other samples, were analyzed for carbon and nitrogen using a CHN analyzer. Carbon (C), nitrogen (N), and phosphorus (P) data were used to calculate %C, %N, and %P (dry weights) and molar C/N/P ratios.

Relationship Between Mississippi River Water Column Nutrients and *T. testudinum* Leaf Tissue Nutrient Levels

The relationship between Mississippi River water column nutrients and *T. testudinum* leaf tissue nutrients was investigated using average annual ambient water column nutrient levels (nitrate + nitrite [mg/L] and phosphorus [mg/L]) in the Mississippi River from 1999 to 2015 collected near Belle Chasse, LA, and *T. testudinum* leaf tissue nutrient data from 1999 to 2015 (see above). Data for Mississippi River nitrate + nitrite for 2011, 2014, and 2015 and phosphorus for 2006, 2011, 2014, and 2015 were obtained from the Louisiana Department of Environmental Quality (LDEQ, Louisiana Department of Environmental Quality 2016). Data for Mississippi River nitrate and nitrite for years 1999, 2003, and 2004 were obtained from the Providence Engineering and Environmental Group (2014).

Hydrodynamic Modeling

To assess water flow and salinity patterns and help explain the origin of nutrient loading to the Chandeleur Islands, we used a hydrodynamic and salinity transport model previously validated by Schindler (2010). We used the finite volume coastal ocean model (FVCOM; Chen et al. 2003) with a model computational domain that includes the northern Gulf of Mexico from Port Fourchon, Louisiana, to Santa Rosa Island, Florida. This domain includes key interior basins such as the Pontchartrain Estuary (including Lakes Maurepas, Pontchartrain, and Borgne as well as the Biloxi Marshes), the Mississippi River Delta, the Barataria Basin, and the Mississippi, Breton, and Chandeleur Sounds. The computational domain consists of 43,768 computational nodes and 79,596 elements. The horizontal grid resolution varies spatially from 80 m in navigation channels and tidal passes to more

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than 10 km near the open boundary. The vertical resolution of the model includes 11 vertical sigma layers equally distributed over the water column. Water flow and salinity distributions surrounding the Chandeleur Islands were modeled under different scenarios. These scenarios included (1) a simulation of typical conditions during cold fronts with dominant South winds, (2) a simulation during a spring flood in the Mississippi River (flow ~35,396 m^3 s^{-1}) with the Bonnet Carré Spillway closed, and (3) during high water spring flood in the Mississippi River (flow >35,396 m^3 s^{-1}) with the Bonnet Carré Spillway open, flowing with an average flow of 4672 m^3 s^{-1}. All three scenarios were simulated for 30 days.

Data Analyses

Mean (± SE) values were calculated for the following parameters sampled in 2014 and 2015: temperature, salinity, dissolved oxygen, water column inorganic nutrients, water column and benthic chlorophyll *a* (2015 only), sediment nutrient concentrations, sediment composition (as the percent of silica, carbonate, and organic matter), grain size, and seagrass percent cover.

To assess spatial variability in leaf nutrient content, one-way ANOVAs were used to test for significant differences in *T. testudinum* nutrient content and molar ratios between sites (where present) during the 2015 sampling event (sites 1–4). To achieve normality of residuals and homogeneity of variance, P data were $\log_{10}$ transformed. There was no significant difference for any of the leaf tissue nutrient variables between sites (Table 1), so all sites were pooled for analyses testing for changes in leaf nutrient content over time.

One-way ANOVAs were used to test for significant differences in change of leaf nutrient content over time (year) for (1) *T. testudinum* %C, %N, and C/N, using data from all sampling events, and (2) *T. testudinum* %P, C/P, and N/P, using data collected from a subset of sampling events (2006, 2011, 2014, and 2015). Tukey HSD tests were performed when significant differences occurred. Data from May and September 2003 for *T. testudinum* %C, %N, and C/N were similar between collection months (May and September; one-way ANOVAs: %C $P = 0.26$; %N $P = 0.89$; C/N $P = 0.43$) and so were pooled for analyses testing for significant differences in change of leaf nutrient content over time. To achieve normality of residuals and homogeneity of variance, C, C/N, C/P, and N/P were $\log_{10}$ transformed.

Pairwise correlations were conducted between *T. testudinum* leaf %N and Mississippi River nitrate + nitrate and *T. testudinum* leaf %P and Mississippi River phosphorus to investigate the relationship between Mississippi River water column nutrient levels and *T. testudinum* leaf tissue nutrient levels. All analyses were conducted in JMP v11 (SAS, Cary, NC, USA). Results are reported as mean ± SE and were considered significant when $P < 0.05$.

