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Patterns in seagrass coverage and community composition along the Texas coast: A three-year trend analysis

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Patterns in seagrass coverage and community composition along the Texas coast: A three-year trend analysis

by

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Abstract

Patterns in seagrass coverage and community composition along the Texas coast: A three-year trend analysis

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Seagrasses are extremely productive coastal plant communities that serve as habitat for various types of marine and estuarine fauna and provide numerous ecosystem services. Seagrass meadows around the world have become threatened by environmental and anthropogenic pressures such as altered hydrologic regimes, physical disturbances, and eutrophication. Monitoring programs that provide high-resolution information and document changes in cover, morphometric characteristics, species composition, and tissue nutrient content across large spatial scales are critical in global conservation and management efforts. In an attempt to address the uncertainties regarding the current distribution and condition of seagrasses in the southwest Gulf of Mexico, I conducted annual sampling from 2011-2013 to examine seagrass cover and condition at 558 permanent stations. Sampling occurred in three regions of the Texas coast: the Coastal Bend (CB), Upper Laguna Madre (ULM), and Lower Laguna Madre (LLM), which together comprise over 94% of the seagrasses in Texas. Significant trends in seagrass coverage and tissue elemental composition were highly location- and species-specific. In the CB, I did not observe significant changes in seagrass cover and no spatial patterns in tissue nitrogen (N) or phosphorus (P) were apparent. However, I observed a species shift in the northern ULM, where significant decreases in *Syringodium filiforme* cover were coupled with significant increases in *Halodule wrightii* cover. Long-term salinity records at four stations throughout the study area suggest that *S. filiforme* mortality in the ULM in 2013 was a product of an extended period of high salinity (> 55) that began in late 2012. In LLM, there were significant increases in *H. wrightii* cover in the north and significant decreases in *T. testudinum* cover in the south, which cannot be explained based on underwater light levels, salinity, or nutrient availability. Both *H. wrightii* and *T. testudinum* displayed lower C:N, C:P, and N:P ratios, along with enriched $\delta^{15}N$ signatures nearest urban areas, particularly in the LLM. This study illustrates the value of integrating rapid-assessment field sampling and rigorous statistical and spatial analysis into a large-scale seagrass monitoring program to uncover patterns in seagrass community structure. I detected significant trends in seagrass coverage and condition across multiple spatial and temporal scales, including a massive species replacement that coincided with a prolonged period of hypersaline conditions.

Table of Contents

List of Tables ix

List of Figures xiv

Introduction.. 1

Methods 4

  Site description 4

  Monitoring design 7

  Sampling methods 10

  Laboratory analyses 11

    Total suspended solids (TSS) 11

    Seagrass elemental and stable isotope analyses................................ 12

  Spatial and statistical analyses 13

  Long-term salinity measurements 14

Results 15

  Seagrass percent cover and canopy height... 15

  Elemental composition and stable isotope signatures 21

  Long-term salinity measurements 27

  Water quality and water clarity 27

Discussion... 31

  Shifts in seagrass coverage and species composition 31

  Comparison of current seagrass distribution to historic maps 34

  Spatial trends in N and P availability 35

  Summary 37

Appendix A – Subregion Delineation 39

Appendix B – Seagrass Percent Cover and Canopy Height 41

Appendix C – Tissue Elemental Composition and Stable Isotope Signatures 71

References.. 93

List of Tables

Table 1. Water quality data for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012, and 2013 (DO = dissolved oxygen). Values are x̄ (mean) and standard error (S.E.). 30

Table 2. Water transparency data for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012, and 2013 (k_d = light attenuation coefficient, TSS = total suspended solids). Values are x̄ (mean) and standard error (S.E.). 31

Table B1. Seagrass percent cover (%) measurements for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.).41

Table B2. Repeated measures ANOVA table for the effect of year on seagrass cover for each species (plus total cover) across each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant effects (α = 0.05) are denoted in bold.......... 42

Table B3. Post hoc Tukey multiple comparison tests for seagrass percent cover change over time for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences (α = 0.05) are denoted in bold.......... 43

Table B4. Seagrass percent cover (%) measurements for each subregion in the Coastal Bend (CB) region (AB = Aransas Bay, RFB-N = Redfish Bay North, RFB-SW = Redfish Bay Southwest, RFB-SE = Redfish Bay Southeast, CCB = Corpus Christi Bay) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.). 44

Table B5. Seagrass percent cover (%) measurements for each subregion in the Upper Laguna Madre (ULM) region (ULM-N = ULM North, ULM-NC = ULM North-Central, ULM-SC = ULM South-Central, ULM-S = ULM South) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.).. 46

Table B6. Seagrass percent cover (%) measurements for each subregion in the Lower Laguna Madre (LLM) region (LLM-N = LLM North, LLM-C = LLM Central, LLM-SW = LLM Southwest, LLM-SE = LLM Southeast) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.).48

Table B7. Repeated measures ANOVA table for the effects of subregion and year on seagrass cover for each species (plus total cover) across each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences (α = 0.05) are denoted in bold. 50

Table B8. Post hoc Tukey multiple comparison tests for seagrass percent cover change over time for each subregion in the Coastal Bend (CB) region (AB = Aransas Bay, RFB-N = Redfish Bay North, RFB-SW = Redfish Bay Southwest, RFB-SE = Redfish Bay Southeast, CCB = Corpus Christi Bay). Significant differences (α = 0.05) are denoted in bold.52

Table B9. Post hoc Tukey multiple comparison tests for seagrass percent cover change over time for each subregion in the Upper Laguna Madre (ULM) region (ULM-N = ULM North, ULM-NC = ULM North-Central, ULM-SC = ULM South-Central, ULM-S = ULM South). Significant differences (α = 0.05) are denoted in bold..................................... 53

Table B10. Post hoc Tukey multiple comparison tests for seagrass percent cover change over time for each subregion in the Lower Laguna Madre (LLM) region (LLM-N = LLM North, LLM-C = LLM Central, LLM-SW = LLM Southwest, LLM-SE = LLM Southeast). Significant differences (α = 0.05) are denoted in bold... 54

Table B11. Seagrass canopy height (cm) measurements for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.)... 55

Table B12. Repeated measures ANOVA table for the effect of year on seagrass canopy height for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences (α = 0.05) are denoted in bold... 56

Table B13. Post hoc Tukey multiple comparison tests for seagrass canopy height change over time for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences (α = 0.05) are denoted in bold... 57

Table C1. Seagrass C:N:P molar ratios for *Halodule wrightii* in each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.)... 71

Table C2. Seagrass C:N:P molar ratios for *Thalassia testudinum* in each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.)... 73

Table C3. Repeated measures ANOVA table for the effect of year on seagrass C:N:P molar ratios and stable isotope (δ^{13}C and δ^{15}N) signatures for *Halodule wrightii* in each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences ($\alpha = 0.05$) are denoted in bold. 75

Table C4. Repeated measures ANOVA table for the effect of year on seagrass C:N:P molar ratios and stable isotope (δ^{13}C and δ^{15}N) signatures for *Thalassia testudinum* in each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences ($\alpha = 0.05$) are denoted in bold. 76

Table C5. Post hoc Tukey multiple comparison tests for seagrass C:N:P molar ratio and stable isotope (δ^{13}C and δ^{15}N) signature changes in *Halodule wrightii* over time for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences ($\alpha = 0.05$) are denoted in bold.. 77

Table C6. Post hoc Tukey multiple comparison tests for seagrass C:N:P molar ratio and stable isotope (δ^{13}C and δ^{15}N) signature changes in *Thalassia testudinum* over time for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences ($\alpha = 0.05$) are denoted in bold...................................... 77

List of Figures

Figure 1. The Texas coast showing the three study regions (Coastal Bend, Upper Laguna Madre, and Lower Laguna Madre). Inset shows an example of the tessellated hexagon grid and sampling stations (n = 72) in Redfish Bay. Green areas indicate seagrass coverage from the NOAA 2004/2007 Benthic Habitat Mapping (http://coast.noaa.gov/digitalcoast/data/benthiccover/)..................... 5

Figure 2. The three regions in this study (the Coastal Bend (A), Upper Laguna Madre (B), and Lower Laguna Madre (C)) divided into thirteen subregions, where n = number of stations. Green areas indicate seagrass coverage from the NOAA 2004/2007 Benthic Habitat Mapping (http://coast.noaa.gov/digitalcoast/data/benthiccover/)..................... 9

Figure 3. Seagrass percent cover (%; mean + standard error) for all regions (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs testing the effect of year and Tukey multiple comparison tests were applied within each region for each species. Results from RM ANOVAs are listed below each region, and significant differences from multiple comparison tests ($\alpha = 0.05$) are listed (A, B, C) where present. Note the difference in y axis ranges... 16

Figure 4. Significant increases in *Halodule wrightii* percent cover and significant decreases of *Syringodium filiforme* percent cover in Upper Laguna Madre (ULM North and ULM North-Central subregions) from 2011-2013... 18

Figure 5. Significant increases in *Halodule wrightii* percent cover in Lower Laguna Madre (LLM North and LLM Central subregions) from 2011-2013.19

Figure 6. Significant decreases in *Thalassia testudinum* percent cover in Lower Laguna Madre (LLM Southeast subregion) from 2011-2013. 20

Figure 7. Lower C:P and N:P molar ratios for *Halodule wrightii* were observed in northern Upper Laguna Madre from 2011-2013. No spatial patterns were observed in C:N molar ratios (Figure C6). 22

Figure 8. Lower C:N and C:P molar ratios for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) were observed in the west and southeast of Lower Laguna Madre from 2011-2013....................... 23

Figure 9. N:P molar ratios for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) were observed in the west and southeast of Lower Laguna Madre from 2011-2013. 25

Figure 10. Stable isotope δ^{13}C and δ^{15}N signatures for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in Lower Laguna Madre from 2011-2013. Note more enriched δ^{15}N signatures in the west and southeast. 26

Figure 11. Salinity time series from 1994 to 2014 at four locations along the Texas coast: Aransas Bay, Upper Laguna Madre, northern Lower Laguna Madre and southern Lower Laguna Madre (see “Methods” section for station coordinates). Arrows indicate major storm events for the region, which are often reflected by subsequent drops in salinity, including Tropical Storms Charley (TSC), Frances (TSF1), Bertha (TSB), and Fay (TSF), and Grace (TSG), and Hurricanes Bret (HB), Erika (HE), Dolly (HD), and Alex (HA). 28

Figure B1. Seagrass percent cover (%; mean + standard error) for all subregions in the Coastal Bend (CB) region (AB = Aransas Bay, RFB-N = Redfish Bay North, RFB-SW = Redfish Bay Southwest, RFB-SE = Redfish Bay Southeast, CCB = Corpus Christi Bay) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs and Tukey multiple comparison tests were applied with subregion and year treated as fixed effects, and the interaction term is reported for each model. Significant differences from multiple comparison tests (α = 0.05) are listed (A, B, C) where present. Note the difference in y-axis ranges.58

Figure B2. Seagrass percent cover in the Coastal Bend from 2011-2013 for total (all species) seagrass and *Halodule wrightii*. 59

Figure B3. Seagrass percent cover in the Coastal Bend from 2011-2013 for *Thalassia testudinum* and *Syringodium filiforme*. 60

Figure B4. Seagrass percent cover in the Coastal Bend from 2011-2013 for *Halophila engelmannii* and *Ruppia maritima*. 61

Figure B5. Seagrass percent cover (%; mean + standard error) for all subregions in the Upper Laguna Madre (ULM) region (ULM-N = ULM North, ULM-NC = ULM North-Central, ULM-SC = ULM South-Central, ULM-S = ULM South) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs and Tukey multiple comparison tests were applied with subregion and year treated as fixed effects, and the interaction term is reported for each model. Significant differences from multiple comparison tests (α = 0.05) are listed (A, B, C) where present. Note the difference in y-axis ranges.. 62

Figure B6. Seagrass percent cover in the Upper Laguna Madre from 2011-2013 for total (all species) seagrass and *Halodule wrightii*.......................... 63

Figure B7. Seagrass percent cover in the Upper Laguna Madre from 2011-2013 for *Thalassia testudinum* and *Syringodium filiforme*. 64

Figure B8. Seagrass percent cover in the Upper Laguna Madre from 2011-2013 for *Halophila engelmannii* and *Ruppia maritima*. 65

Figure B9. Seagrass percent cover (%; mean + standard error) for all subregions in the Lower Laguna Madre (LLM) region (LLM-N = LLM North, LLM-C = LLM Central, LLM-SW = LLM Southwest, LLM-SE = LLM Southeast) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs and Tukey multiple comparison tests were applied with subregion and year treated as fixed effects, and the interaction term is reported for each model. Significant differences from multiple comparison tests (α = 0.05) are listed (A, B, C) where present. Note the difference in y-axis ranges... 66

Figure B10. Seagrass percent cover in the Lower Laguna Madre from 2011-2013 for total (all species) seagrass and *Halodule wrightii*.......................... 67

Figure B11. Seagrass percent cover in the Lower Laguna Madre from 2011-2013 for *Thalassia testudinum* and *Syringodium filiforme*. 68

Figure B12. Seagrass percent cover in the Lower Laguna Madre from 2011-2013 for *Halophila engelmannii* and *Ruppia maritima*. 69

Figure B13. Seagrass canopy height (cm; mean + standard error) for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs testing the effect of year and Tukey multiple comparison tests were applied within each region for each species. Results from RM ANOVAs are listed below each region, and significant differences from multiple comparison tests ($\alpha = 0.05$) are listed (A, B, C) where present. Note the difference in y-axis ranges... 70

Figure C1. *Halodule wrightii* leaf C:N, C:P, and N:P molar ratios and $\delta^{13}C$ and $\delta^{15}N$ signatures (‰; mean + standard error) for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs testing the effect of year and Tukey multiple comparison tests were applied within each region for each species. Results from RM ANOVAs are listed below each region, and significant differences from multiple comparison tests ($\alpha = 0.05$) are listed (A, B, C) where present. Note the difference in y-axis ranges... 78

Figure C2. *Thalassia testudinum* leaf C:N, C:P, and N:P molar ratios and δ^{13}C and δ^{15}N signatures (‰; mean + standard error) for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs testing the effect of year and Tukey multiple comparison tests were applied within each region for each species. Results from RM ANOVAs are listed below each region, and significant differences from multiple comparison tests ($\alpha = 0.05$) are listed (A, B, C) where present. Note the difference in y-axis ranges.. 79

Figure C3. C:N and C:P molar ratios for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in the Coastal Bend from 2011-2013.80

Figure C4. N:P molar ratios for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in the Coastal Bend from 2011-2013.81

Figure C5. δ^{13}C signatures and δ^{15}N signatures for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in the Coastal Bend from 2011-2013... 82

Figure C6. C:N and C:P molar ratios for *Halodule wrightii* in Upper Laguna Madre from 2011-2013. 83

Figure C7. N:P molar ratios for *Halodule wrightii* in Upper Laguna Madre from 2011-2013... 84

Figure C8. δ^{13}C and δ^{15}N signatures for *Halodule wrightii* in Upper Laguna Madre from 2011-2013. 85

Figure C9. C:N and C:P signatures for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in Lower Laguna Madre from 2011-2013. 86

Figure C10. N:P molar ratios for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in Lower Laguna Madre from 2011-2013. 91

Figure C11: $\delta^{13}C$ and $\delta^{15}N$ signatures for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in Lower Laguna Madre from 2011-2013.. 92

Introduction

In many coastal systems, seagrasses are prominent structural features of the benthos, and their condition and productivity can be a valuable indicator of water quality and estuarine health (Dennison et al. 1993; Orth and Moore 1983; Scanes et al. 2007; Montefalcone 2009). Seagrasses form large meadows (beds) which serve as important food sources and habitats for many organisms (Valentine and Heck 1999; Bell et al. 2001; Heck et al. 2003; Bostrom et al. 2006; Vizzini 2009), promote sedimentation (Newell and Koch 2004; Widdows et al. 2008), assist in biogeochemical cycling (Marba et al. 2006; Fourqurean et al. 2012), and are extremely productive (Duarte and Chiscano 1999; Rasheed et al. 2008; Unsworth et al. 2012). Seagrasses provide numerous ecosystem services to coastal areas (Terrados and Borum 2004; Cullen-Unsworth and Unsworth 2013), including protecting shorelines from erosion through wave attenuation (Manca et al. 2012; Christianen et al. 2013), sequestering large amounts of carbon from the water column (Fourqurean et al. 2012; Greiner et al. 2013), and serving as key nursery grounds for many fish and shellfish species of commercial and recreational value (Blandon and zu Ermgassen 2014).

