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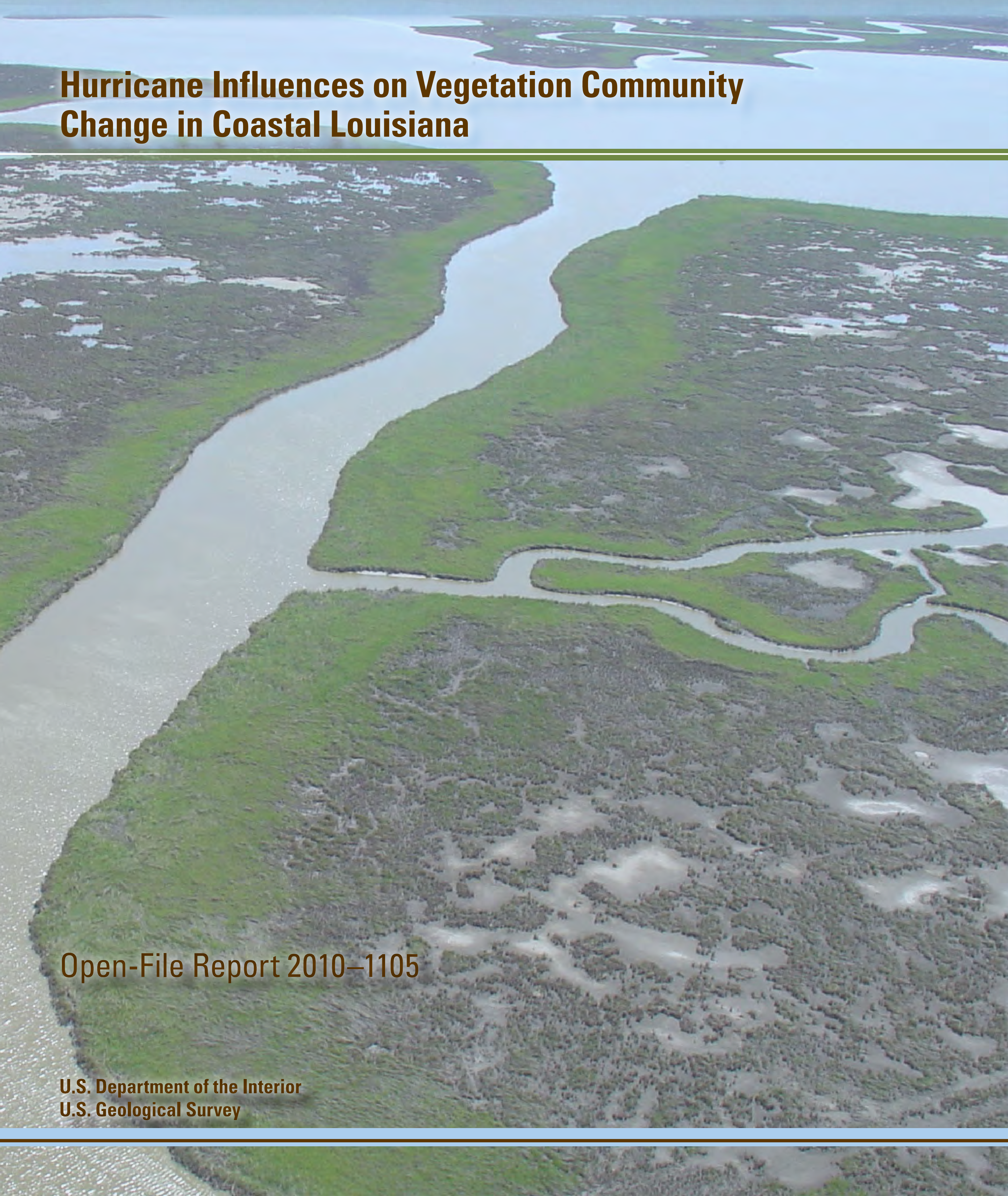
Hurricane Influences on Vegetation Community Change in Coastal Louisiana



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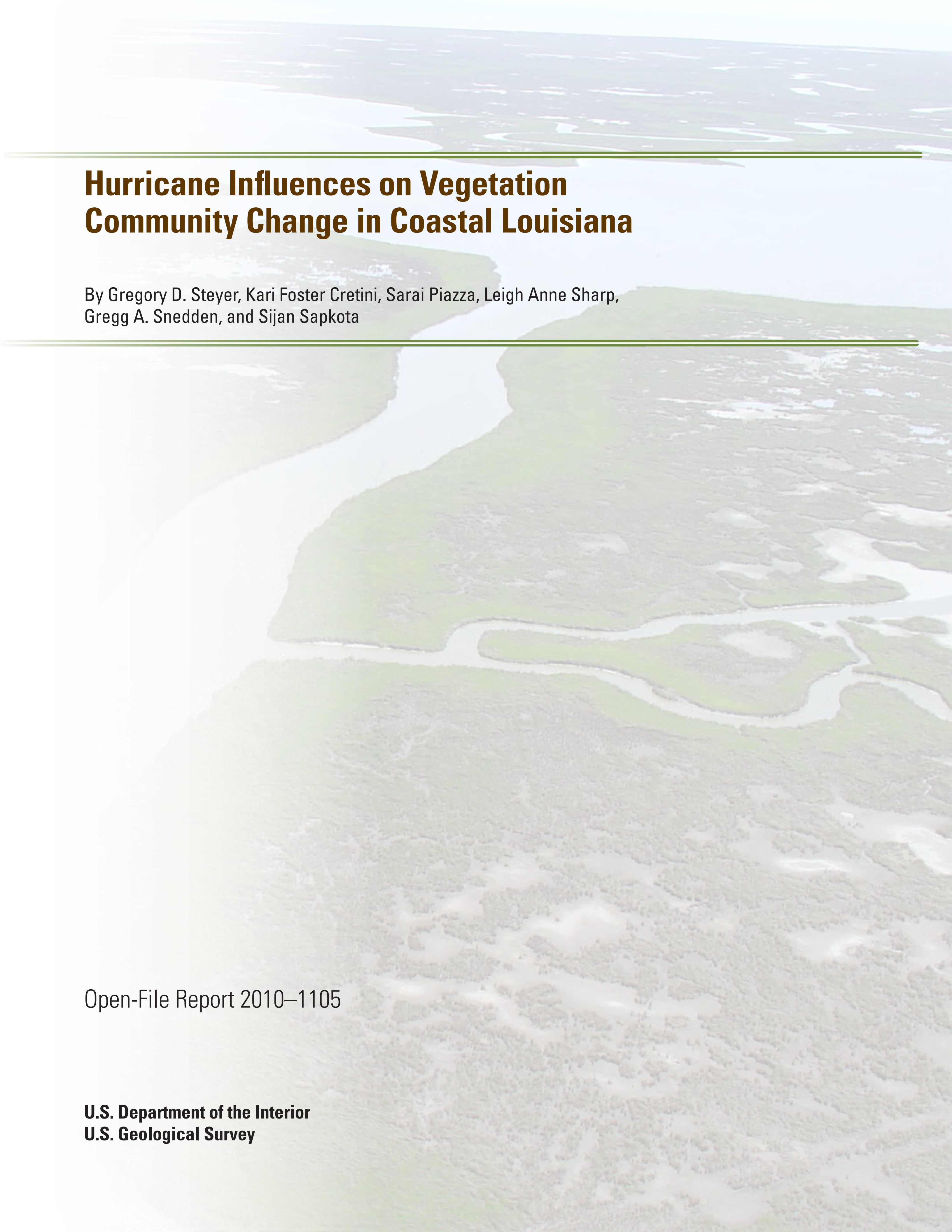

Hurricane Influences on Vegetation Community Change in Coastal Louisiana

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Conversion Factors

SI to Inch/Pound

Multiply	By	To obtain
	Length	
meter (m)	1.094	yard (yd)
	Area	
square meter (m^2)	0.0002471	acre
square kilometer (km^2)	247.1	acre
square meter (m^2)	10.76	square foot (ft^2)

Hurricane Influences on Vegetation Community Change in Coastal Louisiana

By Gregory D. Steyer[1], Kari Foster Cretini[1], Sarai Piazza[1], Leigh Anne Sharp[2], Gregg A. Snedden[1], Sijan Sapkota[1]

Abstract

The impacts of Hurricanes Katrina and Rita in 2005 on wetland vegetation were investigated in Louisiana coastal marshes. Vegetation cover, pore-water salinity, and nutrients data from 100 marsh sites covering the entire Louisiana coast were sampled for two consecutive growing seasons after the storms. A mixed-model nested ANOVA with Tukey's HSD test for post-ANOVA multiple comparisons was used to analyze the data. Significantly ($p<0.05$) lower vegetation cover was observed within brackish and fresh marshes in the west as compared to the east and central regions throughout 2006, but considerable increase in vegetation cover was noticed in fall 2007 data. Marshes in the west were stressed by prolonged saltwater logging and increased sulfide content. High salinity levels persisted throughout the study period for all marsh types, especially in the west. The marshes of coastal Louisiana are still recovering after the hurricanes; however, changes in the species composition have increased in these marshes.

Introduction

Hurricanes are important episodic disturbances that shape coastal, vegetated landscapes in Louisiana and the northern Gulf of Mexico (Conner and others, 1989; Guntenspergen and others, 1995). In addition to physical disturbance to the coastal landscape, these events provide salinity and flooding pulses to coastal marsh ecosystems that can result in significant alteration of vegetation communities (Chabreck and Palmisano, 1973; Neyland, 2007). Although tropical and extratropical storms have decadal scale variability in the North Atlantic Basin (Landsea and others, 1999; Keim and others, 2004), it has been suggested that hurricanes may increase in frequency and intensity in the upcoming decades (Goldenberg and others, 2001; Webster and others, 2005; Intergovernmental Panel on Climate Change, 2007). An investigation of return times by Keim and others (2007), conducted by using records from 1901 to 2005, found that coastal Louisiana averages a 3-year return period for all tropical storms and hurricanes and a 7- to 15-year return period for major hurricanes.

Hurricane disturbances to coastal, wetland vegetation in Louisiana have been previously documented (Ensminger and Nichols, 1957; Chamberlain, 1959; Chabreck and Palmisano, 1973; Meeder, 1987; Doyle and others, 1995); however, most were reported as general observation, and other studies were focused on small geographic areas or specific vegetation species of interest. There are relatively few studies that are comprehensive across broad geographic regions and vegetation communities (Cahoon and others, 1995; Guntenspergen and others, 1995).