Results

Site Characteristics

Water depth was consistently less than 2 m and ranged from 0.61–1.82 m across sites. During both 2014 and 2015 and at all sites, water clarity was high and the Secchi disk was visible on the substrate. Temperature (October 27.3 ± 0.9, April 23.7 ± 0.4 °C), salinity (October 30.7 ± 0.3, April 23.9 ± 0.4), and dissolved oxygen (October 6.8 ± 0.5, April 8.4 ± 0.2 mg L^{-1}) displayed low spatial variability, but high temporal variability. Water column nutrients were consistent across sites, except for site 4, which showed elevated NH_4^+ and NO_2^- + NO_3^- (Table 2). Water column chlorophyll *a* averaged 4.0 ± 1.1 μg L^{-1} across all sites in April 2015 (Table 2).

Sediment nitrate and nitrite levels were below detection limits. Average sediment ammonium displayed high spatial variability, and the range of levels spanned two orders of magnitude (1.5–154 μM). Average sediment grain size was between 0.13 and 0.17 mm across sites and within the range of fine sand in the Wentworth aggregate grain size classification

Table 1 Nutrient content and nutrient molar ratios in *Thalassia testudinum* leaves collected at the Chandeleur Islands, LA, during Spring 2015 at sites spanning the latitudinal extent of *T. testudinum* along the Islands

	C (%)	N (%)	P (%)	C/N	C/P	N/P
Site						
1	39.4 (1.1)	2.87 (0.03)	0.34 (0.03)	16.0 (0.4)	308.8 (31.9)	19.2 (1.7)
2	38.3 (1.0)	2.85 (0.06)	0.29 (0.01)	15.7 (0.6)	342.1 (18.5)	21.8 (0.5)
3	36.9 (0.8)	2.9 (0.17)	0.28 (0.03)	14.9 (0.6)	342.8 (33.0)	23.3 (3.0)
4	38.5 (0.4)	3.0 (0.12)	0.35 (0.03)	15.2 (0.5)	284.9 (22.7)	18.8 (1.3)
ANOVA results						
F	1.4	0.24	1.55	0.85	0.42	1.3
df	3, 8	3, 8	3, 8	3, 8	3, 8	3, 8
P	0.31	0.87	0.28	0.51	0.42	0.34

Data are reported as mean (SE)

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Table 2 Site characteristics from October 2014 and April 2015 sampling at the Chandeleur Islands

		October 2014			April 2015				
		Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 4	Site 5
Water depth	m	1.54	0.72	0.68	1.82	0.78	0.81	0.98	0.61
Water column nutrients	NH_4^+ (μM)	5.32 (0.13)	5.50 (1.3)	4.0 (0.07)	8.64 (0.62)	4.37 (2.13)	3.6 (0.35)	9.2 (4.9)	5.2 (1.6)
	$NO_3^- + NO_2^-$ (μM)	0.41 (0.03)	0.40 (0.01)	0.37 (0.05)	0.46 (0.09)	0.23 (0.03)	0.13 (0.04)	2.2 (0.5)	0.24 (0.18)
	PO_4^{3-} (μM)	0.76 (0.02)	0.71 (0.02)	0.73 (0.03)	0.39 (0.09)	0.48 (0.08)	0.50 (0.02)	0.50 (0.07)	0.5 (0.09)
Sediment nutrients	NH_4^+ (μM)	1.5 (0.6)	61.5 (33.2)	28.5 (0.7)	31.6 (7.9)	154.3 (29)	22.5 (5.3)	29.6 (25.0)	42.2 (3.3)
	$NO_3^- + NO_2^-$ (μM)	ND	ND	ND	ND	ND	ND	ND	ND
Sediment composition	% organic	1.58 (0.16)	2.29 (0.1)	1.85 (0.12)	1.32 (0.19)	2.27 (0.31)	1.54 (0.03)	1.65 (0.20)	0.98 (0.10)
	% carbonate	1.4 (0.52)	0.73 (0.19)	0.96 (0.07)	0.86 (0.16)	1.17 (0.11)	0.87 (0.03)	1.02 (0.20)	0.99 (0.19)
	% silica	97 (0.65)	97 (0.13)	97.2 (0.18)	97.8 (0.08)	96.5 (0.41)	97.6 (0.06)	97.3 (0.30)	98 (0.25)
Grain size	weighted avg., mm	0.17 (0.01)	0.17 (0.02)	0.16 (0.003)	0.17 (0.004)	0.17 (0.003)	0.13 (0.004)	0.16 (0.006)	0.14 (0.004)
BMA	mg m^2	NA	NA	NA	152 (37)	311 (108)	232 (77)	98 (12)	316 (51)
Range of BMA	mg m^2	NA	NA	NA	72–304	80–673	38–571	63–148	105–470
Percent cover	*T. testudinum* (%)	NA	100	15	31.7 (4.4)	75 (12.6)	31.7 (10.1)	21.7 (6.0)	0
	H. wrightii (%)	NA	0	30	0	0	3.3 (3.3)	0	50 (0.0)
	S. filiforme (%)	NA	0	5	1.7 (1.7)	0	0	15 (2.9)	0
	R. maritima (%)	NA	0	0	0	0	15 (12.6)	0	0
	Bare (%)	NA	0	50	66.7 (6.0)	25 (12.6)	50 (5.0)	63.3 (4.4)	50 (0.0)