Despite the ecological importance of seagrasses, their coverage is declining worldwide (Orth et al. 2006; Waycott et al. 2009; Short et al. 2011). In addition to the loss of ecosystem services, decreases in seagrass coverage may exert strong controls on meio- and macrofaunal communities, since seagrasses and epiphytic algae are the base of many marine and estuarine food webs (Moncreiff and Sullivan 2001; Kirsch et al. 2002; Heck et al. 2008). Furthermore, shifts in the seagrass species composition of an area may shape local faunal assemblages, as numerous studies have documented preference for one seagrass species over another by epifauna and invertebrates (Kenyon et al. 1997;

Sanchez-Jerez et al. 1999; Hamilton et al. 2012; but see Leopardas et al. 2014), fishes (Mariani and Alcoverro 1999; MacArthur and Hyndes 2001; Hyndes et al. 2003) and larger seagrass grazers such as green turtles (*Chelonia mydas*; Fuentes et al. 2006; Kelkar et al. 2013) and redhead ducks (*Aythya americana*; McMahan 1970; Mitchell et al. 1994).

Changes in seagrass community structure and condition provide insight into water quality and ecological functioning (Dennison et al. 1993; Orth and Moore 1983; Scanes et al. 2007; Montefalcone 2009), as well as clues to abiotic factors (e.g. environmental disturbances) exerting controls on the system (Boudouresque et al. 2009; Cabaco et al. 2012; Roca et al. 2014). Seagrass tissues are long-term integrators of local environmental conditions, and changes in tissue carbon (C), nitrogen (N), and phosphorus (P) may show evidence of altered nutrient, light, salinity, or hydrologic regimes. Since the primary source of dissolved inorganic carbon (DIC) for seagrasses (bicarbonate) is ubiquitous in seawater, shifts in C:N or C:P molar ratios typically indicate variation in the amount of available dissolved inorganic N (DIN) or P (DIP) in the system, providing a link to nutrient inputs and biogeochemical cycling in the local environment (Duarte 1990). Additionally, stable isotopic ratios such as ^{13}C:^{12}C ($\delta^{13}C$) and ^{15}N:^{14}N ($\delta^{15}N$) provide information about the pool of DIC or DIN utilized by seagrasses for metabolism and growth (Lin et al. 1991; Hemminga and Mateo 1996; Campbell and Fourqurean 2009), and can be useful for seagrass community food web studies (Lepoint et al. 2004).

Given the importance of seagrasses, various monitoring efforts have been utilized over the past several decades to conduct research and document seagrass community changes over time (Duarte et al. 2004; Short et al. 2006). Numerous types of remote sensing approaches have been used to measure seagrass extent and map meadow boundaries, employing satellites (e.g. Phinn et al. 2008; Lyons et al. 2013; Roelfsema et al. 2013), aerial photography (e.g. Ward et al. 1997; Kendrick et al. 2002; Frederiksen et al. 2004; Bernard et al. 2007; Costello and Kenworthy 2011), and side-scan sonar (e.g. Ardizzone et al. 2006; Montefalcone et al. 2013). An alternative to remote sensing is field-based monitoring, which provides accurate and high-resolution measurements of seagrass coverage, biomass, physiology, tissue and morphometric condition, and species assemblage. Using rigorous statistical and geospatial methodology, including linear models and interpolation, I will show that results from *in situ* monitoring coupled with statistical and spatial analysis in a GIS are critical to determine smaller-scale community changes such as increases or decreases in cover or patterns in species succession.

The primary objective of my study was to assess changes in seagrass percent cover and species composition over three years (2011-2013) by employing a rapid-assessment, repeated measures monitoring design over nearly 250 km of Texas coastline. I expected to detect large amounts of interannual variability in seagrass coverage, and hypothesized that major changes in percent cover and species composition along the Texas coast would be highly location-specific (Quammen and Onuf 1993; Onuf 2007). I also hypothesized that seagrass C:N:P molar ratios and stable isotopic signatures would be regionally distinct and show inter-specific differences. The establishment of over 550 permanent stations provided greater assurance for reliable and accurate detection of temporal and spatial change in seagrass parameters than has previously been reported for Texas waters. I attempted to explain temporal changes in seagrass composition and percent cover by examining hydrologic data, and will link variations in tissue elemental content to ambient nutrient regimes. The results of this monitoring show that extensive changes in seagrass community structure and coverage have taken place in as little as one year, and my high-resolution maps illustrate this story across space and through time, providing a vivid analysis of the dynamic nature of Texas seagrass communities.

Methods

SITE DESCRIPTION

The Texas coast is composed of a network of semi-enclosed estuarine bays located behind long barrier islands that run parallel to the shore (Figure 1). Average depths of Texas bays range from 1-3 m with the exception of deeper, dredged inlets and the Gulf Intracoastal Waterway (GIWW). Because of their shallow depths, Texas bays are primarily wind-mixed, with the exception of some tidal mixing near passes and inlets (Solis and Powell 1999). Salinities exhibit wide ranges with an average of around 35 in the central bay systems up to > 50 in parts of Laguna Madre, mainly due to the strong precipitation gradient along the coast, with the highest amounts of precipitation and river discharge in the northeast and the lowest amounts in the southwest.

The southern portion of the Texas coast is dominated by an extensive lagoon, the Laguna Madre, which is divided into two parts (Upper and Lower) by a large expanse of wind-tidal flats. The Upper Laguna Madre (ULM) receives minimal amounts of freshwater inflow from tributaries draining into Baffin Bay, and Lower Laguna Madre (LLM) also receives minimal freshwater inflow from agricultural run-off into the Arroyo-Colorado River (Tunnell 2002). Limited freshwater inflows coupled with long water residence times (up to 350 days) and high evaporation rates across the nearly 185 km expanse of the lagoon create hypersaline conditions (Solis and Powell 1999; Tunnell 2002). The Laguna Madre supports the majority (79%) of the state's seagrass beds (Pulich and Onuf 2007), which historically grew as far north as Galveston Bay (Figure 1) but have suffered large declines since the 1950's (Pulich and White 1991). At this time, 94 % of seagrasses in Texas are found in the central "Coastal Bend" (CB) region and Laguna Madre (Pulich and Onuf 2007).

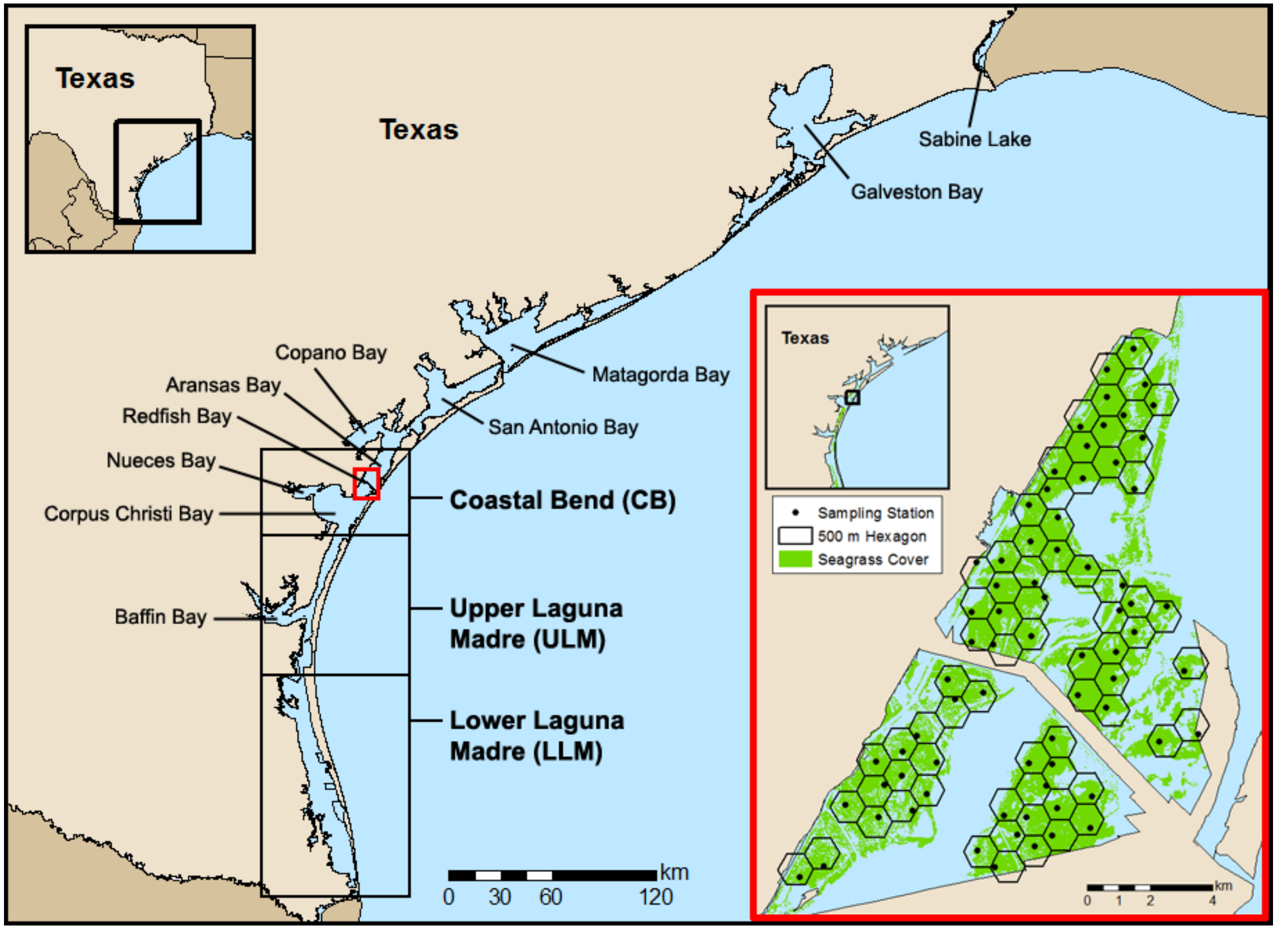

Figure 1. The Texas coast showing the three study regions (Coastal Bend, Upper Laguna Madre, and Lower Laguna Madre). Inset shows an example of the tessellated hexagon grid and sampling stations (n = 72) in Redfish Bay. Green areas indicate seagrass coverage from the NOAA 2004/2007 Benthic Habitat Mapping (http://coast.noaa.gov/digitalcoast/data/benthiccover/).

Texas is home to five species of subtropical seagrasses: *Halodule wrightii* (shoal grass), *Thalassia testudinum* (turtle grass), *Syringodium filiforme* (manatee grass), *Halophila engelmannii* (star grass), and *Ruppia maritima* (widgeon grass). Throughout most of the state, *H. wrightii* is the dominant species, except for some dense meadows of *T. testudinum* present in parts of Redfish Bay and LLM (Onuf 2007). Since *H. wrightii* can tolerate a wide range of salinities and has fast colonization rates, it has long been recognized as the pioneer species in Texas estuaries (Dunton 1996). In succession over time, *H. wrightii* meadows are typically followed by *S. filiforme* and then *T. testudinum*, which is recognized as the climax community species in Texas (Zieman 1982; Zieman and Zieman 1989; Withers 2002). Based on periodic surveys of seagrass coverage in Texas undertaken since the 1960's, it appears that total seagrass cover in ULM has increased over time, but that coverage in LLM has decreased (Onuf 2007). While these irregular surveys have provided valuable snapshots of the extent of existing seagrass beds, they give no information about variability across small temporal scales, which can provide a much more detailed account of changes in the community. Seagrass monitoring in Texas must be completed more regularly in order to provide insight into seagrass meadow dynamics before large-scale changes occur (Neckles et al. 2012). A challenge with annual monitoring, however, is separating meaningful trends in seagrass coverage from natural interannual system variability. Seagrasses in Texas are perennial, growing in late spring and early summer, then senescing and becoming dormant with little growth in winter months (Conover 1964; Dunton 1994). Given this seasonal leaf dieback and regrowth, some inherent variability will exist in seagrass meadow cover from year to year.

MONITORING DESIGN

Based on recommendations of the Texas Seagrass Monitoring Plan (Dunton et al. 2011), researchers at the University of Texas Marine Science Institute (UTMSI) created a "statewide" seagrass monitoring program to study seagrass meadows in Texas and investigate the environmental drivers of seagrass community change (www.texasseagrass.org). This monitoring program is based on a smaller, three-tiered seagrass monitoring program used by Neckles et al. (2012) in New York and Massachusetts. Following this design, 'tier 1' involves the use of remotely sensed imagery to delineate seagrass meadow extent across a large geographic area, 'tier 2' involves rapid assessment sampling across broad geographic areas, where the data collected from each station is limited and thus provides a snapshot of major trends (this study), while 'tier 3' incorporates intensive sampling efforts at a small number of representative stations, gathering data on parameters such as sediment characteristics and seagrass biomass that are too time- and resource-intensive to sample over the whole region (Neckles et al. 2012). Monitoring followed a restricted random sampling design to ensure even coverage across the study region while still maintaining random station selection (Elzinga et al. 2001; Dunton et al. 2011; Neckles et al. 2012). To generate the sampling stations, maps from the National Oceanic and Atmospheric Administration's (NOAA) 2004/2007 Benthic Habitat Mapping program (http://coast.noaa.gov/digitalcoast/data/benthiccover/) were used to create a shapefile delineating seagrass extent along the Texas coast, which was overlaid with a grid of tessellated hexagons (Stevens 1997). Hexagons created for Aransas, Redfish, and Corpus Christi Bays had 500 m sides (~0.65 km^2 area) and hexagons created for ULM and LLM had 750 m sides (~1.46 km^2 area), reflecting the different sizes of the study areas (Neckles et al. 2012). One sampling station was assigned within each hexagon containing

> 50% seagrass cover. A random number generator was used to assign latitude and longitude coordinates of the station (Figure 1). This design resulted in a total of 567 permanent sampling stations.