Hurricanes can greatly alter vegetation community development, yet very few studies have tracked recovery beyond one growing season. The resilience of ecosystems, defined as the ability of a system to return to a predisturbance state after a disturbance (Leps and others, 1982), is also difficult to evaluate in coastal wetlands because of the variety of stressors constantly operating in the system. Vogt and others (1997) suggest that an ecosystem is resilient if its recovery periods are shorter than the recurrence interval of disturbance events.

Wetland plant associations are well established along estuarine salinity gradients (Odum and Hoover, 1988; Latham

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and others, 1994; Mitsch and Gosselink, 2000). Distributions of plant species in fresh marshes are primarily driven by competitive dominance, whereas the distributions in salt marshes are primarily driven by physical factors, such as salinity (Wilson and Keddy, 1986; Crain and others, 2004). Disturbances that alter salinity regimes provide opportunities to directly evaluate salt tolerance and indirectly evaluate competitive ability, which have been suggested to be inversely related (Barbour, 1978; LaPeyre and others, 2001; Crain and others, 2004). Additionally, disturbances commonly promote invasions by nonnative or opportunistic plant species (Ewel, 1986).

Sulfide also is considered an important stressor that has been shown to be detrimental to plant growth at elevated concentrations, either directly through its toxicity or indirectly by interfering with nutrient uptake (Havill and others, 1985; Mendelssohn and McKee, 1988; Bradley and Dunn, 1989; Koch and Mendelssohn, 1989; Bradley and Morris, 1990; Koch and others, 1990; Chambers and others, 1998); however, most studies that have assessed the synergistic influences of both salinity and sulfide on plant growth (McKee and Mendelssohn, 1989; Naidoo and Mundree, 1993; Broome and others, 1995; Flynn and others, 1995; Chambers and others, 1998; Pahl, 2002) are limited to controlled exposures of single or multiple species.

Hurricanes Katrina and Rita were important vectors for physical landscape disturbance and saltwater intrusion into Louisiana's coastal, freshwater swamps and marshes. In the east region, Hurricane Katrina surge (estimated between 3 and 6 m by Ebersole and others, 2007) flipped, compressed, scoured, and sheared the marsh landscape (Barras, 2007). Persistent, new water bodies formed in the east region with a broad area of disturbance in the Breton Sound estuary (Barras, 2007). The coast-parallel track of Hurricane Rita pushed a storm surge across all regions of the coast with surge that exceeded 2 to 4 m in the west region (McGee and others, 2007) and 1 to 2 m in the central region (Doyle and others, 2007). Surge-created shears and wrack deposits were present throughout the west region (Barras, 2007; Michot and others, 2007). In fresh and intermediate marsh communities coastwide, 334 km^2 of new water area formed between fall 2004 and fall 2005 (Barras, 2007). Barras (2007) used biweekly satellite images to identify areas of the west region that were persistently flooded by Hurricane Rita from September 2005 through February 2006. The saltwater storm surge into coastal marsh communities was evident from initial field sampling of surface waters immediately after the storms (Steyer and others, 2007), because discrete salinity concentrations were as high as 26 in fresh marsh, 26 in intermediate marsh, and 34 in brackish marsh (Steyer and others, 2007).

Hurricane-induced saltwater intrusion and flooding provide an ideal situation to assess how wetland plant communities and species respond to catastrophic disturbances. Our objective was to document the effect of saltwater storm surge from Hurricanes Katrina and Rita in 2005 on marsh community dynamics in coastal Louisiana. We specifically addressed the following questions: (1) What was the extent of the impact to herbaceous, emergent marsh communities across coastal Louisiana, and to what extent did they recover over two growing seasons? (2) Were there any changes in species dominance and/or shifts in marsh community types? (3) How did the level of salinity and/or sulfide concentrations in soil pore water influence marsh community dynamics and recovery?

Materials and Methods

Study Area

The study area consists of 33,457.6 km^2 of wetlands and associated waters, with boundaries consistent with the Louisiana Coastal Area (LCA) trend assessment boundary (Barras and others, 2003; fig. 1). It includes coastal, wetland community types in two physiographic units, the eastern Deltaic Plain and the western Chenier Plain (Roberts, 1997). Marsh types reflect gradients in salinity and elevation (Visser and others, 1998) and are roughly distributed in zones that run parallel to the Gulf of Mexico, with salt marshes farthest south, followed by brackish, intermediate, and fresh marshes farther inland. These zones were initially described by Penfound and Hathaway (1938) followed by a comprehensive description and mapping of marsh communities conducted by O'Neil (1949). Subsequent coastwide surveys were conducted in 1968 (Chabreck and others, 1968; Chabreck, 1970) and in 1978, 1988, 1997, and 2001 (Chabreck and Linscombe, 1978; 1988; 1997; 2001). Coastwide survey data were mapped and habitat types were classified as fresh, intermediate, brackish, and salt marsh zones by using the same methodology described in Chabreck and others (1968).

Within the study area, regions were assigned on the basis of a predominance of storm-surge elevations exceeding approximately 2 m at the coast (Ebersole and others, 2007; McGee and others, 2007) to assess direct versus indirect hurricane effects (fig. 1). The effects of Hurricane Katrina were predominant in the east region, whereas Hurricane Rita's effects occurred mostly across the Chenier Plain in the west region. The central region also experienced tropical storm force winds and some degree of storm-surge effects, mainly from Hurricane Rita.

The assessment of hurricane effects is confounded by drought conditions that occurred in the west and central regions prior to Hurricanes Katrina and Rita. Furthermore, all Louisiana coastal regions suffered a long period of drought conditions after these hurricanes (fig. 2). The National Oceanic and Atmospheric Administration's National Climatic Data Center (NCDC) provides the Palmer Drought Severity Index

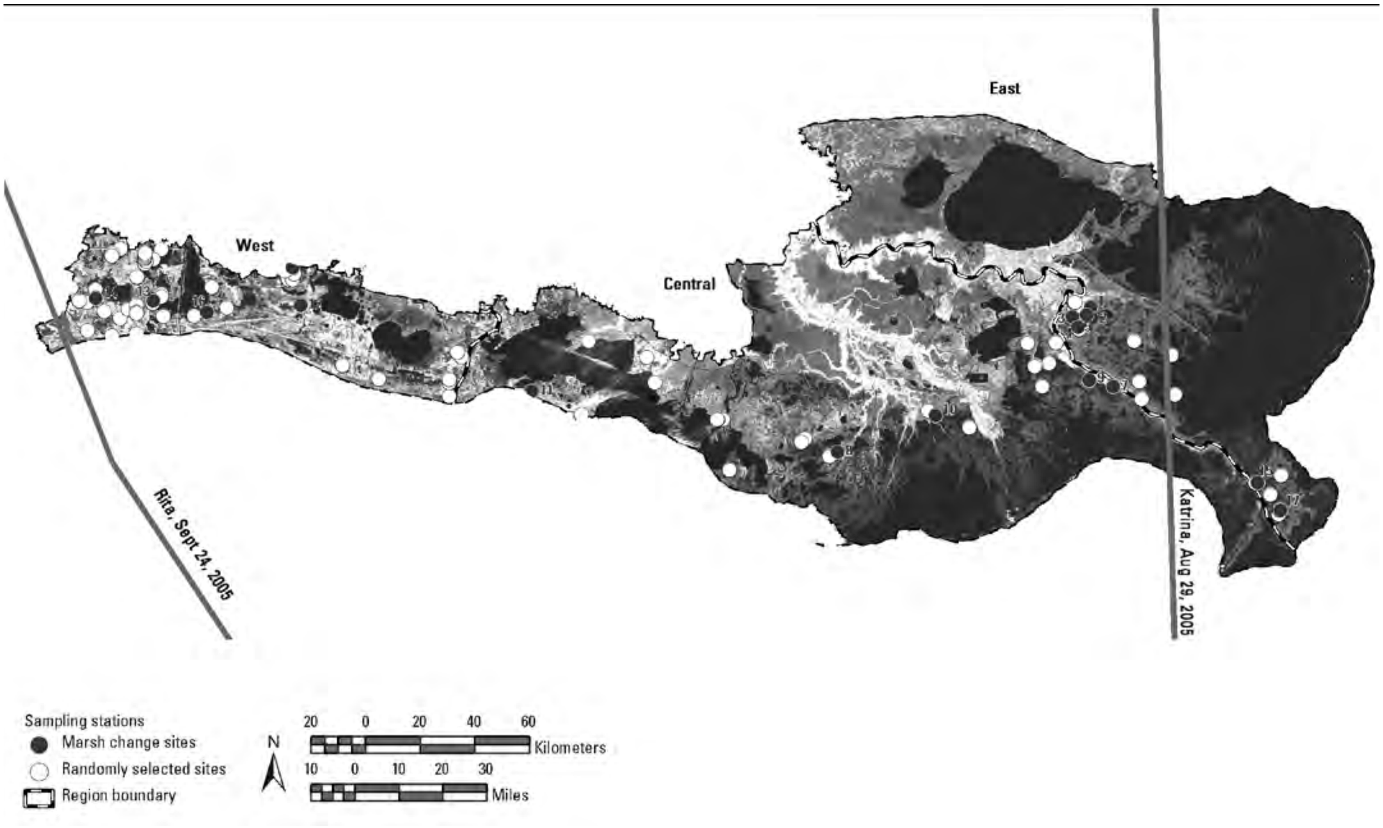

Figure 1. The 33,457.6-km^2 study area defined by the Louisiana Coastal Area (LCA) trend assessment boundary (Barras and others, 2003) showing 100 randomly selected sampling sites, hurricane tracks, and regional assessment areas. Numbers represent sites that changed marsh type between fall 2006 and fall 2007.

(PDSI), which classifies drought conditions with values that range from equal to or less than -1 for mild drought condition to values less than -4 for extreme drought. The NCDC's three climatic divisions in south Louisiana are classified as the southwest, south-central, and southeast, which approximately correspond to the west, central, and east regions in our study.

Vegetation and Pore-water Collection

Sampling sites were randomly selected from a population of 741 existing, coastal monitoring stations established under the Coastal Wetlands Planning, Protection and Restoration Act of 1990 (CWPPRA) and Coastwide Reference Monitoring System (Steyer and others, 2003). Sample size was regionally weighted by the spatial extent of storm surge and exposure to hurricane impacts. A total of 100 sites representing fresh, intermediate, and brackish marsh community types was sampled by helicopter across coastal Louisiana. Because of the spatial extent of the impacted area, 49 stations were sampled in the west, 28 in the east, and 23 stations in the central region (fig. 1). The marsh types were initially assigned using methods described in Chabreck (1970) on a coastwide survey conducted in summer and early fall of 2001 by Chabreck and Linscombe (2001).