$N = 3$ per site, except for percent cover values from October 2014, which are $N = 1$ per site. Levels of sediment nitrate and nitrite ($NO_3^- + NO_2^-$ (μM)) were too low for detection on the instrument. Numbers are represented as mean (SE)

ND not detectable

scheme (Table 2). Sediments were predominantly composed of silica (>96% at all sites), with minimal contributions of carbonate (<1.5%) and organic matter (<2.5%) (Table 2). Chlorophyll *a* attributed to benthic microalgae displayed high within-site variability, and site averages ranged from 98 to 316 mg m^2 (Table 2).

Thalassia testudinum was the most abundant seagrass species at all sites during both 2014 and 2015, although *H. wrightii*, *S. filiforme*, *R. maritima*, and *H. englemannii* were also present. Seagrass cover at most sites was composed of mixed species assemblages, with the exceptions of site 2 in October 2014 and site 5 in April 2015, which had monospecific beds of *T. testudinum* and *H. wrightii*, respectively (Table 2). *Thalassia testudinum* leaf tissue nutrients (%C, %N, %P, and molar ratios) were similar across sites (Table 1).

Seagrass Reproductive Status and History

Seagrass flowering was observed in April 2015, with *S. filiforme* at site 1 and *R. maritima* at site 3 bearing flowers. *Thalassia testudinum* shoots, however, showed little evidence of past flowering. Two of the 105 shoots examined had flower scars on the short shoots, one of which was collected in October 2014 at site 2 and the other collected in April 2015 at site 1. The shoot collected in 2014 produced 30 leaves prior to flowering (as indicated by counting leaf scars), and the shoot collected in 2015 produced 9 leaves prior to flowering. Evidence of grazing on *T. testudinum* leaf tissue was only present at the most northern site (site 1) during April 2015.

Thalassia testudinum leaf nutrient content over time

Thalassia testudinum leaf %C, %N, and %P and molar ratios were variable between 1998 and 2015 (%C $F_{7,115} = 21.1$ $P < 0.0001$; %N $F_{7,108} = 53.9$, $P < 0.0001$; %P $F_{3,40} = 11.8$ $P < 0.0001$; C/N $F_{7,115} = 32.1$, $P < 0.0001$; C/P $F_{3,40} = 4.23$, $P = 0.0114$; N/P $F_{3,40} = 4.52$, $P = 0.0085$) (Fig. 2). Leaf tissue %C, %N, and %P were all highest in 2015, tissue %C was lowest in 2003, and %N and %P were lowest in 2006 (Fig. 2). Leaf tissue C/N, C/P, and N/P ratios were all highest in 2006, C/N and C/P were lowest in 2015, and N/P was lowest in 2011 (Fig. 2).

Mississippi River water column nutrients and *T. testudinum* leaf tissue nutrient levels

Average annual ambient water column nitrate + nitrite in the Mississippi River at Belle Chasse, LA, ranged from 1.2 mg/L (2003 and 2011) to 2.4 mg/L (1999), and average annual ambient water column phosphorus ranged from 0.16 mg/L (2006) to 0.27 mg/L (2011) across the study period (Fig. 2). Mississippi River water column nitrate + nitrate and