Annual ‘tier 2’ seagrass monitoring was conducted across three regions of the Texas coast (Figure 1) from 2011-2013, and within each region (CB, ULM, LLM) stations were divided into subregions for statistical analyses (Figure 2). Often, distinctions between subregions were obvious and subregion extent was easily determined based on natural environmental or geographic features. In the few instances where distinctions between subregions were not immediately discernible, the grid of tessellated hexagons was used to assist in bounding subregion extent. Nine of the original 567 sampling stations were removed prior to analysis either because they were extremely isolated from any other subregion or because they could not be sampled annually. This resulted in a total of 558 stations: 98 in CB, 178 in ULM, and 282 in LLM. The CB region was divided into five subregions: Aransas Bay (AB; n=10), Redfish Bay North (RFB-N; n=43), Redfish Bay Southwest (RFB-SW; n=15), Redfish Bay Southeast (RFB-SE; n=14), and Corpus Christi Bay (n=16; Figure 2). The ULM region was divided into four subregions: ULM North (ULM-N; n=34), ULM North-Central (ULM-NC; n=72), ULM South-Central (ULM-SC; n=39), and ULM South (ULM-S; n=33), and the LLM region was also divided into four subregions: LLM North (LLM-N: n=48), LLM Central (LLM-C; n=71), LLM Southwest (LLM-SW; n=45), and LLM Southeast (LLM-SE; n=118; Figure 2). A further discussion of subregion delineation can be found in Appendix A.

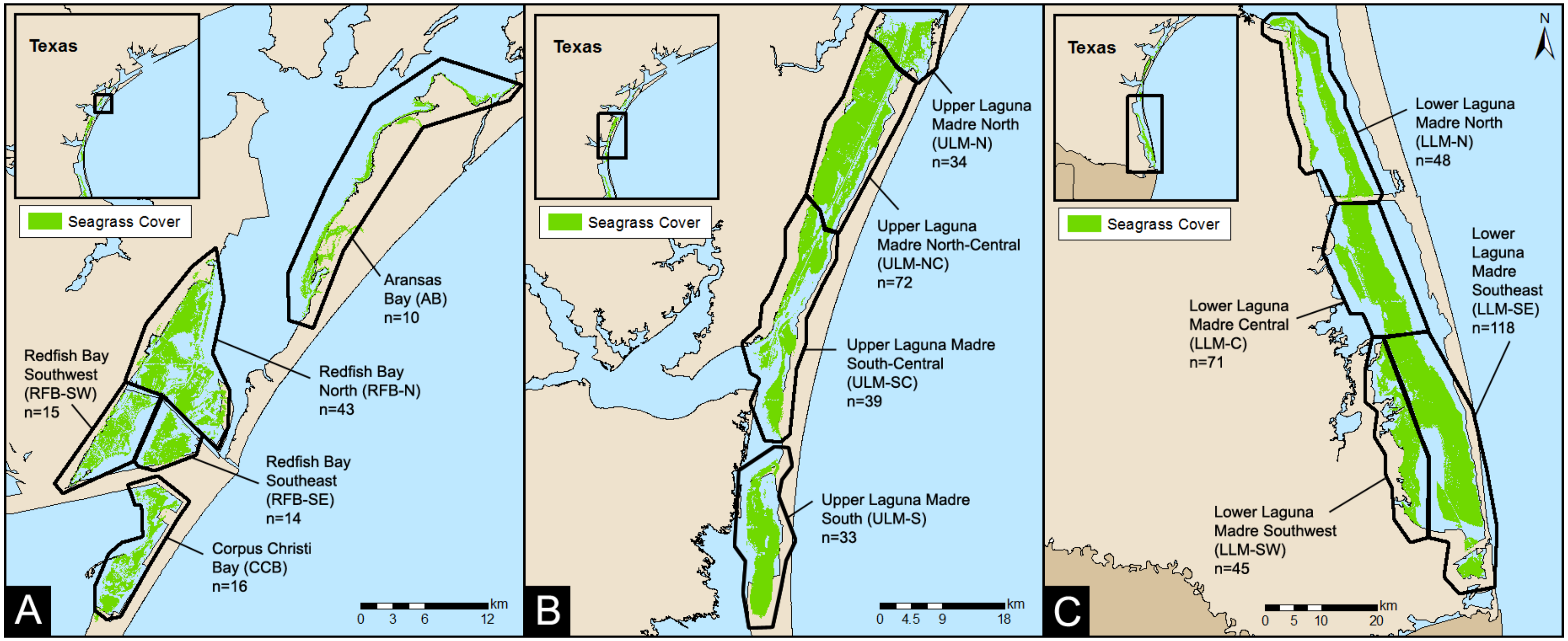

Figure 2. The three regions in this study (the Coastal Bend (A), Upper Laguna Madre (B), and Lower Laguna Madre (C)) divided into thirteen subregions, where n = number of stations. Green areas indicate seagrass coverage from the NOAA 2004/2007 Benthic Habitat Mapping (http://coast.noaa.gov/digitalcoast/data/benthiccover/).

SAMPLING METHODS

Monitoring took place from the late summer to early fall each year, during the time of peak seagrass biomass. Sampling always began at the northernmost stations in CB and worked south to end in LLM. Sampling efforts employed 2-4 personnel, and spanned 21 days from August through October in 2011, 24 days from July through October in 2012, and 25 days from July through November in 2013. Sampling was conducted from an airboat, which minimized travel time between sites and allowed access to areas that would have been difficult to reach with an outboard motor. Generally, sampling took place on days with little cloud cover and winds below 15 mph.

Following the methods of Neckles et al. (2012), each sampling station was defined as a circle 10-m in diameter around the assigned coordinates, to account for the length of the boat and limitations in GPS accuracy. At each station the vessel was anchored within 10-m of the assigned coordinate, and water quality and clarity measurements were made before research technicians entered the water to avoid stirring up sediment. Water depth was measured with a meter stick and Secchi depth (a proxy of water clarity) was measured with a Secchi disk. A 1-L water sample was collected and stored on ice for total suspended solid (TSS) analysis in the laboratory. A YSI 6920 datasonde (YSI Inc., Yellow Springs, OH) was used to collect instantaneous measurements of water temperature, salinity, dissolved oxygen (DO), pH, and chlorophyll *a* concentrations. A custom-built lightmeter consisting of two LI-COR spherical quantum scalar sensors (LI-COR, Lincoln, NE) mounted at a fixed distance of 25 cm apart on a PVC lowering frame, attached to a LI-COR 1000 datalogger, was deployed to measure underwater irradiance (μmol photons m^{-2} s^{-1}), which can be a limiting factor to seagrass growth if sufficient irradiance does not reach the canopy. The light attenuation coefficient (k_d) was calculated using the Beer-Lambert Law (Equation 1), where I_z = irradiance at depth (μmol photons m^{-2} s^{-1}), I_0 = irradiance at the surface (μmol photons m^{-2} s^{-1}), and z = sensor depth (m):

$$k_d = \frac{-[\ln(I_z / I_0)]}{z} \tag{1}$$

Visual assessments of seagrass percent cover were made underwater at four ordinal points around the vessel using a 0.25 m^2 PVC quadrat frame subdivided into 100 cells with monofilament line. Four replicates were chosen because Neckles et al. (2012) demonstrated that four replicate estimates of seagrass percent cover with a 0.25 m^2 quadrat were sufficient to estimate an overall mean percent cover ± 5% of the true mean 80% of the time, and were sufficient to estimate an overall mean percent cover ± 10% of the true mean > 99% of the time. Percent cover measurements were always made by an experienced field technician to ensure accuracy. At each of the four ordinal points, five blades of each species present within the quadrat were randomly collected and the length of their longest blade was recorded to measure seagrass canopy height. Finally, if *H. wrightii* or *T. testudinum* was present at the station, a small tissue sample (consisting of shoots from multiple plants) was collected randomly by hand and stored on ice for transport back to the laboratory for stable isotope and tissue elemental analyses.

LABORATORY ANALYSES

Total suspended solids (TSS)

Each 1-L water sample was poured over a pre-dried, pre-weighed glass fiber filter (Whatman 47 mm GF/F, 7 micron retention) and filtered using a vacuum pump. The filter and retained residue were dried to a constant weight at 60 °C in a drying oven and then re-weighed. This weight was used to determine TSS (mg L^{-1}) concentration, where A = weight of filter + residue (mg), B = weight of filter (mg), and C = amount of sample filtered (L):

$$\mathrm{TSS} = \frac{(\mathrm{A} - \mathrm{B})}{\mathrm{C}} \qquad (2)$$

Seagrass elemental and stable isotope analyses

Tissue samples from 2011 were processed from every station and a subset (approximately half) of the tissue samples from 2012 and 2013 were processed due to time and cost constraints. The subset of 2012 and 2013 samples was chosen randomly but checked on a map to ensure roughly even spatial coverage of each region. Tissue samples were cleaned by lightly scraping above-ground (leaf) tissue with a razor blade to remove sediment or epiphytic material. Samples were then dried to a constant weight at 60 °C in a drying oven and ground to a fine powder using a Wig-L-Bug (Dentsply Rinn, Elgin, IL) grinding mill. For stable isotope ($\delta^{13}C$ and $\delta^{15}N$) and tissue C and N content analyses, a small amount of ground material was wrapped inside a 35-mm tin capsule. Samples collected in 2011 were sent to the University of California at Davis Stable Isotope Facility for analysis using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Samples from 2012 and 2013 were processed at UTMSI using a Finnigan MAT Delta Plus stable isotope mass spectrometer (Thermo Fisher Scientific, Waltham, MA) coupled to an NC 2500 elemental analyzer (CE Instruments, Milan, Italy). Seagrass leaf P was analyzed with a Shimadzu UV-2401 PC UV-VIS Recording Spectrophotometer using modified methods from Chapman and Pratt (1961).

SPATIAL AND STATISTICAL ANALYSES

For each region, I performed a repeated measures analysis of variance (RM ANOVA) to test the effect of year on seagrass percent cover, canopy height, molar C:N:P ratios, and stable isotope signatures, with year treated as a fixed effect and station treated as a random effect. I also performed RM ANOVAs to test the effect of year and subregion (both treated as fixed effects with station treated as a random effect) on seagrass percent cover within each region. I applied post hoc Tukey multiple comparison tests to all RM ANOVAs to determine which years displayed changes in the parameter of interest. I transformed data when necessary to meet assumptions of normality for all RM ANOVAs, and checked normality with Shapiro-Wilk tests. Typically, I applied square root or logarithmic transformations to skewed data and arcsine transformations to proportion (percent cover) data (Zar 2010). All statistical analyses were performed in R Statistical Software 3.0.2 (R Core Team 2013) and results considered significant at $\alpha = 0.05$. Results from RM ANOVAs and multiple comparisons not reported in the text, as well as additional graphics, are included in Appendix B (seagrass percent cover and canopy height) and Appendix C (tissue elemental composition and stable isotope signatures).

To generate a continuous surface estimating seagrass cover in each system, I used Inverse-Distance Weighting (IDW) interpolation. IDW is a form of deterministic interpolation that generates predicted values for unsampled points based off the values of sampled points at nearby locations, weighted by distance (Shepard 1968). I used 12 sampling stations identified from a variable search radius to generate a predicted value at each unknown point (100 m^2). Interpolations of seagrass cover were bound to the extent of each subregion, while interpolations of tissue elemental composition and stable isotope signatures were bound to each region, to reflect statistical procedures. All spatial analyses were performed in ArcMap v10.1 (Environmental Systems Research Institute). Interpolations not shown in this manuscript are reported in Appendix B (seagrass percent cover) and Appendix C (tissue elemental composition and stable isotope signatures).

LONG-TERM SALINITY MEASUREMENTS

In order to better understand regional hydrologic regimes, salinity measurements from 1994 to 2014 were obtained from four locations along the Texas coast, which ranged throughout the monitoring area. CB salinity measurements taken every 15 minutes from the Mission-Aransas National Estuarine Research Reserve's Station #4 in Aransas Bay (28°58'47" N, 97°01'43" W; beginning in 2007) were averaged into weekly salinity measurements for this analysis. ULM salinity measurements were taken approximately bi-weekly at the LM-151 long-term monitoring station (27°21' N, 97°22' W; see Dunton 1994), and salinity measurements for two locations in LLM (northern LLM and southern LLM) were obtained from Texas Parks and Wildlife Department trawls that took place approximately bi-weekly. Northern LLM salinity data was obtained from trawls between 26°47'30" N, 97°28'30" W and 26°20'30" N, 97°18'30" W, and southern LLM salinity data was obtained from trawls between 26°19'30" N, 97°17'30" W and 26°09'30" N, 97°10'30" W.

Results

SEAGRASS PERCENT COVER AND CANOPY HEIGHT

Total seagrass coverage was consistently highest in ULM (~77%), followed by the CB (~72%) and LLM (~49%; Figure 3). *H. wrightii* was the dominant species across all regions, accounting for ~85% of total seagrass cover in ULM, ~60% in LLM, and ~50% in CB. *T. testudinum* was the second most abundant species in the CB and LLM, but was completely absent from ULM except at one sampling station in 2011. *S. filiforme* was the third most abundant species in the CB and LLM and the second most abundant species in ULM. *H. engelmannii* was present in amounts < 1% in the CB and ULM, and was absent from LLM except at three stations in 2013. *R. maritima* was present in small amounts (< 3%) across all regions.

In the CB region, percent cover did not change significantly over time for any species, but there was a small effect of year on total seagrass cover (p=0.057), which decreased from 2012-2013 (p=0.045; Figure 3). There was no effect of year on percent cover for any species at the subregion level, and seagrass cover appeared quite stable in all subregions except AB, which experienced a large increase in *H. wrightii* cover from 2011-2012 then a large decrease from 2012-2013 (Figure B1). *H. wrightii* dominated the eastern portion of CB, with particularly high percent cover in west RFB-N, in RFB-SE and in CCB (Figure B2). The western portion of CB contained expansive coverage of *T. testudinum*, especially in western RFB-N and RFB-SW (Figure B2).