Measurements of the percentage of vegetation cover, species composition, and height of dominant plants and of soil pore-water salinity, temperature, pH, sulfide, and nutrients (i.e., ammonium, nitrate, nitrite, and phosphorous) were taken in spring, summer, and fall 2006 and in fall 2007. The percentage of vegetation cover was estimated at each site through visual examination of a 4-m^2 quadrat assessed by following the Braun-Blanquet method described in Steyer and others (1995). Plant nomenclature was established by using the criteria described by Godfrey and Wooten (1979). The percentage of cover of individual plant species and nonvegetated area (e.g., bare ground, standing water, wrack, and dead material) also were identified. Vegetation data for fall 2006 and 2007 were classified by marsh type by identifying the dominant and codominant species and assigning a salinity score based on the overall species composition and abundance, as well as the distribution of those species within fresh, intermediate, and brackish zones as described in Chabreck (1970) and Visser and others (2002).

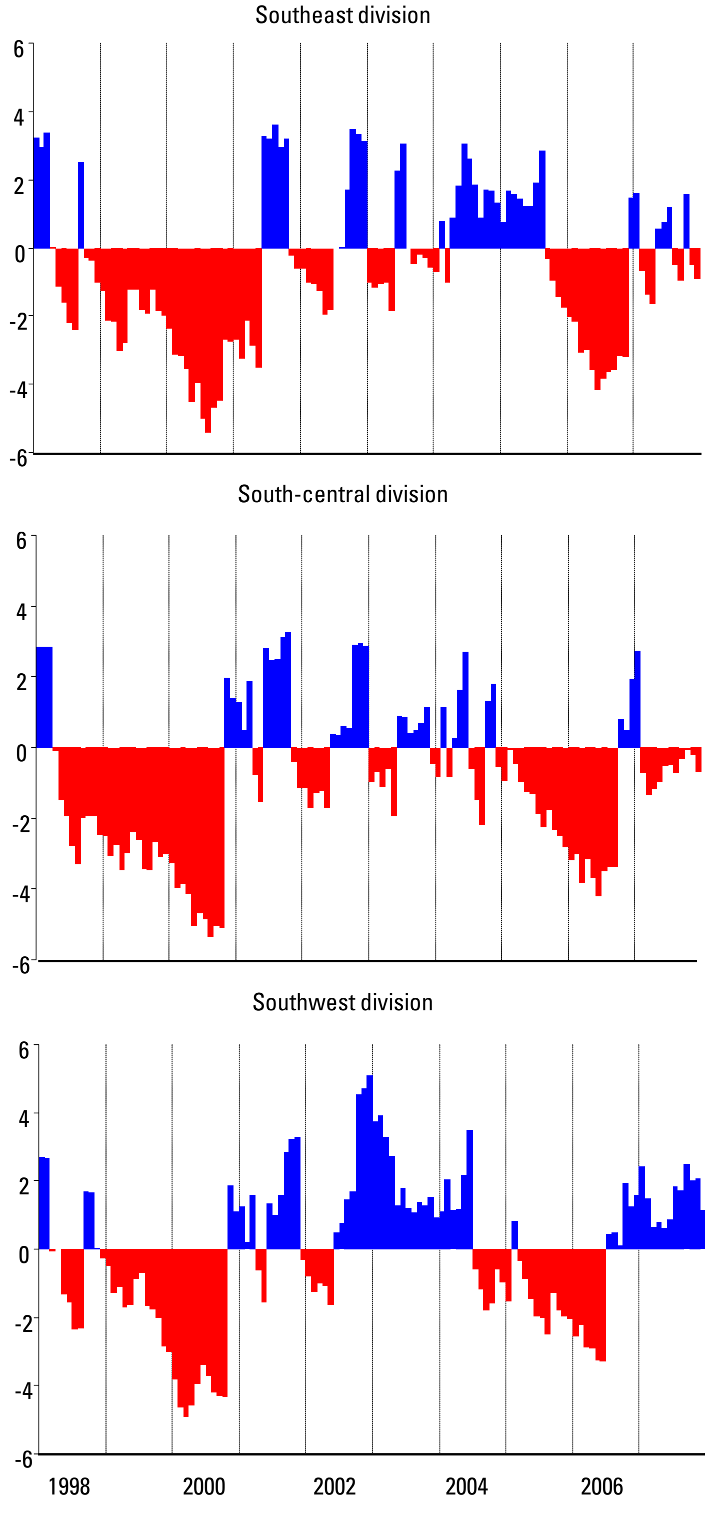

Figure 2. The Palmer Drought Severity Index (PDSI) reflects drought conditions (negative values) that were persistent between 1998 and 2000 and again in 2005 and 2006 in the National Climatic Data Center's Louisiana climate divisions. The south-central and southwest divisions experienced drought before Hurricanes Katrina and Rita in 2005, and drought extended into summer 2006 in the southwest, fall 2006 in the south-central, and winter 2006 in the southeast division.

At each site, three water samples at 10-cm depth were to be collected adjacent to the vegetation plot by using a sipper probe to aid in extracting interstitial water at the desired depth (McKee and others, 1988). There was no pore water available at 10-cm depth, so all water samples were collected from a 30-cm depth. Three 3-ml samples were buffered onsite with an antioxidant and were analyzed within 24 hours of collection. Serial dilutions were prepared, and sulfides were measured with an Orion 9416BN Silver/Sulfide electrode (Thermo Fisher Scientific, Inc., Waltham, Massachusetts, USA) by following the manufacturer's specified standard operating procedures for quality control. The remaining interstitial water was measured onsite for water temperature, salinity, and pH with a YSI Model 30 handheld instrument (YSI Inc., Yellow Springs, Ohio, USA) by following procedures described by Folse and West (2005).

Two additional 25-ml interstitial water samples were extracted and analyzed for inorganic nitrogen (NO_2-N, NO_3-N, and NH_4-N), and phosphorus (PO_4). Samples were filtered in the field by using GF/F filters and were then placed on ice until returned to the laboratory. Concentrations of NO_2, NO_3, NH_4, and PO_4 were measured on a Flow Solution IV automated colorimetric analyzer (O.I. Analytical, Inc., College Station, Texas, USA) by using Environmental Protection Agency standard methods 349.0, 353.4, and 365.5. The fall 2006 NH_4 and PO_4 samples were contaminated and therefore were not used for further analyses.

Statistical Analyses

The PROC GLM procedure was used to perform a mixed-model, nested analysis of variance (ANOVA) to statistically compare data among regions and marsh types. Tukey's HSD tests were used to evaluate differences among the means of main effects. Vegetation cover and all other environmental data were examined for normality by using PROC UNIVARIATE. Vegetation cover data were arc-sine square root transformed and other data were log transformed; however, the assumption of normality was not met. Nonparametric rank transformations (Conover and Iman, 1981) of vegetation cover and environmental data were conducted, and differences among regions and marsh types were similar to findings from the nontransformed parametric GLM procedure. Likewise, both parametric (Pearson's) and nonparametric (Spearman's) partial correlations were evaluated for vegetation cover and environmental variables. No considerable differences in the slopes or in the strength of the relationship were found on the basis of these two correlation techniques. Because inferences from the parametric and nonparametric results are the same, nontransformed parametric results are presented for clarity. We performed the statistical analyses using SAS® software (SAS Institute, Inc., 2002). An alpha=0.05 was used to determine significance for all statistical analyses.

Results

Pore-water Salinity and Sulfide

Measurements of seasonal, mean pore-water salinities show that high salinity conditions persisted throughout 2006 (table 1). In fresh marsh, mean pore-water salinities remained above 1.7 in the east, 2.5 in the central, and 7.1 in the west (table 1). In intermediate marsh, mean pore-water salinities generally increased throughout 2006 with fall mean salinity of 4.7 in the east and 11.3 in the central region (table 1). Intermediate marsh salinities remained high throughout the first growing season in the west region, averaging over 11.1. Brackish marsh salinities were highest in summer and fall 2006 with means across regions ranging from 13.5 to 19.0. Site-specific salinity values within marsh types were wide-ranging (fig. 3), illustrating the extent of exposure to saltwater storm surge.

Within marsh types across the three regions, there were significant differences ($p<0.0001$) in the 2006 pore-water salinities. A multiple comparisons test showed that pore-water salinities in fresh and brackish marshes were significantly higher in the west compared to the east and central regions; furthermore, within intermediate marshes, salinities in the west and central regions were significantly higher than in the east (fig. 4a). Within fresh and brackish marshes, there were no statistically significant differences between the central and east regions in 2006 (fig. 4a). Mean pore-water salinities differed between fall 2006 and fall 2007 among marsh types ($p=0.0007$). Tukey's HSD test indicated that pore-water salinities were significantly lower in fall 2007 compared to fall 2006 in intermediate and brackish marshes, but not in fresh marsh (table 1). The patterns within marsh types found among regions in fall 2007 were similar to 2006 (fig. 4b).

Pore-water sulfide levels were also highly variable, with values in excess of 3.0 mM at some fresh, intermediate, and brackish sites in the west and at some brackish sites in the central region (fig. 3). Sulfide levels in 2006 were greatest in brackish marsh with an average of 0.99 mM, compared to 0.74 mM in intermediate marsh and 0.43 mM in fresh marsh. In 2006 and fall 2007, there were significant differences in pore-water sulfides within marsh types across the three regions ($p<0.0001$). Brackish marshes in the central region had higher sulfides than those in the west and east regions in 2006 (fig. 5a, 5b). No other patterns existed within marsh types among the regions. Although not significantly different, the mean sulfide concentration of 0.62 mM in fresh marsh within the west region in 2006 was more than twice as high as in the other regions (table 1). Mean pore-water sulfides did not differ between fall 2006 and fall 2007 ($p=0.8741$). The mean sulfide values in the fresh marsh (0.44 mM) and the intermediate marsh (1.23 mM) in the west region in fall 2007 nearly doubled that of the other regional values within the same marsh type.

Inorganic Nutrients

There were no distinct differences in mean nitrate and nitrite levels in 2006 across regions and marsh types. Nitrite and nitrate levels were highest in the brackish marsh in the west and in fresh and brackish marshes in the east. The highest nitrate and nitrite levels were observed in summer 2006 and the lowest in fall 2007. Mean nitrate and nitrite levels were higher in fall 2006 than in fall 2007 ($p<0.0001$). Averaged across all marsh types and regions, mean concentrations of nitrate at 4.64 µM and nitrite at 1.41 µM were found in fall 2006 compared to a nitrate concentration of 1.7 µM and a nitrite concentration of 0.45 µM in fall 2007.

Mean phosphate concentrations in 2006 and 2007 were highest in all marsh types in the east and lowest in the west region. Mean phosphate concentrations were also significantly ($p <0.0001$) highest in brackish marsh (27.34 µM) and lowest in fresh marsh (14.07 µM) across all regions. Ammonium levels were highly variable with no patterns among marsh types and regions (fig. 3), other than in the east region, where ammonium concentrations in intermediate marsh (637.8 µM) were more than twice as high as in the west (273.9 µM) and central (172.2 µM) regions.