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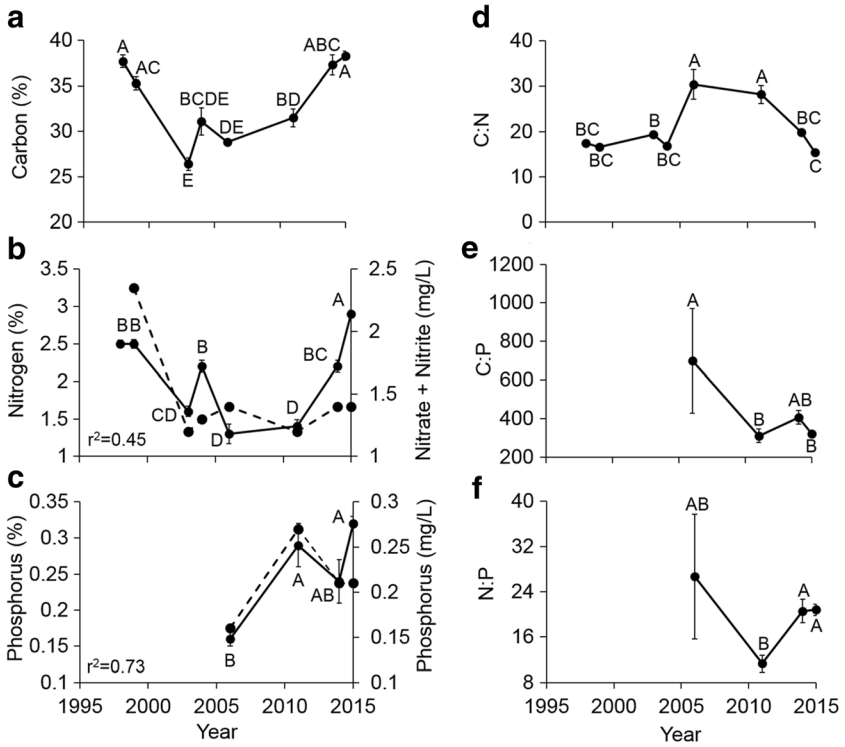

Fig. 2 Leaf nutrient content of *T. testudinum* as carbon (%) (**a**), nitrogen (%) (**b**), phosphorus (%) (**c**), molar ratios (C/N) (**d**), C/P (**e**), and N/P (**f**) over time, denoted by the *solid lines*, and average annual ambient water quality data for nitrate and nitrite (mg/L) (**b**) and phosphorus (mg/L) (**c**) collected in the Mississippi River at Belle Chasse, LA, denoted by *dashed lines*. Data for Mississippi River nitrate and nitrite for 2011, 2014, and 2015 and phosphorus for 2006, 2011, 2014, and 2015 were obtained from the Louisiana Department of Environmental Quality (LDEQ, Louisiana Department of Environmental Quality 2016). Data for Mississippi River nitrate and nitrite for years 1999, 2003, and 2004 were obtained from Providence Engineering and Environmental Group (2014). Results of correlations between *T. testudinum* leaf %N and Mississippi River nitrate and nitrate (**b**) and *T. testudinum* leaf %P and Mississippi River phosphorus (**c**) are denoted by r^2 values. *Letters* represent significant differences as determined from Tukey HSD tests

phosphorus explained 45% of the variation in *T. testudinum* leaf tissue %N and 73% of the variation in *T. testudinum* leaf tissue %P, respectively (N r^2 = 0.45, P = N.S.; P r^2 = 0.73, P = N.S.).

Hydrodynamic Modeling

Modeled hydrologic circulation patterns demonstrated the potential for multiple scenarios that would deliver Mississippi River water (and thus nutrients) to seagrass meadows at the Chandeleur Islands (Fig. 3). Pre-frontal wind patterns resulting from winter frontal weather often blow onshore from the southeast (Georgiou et al. 2005), move water in the direction of the wind, and typically cause water level setup in interior bays and sounds (Fig. 3a) evidenced by the average currents (vectors) which point onshore. Low salinity indicative of freshwater resulting from this scenario, however, is absent, with regional average salinity ranging from 21 to 23 psu. Scenario 2 (Fig. 3b), designed to simulate a spring flood, shows that current direction is generally northward, with water from the Mississippi River Delta moving north, and evidence of a slight lowering of salinity resulting in a range of 18–21 psu. Although a visible freshwater plume is present, it is largely constrained within Breton Sound. Finally, the scenario evaluating the effect of the Bonnet Carré Spillway (Fig. 3c) shows that currents, as expected, are directed offshore and salinities near the Chandeleur seagrass meadows are reduced further, ranging from 12 to 18 psu. From this simulation, there is evidence of lower salinity water west of the barrier arc, in Chandeleur Sound, with salinities of 6–10 psu.