Significant changes in percent cover were observed for *H. wrightii*, *S. filiforme*, and total seagrass in ULM (p<0.001 for all; Figure 3). Cover of both *H. wrightii* and *S. filiforme* increased from 2011-2012 (*H. wrightii*: p<0.001), then from 2012-2013 *S. filiforme* cover sharply decreased (p<0.001) while *H. wrightii* cover remained stable

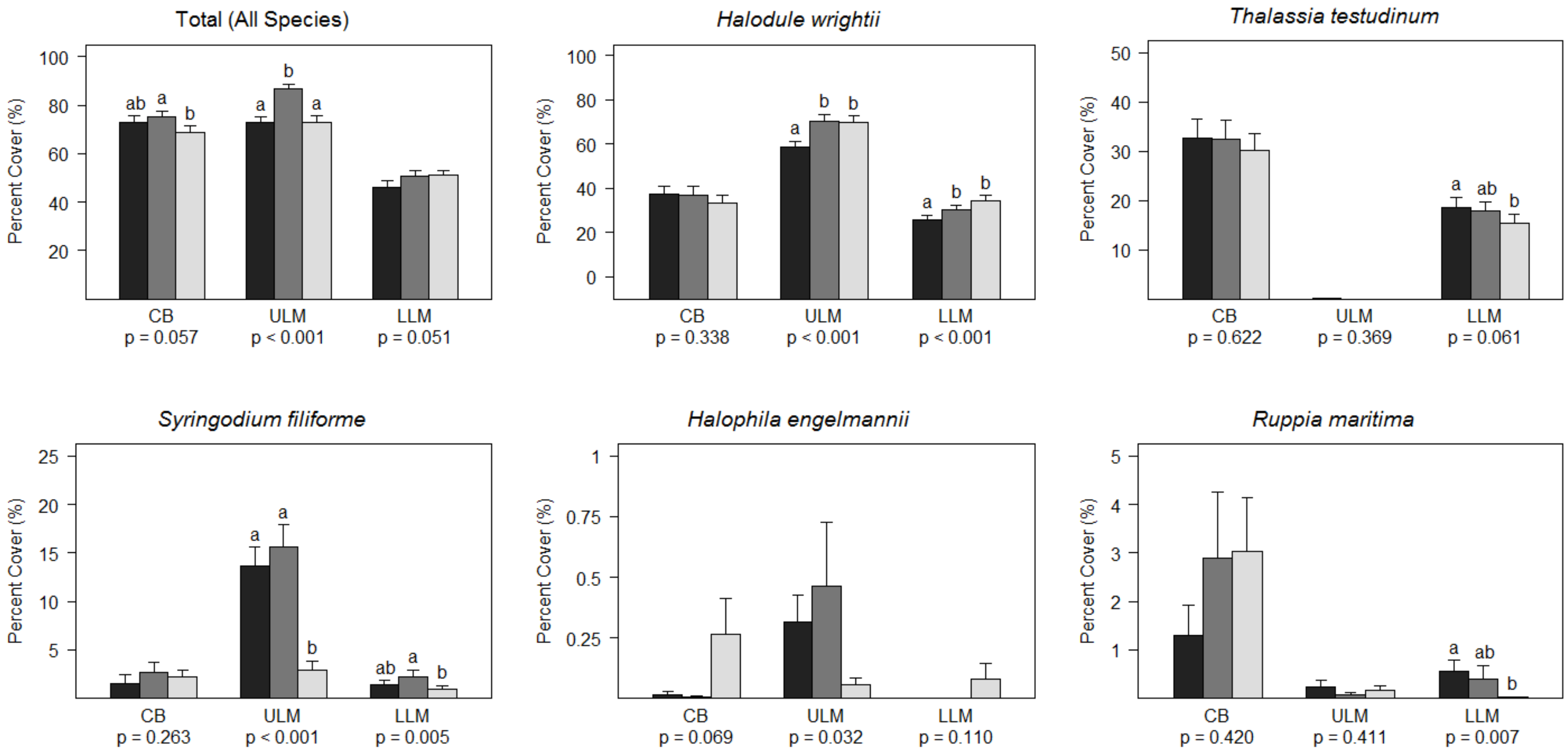

Figure 3. Seagrass percent cover (%; mean + standard error) for all regions (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs testing the effect of year and Tukey multiple comparison tests were applied within each region for each species. Results from RM ANOVAs are listed below each region, and significant differences from multiple comparison tests (α = 0.05) are listed (A, B, C) where present. Note the difference in y axis ranges.

(Figure 3). Across ULM subregions, significant changes in cover of *H. wrightii* (p<0.001), *S. filiforme* (p<0.001), *H. engelmannii* (p=0.007), *R. maritima* (p=0.001), and total seagrass (p=0.017) occurred. There was a significant increase in *H. wrightii* cover across every subregion in ULM from 2011-2012 (ULM-N: p=0.028, ULM-NC: p=0.011, ULM-SC: p=0.043, ULM-S: p=0.002; Figure B5). From 2012-2013, change in *H. wrightii* cover was variable across subregions, but percent cover in 2013 was always greater than in 2011 (Figure B5). Large declines of *S. filiforme* in ULM-NC (p<0.001) and ULM-SC occurred between 2012 and 2013 (Figure 4). The increases in *H. wrightii* and decreases in *S. filiforme* cover in ULM-NC occurred throughout the entire subregion and were not confined to a specific area (Figure 4). By 2013, the only remaining *S. filiforme* meadow in ULM was located at the northwestern edge of ULM-N (Figure 4).

Significant changes in percent cover were observed for every species in LLM except for *H. engelmannii*, which was only present in very low (< 1%) amounts (Figure 3). There was a general trend of increasing *H. wrightii* cover through time, with significant increases in LLM-N (p<0.001) and LLM-C (p=0.028), and smaller increases in LLM-SW and LLM-SE (Figure B9). *H. wrightii* cover increased evenly throughout LLM-N but increases in LLM-C were largely confined to the west and south, with a strip of very low *H. wrightii* cover in the eastern portion of the subregion (Figure 5). There was a small increase in *T. testudinum* cover in LLM-N, which occurred across several stations in the central portion of the subregion (Figure B11). However decreases in *T. testudinum* cover occurred in LLM-SW and to a greater extent in LLM-SE (p<0.001; Figure B9). In both LLM-SW and LLM-SE, *T. testudinum* communities in the southernmost areas appear stable, while meadows in the central parts of both subregions experienced declines in cover (Figure 6). Although mean *S. filiforme* cover was low in

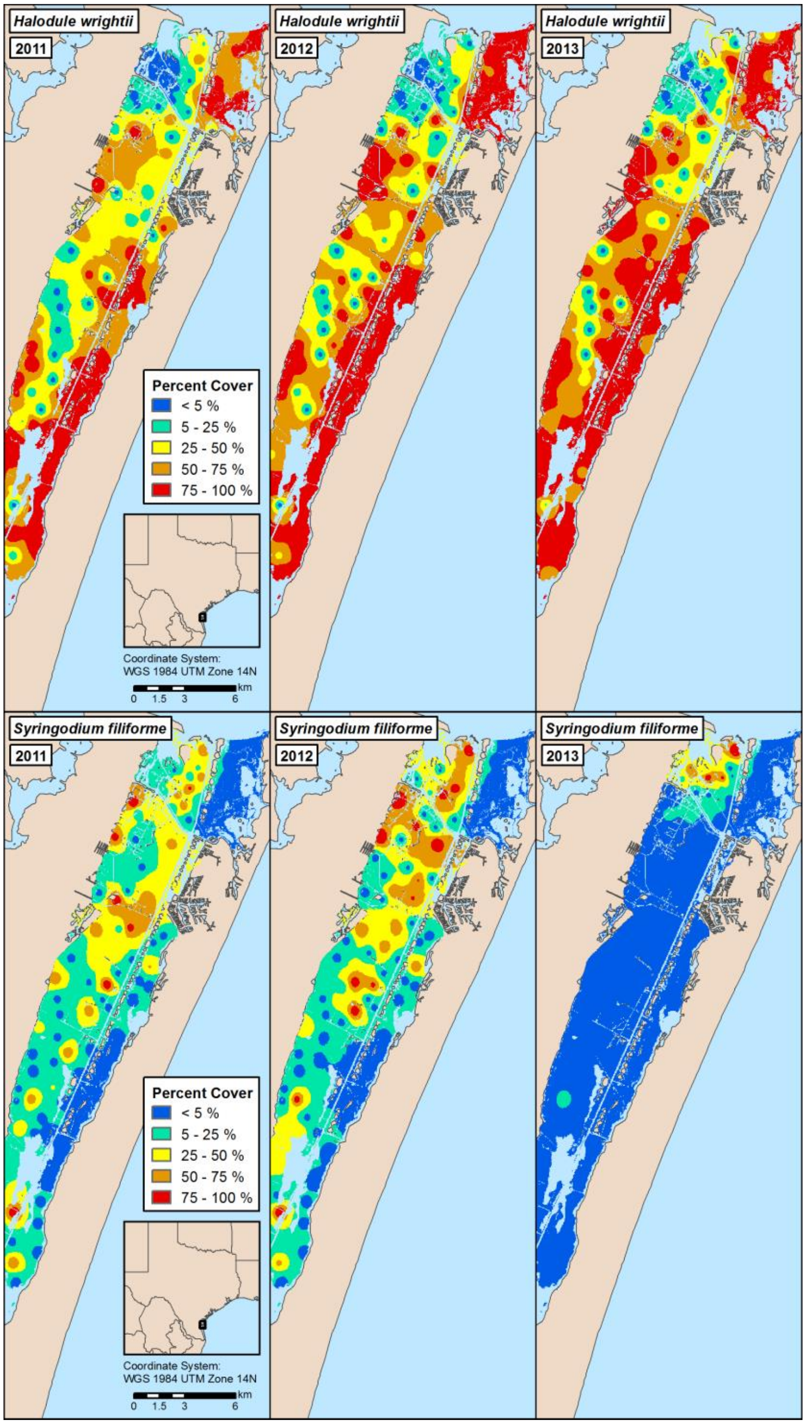

Figure 4. Significant increases in *Halodule wrightii* percent cover and significant decreases of *Syringodium filiforme* percent cover in Upper Laguna Madre (ULM North and ULM North-Central subregions) from 2011-2013.

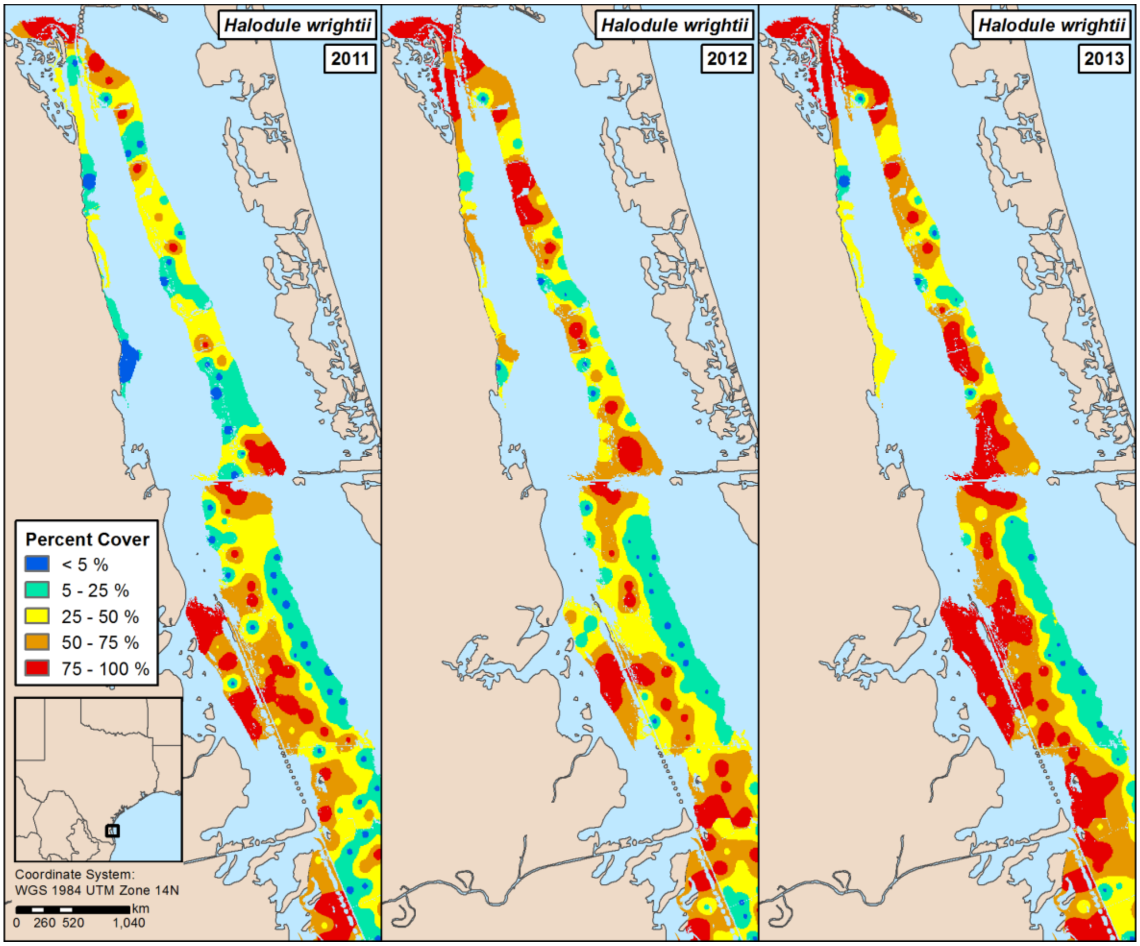

Figure 5. Significant increases in *Halodule wrightii* percent cover in Lower Laguna Madre (LLM North and LLM Central subregions) from 2011-2013.

LLM-SE, it should be noted that at several stations near Brownsville Ship Channel, *S. filiforme* cover was between 25-50% (Figure B11).

Canopy height of *H. wrightii* changed significantly through time across all regions ($p<0.001$ for all; Table B12). From 2011-2012, *H. wrightii* canopy height increased across every region, then decreased from 2012-2013 in CB and ULM but remained stable in LLM (Figure B13). Interestingly, changes in *H. wrightii* canopy height seemed to

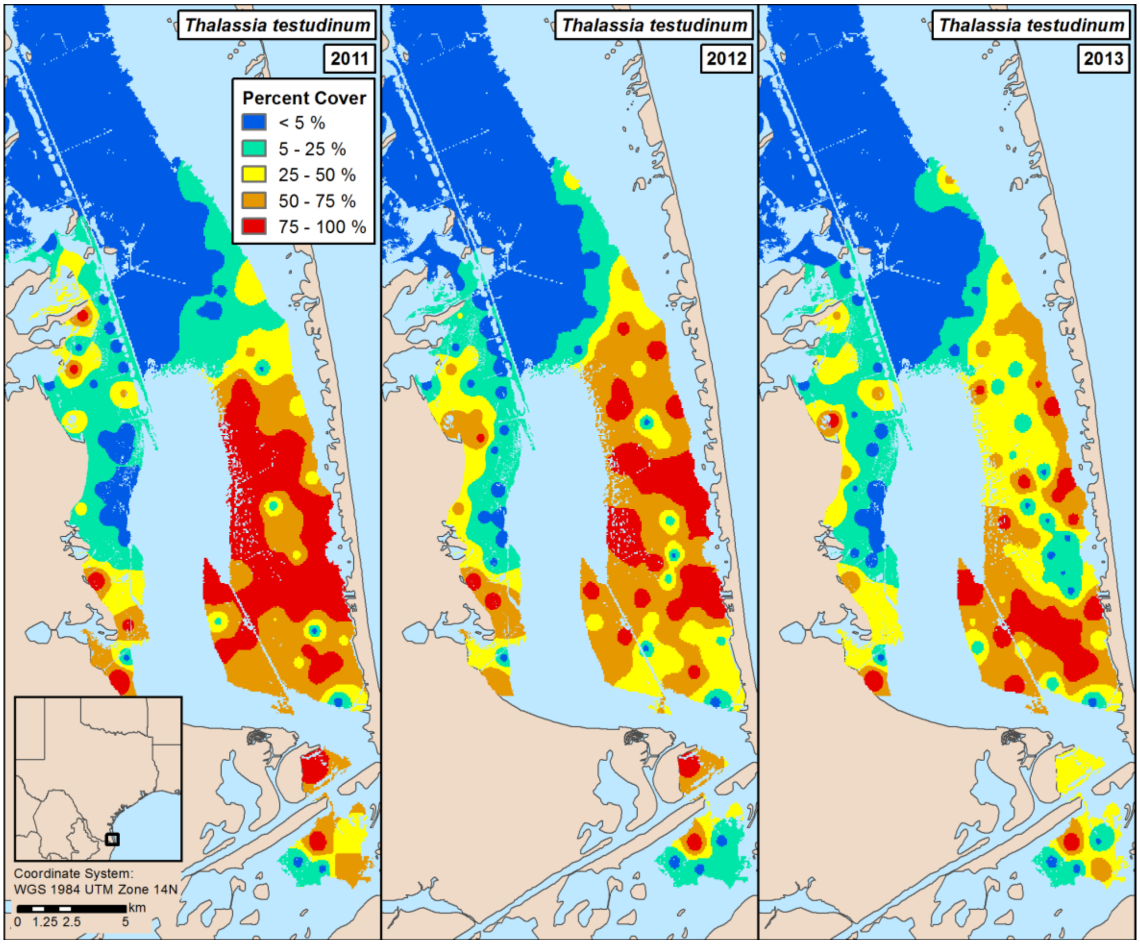

Figure 6. Significant decreases in *Thalassia testudinum* percent cover in Lower Laguna Madre (LLM Southeast subregion) from 2011-2013.

reflect changes in *H. wrightii* percent cover. *T. testudinum* canopy height changed little in the CB but decreased significantly in LLM ($p<0.001$), again displaying a similar pattern as changes in percent cover for the two regions. *S. filiforme* canopy height changes through time also reflect changes in percent cover relatively well, with significant decreases in canopy height occurring across every region (CB: $p=0.24$; ULM and LLLM: $p<0.001$). No significant changes in *H. engelmannii* canopy height were observed, and changes in *R. maritima* canopy height did not correspond to changes in cover.