Vegetative Cover

Mean total percentage of cover differed among regions within marsh types in 2006 ($p<0.0001$). Multiple comparisons indicated that the mean total percentage of cover was lower in the west among fresh and brackish marsh types in 2006 compared to the other regions (fig. 6a). There were no significant differences in vegetation cover among regions within the intermediate marsh type in 2006 (fig. 6a). In fall 2007, there were no significant differences in vegetation cover among regions within marsh types ($p=0.0548$; fig. 6b). Mean vegetation cover values were also compared between fall 2006 and fall 2007 to evaluate the first 2 years of posthurricane impact recovery. In the entire study area, irrespective of marsh types and regions, ANOVA indicated that the mean total percentage of cover of 70.8 in fall 2007 was significantly higher ($p=0.0103$) than the mean total cover of 54.8 in fall 2006. Within marsh types, across regions, there were no significant differences in total cover between fall 2006 and fall 2007 ($p =0.8515$).

Table 1. Pore-water chemistry means by region, marsh type (F = fresh, I = intermediate, B = brackish), and season (Sp = spring, Su = summer, Fa = fall). Standard error (SE) and sample size (N) are provided.

Marsh	Season	East region				Central region				West region			
		Salinity		Sulfide (mM)		Salinity		Sulfide (mM)		Salinity		Sulfide (mM)	
		Mean ± SE (N)	Min – Max	Mean ± SE (N)	Min – Max	Mean ± SE (N)	Min – Max	Mean ± SE (N)	Min –Max	Mean ± SE (N)	Min – Max	Mean ± SE (N)	Min –Max
F	Sp06	1.74±0.09 (23)	0.7–2.7	0.13±0.05 (23)	0.00–0.90	2.51±0.39 (16)	0.1–5.1	0.10±0.03 (16)	0.01–0.44	8.11±0.65 (48)	0.0–15.0	0.45±0.07 (48)	0.00–1.74
	Su06	1.81±0.18 (25)	0.5–3.9	0.19±0.08 (25)	0.00–1.69	3.03±0.39 (18)	0.6–5.4	0.39±0.11 (18)	0.00–1.34	10.41±0.95 (45)	0.1–19.8	1.00±0.18 (45)	0.00–3.88
	Fa06	2.87±0.25 (26)	0.6–5.6	0.27±0.09 (26)	0.00–1.55	2.53±0.29 (18)	0.5–4.6	0.35±0.08 (18)	0.01–1.00	7.19±0.82 (39)	0.1–14.8	0.39±0.09 (39)	0.00–2.35
	Fa07	1.35±0.13 (24)	0.3–2.4	0.18±0.06 (9)	0.04–0.52	1.47±0.18 (14)	0.6–2.6	0.14±0.03 (14)	0.00–0.33	6.12±0.70 (38)	0.1–11.7	0.44±0.12 (37)	0.00–2.65
I	Sp06	2.31±0.06 (40)	1.7–3.5	0.36±0.06 (40)	0.00–1.43	6.05±0.81 (20)	1.7–12.1	0.39±0.07 (20)	0.01–1.08	11.10±0.55 (66)	1.7–17.9	0.67±0.09 (64)	0.00–3.22
	Su06	3.11±0.25 (37)	0.9–7.5	0.97±0.11 (37)	0.01–2.54	10.18±1.48 (24)	1.5–21.7	0.64±0.14 (24)	0.00–2.56	12.35±0.56 (72)	1.9–23.5	0.70±0.09 (73)	0.00–4.16
	Fa06	4.65±0.24 (48)	1.6–7.6	0.76±0.11 (48)	0.01–2.44	11.32±1.40 (21)	2.2–20.6	0.67±0.15 (21)	0.00–1.82	11.29±0.50 (74)	2.4–21.4	1.04±0.11 (75)	0.00–3.57
	Fa07	1.85±0.12 (46)	0.7–4.4	0.59±0.08 (39)	0.03–1.83	6.48±1.01 (24)	1.1–14.3	0.55±0.13 (24)	0.00–1.70	8.69±0.42 (69)	0.9–15.6	1.23±0.18 (69)	0.00–5.48
B	Sp06	8.47±0.30 (6)	7.5–9.5	0.76±0.14 (6)	0.18–1.09	9.33±0.54 (24)	6.3–17.1	0.74±0.14 (24)	0.04–2.10	14.02±0.65 (21)	8.9–19.2	0.46±0.10 (21)	0.00–1.37
	Su06	15.51±2.50 (9)	4.9–22.0	0.62±0.32 (9)	0.00–2.36	13.53±0.92 (27)	6.7–23.6	1.45±0.17 (27)	0.02–3.38	19.00±1.27 (21)	9.7–27.0	0.70±0.20 (18)	0.00–2.72
	Fa06	15.20±0.34 (6)	14.1–16.1	0.38±0.33 (6)	0.00–2.00	13.89±0.61 (24)	9.3–19.0	1.87±0.21 (24)	0.03–4.05	17.04±1.78 (18)	0.9–24.6	0.85±0.23 (18)	0.00–2.67
	Fa07	7.94±1.75 (7)	2.8–13.3	0.16±0.07 (3)	0.01–0.23	8.31±0.85 (27)	2.4–15.9	1.73±0.18 (24)	0.05–3.86	13.76±1.20 (21)	6.6–21.3	1.43±0.34 (21)	0.01–3.87

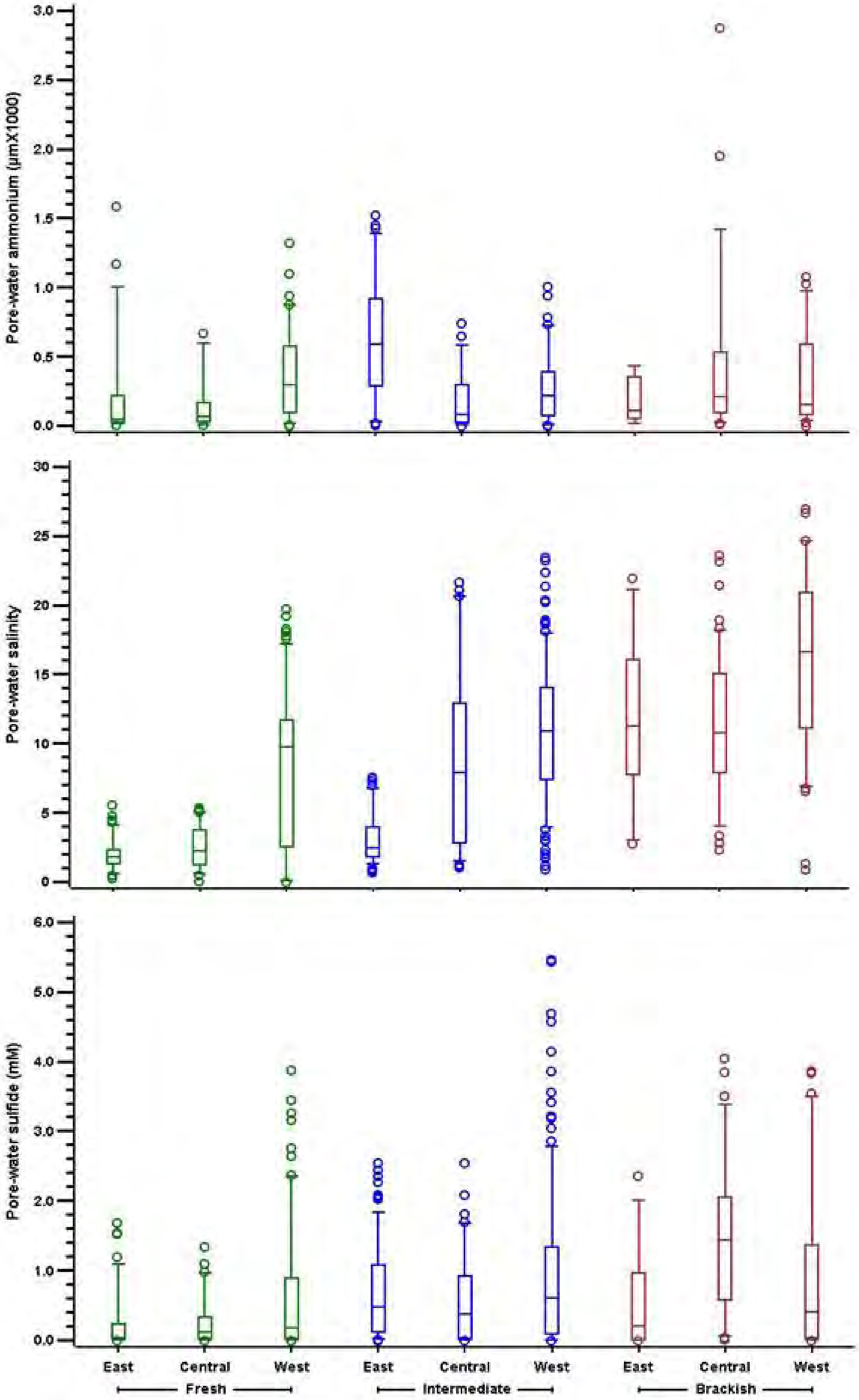

Figure 3. Ammonium(µM), pore-water salinity, and sulfide (mM) concentrations by marsh type and region for 2006 and 2007. Horizontal lines represent 5th, 25th, 50th, 75th, and 95th percentiles. Open circles symbolize outliers that represent data points outside the 95 percent confidence interval.