Discussion

Chandeleur Islands *Thalassia testudinum* nutrients in the global context

Thalassia testudinum, the climax indicator species targeted in this study, showed considerable interannual variation in leaf nutrient content over the duration of the study. There was no general trend over nearly two decades of observations in the leaf nutrient contents that would indicate gradual coastal eutrophication was occurring on the Islands, suggesting they remain a relatively pristine system in the Gulf of Mexico, as has been previously noted (Poirrier and Handley 2007).

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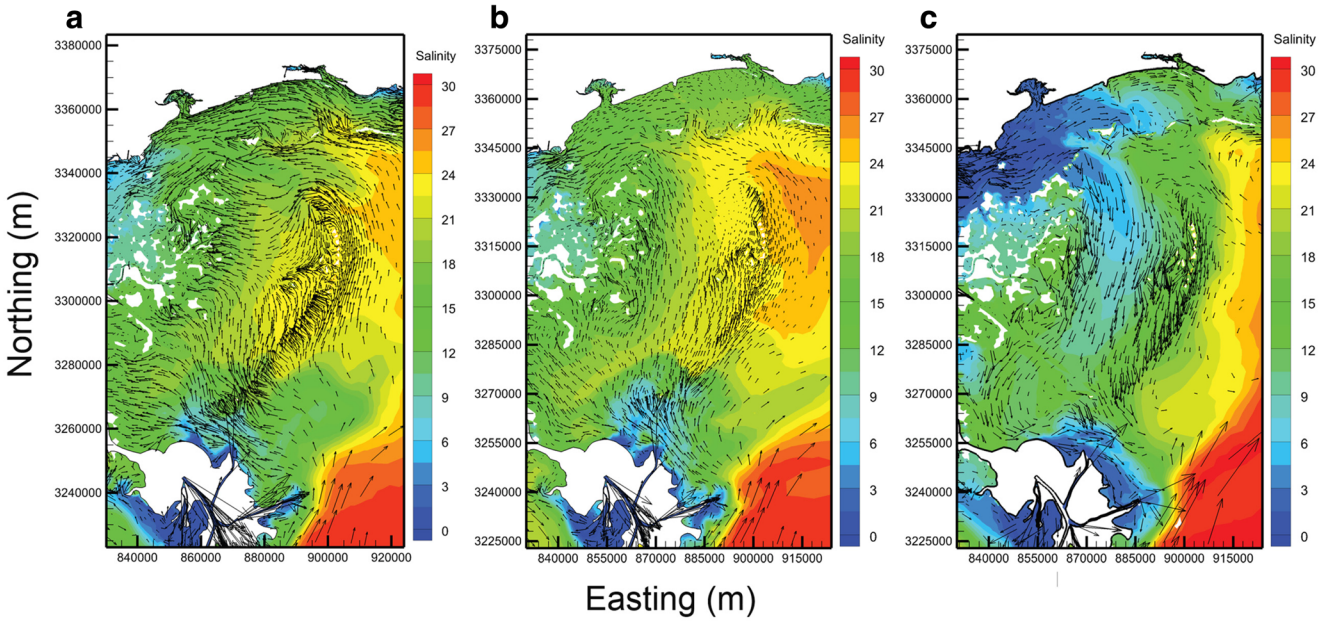

Fig. 3 Model simulations of water flow (vectors) and salinity distribution (*color map*) under different scenarios, conducted for this study, as a simulation of typical conditions during cold fronts with dominant South winds, where vectors in this panel indicate residual direction (time-mean) (**a**); simulation during a spring flood in the Mississippi River (flow ~35,396 m^3 s^{-1}) but with the Bonnet Carré Spillway closed, where vectors show a snapshot after 25 days of simulation (**b**); and during high water spring flood in the Mississippi River (flow >35,396 m^3 s^{-1}) with the Bonnet Carré Spillway open, flowing with an average flow of 4672 m^3 s^{-1}, where vectors show a snapshot after 20 days of simulation (**c**)

Nutrient levels spanned the range of reported values for this species, both in the Gulf of Mexico and globally (Duarte 1990) (Table 3).

The nutrient status of seagrass tissue can be a useful and reliable indicator of surrounding nutrient conditions and overall plant status (Fourqurean and Rutten 2003; Lee et al. 2004). As a result, several attempts have been made to estimate median nutrient ratios (C/N/P), or Redfield ratios, against which nutrient status can be compared. Atkinson and Smith (1983) first reported a ratio of 550:30:1 for aquatic plants. This was followed by Duarte (1990), who reported a global seagrass median of 474:24:1. Using these ratios, N/P values of 30 and 24 reflect a balance between N and P within the plant, and deviations indicate either N or P limitation. In this study, N/P was consistently below 30 and, during 2011 and 2015, below 24, suggesting potential N limitation for *T. testudinum*. Duarte (1990) further suggested that seagrasses with nutrient concentrations less than 1.8% N and 0.20% P were limited by each of these nutrients, respectively. With the exception of 2006, *T. testudinum* at the Islands consistently had higher leaf %P than the suggested thresholds, but leaf tissue %N was lower than the suggested threshold in 2003, 2006, and 2011, and below the seagrass global median during 2003–2006, further suggesting potential N limitation (Duarte 1990; Fourqurean and Rutten 2003).