ELEMENTAL COMPOSITION AND STABLE ISOTOPE SIGNATURES

For seagrasses in CB, significant changes in C:N (*H. wrightii*: $p=0.014$, *T. testudinum*: $p=0.041$), C:P ($p<0.001$ for both), and N:P ($p<0.001$ for both) molar ratios occurred over time. There was a general trend of decreasing C:N, C:P, and N:P ratios over time for both *H. wrightii* and *T. testudinum* (although *H. wrightii* C:N and C:P increased from 2012-2013; Figures C1 and C2), reflecting increased assimilation of N and P. No spatial patterns were observed for C:N, C:P, or N:P ratios in *H. wrightii* or *T. testudinum* in the CB region (Figures C3 and C4).

In ULM, significant changes in *H. wrightii* C:N, C:P, and N:P molar ratios occurred through time. *H. wrightii* C:N increased significantly ($p<0.001$), while C:P and N:P decreased significantly ($p<0.001$ for both), suggesting a shift towards less N and more P assimilation. No spatial patterns were obvious in *H. wrightii* C:N ratios, but C:P and N:P ratios were always lower in northern parts of ULM, and C:P ratios were always low in southern ULM (Figure 7).

For LLM, significant changes through time were almost always observed in *H. wrightii* and *T. testudinum* in C:N ($p<0.001$ for both), C:P (*H. wrightii*: $p<0.001$, *T. testudinum*: $p=0.059$), and N:P (*H. wrightii*: $p<0.001$, *T. testudinum*: $p=0.002$) molar ratios, although *H. wrightii* and *T. testudinum* C:N ratios showed different trends. *H. wrightii* C:N ratios increased (2011-2013: $p<0.001$), but *T. testudinum* C:N ratios decreased (2011-2013: $p<0.001$; Figures C1 and C2). Higher *H. wrightii* C:N ratios were always observed on the western side of the bay near the mouth of the Arroyo-Colorado River (Figure 8), and *T. testudinum* C:N ratios were always lower in the southeast near South Padre Island (Figure 8). C:P ratios for both species in LLM decreased from 2011-2012 (*H. wrightii*: $p<0.001$, *T. testudinum*: $p=0.052$), then increased from 2012-2013 (*H. wrightii*: $p<0.001$); however, the changes were much more pronounced in *H. wrightii*

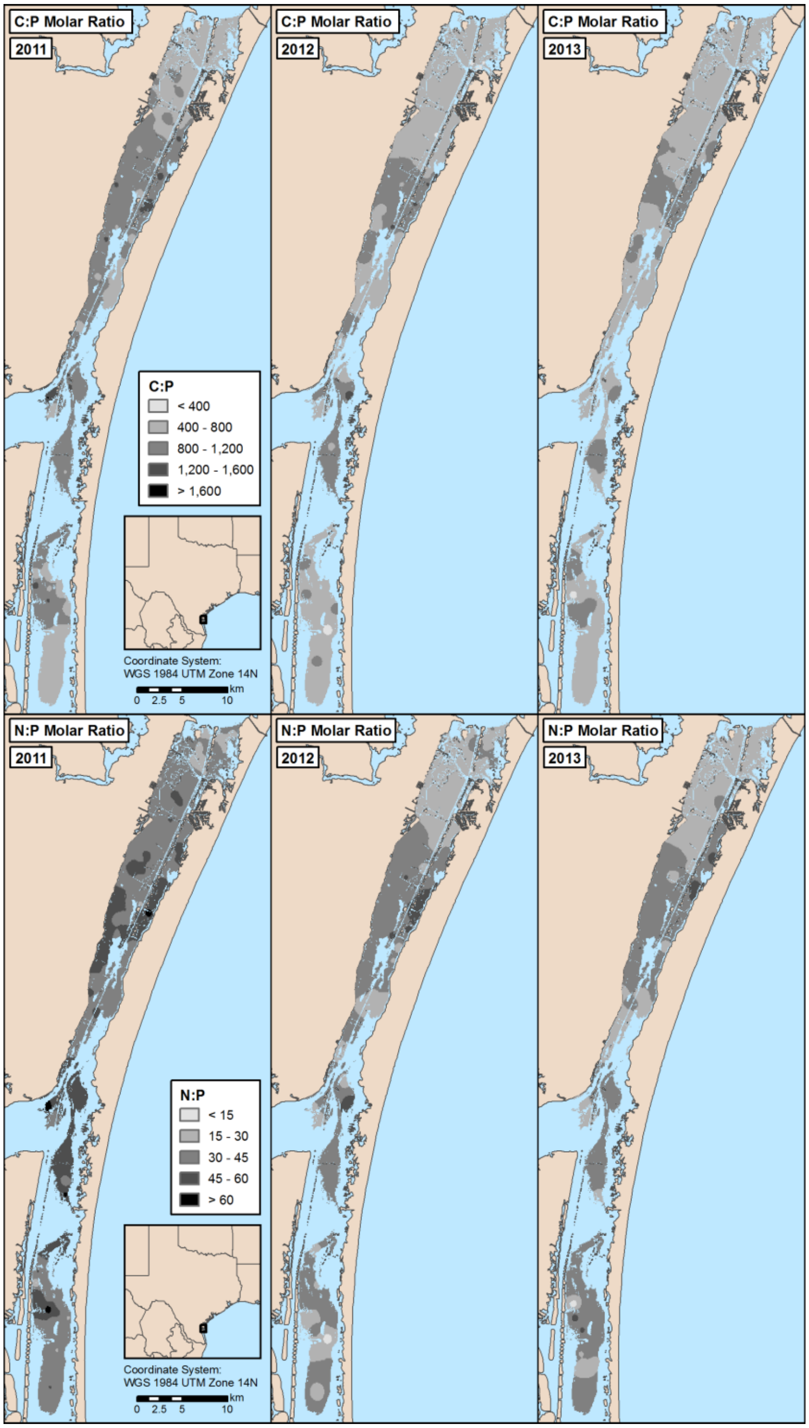

Figure 7. Lower C:P and N:P molar ratios for *Halodule wrightii* were observed in northern Upper Laguna Madre from 2011-2013. No spatial patterns were observed in C:N molar ratios (Figure C6).

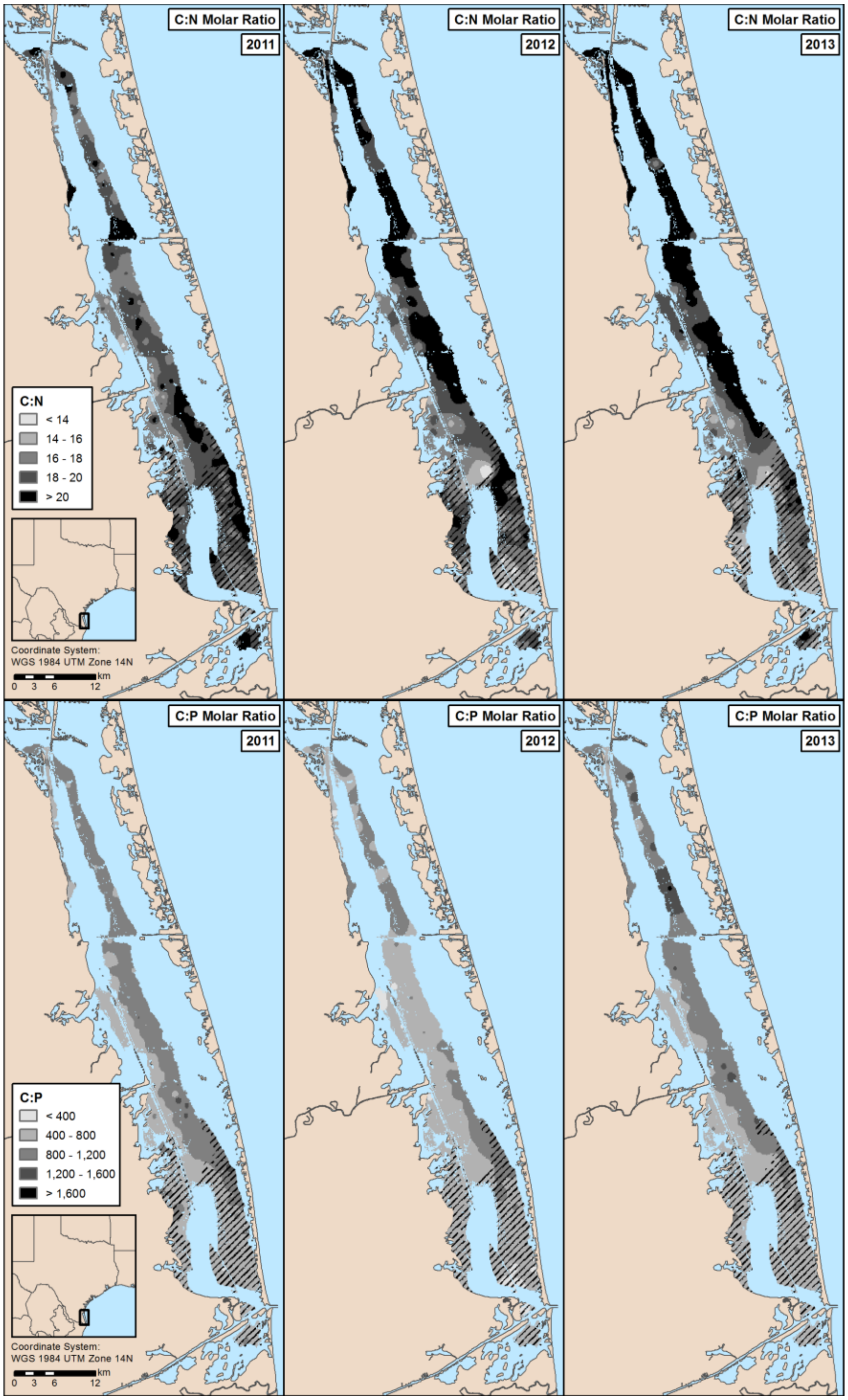

Figure 8. Lower C:N and C:P molar ratios for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) were observed in the west and southeast of Lower Laguna Madre from 2011-2013.

than *T. testudinum* tissue (Figures C1 and C2). C:P ratios for *H. wrightii* lower on the western side of the bay, particularly in 2011 and 2013 (Figure 8). *H. wrightii* N:P changes in LLM were variable, with a large decrease from 2011-2012 followed by an increase from2012-2013 (*H. wrightii*: $p<0.001$, *T. testudinum*: $p=0.002$; Tables C5 and C6). *T. testudinum* N:P ratios remained constant from 2011-2012, then increased in 2013 (Table C2; Figure C2). Lower N:P ratios in LLM *H. wrightii* were always observed in the western side of the bay, and the lowest *T. testudinum* N:P ratios were observed in southwest LLM-SE from 2011-2012 (Figure 9).

Changes in $\delta^{13}C$ signatures over time varied by region and species (Figures C1 and C2). I found that *T. testudinum* had more enriched (~ -8.7‰) $\delta^{13}C$ signatures compared to *H. wrightii* (~ -10.2‰). Significant changes in leaf $\delta^{13}C$ signatures were observed across all regions in *H. wrightii* (CB: $p=0.019$, ULM and LLM: $p<0.001$), but not *T. testudinum*. In CB, both *H. wrightii* and *T. testudinum* $\delta^{13}C$ signatures became more depleted from 2011-2012, and then more enriched from 2012-2013, but 2011 $\delta^{13}C$ was not significantly different than 2013 $\delta^{13}C$ for either species (Figures C1 and C2). *H. wrightii* $\delta^{13}C$ signatures in ULM became more enriched from 2011-2012 then more depleted from 2012-2013 ($p<0.001$ for both). In LLM, *H. wrightii* $\delta^{13}C$ signatures also became more enriched from 2011-2012 then more depleted from 2012-2013 ($p<0.001$ for both), however *T. testudinum* $\delta^{13}C$ signatures remained stable. While no spatial trends in seagrass $\delta^{13}C$ signatures were observed in CB or ULM, the southern edge of *H. wrightii* meadows and the northern edge of *T. testudinum* meadows in LLM-SE displayed consistently enriched $\delta^{13}C$ signatures (Figure 10).