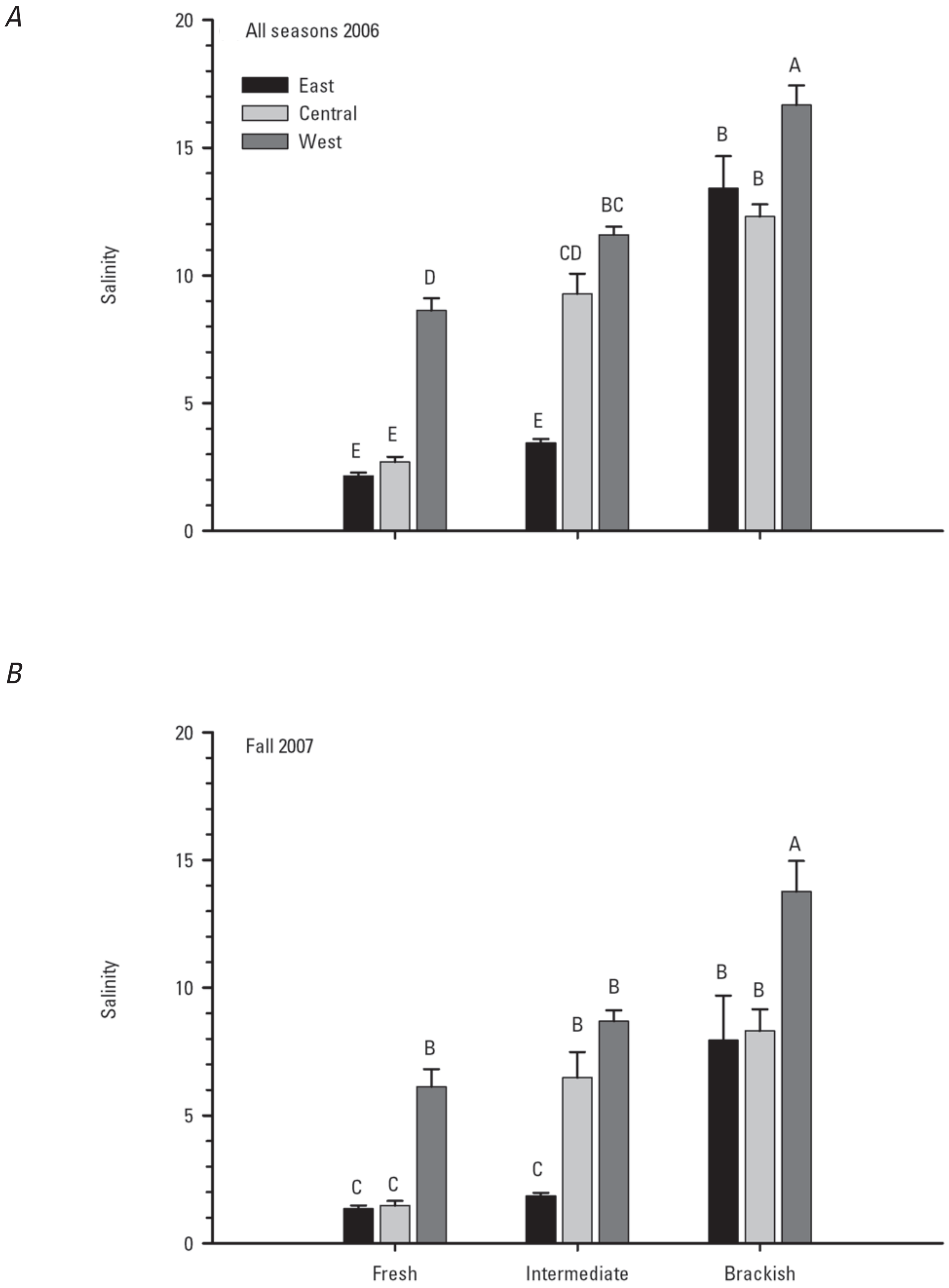

Figure 4. Average pore-water salinity across coastal Louisiana for (a) all seasons in 2006 and (b) fall 2007. Bars with the same letter are not statistically different at $p \leq 0.05$ (Tukey's HSD test).

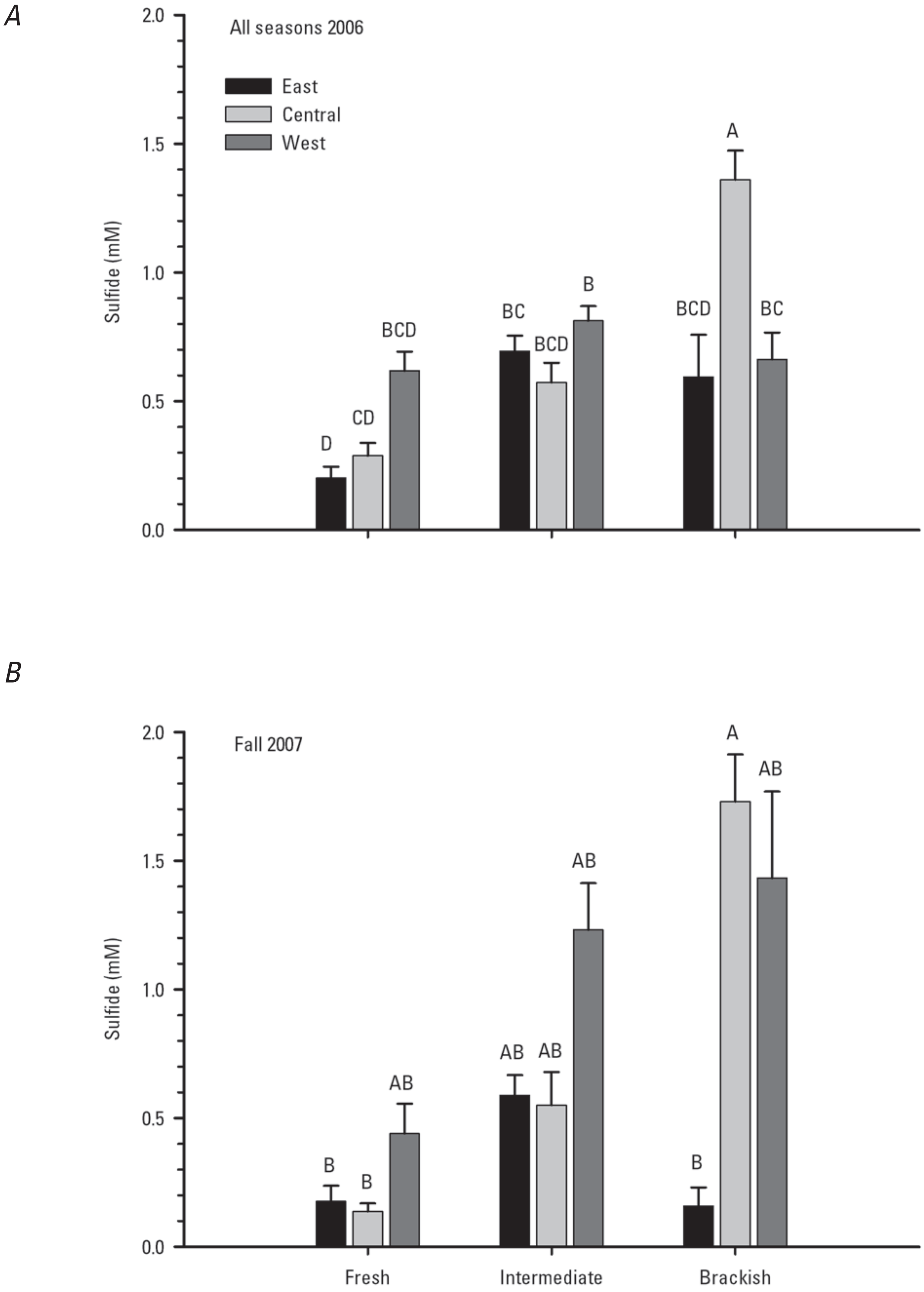

Figure 5. Average pore-water sulfide (mM) across coastal Louisiana for (a) all seasons in 2006 and (b) fall 2007. Bars with the same letter are not statistically different at $p \leq 0.05$ (Tukey's HSD test).

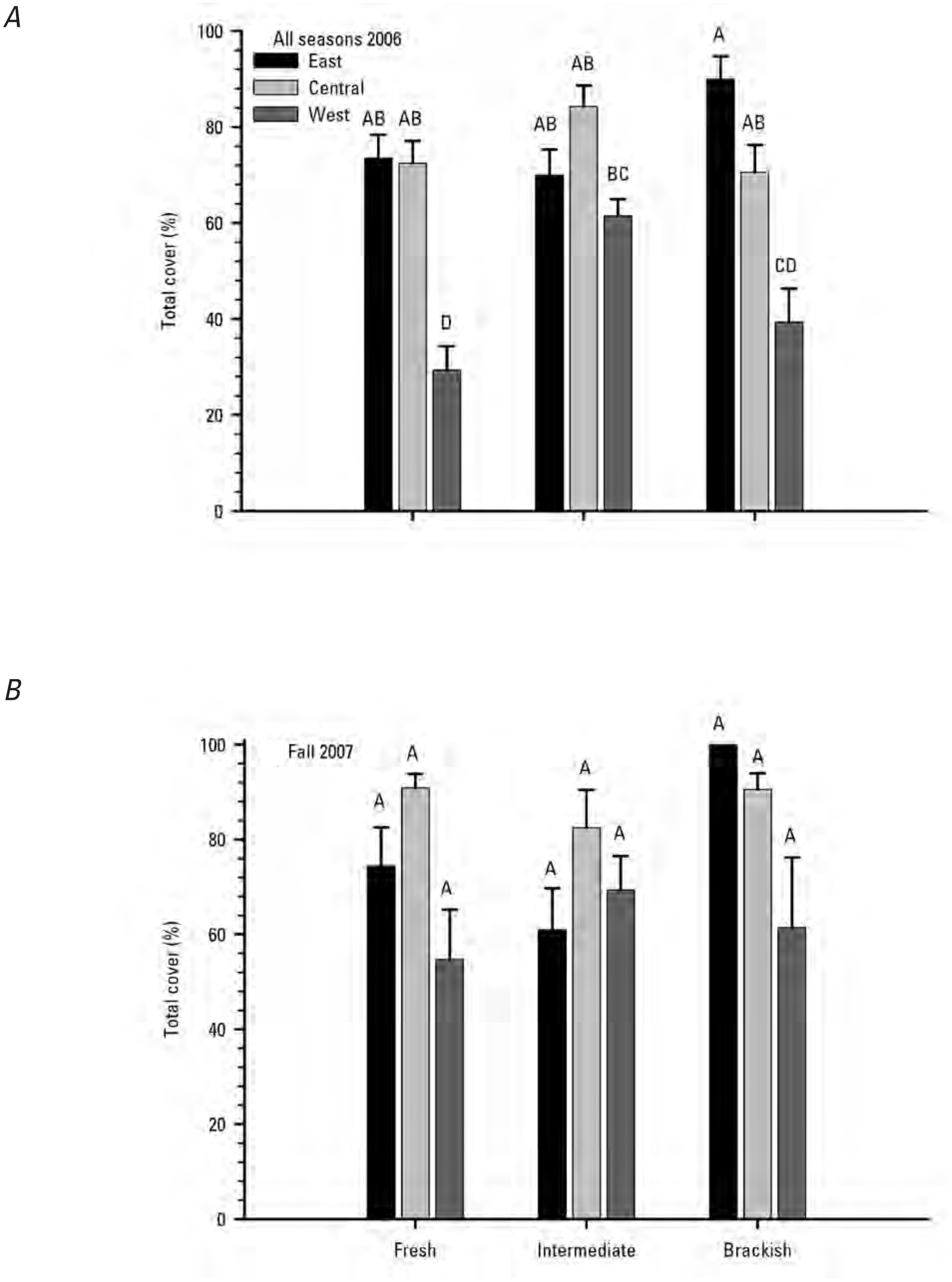

Figure 6. Average total percentage of cover across coastal Louisiana for (a) all seasons in 2006 and (b) fall 2007. Bars with the same letter are not statistically different at $p \leq 0.05$ (Tukey's HSD test).