Several studies, in both temperate and tropical systems, including the northern Gulf of Mexico, have previously reported P limitation in seagrasses (Short 1987; Fourqurean et al. 1992; Fourqurean and Zieman 2002). The paradigm that seagrasses in the Gulf of Mexico are limited by P results from studies conducted primarily in carbonate-rich sediments where P readily adsorbs to carbonate particles, thus restricting P availability to the plant (Short 1987; Erftmeijer 1994). In Florida Bay, for example, Fourqurean et al. (1992) demonstrated that P availability in the carbonate-rich sediments limits *T. testudinum* growth and distribution. Sediments along the Chandeleur Islands, however, are predominantly composed of silica (>96%), with minimal carbonate (<2%). In these terrigenous sediments, P does not readily bind to the sediment particles and is therefore available for uptake by the plant from the porewater, potentially resulting in a switch to N limitation in siliclastic sediments. For instance, Udy and Dennison (1999) reported N limitation of other seagrass species in siliceous sediment in Moreton Bay, Southeast Queensland, Australia, and Lapointe et al. (1992) reported N limitation in macroalgae productivity in siliclastic sediments, but P limitation in carbonate sediments. Caution should be taken, though, that when inferring nutrient limitation from ratios and concentrations alone, as in some species and locations, increased nutrient availability may not result in increased uptake and assimilation by the plant (Udy and Dennison 1999).

Potential Drivers of Seagrass Nutrient Content

In the northern Gulf of Mexico, water circulation in Mississippi Sound and Chandeleur Sound is influenced by geomorphology, freshwater discharge, tidal energy, and

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Table 3 Gulf of Mexico and worldwide leaf tissue nutrient levels of seagrasses in the subtropical genus *Thalassia*, and the global median for all seagrass genera

Location	C (%)	N (%)	P (%)	C/N	C/P	N/P	Species	Reference
Gulf of Mexico								
South Florida	34.6	2.2	0.095	18.5	1070	59	*T. testudinum*	Fourqurean and Zieman (2002)
South Florida	36.9	1.82	0.113	25	937	40	*T. testudinum*	Fourqurean and Zieman (2002)
Chandeleur Islands	33.9	2.15	0.25	20	443	20	*T. testudinum*	This study
Texas Coastal Bend	35.5	2.64	–	16	–	–	*T. testudinum*	Lee and Dunton (1999)
South Texas	34.8	1.75	–	23.3	–	–	*T. testudinum*	Lee and Dunton (1999)
East Gulf of Mexico	–	2.27	0.23	–	–	22	*T. testudinum*	Fourqurean and Cai (2001)
Yucatán	32.8	2.72	0.139	14	669	47	*T. testudinum*	Gallegos et al. (1993)
Yucatán	36.9	2.04	0.14	21	680	32	*T. testudinum*	van Tussenbroek et al. (1996)
Yucatán	34.8	2.77	0.12	15	749	51	*T. testudinum*	Carruthers et al. (2005)
Worldwide								
Bermuda	33.4	2.11	0.187	19	464	25	*T. testudinum*	McGlathery (1995)
Indonesia	32	2.07	0.15	–	–	–	*T. hemprichii*	Erftemeijer and Herman (1994)
Southeast Asia	–	1.98	0.22	–	–	–	*T. hemprichii*	Terrados et al. (1999)
Thailand	33.5	2.33	0.241	–	–	–	*T. hemprichii*	Yamamuro and Chirapart (2005)
Global median	33.5	1.9	0.24	22	435	20	all	Duarte (1992)