Changes in $\delta^{15}N$ signatures over time were similar between *H. wrightii* and *T. testudinum*. *H. wrightii* $\delta^{15}N$ changed significantly across all regions (CB: $p=0.023$, ULM

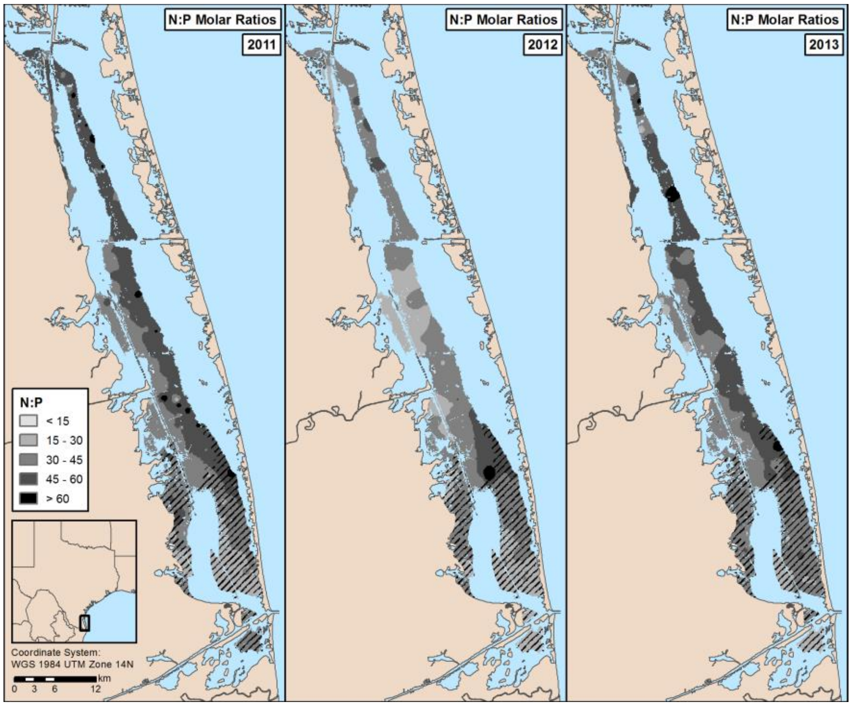

Figure 9. N:P molar ratios for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) were observed in the west and southeast of Lower Laguna Madre from 2011-2013.

and LLM: $p<0.001$), and *T. testudinum* δ^{15}N signatures displayed significant changes in CB ($p=0.016$). For every region and for both species, δ^{15}N signatures were more enriched in 2013 than in 2011 (Figures C1 and C2). The δ^{15}N signatures from *T. tesudinum* in CB (~ 3.4‰) were more enriched than *H. wrightii* signatures (~ 1.4‰), but the two species had similar δ^{15}N signatures in LLM (*H. wrightii*: ~ 2.5‰, *T. testudinum*: ~ 2.9 ‰). Although no spatial patterns were observed in δ^{15}N signatures for either species in CB or ULM, distinct spatial trends were apparent in LLM. In the *H. wrightii* communities in northern LLM, δ^{15}N signatures were always more enriched on the western sides of the bay (Figure 10). In southern areas with *T. testudinum* meadows, δ^{15}N signatures were

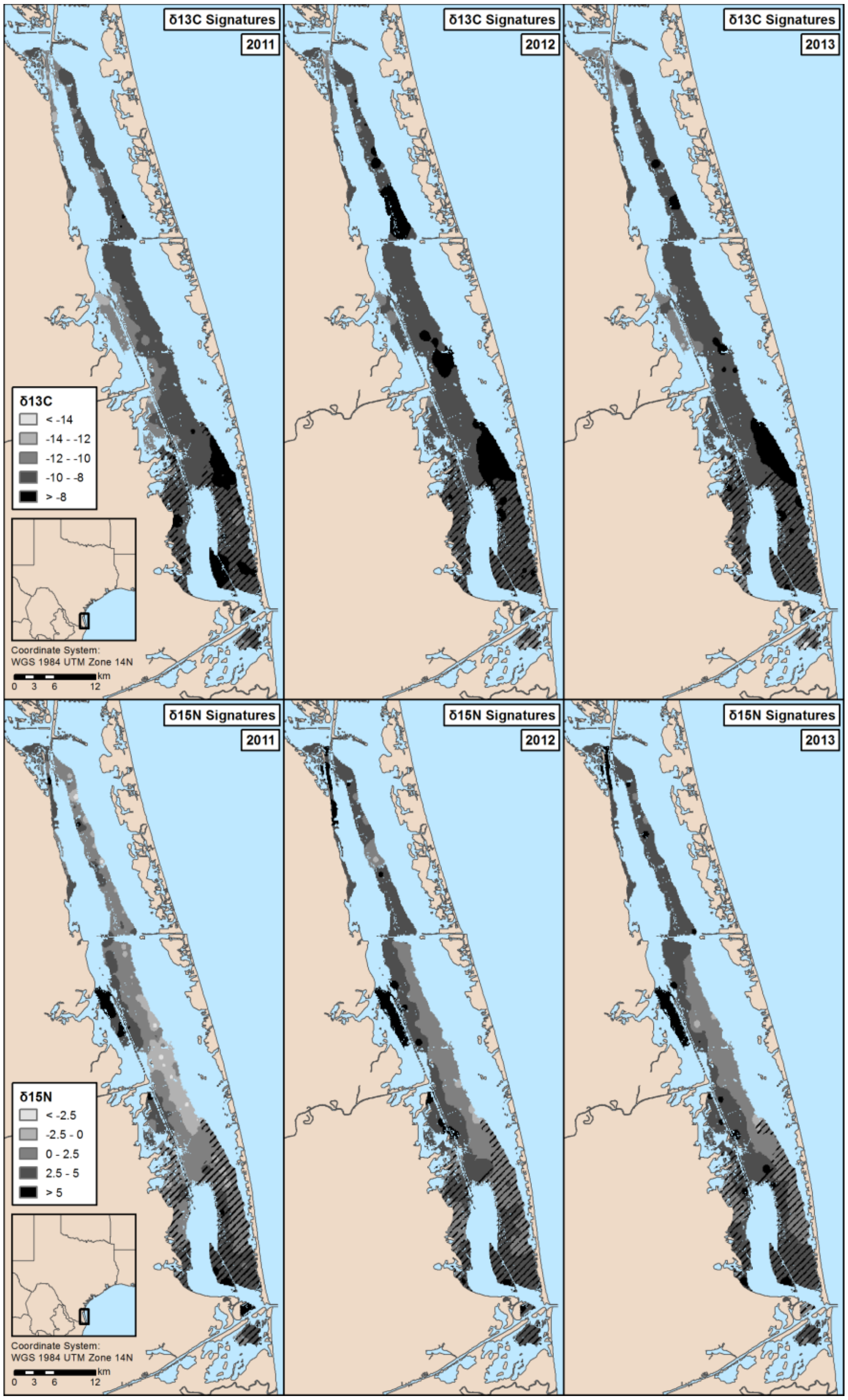

Figure 10. Stable isotope δ^{13}C and δ^{15}N signatures for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in Lower Laguna Madre from 2011-2013. Note more enriched δ^{15}N signatures in the west and southeast.

consistently more enriched near South Padre Island and at stations east of the large bare area between LLM-SW and LLM-SE (Figure 10).

LONG-TERM SALINITY MEASUREMENTS

Salinity records showed regional variability but similar patterns through time (Figure 11). As suggested by instantaneous sonde water quality measurements, ULM tended to display much higher, but variable, salinities than the other areas, whereas southern LLM salinity exhibited minimal variability. The lowest salinities in the twenty year record occurred in northern LLM, where salinity dropped below 5 in July and August 2010, the summer before this monitoring began. These low salinities were due to large amounts of precipitation from Hurricane Alex, which made landfall in northern Mexico on June 30th (NOAA 2010). Since the storm, seasonal freshwater inflows have produced smaller fluctuations in salinity across the coast, and salinities became very high in ULM throughout 2012 and 2013 (Figure 11). The highest salinities in this record (> 55) were observed in ULM during early 2013, likely driven by regional drought conditions and limited freshwater inflow.

WATER QUALITY AND WATER CLARITY

Instantaneous water quality (depth, salinity, DO, pH) and water clarity (k_d, chlorophyll *a*, TSS) measurements showed high regional and temporal variability (Tables 1 and 2). CB was characterized by having shallow (~57 cm) stations, moderately high salinities (~40), and high DO levels (~6.7 mg L^{-1}). ULM stations were of intermediate depth (~79 cm) and consistently had the highest salinities (~48), and the lowest DO levels (~6 mg L^{-1}) of any region. LLM stations were the deepest (~85 cm) and exhibited

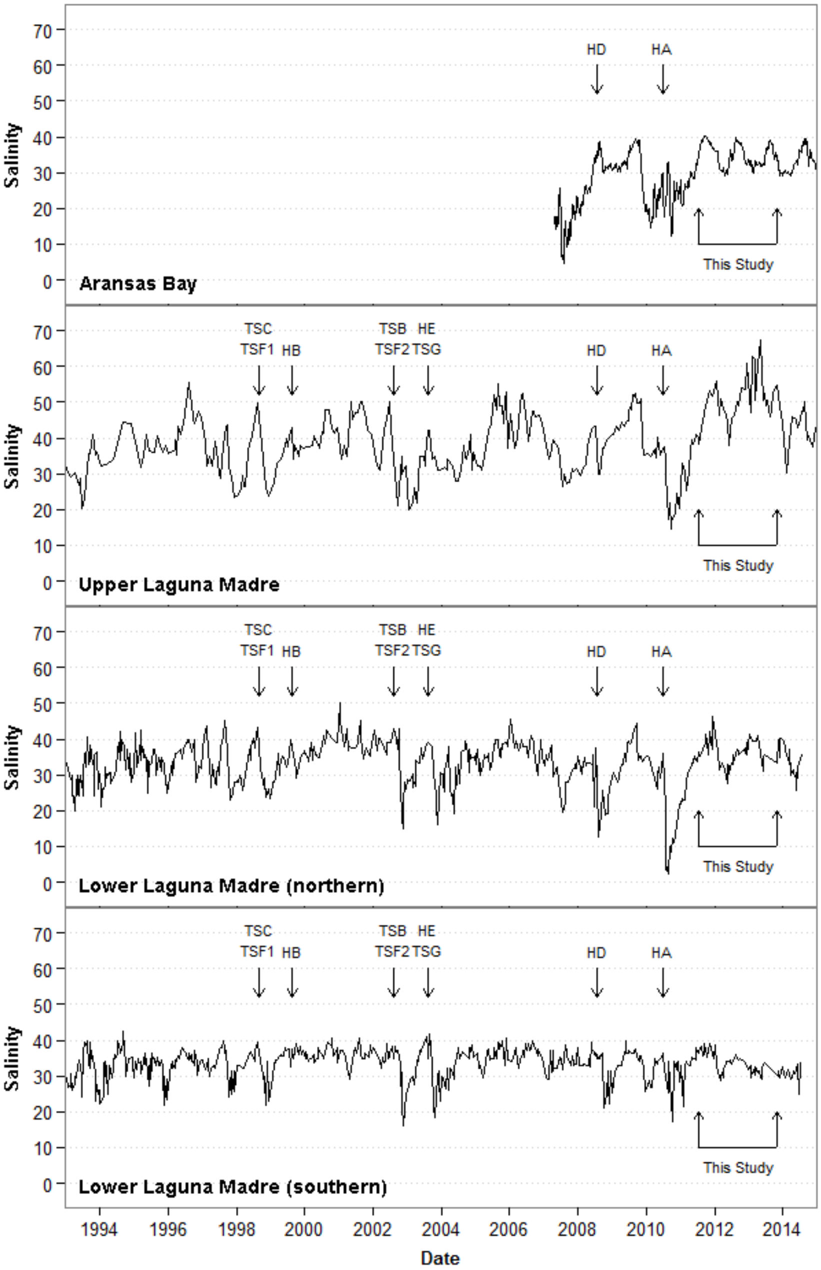

Figure 11. Salinity time series from 1994 to 2014 at four locations along the Texas coast: Aransas Bay, Upper Laguna Madre, northern Lower Laguna Madre and southern Lower Laguna Madre (see "Methods" section for station coordinates). Arrows indicate major storm events for the region, which are often reflected by subsequent drops in salinity, including Tropical Storms Charley (TSC), Frances (TSF1), Bertha (TSB), and Fay (TSF), and Grace (TSG), and Hurricanes Bret (HB), Erika (HE), Dolly (HD), and Alex (HA).

Table 1. Water quality data for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012, and 2013 (DO = dissolved oxygen). Values are $\bar{x}$ (mean) and standard error (S.E.).

		Depth (cm)			**Salinity**			**DO (mg L^{-1})**			**pH**		
Region		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
CB	$\bar{x}$	53.67	63.41	58.73	41.31	37.91	40.11	6.59	7.15	6.28	7.88	8.02	8.30
	S.E.	2.37	2.63	2.72	0.32	0.33	0.66	0.21	0.25	0.18	0.03	0.03	0.02
	n	98	97	98	98	98	98	98	98	92	98	98	98
ULM	$\bar{x}$	74.08	81.49	84.11	48.65	47.12	48.04	5.44	6.55	6.11	7.95	8.17	8.41
	S.E.	3.13	3.07	3.21	0.45	0.29	0.36	0.15	0.17	0.21	0.03	0.02	0.02
	n	178	178	177	178	174	152	178	173	130	178	174	152
LLM	$\bar{x}$	84.37	83.79	89.16	41.64	39.57	34.50	7.21	6.76	7.14	8.09	7.91	8.25
	S.E.	2.16	2.12	1.84	0.23	0.21	0.24	0.08	0.09	0.09	0.02	0.02	0.01
	n	282	282	282	282	282	281	282	238	262	282	281	282

intermediate salinities (~39) and high DO levels (~7 mg L^{-1}). Despite high variability between years, CB appears to have the highest water transparency of the three regions, based upon low light attenuation coefficients (k_d) in 2011 (0.59 m^{-1}) and 2012 (0.73 m^{-1}), and relatively low concentrations chlorophyll *a* (~3 µg L^{-1}), and TSS (~12.5 mg L^{-1}). ULM and LLM water transparency measurements were similar, except that stations in the LLM always had much lower chlorophyll *a* concentrations (~2.5 µg L^{-1}) than stations in ULM (~4 µg L^{-1}).

Table 2. Water transparency data for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012, and 2013 (k_d = light attenuation coefficient, TSS = total suspended solids). Values are x̄ (mean) and standard error (S.E.).

		k_d (m^{-1})			**Chlorophyll *a* (µg L^{-1})**			**TSS (mg L^{-1})**		
Region		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
CB	x̄	0.59	0.73	1.25	4.35	2.62	1.82	13.01	13.82	10.54
	S.E.	0.08	0.11	0.14	0.28	0.16	0.17	0.81	0.62	0.69
	n	29	46	50	98	98	98	97	98	89
ULM	x̄	0.75	1.05	1.05	4.32	4.95	2.91	13.92	17.38	10.59
	S.E.	0.04	0.06	0.06	0.19	0.34	0.21	0.57	0.69	0.47
	n	102	108	118	177	174	152	177	176	174
LLM	x̄	1.46	1.06	1.08	2.94	2.01	2.73	23.81	17.58	9.98
	S.E.	0.09	0.05	0.06	0.20	0.12	0.19	1.56	0.73	0.46
	n	176	174	248	279	282	282	276	278	277

Discussion

SHIFTS IN SEAGRASS COVERAGE AND SPECIES COMPOSITION

As predicted, changes in seagrass cover along the Texas coast were highly variable and location-specific. I observed dramatic changes in plant community composition and percent cover in both ULM and LLM, while CB seagrass coverage remained relatively stable throughout the three-year study period. The largest changes occurred in northern and central ULM, where I witnessed a transition from a mixed species assemblage to an almost entirely monospecific *H. wrightii* population following extensive *S. filiforme* mortality.

The species shift that I observed seems to have been strongly driven by salinity. Following low salinities in late 2010 caused by Hurricane Alex, salinities in ULM in late 2012 and early 2013 rose above 55 for the first time in nearly 20 years, and remained elevated for several months (Figure 11). In previous studies, *S. filiforme* growth has stopped at salinities between 45 (McMillan and Moseley 1967) and 52.5 (McMahan 1968), so I hypothesize that *S. filiforme* communities in ULM were unable to tolerate the extended periods of hypersalinity, causing mortality throughout the bay. During this period of elevated salinity, *H. wrightii* was able to quickly re-colonize areas previously dominated by mixed meadows, and effectively outcompete *S. filiforme*. Continued tier 2 monitoring in summer 2014 showed small increases in *S. filiforme* cover in ULM (S. Wilson, unpubl. data), but major recolonization is unlikely unless salinity decreases. However, if salinities lower and a *S. filiforme* seed bank still exists, re-colonization may be possible. McMillan (1981) showed that *S. filiforme* seeds collected from Florida germinated at salinities between 10 and 50, and also observed that *S. filiforme* seeds collected from Padre Island, Texas continued to germinate for three years (McMillan 1983).