A total of 95 vegetation species was identified in all marsh types throughout the study, of which 22 were identified as disturbance species or taxa (table 2). Disturbance species were identified in fall 2006 and 2007 as the dominant vegetation species in 38.5 percent of the sites in the east (n=28), 13.6 percent in the central (n=23), and 2.5 percent in the west (n=49) region. The vegetation species that composed the greatest percentage of cover in fresh marsh throughout the study were *Alternanthera philoxeroides* in the east and central regions and *Spartina patens* in the west region (fig. 7). *Alternanthera philoxeroides* and other identified disturbance species (table 2) occupied over 40 percent of the total species cover in the east region and 25 percent in the west region. *Panicum hemitomon*, the dominant fresh marsh species (along with *Sagittaria lancifolia*) in the central and west regions prior to the hurricanes, contributed less than 3 percent cover in spring 2006. *Panicum hemitomon* then became codominant in the central and west regions in fresh marsh during summer and fall 2006 and dominant once again in the west region during fall 2007, then accounting for 18 percent of cover.

Table 2. Observed taxa that are characterized as disturbance because they are commonly present in marshes that have been recently disturbed by physical or biological forces (Jenneke Visser, University of Louisiana at Lafayette, and Charles Sasser, Louisiana State University, written communs.)

Disturbance taxa
Aeschynomene indica L.
Alternanthera philoxeroides (Mart.) Griseb.
Amaranthus L.
Andropogon L.
Cyperus L.
Cyperus odoratus L.
Echinochloa Beauv.
Echinochloa crus-galli (L.) Beauv.
Echinochloa walteri (Pursh) Heller
Eupatorium capillifolium (Lam.) Small
Leptochloa fusca (L.) Kunth ssp. *fasicularis* (Lam.) N. Snow
Mikania scandens (L.) Willd.
Panicum dichotomiflorum Michx.
Pluchea camphorata (L.) DC.
Ranunculus L.
Rorippa palustris (L.) Bess. ssp. *fernaldiana* (Butters & Abbe) Jonsell
Sesbania drummondii (Rydb.) Cory
Sesbania herbacea (P. Mill.) McVaugh
Sesbania Scop.
Symphyotrichum subulatum (Michx.) Nesom
Symphyotrichum tenuifolium (L.) Nesom
Vigna luteola (Jacq.) Benth.

Spartina patens dominated the intermediate marsh sites in all regions, and percentage of cover changed very little over time (fig. 8). *Spartina patens* maintained over 20 percent cover in the central region, 30 percent in the east region, and 40 percent in the west region throughout the study. The codominant species varied by regions: the east region consisted of disturbance species, the central of *Spartina alterniflora* and *Distichlis spicata*, and the west of *Schoenoplectus americanus*. In spring 2006, *Schoenoplectus americanus* had 15 percent cover in the central region and 8 percent cover in the west region, but declined throughout 2006 and contributed less than 5 percent cover in central or west regions by fall 2007.

Brackish marsh cover was also dominated by *Spartina patens*, especially in the central region where it contributed over 47 percent of the total species cover, but varied seasonally and annually within regions (fig. 9). *Distichlis spicata* was codominant with *Spartina patens* at different times throughout the study period. In fall 2007, *Distichlis spicata* accounted for 15 percent of the cover in each of the three regions. The west region had the smallest percentage of *Spartina patens* but also the largest percentages of *Spartina alterniflora* and *Schoenoplectus robustus*.

Nine of the 100 sample sites across all regions did not recover from initial hurricane impacts and were converted to open water by fall 2007; of these, eight were located in the west region and one in the east region. Additionally, one site in the east and one in the central region that deteriorated to 0 percent cover by fall 2006 had recovered to 100 percent cover by fall 2007. Between fall 2006 and fall 2007, changes in species dominance occurred at 53.8 percent of the vegetated sites in the east region, 40.9 percent in the central, and 22.5 percent in the west region. Species richness increased from fall 2006 to fall 2007 in 47.5 percent of the sites in the west region and 54.5 percent of the sites in the central region. Decreases in species richness were observed at 23.1 percent of the sites in the east region, compared to 9.1 percent in the central, and 10.0 percent in the west region.

Vegetation data collected in fall 2006 and 2007 were classified by marsh type by using salinity scores from Visser and others (2002) and zones of peak occurrence from Chabreck (1970). Five sites in the east region, four sites in the central region, and four sites in the west region changed marsh classification from fall 2006 to

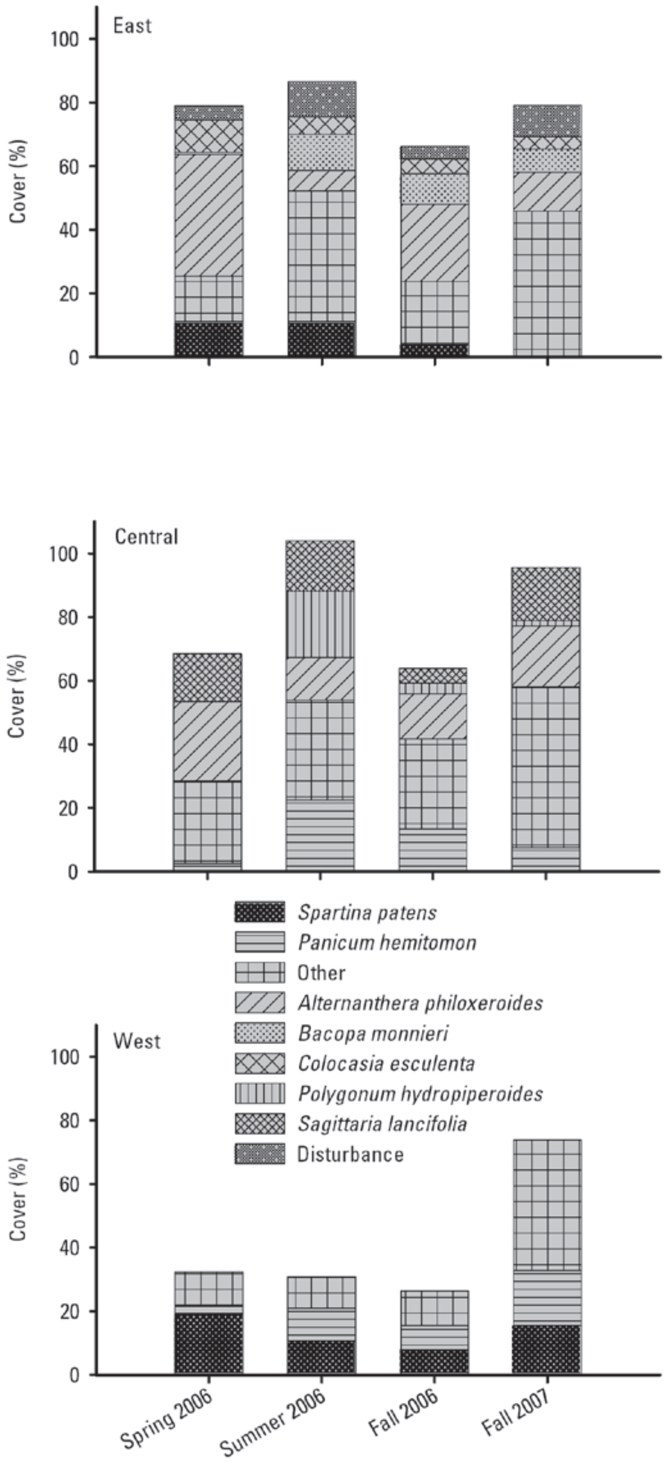

Figure 7. Percentage of cover of fresh marsh species in east, central, and west regions for all four seasons considered in the study. The "other" category includes 53 different species, each of which had less than 5 percent cover. The species that make up the disturbance category are identified in table 2. Although *Alternanthera philoxeroides* is a disturbance species, it was identified separately because it represents a high percentage of cover.

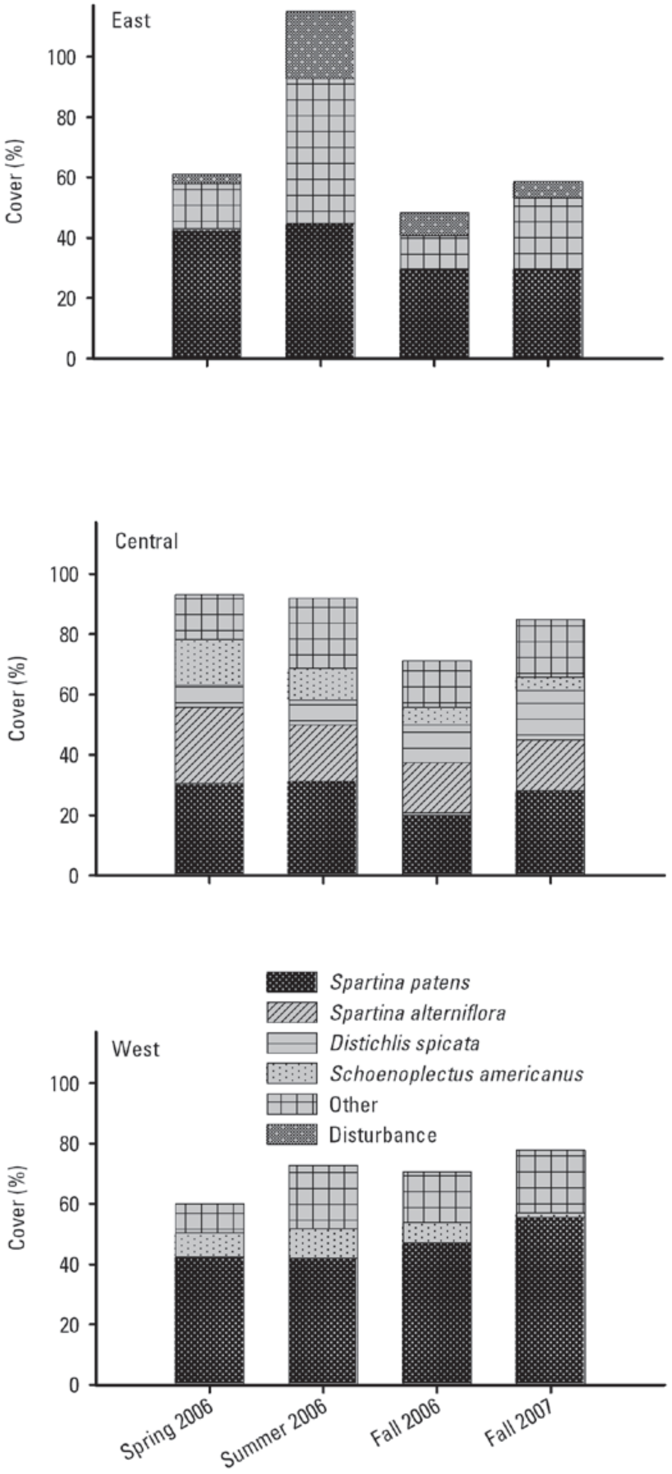

Figure 8. Percentage of cover of intermediate marsh species in east, central, and west regions for all four seasons considered in the study. The "other" category includes 40 different species, each of which had less than 5 percent cover. The species that make up the disturbance category are identified in table 2.