atmospheric and meteorological conditions. The Chandeleur Islands are part of the Lake Pontchartrain Basin, and circulation models indicate that the Islands receive freshwater input largely from the basin, including Lake Pontchartrain, Lake Borgne, and the Pearl River, although input from the westward-flowing waters through Mississippi Sound and from the Alabama shelf can also occur (Blumberg et al. 2000; Dzwonkowski and Park 2012). The Lake Pontchartrain Basin is a 26,000-km^2 watershed that encompasses 20% of Louisiana's area, containing rural and urban areas including metro New Orleans and Baton Rouge and bordered by the Mississippi River on the west and the Pearl River on the east. Rain events resulting in surface runoff from the land and non-point source pollution from the northern and southern shores can decrease water quality in the lake (Demcheck 1995). Recently, large (>1000 m^2) hypoxic events in Chandeleur Sound have received attention (Dillon et al. 2010; Moshogianis et al. 2013) with potential linkage to nutrients from the Mississippi River discharge via the Bonnet Carré Spillway, but this may not be a new phenomenon in the area (Brunner et al. 2006). Modeled hydrologic circulation patterns conducted for this study to assess the linkage between Mississippi River outflow and seagrasses at the Chandeleur Islands demonstrated the potential for multiple scenarios that would deliver Mississippi River water to the seagrass meadows (Fig. 3). Further, ambient average annual levels of water column nutrients measured by the Louisiana Department of Environmental Quality (LDEQ) in the Mississippi River at Belle Chasse, LA, explain nearly 50 and 75% of the variability in *T. testudinum* leaf tissue %N (r^2 = 0.43) and %P (r^2 = 0.73) across the study period (Fig. 2), suggesting that the Mississippi River may be a potential source of nutrients to seagrasses along the Chandeleur Islands (Providence Engineering and Environmental Group 2014; LDEQ, Louisiana Department of Environmental Quality 2016). We recommend that future studies not only collect finer-resolution Mississippi River water column nutrient data with paired seagrass tissue nutrient data to better evaluate this potential relationship but also investigate other potential nutrient sources to the Chandeleur Islands, such as outflow from the Pontchartrain Basin and the Pearl River.

During extreme water events in the Mississippi River, Lake Pontchartrain receives diverted floodwater from the river through the Bonnet Carré Spillway. The spillway was constructed in 1931 to protect New Orleans from flooding and, with a flow capacity of 7079 m^3 s^{-1}, can divert a large amount of water (Moncreiff 2007). Nutrient-enriched waters pass through Lake Pontchartrain to the Mississippi and Chandeleur Sounds relatively quickly, as the residence time in Lake Pontchartrain during Bonnet Carré openings is only

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~13 days with a flow of 4729 m^3 s^{-1} (Haralampides 2000). The Bonnet Carré Spillway has been opened 11 times, and recently, it was opened for 42 days in 2011 (May 9–June 20) and 22 days in 2016 (January 11–February 1) during peak river flow. The diverted flood waters can reduce salinities in western Mississippi Sound for 2–3 months following the spillway opening (Moncreiff 2007). In the current study, the 2011 sampling event occurred during September and it is therefore possible that the high tissue nutrients (P primarily) observed during this time were partially a result of the nutrient-rich diverted Mississippi River floodwater, as model simulations indicate that during times of Bonnet Carré opening, waters are transported to the Islands (Fig. 3).

Another potential, although less likely, driver of seagrass nutrient concentrations, in particular P, may be related to the use of the islands by waterfowl and nesting birds. The Chandeleur Islands are habitat for piping plovers (*Charadrius melodus*), royal (*Thalasseus maximus*) and sandwich terns (*T. sandvicensis*), reddish egrets (*Egretta rufescens*), magnificent frigate birds (*Fregata magnificens*), and Eastern brown pelicans (*Pelecanus occidentalis*), a species that has been restocked on the Islands (Nicholls and Baldassarre 1990; McNease et al. 1984). Additionally, the islands are important wintering habitat for redhead ducks (Michot 1997). It is well known that colonies of birds can enrich waters in coastal systems and deposited nutrients can be assimilated by seagrasses such as *T. testudinum* (Powell et al. 1989, 1991). The loading rate of P, specifically, can be very high. For example, in a 109-acre pond in Cape Cod, Portnoy (1990) estimated that gull feces could result in P loading of 52 kg $year^{-1}$. It is possible that changes in nesting bird densities may, at least partially, drive the interannual variability observed in *T. testudinum* %N and %P.

Storm activity can dramatically impact the condition and functioning of seagrass beds (Fourqurean and Rutten 2004), and it is possible that storm activity is in part responsible for the variability in seagrass %N and %P over this 20-year study, with variability resulting from storm-induced sediment suspension, subsequent nutrient release, and changes to local water flow patterns in channels between the islands. It is also possible that methodological differences across years contributed to the observed differences in leaf tissue nutrients. However, these effects are likely minimal, as plant collection, epiphyte removal, and chemical analyses were conducted using similar, established methods. Additionally, any instrumental (e.g., CHN analyzer) differences would likely also be minimal, as samples were analyzed against a common standard.