Since morphology, canopy height, surface area, and shoot density of *H. wrightii*, *T. testudinum*, and *S. filiforme* create vastly different benthic landscapes for nekton and invertebrates, the species shifts that I observed will likely drive differences in benthic faunal diversity and abundance in the Laguna Madre, and may have food web implications. Research suggests that marine faunal habitat preference is largely controlled by structural characteristics of different seagrass species (i.e. blade density or morphology; Martin and Cooper 1981; Stoner 1983; Tolan et al. 1997; Hyndes et al. 2003; Prado and Heck 2011) or differences in seagrass nutritional quality (Mariani and Alcoverro 1999; Prado and Heck 2011). When comparing meadows of *H. wrightii*, *T. testudinum*, and *S. filiforme* in Laguna Madre, studies indicate that *H. wrightii* beds support higher mean abundances of blue crab (*Callinectes sapidus*), lesser blue crab (*C. similis*), arrow shrimp (*Tozeuma carolinense*), and total fish, while *T. testudinum* beds support higher mean abundances of the code goby (*Gobiosoma robustum*), pinfish (*Lagodon rhomboides*), and the big claw snapping shrimp (*Alpheus heterochaelis*), and *S. filiforme* beds support higher mean abundances of total shrimp and total organisms (Sheridan and Minello 2003; Ray et al. 2014).

Tolan et al. (1997) demonstrated that juvenile-stage ichthyofauna in Laguna Madre showed clear habitat preferences with respect to vegetated versus unvegetated bottom, usually choosing *H. wrightii* beds over *S. filiforme* beds or unvegetated substrate. One of the most popular gamefish in Texas, red drum (*Sciaenops ocellatus*), is found at higher densities in *H. wrightii* than *T. testudinum* beds (Rooker and Holt 1997), and juveniles of another popular Texas sportfish, the spotted sea trout (*Cynoscion nebulosus*), are also found in greater abundances in *H. wrightii* than *S. filiforme* beds (Tolan et al.

1997). Furthermore, it is well documented that the redhead duck (*Aythya americana*), a common wintering species in Texas bay systems, has a clear preference for feeding on *H. wrightii* rhizomes (McMahan 1970; Mitchell et al. 1994). Therefore, the significant increases in *H. wrightii* coverage documented in both ULM (Figure 4) and LLM (Figure 5) may suggest increased habitat quality of the Laguna Madre for many resident species (McMahan 1968; Tolan et al. 1997).

The loss in *T. testudinum* cover that I observed in southern LLM (Figure 6) is concerning, as decreases in percent cover create a more patchy landscape, and organisms cannot move freely between fragmented seagrass patches as they would in a continuous bed (Irlandi 1994; Bell et al. 2006). It is widely recognized that faunal species richness and density can be severely altered by changes in the amount of seagrass cover (Edgar and Robertson 1992; Gambi et al. 1998; Battley et al. 2011). For example, during experiments with the seagrass *Amphibolis* spp., thirteen of the thirty-five most common faunal species were present at significantly lower densities and three species showed significantly higher densities following *in situ* seagrass leaf reduction (Edgar and Robertson 1992). The drivers of *T. testudinum* decline in southern LLM remain unknown, as none of my data suggest the loss in cover is related to salinity, nutrients, or underwater light levels in this area. If this decline continues, it could be possible for *H. wrightii* to re-colonize southern LLM, where it has not been documented since the 1960's (Singleton 1964), illustrating the importance of placing these monitoring results in the context of past studies.

COMPARISON OF CURRENT SEAGRASS DISTRIBUTION TO HISTORIC MAPS

Previous seagrass surveys were made across ULM and LLM in 1961 (LLM only; Singleton 1964), 1965-67 (LLM only; McMahan 1966; ULM and LLM; McMahan 1969), 1974-76 (Merkord 1978), 1988 (Quammen and Onuf 1993), and 1998 (Onuf 2007), though to my knowledge no other bay-wide mapping efforts have been undertaken since 1998. Based off historic maps and this monitoring, it is apparent that large changes in seagrass cover and species composition have occurred in the Laguna Madre, especially in LLM. Maps from the 1960's indicate that *H. wrightii* was widespread in the LLM, except for a large mixed *T. testudinum* and *S. filiforme* meadow present near the Brownsville Ship Channel, one of the LLM's only open connections to the Gulf of Mexico (Singleton 1964; McMahan 1966, 1969). Surveys from 1988 showed *S. filiforme* present in a strip along much of the western LLM, and a small *T. testudinum* meadow present near the mouth of Brownsville Ship Channel (Quammen and Onuf 1993). In 1998, the *S. filiforme* band was still present, but *T. testudinum* had expanded farther northwards and also west near Port Isabel (Onuf 2007). My monitoring revealed that a large meadow of *T. testudinum* documented in 1998 across from the mouth of the Arroyo-Colorado River is now entirely dominated by *H. wrightii*. Additionally, this survey showed that the extensive strips of *S. filiforme* present through LLM in 1998 have vanished, and are now completely filled in by *H. wrightii*.

There are several possible reasons for the observed species shift from *S. filiforme* to *H. wrightii* in northern and central LLM that occurred sometime between 1998 and 2011. While *S. filiforme* can outcompete and displace *H. wrightii* when light and nutrient conditions are favorable, *H. wrightii* is much more tolerant of salinity fluctuation than *S. filiforme* (McMahan 1968; Quammen and Onuf 1993; Lirman and Cropper 2003).

However, salinity fluctuation does not appear to be the cause of *S. filiforme* decline in LLM, as the long-term salinity record does not reflect extended periods of hypersalinity for this area (Figure 11). In fact, salinities in northern and southern LLM dropped to ~20 several times in the past 20 years, potentially creating good conditions for expansion of *S. filiforme*, which was observed to have maximum leaf elongation rates at salinities of 25 by Lirman and Cropper (2003). Since the salinity regime does not seem to have precluded *S. filiforme* growth and expansion across northern and central LLM, it is therefore possible that some other factor such as light penetration or the ambient nutrient regime was unfavorable for *S. filiforme* growth in these areas. Then, during or directly after *S. filiforme* decline, *H. wrightii* was able to successfully re-colonize those portions of LLM.

SPATIAL TRENDS IN N AND P AVAILABILITY

The C:N:P molar ratios along with the $\delta^{13}C$ and $\delta^{15}N$ signatures measured in both *H. wrightii* and *T. testudinum* were comparable to findings from other studies in the Gulf of Mexico (Hemminga and Mateo 1996; Johnson et al. 2006; Campbell and Fourqurean 2009; Kowalski et al. 2009; Baggett et al. 2010; Campbell et al. 2012; K. Darnell, unpubl. data), and the spatial patterns I observed in ULM and LLM provide insight to regional nutrient availability. Not surprisingly, spatial availability of N and P in seagrass tissues in Laguna Madre largely reflects land use and land cover for south Texas. The area adjacent to northernmost ULM as well as most of the South (Lower) Laguna Madre Watershed, which drains into the Arroyo-Colorado River on the western side of LLM, contain relatively large population centers (Corpus Christi and Brownsville) as well as large expanses of cultivated agricultural cropland (USGS 2011). Therefore, I believe the spatial differences in C:N:P molar ratios and enriched $\delta^{15}N$ signatures in northernmost ULM (Figure 7) and western/southern LLM (Figures 8-10) compared to the rest of the Laguna are likely indicative of anthropogenically derived nutrient sources that were assimilated by seagrasses (McClelland and Valiela 1998; Cole et al. 2005; Campbell and Fourqurean 2009).

In all regions the variation in C:N:P ratios for *H. wrightii* and *T. testudinum* through time tracked one another relatively well, but the same trends were not always observed. This phenomenon may be an artifact of each species' spatial distribution, or physiological differences between *H. wrightii* and *T. testudinum* could be driving differential nutrient assimilation into leaf tissues (Kraemer and Mazzella 1999; Lee and Dunton 2000; Morris et al. 2008). For example, lower C:N ratios in *T. testudinum* may reflect greater N storage in rhizomes, thus creating more N availability for leaves. Differences in C:N and C:P ratios between species could also indicate different rates of water-column versus porewater nutrient assimilation, or differential amounts of nutrient allocation to leaf tissues.

Stable isotope signatures exhibited the same patterns over time in both species, although *T. testudinum* had more enriched $\delta^{13}C$ and $\delta^{15}N$ signatures than *H. wrightii*. The $\delta^{13}C$ signatures that I measured were within previously reported ranges for each species, but were more enriched than the mean *H. wrightii* and *T. testudinum* signatures reviewed by Hemminga and Mateo (1996). Both $\delta^{13}C$ and $\delta^{15}N$ signatures were similar to another Gulf of Mexico study, although $\delta^{15}N$ was much more enriched for both species (Campbell and Fourqurean 2009). Furthermore, both species displayed more enriched $\delta^{15}N$ signatures over time across all regions, perhaps indicating an increased reliance on anthropogenically derived N sources (McClelland and Valiela 1998; Cole et al. 2005; Campbell and Fourqurean 2009). These results serve as further evidence that changes in seagrass tissue composition and community structure can be utilized to characterize local hydrographic conditions, and illustrates their sensitivity as valuable indicators of regional environmental conditions.

SUMMARY

In conclusion, I believe that annual sampling was a major strength of this monitoring program because this design provided information about percent cover changes that occurred over a relatively short temporal scale (one year), as opposed to comparing seagrass percent cover measurements taken many years apart, possibly with different field methods. This study complements remotely sensed data through confirmation of seagrass presence and provision of quantitative information on species composition, which is critical for examining unique within-bed species shifts (such as those observed in ULM-NC), which may have important ecological consequences for the region. However, a limitation of my monitoring design was that sampling was constrained by the remote imagery used to delineate seagrass extent, taken in either 2004 or 2007. Updated imagery delineating seagrass coverage for Texas (e.g. the semi-automated approach employed by Fletcher et al. in 2009 in Redfish Bay, or current aerial mapping efforts, see http://tpwd.texas.gov/gis/seagrass) is a high priority, since additional hexagons and stations could be easily incorporated into this monitoring design where seagrass meadow edges may have expanded. Ideally, remote imagery to assess seagrass extent should be collected at intervals of 5-10 years to supplement field-based monitoring efforts (Pulich et al. 1997; Pulich and Onuf 2007; Dunton et al. 2011).

Overall, this study demonstrates the value of a field-based monitoring program to rapidly sample seagrasses across nearly 250 km of coast. I was able to successfully detect various changes in seagrass percent cover and species composition at both the region and subregion scale over one year, as well as assess trends in these parameters through time. By assigning random stations nested into a grid of hexagons I ensured even spatial coverage while still incorporating a degree of randomness, demonstrating the utility of tiered seagrass monitoring for conducting seagrass research at the landscape scale (Neckles et al. 2012). I believe that a similar, coordinated approach to seagrass monitoring across the Gulf of Mexico will be extremely beneficial in the future, as seagrass communities continue to face threats both environmental and anthropogenic in nature. My monitoring framework is adaptable in that additional laboratory (e.g. tissue elemental content) or statistical and geospatial analyses (e.g. ordination) can be employed to field data when feasible to provide stronger evidence for seagrass stability or change (Neckles et al. 2012).

In conclusion, I observed significant seagrass percent cover changes and species shifts across the Texas coast, indicative of the dynamic nature of Texas seagrass meadows undoubtedly influenced by environmental drivers such as salinity and gradients of nutrient availability. I am confident that a similar tiered monitoring framework can be adapted to other systems, and used in conjunction with statistical and geospatial analyses to analyze trends in seagrass community structure at the landscape scale.

Appendix A – Subregion Delineation

Coastal Bend

Stations in the Coastal Bend region were classified into five subregions: Aransas Bay (AB), Redfish Bay North (RFB-N), Redfish Bay Southwest (RFB-SW), Redfish Bay Southeast (RFB-SE), and Corpus Christi Bay (CCB). AB stations (n = 10) were clearly separated from Redfish Bay stations to the southwest by the Lydia-Ann Channel and a large expanse of Aransas Bay. RFB-N stations (n = 43) are geographically distinct from RFB-SW and RFB-SE stations (n = 15 and n = 14, respectively) as they are separated by Harbor Island and State Highway 361. A moderately sized portion of Aransas Bay that was devoid of seagrasses in the 2004/2007 NOAA Benthic Habitat Mapping separates RFB-SW from RFB-SE. Finally, CCB stations to the southeast are naturally separated from RFB-SE stations by the Gulf Intracoastal Waterway (GIWW) and the northern edge of Mustang Island.

Upper Laguna Madre

Stations in the Upper Laguna Madre (ULM) region were classified into four subregions: ULM North (ULM-N), ULM North-Central (ULM-NC), ULM South-Central (ULM-SC), and ULM South (ULM-S). The ULM-N stations (n = 34) were surrounded to the north by Corpus Christi Bay, and were separated from ULM-NC stations (n = 72) in the south by Packery Channel and by the JFK Causeway. Division of ULM-NC stations from ULM-SC stations (n = 39) was based upon a natural northwest to southeast break in seagrass extent as delineated by the 2004/2007 NOAA Benthic Habitat Mapping, and by the tessellated hexagon grid. Finally, the ULM-SC stations were clearly separated from ULM-S stations (n = 33) by a large expanse of water and wind-tidal flats. The ULM-S subregion (“Nine-Mile Hole”) contains the southernmost seagrass meadows in the Laguna Madre north of the Land Cut.

Lower Laguna Madre

Stations in the Lower Laguna Madre (LLM) region were classified four subregions: LLM North (LLM-N), LLM Central (LLM-C), LLM Southwest (LLM-SW), and LLM Southeast (LLM-SE). The LLM-N stations (n = 48) begin south of the Land Cut and extend southward. LLM-N stations are separated from LLM-C stations (n = 74) where Mansfield Pass creates a natural break in seagrass extent (as seen in the 2004/2007 NOAA Benthic Habitat Mapping). The LLM-C subregion extends south from Mansfield Pass to the mouth of the Arroyo-Colorado River. Here, the tessellated hexagon grid was used to separate LLM-C stations from LLM-SE stations (n = 117) based on the natural eastward path of the Arroyo Colorado River. Finally, LLM-SE stations are separated from LLM-SW stations (n = 46) based upon the GIWW and the tessellated hexagon grid. The LLM-SE subregion extends southward just past the Brownsville Ship Channel into South Bay, where the southernmost seagrass meadows in Texas are located.

Appendix B – Seagrass Percent Cover and Canopy Height

Table B1. Seagrass percent cover (%) measurements for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.).

		Total (All Species)			***Halodule wrightii***			***Thalassia testudinum***			***Syringodium filiforme***		
Region		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
CB	x̄	72.75	75.07	68.95	37.28	37.01	33.41	32.63	32.44	30.08	1.53	2.72	2.17
	S.E.	2.80	2.68	2.51	3.50	3.78	3.56	3.82	3.85	3.57	0.89	1.05	0.78
	n	98	98	98	98	98	98	98	98	98	98	98	98
ULM	x̄	72.81	86.80	72.92	58.54	70.60	69.85	0.04	0.00	0.00	13.66	15.67	2.86
	S.E.	2.35	1.96	2.69	2.79	2.81	2.85	0.04	0.00	0.00	1.93	2.23	1.01
	n	178	178	178	178	178	178	178	178	178	178	178	178
LLM	x̄	46.31	50.69	50.99	25.75	30.18	34.44	18.62	17.85	15.49	1.38	2.26	0.96
	S.E.	2.38	2.29	2.27	2.14	2.22	2.37	2.00	1.90	1.75	0.45	0.66	0.39
	n	282	282	282	282	282	282	282	282	282	282	282	282

Table B1 (continued).