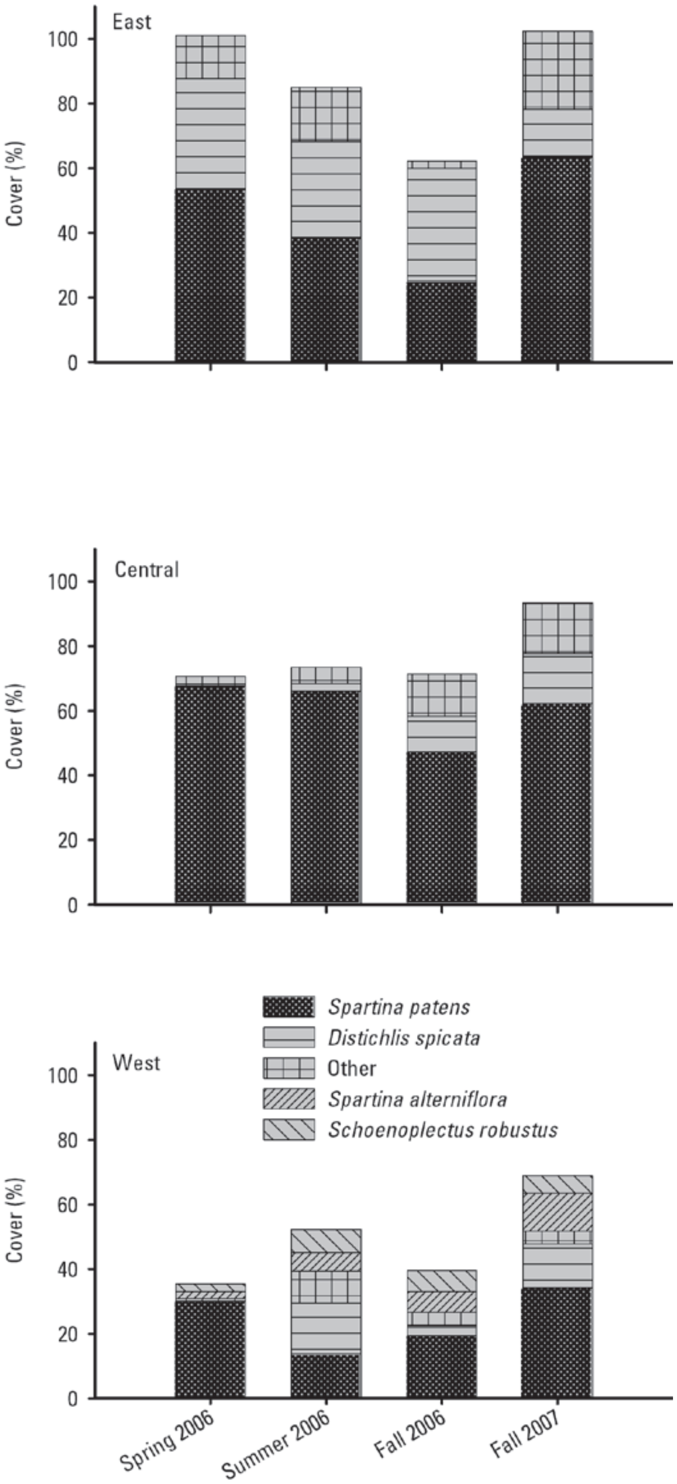

Figure 9. Percentage of cover of brackish marsh species in east, central, and west regions for all four seasons considered in the study. The “other” category includes 19 different species, each of which had less than 5 percent cover. The species that make up the disturbance category are identified in table 2.

fall 2007 (fig. 1; table 3). In the east region, composition changes in four sites were to fresher marsh classifications, and all sites had a change in species dominance. At the one site, where composition switched classification from fresh marsh to intermediate marsh, change was driven by high species richness in 2007, compared to dominance by a single species, *Bacopa monnieri*, in 2006 (table 3). In the central region, marsh composition of all 4 sites changed to a more saline classification, which was consistent with fall 2006 high mean salinities that exceeded mean pore-water salinity levels tolerated by the dominant species, as identified by Chabreck (1970). There were minimal changes in both species dominance and species richness between fall 2006 and 2007 in the central region. Three sites in the west region shifted to more saline classifications, even though only one site had a change in species dominance. Increased species richness and more saline compositions at all sites coincided with salinity values exceeding toleration limits of dominant species identified by Chabreck (1970).

Vegetation and Environmental Correlations

Pearson correlation coefficients suggested relational trends between the variables measured in this study from 2006 and 2007 datasets for each marsh type (table 4). Across all marsh types, total percentage of cover was significantly negatively correlated ($p<0.05$) with salinity and ammonium. Additionally, in fresh marsh, total percentage of cover was negatively correlated with sulfide ($r=-0.35$, $p<0.0001$) and positively correlated with pH ($r=0.18$, $p=0.0021$), nitrate ($r=0.17$, $p=0.0144$), and phosphate ($r=0.17$, $p<0.0283$). In brackish marsh, total percentage of cover was negatively correlated with nitrite and nitrate ($r=-0.29$, $p=0.0008$; $r=-0.25$, $p=0.0035$, respectively) and was positively correlated with pH ($r=0.28$, $p=0.0001$) and phosphate ($r=0.24$, $p=0.0122$). In pairwise partial correlations among independent variables across marsh types, nitrite and salinity were found to be significantly correlated with the most of the variables. The strongest positive correlations were between ammonium and sulfide in fresh marshes ($r=0.53$, $p<0.0001$) and between ammonium and phosphate ($r=0.53$, $p<0.0001$) in intermediate marshes, followed by nitrate and nitrite for all marsh types (table 4). The strongest negative correlations were between salinity and phosphate in fresh marshes ($r=-0.36$, $p<0.0001$) and between pH and nitrate in brackish marshes ($r=-0.52$, $p<0.0001$), followed by pH and nitrite in all marsh types (table 4).

Table 3. Dominant taxa, species richness, mean pore-water salinity, and vegetation type (classified based on Visser and others, [2002] salinity scores) for field sampling sites where marsh species composition changed type classification between fall 2006 and 2007. Vegetation types are fresh (F), intermediate (I), brackish (B), and saline (S). Underlined salinities indicate ≥ 1 SD, and bold pore-water salinities indicate ≥ 2 SD higher than the mean pore-water salinity of the dominant species identified from Chabreck (1970). Pore-water salinity data from Chabreck (1970) was not available for taxa indicated with (*).

Region	Site number	Vegetation type		Dominant taxa		Species richness		Pore-water salinity	
		Fall 2006	Fall 2007	Fall 2006	Fall 2007	Fall 2006	Fall 2007	Fall 2006	Fall 2007
East	1	I	F	*Panicum dichotomiflorum**	*Polygonum* spp.	2	4	7.13	1.80
	2	I	F	Vigna luteola	Panicum hemitomon	4	3	2.37	1.17
	3	F	I	Bacopa monnieri	Spartina patens	1	6	5.53	1.60
	4	I	F	Spartina patens	Ipomoea sagittata	3	3	3.93	1.60
	5	S	B	Distichlis spicata	Spartina patens	3	5	15.50	11.03
Central	6	B	S	Spartina patens	Distichlis spicata	4	2	20.43	4.37
	7	I	B	*Juncus* spp.	*Juncus* spp.	2	2	**9.10**	4.87
	8	I	B	Spartina patens	Spartina patens	2	3	16.77	5.30
	9	B	S	Spartina patens	Distichlis spicata	2	2	15.87	12.77
West	10	F	I	*Typha* spp.	*Typha* spp.	2	4	9.27	6.80
	11	B	I	Spartina patens	Spartina patens	1	2	9.07	6.50
	12	I	B	Spartina patens	Spartina patens	1	2	20.47	17.70
	13	B	S	*Spartina patens*	*Distichlis spicata*	3	4	**23.83**	21.03

Table 4. Pearson correlation coefficients for independent and dependent variables derived by using 2006 and 2007 datasets for (a) fresh marsh, (b) intermediate marsh, and (c) brackish marsh. Bold values represent significant correlations at $p<0.05$.

(a) Fresh marsh

Variable	Total cover	Salinity	pH	Sulfide	NO_2-N	NO_3-N	NH_4-N	PO_4
Total cover	1.00	-0.54	**0.18**	**-0.35**	-0.04	**0.17**	**-0.38**	**0.17**
Salinity		1.00	0.23	0.42	0.19	-0.14	0.28	-0.36
pH			1.00	**0.23**	**-0.27**	0.05	0.05	**0.39**
Sulfide				1.00	**-0.22**	-0.08	**0.53**	0.04
NO_2-N					1.00	**0.52**	**-0.16**	-0.11
NO_3-N						1.00	**-0.16**	0.09
NH_4-N							1.00	**0.45**
PO_4								1.00

Table 4. Pearson correlation coefficients for independent and dependent variables derived by using 2006 and 2007 datasets for (a) fresh marsh, (b) intermediate marsh, and (c) brackish marsh. Bold values represent significant correlations at $p<0.05$.—Continued

(b) Intermediate marsh

Variable	Total cover	Salinity	pH	Sulfide	NO_2-N	NO_3-N	NH_4-N	PO_4
Total cover	1.00	**-0.15**	0.09	-0.03	-0.10	0.10	-0.16	-0.02
Salinity		1.00	**-0.11**	**0.15**	**0.23**	0.06	**-0.26**	**-0.22**
pH			1.00	**0.36**	**-0.40**	**-0.17**	**0.32**	**0.25**
Sulfide				1.00	**-0.17**	-0.01	**0.39**	0.03
NO_2-N					1.00	**0.51**	**-0.14**	**-0.16**
NO_3-N						1.00	0.01	-0.03
NH_4-N							1.00	**0.53**
PO_4								1.00