Seagrass Decline Along the Chandeleur Islands

The Chandeleur Islands support the only marine seagrass beds in Louisiana, are the sole location of *T. testudinum* across nearly 1000 km of coastline from west Florida to central Texas, and support a unique mixed species assemblage of *T. testudinum* and *R. maritima*. While coastal eutrophication is generally accepted as the proximate cause for seagrass loss globally, there does not appear to be strong evidence that nutrients are behind the dramatic declines observed in seagrasses at the Chandeleur Islands. Rather, seagrass cover along the Chandeleur Islands appears to be strongly influenced by island geomorphological processes. Island erosion, narrowing, storm-induced overwash, and the lack of sediment supply have resulted in substantial land loss (Ellis and Stone 2006; Fearnley et al. 2009; Sallenger et al. 2009). Although partial recovery is possible after storms by sealing breaches in the land through redistribution of sediment via longshore transport (as seen in Fig. 1 following Hurricane Katrina in 2005; Georgiou and Schindler 2009), the Islands are predicted to transition to ephemeral barrier island/shoal sand bodies before 2037 per regression analysis using shoreline erosion rates (Fearnley et al. 2009). Seagrass loss between 1992 and 2005 was 41 km^2, losing more than 80% of the 50 km^2 present in 1992, and estimates from 1969 through the mid-1990s indicate that the seagrass area was at times as high as 65 km^2 (Pham et al. 2014; Poirrier and Handley 2007).

Considering this historical loss of seagrass along the Islands, it is likely that remaining seagrass beds will be largely or completely removed if the Islands transition to ephemeral shoals. Altered island geomorphology may also result in a shift in the relative abundance/composition and biodiversity of remaining seagrass meadows. Historic data suggest *T. testudinum* has been a dominant seagrass species along the Chandeleur Islands (Neckles and Michot, USGS, unpublished, as cited in Michot and Chadwick 1994 and Michot 1997; Poirrier and Handley 2007; Pham et al. 2014), but altered island geomorphology and increasing temperatures may be pushing this climax species beyond its tolerance limits (Fourqurean and Rutten 2003). Surveys conducted in 2010 and 2011 following the Deepwater Horizon oil spill reported *H. wrightii* and *R. maritima* as the two most commonly encountered seagrass species, followed by *T. testudinum* (Kenworthy et al. in press). In this study, *T. testudinum* was present at most of the sites we visited and occurred mostly in mixed beds. Although our sampling area extended from the northern to the southern range of seagrasses along the Islands, our sampling area did not comprehensively sample across the entire back barrier shelf in an east to west direction, so our sites may not fully represent local variability within the system. But it is also important to note that the timing of sampling can affect estimates of percent cover, as the biomass of *R. maritima*, for example, is substantially greater during the spring/summer reproductive season than not (pers. obs.). Composition of the remaining seagrass meadows at the Chandeleur Islands may also shift as a response to nutrient supply. Across our 20-year study, *T. testudinum* leaf nutrient

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levels were periodically elevated. If the Islands' seagrass beds are subject to prolonged exposure to nutrient-rich waters, outcompetition of *T. testudinum* by a species with a higher nutrient demand, such as *H. wrightii* (Fourqurean et al. 1995) or *R. maritima* (Cho et al. 2009), may occur.

The potential decrease in *T. testudinum* cover and replacement by species more tolerant to low light and higher variability in salinity and temperature, such as *R. maritima* or *H. wrightii*, would result in a less predictable and stable seagrass system over time. This, coupled with reduced biodiversity, would tend to decrease functional redundancy and resiliency, thus increasing the system's susceptibility to future stressors (Duffy 2006; Bjork et al. 2008). Additionally, such a shift would affect the provision of ecosystem services, as physical differences between these species influence secondary production, carbon and nutrient sequestration, predation, and herbivory and can have ecosystem-level consequences (Duffy 2006; Ray et al. 2014).

Conclusion

Coastal eutrophication is generally accepted as the proximate cause for seagrass loss globally. However, there does not appear to be strong evidence that nutrients are driving the dramatic declines observed in the locally unique seagrasses at the Chandeleur Islands. Although variable over time, the often-elevated nutrient levels of the climax seagrass species, *T. testudinum*, which are potentially influenced by Mississippi River-derived nutrient inputs, raise an important consideration of the potential loss of the ecosystem functions and services associated with these declining seagrass meadows.

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