(c) Brackish marsh

Variable	Total cover	Salinity	pH	Sulfide	NO_2-N	NO_3-N	NH_4-N	PO_4
Total cover	1.00	**-0.24**	**0.28**	0.02	**-0.29**	**-0.25**	**-0.38**	**0.24**
Salinity		1.00	**-0.25**	-0.06	**0.26**	**0.44**	-0.08	-0.04
pH			1.00	**0.37**	**-0.70**	**-0.52**	-0.10	**0.22**
Sulfide				1.00	**-0.26**	-0.15	**0.25**	0.14
NO_2-N					1.00	**0.44**	0.17	-0.09
NO_3-N						1.00	**0.24**	-0.10
NH_4-N							1.00	**0.19**
PO_4								1.00

Discussion

Fresh Marsh

The results indicated that elevated pore-water salinity and sulfide were significant stressors on vegetative cover in fresh marsh. Fresh marsh sites that converted to open water were exposed to salinities and sulfides during 2006 in excess of 10 and 1.6 mM, respectively. Mean salinities in fresh marsh greatly exceeded the typical range of 0–0.5 (Chabreck 1970) in all sampled time periods in the west region. The persistence of mean salinities above 7.1 in 2006 may have significantly affected cover values of *Panicum hemitomon*, the dominant freshwater species in the Chenier Plain (Visser and others, 2000), and limited the extent of its regrowth (fig. 7). Salinity levels in excess of 7.6 and sulfide in excess of 0.6 mM have been reported to significantly reduce productivity and increase plant mortality in fresh marsh vegetation communities (Hester and others, 1998; Koch and Mendelssohn 1989). La Peyre and others (2001) found that *Panicum hemitomon*, when grown in a mixture of more salt-tolerant species, decreased as salinity increased, until death occurred at 8.0, and Howard and Mendelssohn (1999) reported sharp decreases in production by *Panicum hemitomon* in response to three-month pulses of water with salinity of 6.0. Spalding and Hester (2007) observed reduced biomass production above salinity of 2.0 for *Panicum hemitomon*, but no such reduction was observed for *Spartina patens*. Those findings, consistent with observations from this study, suggest that *Panicum hemitomon* dieback at initial salinity exposure provided opportunities for *Spartina patens*, one of the dominant intermediate marsh species, to dominate cover by spring 2006.

Fresh marsh in the central and east regions was exposed to salinities and sulfides on the higher end of their typical range (0–3 and 0–0.5 mM, respectively). In October 2005, leaf browning from salt burn was observed in all regions (Steyer and others, 2007); however, we observed little effect on fresh marsh cover values in the central and east regions. The fall 2006 and 2007 fresh marsh cover values measured in this study (fig. 7), were similar to fresh marsh cover values measured in 2003 and 2004 (mean = 69.2%; n = 218) under the CWPPRA monitoring program (LaCoast, 2008). The difference we observed was a higher percentage of disturbance species occurring, in particular *Alternanthera philoxeroides*, which is commonly found flanking marsh edges adjacent to open water. The significant area of new open water and the physical disruption of the marsh surface in fresh and intermediate marshes found by Barras (2007) after Hurricane Katrina may contribute to the predominance by *Alternanthera philoxeroides* and other disturbance species in these regions.

Intermediate Marsh

Intermediate marshes in the central and west regions were exposed to salinities well outside the 0.5–5.0 range as described in Chabreck (1970); however, they were not at levels that are lethal to the dominant marsh species. *Spartina patens*, the dominant species in all regions of the coast, generally experiences reduced growth and net photosynthesis when exposed to salinity above 10 (Pezeshki and others, 1987; Pezeshki and DeLaune 1993; Broome and others, 1995; Ewing and others, 1995) but has a high tolerance of salinity conditions and is commonly found to coexist with *Spartina alterniflora* in brackish communities. In the central region, *Distichlis spicata* became codominant, suggesting that parts of this region are transitioning to more brackish marsh communities (table 3). The intermediate marsh in the east region appears to be transitioning to fresh marsh, with much lower salinities, high species richness, and an increase of annuals and disturbance species; however, it is not uncommon for fresh and intermediate marsh communities to transition between marsh types, even in nondisturbance time periods, because of similarities in species composition. The intermediate marsh in the east region had the greatest amount of new open water formation and physical disruption following Hurricane Katrina (Barras, 2007). The physical disruption covered the landscape with displaced patches of *Spartina patens*, commonly referred to as marsh balls. Marsh balls that were relocated during the storm were commonly a few meters in size. By fall 2007, most of the identified annuals and disturbance species were growing through the marsh balls in the east region, and there was limited expansion of *Spartina patens* cover.

The intermediate marsh cover values measured in the central and west regions in our study (fig. 8) were comparable to the cover values from intermediate marshes measured in 2003 and 2004 (mean = 78.4%; n = 103) under the CWPPRA monitoring program. The highest cover values in the central region may be related to the transition in dominant perennials and the lowest sulfide stress among the regions.

Brackish Marsh

Salinity and sulfide concentrations were variable among sites within all three coastal regions of the brackish marsh communities. Although mean salinities were significantly higher in the west, concentrations were primarily in the typical range of 5 to 18 (Chabreck 1970) in all regions. Sulfides generally increased from season to season in the central and west regions and decreased in the east region. *Spartina patens* and *Distichlis spicata* were found to be the dominant brackish marsh species in all regions of the coast during the study. The high relative cover of *Distichlis spicata* in the east region appeared to be associated with physical disturbance of the marsh substrate. Observed areas of scour had some of the highest cover values. Bertness (1991) found that *Distichlis spicata* is adept at colonizing hypersaline bare space and resistant to wrack burial, which is consistent with our observations. The brackish marsh cover values in the west region in 2006 and 2007 were low compared to average conditions measured in 2003–04 by the CWPPRA monitoring program (mean = 75.4%, n = 159), and strongly reflect the low *Spartina patens* cover and slow recovery by *Spartina patens*. Our observations of reduced *Spartina patens* cover may be the result of reduced seed germination, which has been observed to occur in *Spartina patens* when salinities exceed 3.5 (Baldwin and others, 1996). The combined influences of high salinity and sulfide appear to favor the expansion of more tolerant *Spartina alterniflora* and *Schoenoplectus robustus*.

Landscape Response

A prolonged drought began in late 2004 in the south-central and southwest climatic regions in Louisiana and in summer 2005 in the southeast region. The drought extended into summer 2006 in the southwest, fall 2006 in the south-central, and winter 2006 in the southeast region (fig. 2). Visser and others (2002) were able to identify vegetation community changes between 1997 and 2000 that included changes due to an extreme drought in 1999 and 2000 across the Barataria estuarine landscape in coastal Louisiana. Because of the lack of immediate prehurricane salinity data, the vegetation change results presented in this study represent the combined effects of both hurricane and drought conditions.

Changes in marsh type from fall 2006 to fall 2007 were identified at 13 sampling sites, equally distributed among the three regions. The changes that occurred in the east region were primarily to fresher marsh classifications. Though the hurricanes physically disturbed the marsh landscape, stress associated with salinity and sulfide appeared to have been minimal. From January through May 2006, this region received an average freshwater discharge of 85.8 m^3/s from the Caernarvon Freshwater Diversion Project located at river mile 81.5 (131.2 km). Even though the region was in an extended drought, it appears that the freshwater from the diversion structure moderated salinities, and the high nutrient loads may have contributed to rapid colonization by disturbance species in the fresh and intermediate marshes. Lane and others (2007) showed strong inverse relationships between diversion discharge and salinity in upper Breton Sound. A box model developed by Swenson and others (2006) showed that river diversions can significantly reduce water residence times and salinities within upper portions of their receiving basins. The central region was only indirectly exposed to storm surge from the hurricanes, and salinity data suggested elevated exposures primarily in intermediate and brackish marshes. Changes in vegetation composition to more saline marsh classifications occurred, but ancillary salinity data (2004 and 2005) from CWPPRA suggested that, prior to the hurricanes of 2005, some intermediate marsh sites had drought-induced salinities above typical ranges.

The west region was most highly impacted and showed both physical and plant stress effects. The effects of salinity on plant cover appeared to be amplified when sulfide stress was present. Sulfide is a phytotoxic substance that accumulates in waterlogged soils and has been shown to reduce growth in marine and freshwater species (Joshi and others, 1975; Ingold and Havill, 1984; Koch and others, 1990). The excessive and prolonged flooding in the west region, identified from satellite imagery, corresponded to the many sites that had high concentrations of mean pore-water sulfide in spring and summer 2006, which may have contributed to the low percentage of vegetation cover in this region. Buresh and Patrick (1978) found that NH_4-N, rather than NO_3-N, was the primary form of nitrogen assimilated by marsh plants. Across all marsh types, total cover was inversely correlated with ammonium, suggesting uptake by the vegetation. The uptake of NH_4-N in fresh and salt marsh has been shown to be limited by high sulfide concentration (Mendelssohn and McKee 1988; Bradley and Morris 1990; Koch and others, 1990; Flynn and others, 1995). High interstitial NH_4-N was found at many of the high sulfide sites, and low cover values suggested that sulfide may have reduced plant uptake of NH_4-N. The high correlation between ammonium and phosphate in fresh and intermediate marshes might have suggested that phosphate was also not taken up at sites with high sulfide. The mobilization of phosphate and ammonium combined with phytotoxicity from sulfide was shown to favor fast-growing species that are resistant to sulfide (Lamers and others, 1998).

Summary

The hurricanes of 2005 contributed to vegetation community change across the Louisiana coast through the stress induced by saltwater storm surge, primarily from Hurricane Rita, and physical impacts to the marsh substrate, primarily from Hurricane Katrina. Salinity and sulfide stress were persistent in the west region throughout 2006 and in fall 2007, contributing to low vegetative cover and shifts towards more saline marsh compositions with minor changes in species dominance. Although hurricane landfalls did not directly impact the central region, saltwater storm surge from Hurricane Rita did reach fresh, intermediate, and brackish marshes. Salinity intrusion in the central region combined with drought conditions may have contributed to shifts towards more saline marsh classifications, but with minimal changes in species dominance. Physical disruption of the marsh surface through shearing and removal was predominant in the east region, contributing to a high abundance of disturbance species and major changes in species dominance from fall 2006 to fall 2007. Low salinity and sulfide stress, together with abundant nutrients, contributed to high vegetative cover in the east compared to the central and west regions. The variability depicted among sites within marsh types suggested the importance of species-specific tolerances to salinity and sulfide. Two full growing seasons after the hurricanes of 2005, marshes directly impacted in the east and west regions were still recovering. Although vegetation cover values were approaching prehurricane levels, species compositions were still indicative of a disturbance environment. Continued assessment of these vegetation communities over time should provide important insights into factors contributing to ecosystem resilience.

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