		Halophila engelmannii			*Ruppia maritima*		
Region		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
CB	x̄	0.02	0.01	0.26	1.30	2.90	3.03
	S.E.	0.01	0.01	0.15	0.63	1.37	1.13
	n	98	98	98	98	98	98
ULM	x̄	0.32	0.46	0.06	0.24	0.07	0.16
	S.E.	0.11	0.26	0.03	0.13	0.06	0.10
	n	178	178	178	178	178	178
LLM	x̄	0.00	0.00	0.08	0.57	0.40	0.02
	S.E.	0.00	0.00	0.06	0.21	0.28	0.02
	n	282	282	282	282	282	282

Table B2. Repeated measures ANOVA table for the effect of year on seagrass cover for each species (plus total cover) across each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant effects (α = 0.05) are denoted in bold.

		Total (All Species)		***Halodule wrightii***		***Thalassia testudinum***		***Syringodium filiforme***		***Halophila engelmannii***	
Region	**df**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
CB	2, 194	2.9000	0.0574	1.0922	0.3375	0.4763	0.6218	1.3458	0.2628	2.7182	0.0685
ULM	2, 354	34.9426	**<0.0001**	25.6487	**<0.0001**	1.0000	0.3689	32.8784	**<0.0001**	3.4645	**0.0324**
LLM	2, 562	2.9999	0.0506	14.1465	**<0.0001**	2.8173	0.0606	5.4288	**0.0046**	2.2177	0.1098

Table B2 (continued).

Region	df	*Ruppia maritima* F	 p
CB	2, 194	0.8708	0.4202
ULM	2, 354	0.8922	0.4107
LLM	2, 562	5.0658	**0.0066**

Table B3. Post hoc Tukey multiple comparison tests for seagrass percent cover change over time for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences (α = 0.05) are denoted in bold.

Region	Years	Total (All Species)	*Halodule wrightii*	*Thalassia testudinum*	*Syringodium filiforme*	*Halophila engelmannii*	*Ruppia maritima*
CB	2011-2012	0.636	0.862	0.994	0.299	0.974	0.826
	2011-2013	0.301	0.311	0.710	0.368	0.139	0.385
	2012-2013	**0.045**	0.615	0.645	0.990	0.086	0.747
ULM	2011-2012	< **0.001**	< **0.001**	0.438	0.973	0.990	0.376
	2011-2013	0.239	< **0.001**	0.438	< **0.001**	0.050	0.748
	2012-2013	< **0.001**	0.882	1.000	< **0.001**	0.070	0.816
LLM	2011-2012	0.106	**0.005**	0.551	0.124	1.000	0.246
	2011-2013	0.070	< **0.001**	**0.047**	0.383	0.162	**0.004**
	2012-2013	0.982	0.078	0.380	**0.003**	0.162	0.253

Table B4. Seagrass percent cover (%) measurements for each subregion in the Coastal Bend (CB) region (AB = Aransas Bay, RFB-N = Redfish Bay North, RFB-SW = Redfish Bay Southwest, RFB-SE = Redfish Bay Southeast, CCB = Corpus Christi Bay) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.).

		Total (All Species)			***Halodule wrightii***			***Thalassia testudinum***			***Syringodium filiforme***		
Subregion		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
AB	x̄	48.55	73.25	54.48	46.93	73.25	54.35	0.00	0.00	0.00	0.00	0.00	0.00
	S.E.	9.60	6.45	9.85	8.91	6.45	9.85	0.00	0.00	0.00	0.00	0.00	0.00
	n	10	10	10	10	10	10	10	10	10	10	10	10
RFB-N	x̄	82.16	81.47	71.58	34.31	31.34	24.26	43.75	43.93	39.26	2.18	1.42	3.01
	S.E.	3.27	3.76	3.67	5.08	5.34	4.52	5.66	6.02	5.60	1.79	1.00	1.26
	n	43	43	43	43	43	43	43	43	43	43	43	43
RFB-SW	x̄	61.00	57.92	60.12	10.50	2.03	2.82	49.58	49.13	56.20	0.92	6.75	1.10
	S.E.	9.94	9.50	7.39	7.03	1.67	2.56	10.35	10.90	8.33	0.83	3.97	1.00
	n	15	15	15	15	15	15	15	15	15	15	15	15
RFB-SE	x̄	68.30	75.20	73.52	40.45	40.25	44.95	27.32	28.77	22.50	0.18	1.07	0.73
	S.E.	7.11	5.20	5.73	9.31	10.01	11.06	10.33	9.39	8.84	0.18	1.07	0.73
	n	14	14	14	14	14	14	14	14	14	14	14	14
CCB	x̄	77.50	75.00	75.19	61.56	59.58	63.52	11.88	9.38	6.34	2.50	5.55	3.52
	S.E.	4.35	6.03	4.50	7.92	9.27	7.38	6.81	4.86	3.39	2.50	4.39	3.20
	n	16	16	16	16	16	16	16	16	16	16	16	16

Table B4 (continued).

		Halophila engelmannii			*Ruppia maritima*		
Subregion		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
AB	x̄	0.00	0.00	0.08	1.63	0.00	0.05
	S.E.	0.00	0.00	0.08	1.54	0.00	0.05
	n	10	10	10	10	10	10
RFB-N	x̄	0.04	0.01	0.44	1.88	4.76	4.62
	S.E.	0.03	0.01	0.31	1.34	2.64	2.33
	n	43	43	43	43	43	43
RFB-SW	x̄	0.00	0.00	0.00	0.00	0.00	0.00
	S.E.	0.00	0.00	0.00	0.00	0.00	0.00
	n	15	15	15	15	15	15
RFB-SE	x̄	0.00	0.00	0.00	0.36	5.11	5.34
	S.E.	0.00	0.00	0.00	0.36	5.00	2.91
	n	14	14	14	14	14	14
CCB	x̄	0.00	0.00	0.39	1.56	0.50	1.42
	S.E.	0.00	0.00	0.39	1.05	0.50	1.03
	n	16	16	16	16	16	16

Table B5. Seagrass percent cover (%) measurements for each subregion in the Upper Laguna Madre (ULM) region (ULM-N = ULM North, ULM-NC = ULM North-Central, ULM-SC = ULM South-Central, ULM-S = ULM South) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.).

		Total (All Species)			***Halodule wrightii***			***Thalassia testudinum***			***Syringodium filiforme***		
Subregion		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
ULM-N	x̄	62.89	82.82	70.24	48.63	59.98	56.20	0.00	0.00	0.00	13.96	20.93	13.36
	S.E.	5.45	4.91	5.85	6.40	7.27	6.99	0.00	0.00	0.00	4.25	5.57	4.89
	n	34	34	34	34	34	34	34	34	34	34	34	34
ULM-NC	x̄	74.52	85.66	67.12	51.30	60.52	66.15	0.10	0.00	0.00	22.64	24.89	0.76
	S.E.	3.71	3.55	4.35	4.42	4.88	4.40	0.10	0.00	0.00	3.56	4.17	0.28
	n	72	72	72	72	72	72	72	72	72	72	72	72
ULM-SC	x̄	86.53	95.90	88.11	77.79	88.53	88.11	0.00	0.00	0.00	8.40	7.33	0.00
	S.E.	3.79	2.03	4.01	5.05	3.75	4.01	0.00	0.00	0.00	3.63	3.19	0.00
	n	39	39	39	39	39	39	39	39	39	39	39	39
ULM-S	x̄	63.05	82.65	70.39	61.80	82.33	70.39	0.00	0.00	0.00	0.00	0.00	0.00
	S.E.	5.78	4.19	7.39	6.09	4.28	7.39	0.00	0.00	0.00	0.00	0.00	0.00
	n	33	33	33	33	33	33	33	33	33	33	33	33

Table B5 (continued).

		Halophila engelmannii			*Ruppia maritima*		
Subregion		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
ULM-N	x̄	0.25	1.86	0.29	0.05	0.05	0.39
	S.E.	0.22	1.32	0.16	0.05	0.05	0.28
	n	34	34	34	34	34	34
ULM-NC	x̄	0.48	0.25	0.00	0.00	0.00	0.21
	S.E.	0.22	0.18	0.00	0.00	0.00	0.21
	n	72	72	72	72	72	72
ULM-SC	x̄	0.33	0.04	0.00	0.00	0.00	0.00
	S.E.	0.23	0.02	0.00	0.00	0.00	0.00
	n	39	39	39	39	39	39
ULM-S	x̄	0.00	0.00	0.00	1.25	0.32	0.00
	S.E.	0.00	0.00	0.00	0.67	0.31	0.00
	n	33	33	33	33	33	33

Table B6. Seagrass percent cover (%) measurements for each subregion in the Lower Laguna Madre (LLM) region (LLM-N = LLM North, LLM-C = LLM Central, LLM-SW = LLM Southwest, LLM-SE = LLM Southeast) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.).

		Total (All Species)			***Halodule wrightii***			***Thalassia testudinum***			***Syringodium filiforme***		
Subregion		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
LLM-N	x̄	36.94	56.57	63.56	36.70	54.77	60.36	0.21	1.81	3.07	0.00	0.00	0.03
	S.E.	5.60	5.54	5.32	5.62	5.61	5.46	0.14	0.99	1.65	0.00	0.00	0.03
	n	48	48	48	48	48	48	48	48	48	48	48	48
LLM-C	x̄	49.16	45.81	56.17	48.22	44.69	56.16	0.00	0.00	0.00	0.00	0.00	0.00
	S.E.	4.56	4.41	4.62	4.59	4.35	4.63	0.00	0.00	0.00	0.00	0.00	0.00
	n	71	71	71	71	71	71	71	71	71	71	71	71
LLM-SW	x̄	41.64	46.62	44.59	20.83	26.08	26.48	19.85	20.26	17.99	0.00	0.00	0.00
	S.E.	6.00	5.93	5.66	5.25	5.60	5.83	4.58	4.55	4.17	0.00	0.00	0.00
	n	45	45	45	45	45	45	45	45	45	45	45	45
LLM-SE	x̄	50.20	52.79	45.20	9.64	13.02	13.87	36.84	34.20	28.90	3.29	5.39	2.28
	S.E.	3.77	3.55	3.40	2.04	2.48	2.51	3.76	3.56	3.37	1.06	1.54	0.92
	n	118	118	118	118	118	118	118	118	118	118	118	118

Table B6 (continued).

Subregion		*Halophila engelmannii* 2011	*Halophila engelmannii* 2012	*Halophila engelmannii* 2013	*Ruppia maritima* 2011	*Ruppia maritima* 2012	*Ruppia maritima* 2013
LLM-N	x̄	0.00	0.00	0.10	0.02	0.00	0.00
	S.E.	0.00	0.00	0.10	0.02	0.00	0.00
	n	48	48	48	48	48	48
LLM-C	x̄	0.00	0.00	0.01	0.94	1.12	0.004
	S.E.	0.00	0.00	0.01	0.43	1.09	0.004
	n	71	71	71	71	71	71
LLM-SW	x̄	0.00	0.00	0.00	0.96	0.28	0.12
	S.E.	0.00	0.00	0.00	0.94	0.28	0.11
	n	45	45	45	45	45	45
LLM-SE	x̄	0.00	0.00	0.15	0.42	0.18	0.00
	S.E.	0.00	0.00	0.15	0.24	0.12	0.00
	n	118	118	118	118	118	118

Table B7. Repeated measures ANOVA table for the effects of subregion and year on seagrass cover for each species (plus total cover) across each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences (α = 0.05) are denoted in bold.

			Total (All Species)		***Halodule wrightii***		***Thalassia testudinum***	
Region	**Fixed Effect**	**df**	**F**	**p**	**F**	**p**	**F**	**p**
Coastal Bend (CB)	Subregion	4, 93	4.6153	**0.0019**	13.1543	**<0.0001**	10.4364	**<0.0001**
	Year	2, 186	2.8713	0.0591	1.1065	0.3329	0.4620	0.6308
	Subregion x Year	8, 186	0.7601	0.6384	1.3171	0.2372	0.2705	0.9748
Upper Laguna Madre (ULM)	Subregion	3, 174	5.5787	**0.0011**	8.4611	**<0.0001**	0.4865	0.6921
	Year	2, 348	35.8968	**<0.0001**	25.4480	**<0.0001**	0.9913	0.3721
	Subregion x Year	6, 348	2.6111	**0.0173**	0.5383	0.7791	0.4865	0.8184
Lower Laguna Madre (LLM)	Subregion	3, 278	0.5680	0.6365	41.8479	**<0.0001**	37.5551	**<0.0001**
	Year	2, 556	3.1947	**0.0417**	14.7248	**<0.0001**	2.8598	0.0581
	Subregion x Year	6, 556	7.0825	**<0.0001**	4.8295	**<0.0001**	2.4152	**0.0259**

Table B7 (continued).

Region	Fixed Effect	df	*Syringodium filiforme* F	*Syringodium filiforme* p	*Halophila engelmannii* F	*Halophila engelmannii* p	*Ruppia maritima* F	*Ruppia maritima* p
Coastal Bend (CB)	Subregion	4, 93	0.6754	0.6107	0.5660	0.6879	1.1126	0.3554
	Year	2, 186	1.3656	0.2578	2.6413	0.0739	0.8694	0.4209
	Subregion x Year	8, 186	1.3582	0.2176	0.3132	0.9604	0.9593	0.4693
Upper Laguna Madre (ULM)	Subregion	3, 174	10.8765	**<0.0001**	2.9206	**0.0355**	3.9233	**0.0097**
	Year	2, 348	36.4176	**<0.0001**	3.5844	**0.0288**	0.9337	0.3941
	Subregion x Year	6, 348	7.3511	**<0.0001**	3.0427	**0.0065**	3.7456	**0.0013**
Lower Laguna Madre (LLM)	Subregion	3, 278	7.0004	**0.0001**	0.3236	0.8083	1.4403	0.2313
	Year	2, 556	5.5322	**0.0042**	2.2017	0.1116	5.0452	**0.0067**
	Subregion x Year	6, 556	2.7839	**0.0112**	0.3236	0.9247	0.6191	0.7151

Table B8. Post hoc Tukey multiple comparison tests for seagrass percent cover change over time for each subregion in the Coastal Bend (CB) region (AB = Aransas Bay, RFB-N = Redfish Bay North, RFB-SW = Redfish Bay Southwest, RFB-SE = Redfish Bay Southeast, CCB = Corpus Christi Bay). Significant differences (α = 0.05) are denoted in bold.

Subregion	**Years**	**Total (All Species)**	***Halodule wrightii***	***Thalassia testudinum***	***Syringodium filiforme***	***Halophila engelmannii***	***Ruppia maritima***
AB	2011-2012	0.625	0.329	1.000	1.000	1.000	0.989
	2011-2013	1.000	1.000	1.000	1.000	1.000	0.996
	2012-2013	0.935	0.814	1.000	1.000	1.000	1.000
RFB-N	2011-2012	1.000	0.949	1.000	1.000	1.000	0.965
	2011-2013	0.254	0.198	0.996	0.819	0.743	0.973
	2012-2013	0.143	0.953	0.987	0.676	0.490	1.000
RFB-SW	2011-2012	1.000	0.975	1.000	0.125	1.000	1.000
	2011-2013	1.000	0.979	0.999	1.000	1.000	1.000
	2012-2013	1.000	1.000	1.000	0.154	1.000	1.000
RFB-SE	2011-2012	1.000	1.000	1.000	1.000	1.000	0.938
	2011-2013	1.000	1.000	1.000	1.000	1.000	0.189
	2012-2013	1.000	1.000	0.994	1.000	1.000	0.957
CCB	2011-2012	1.000	1.000	1.000	0.967	1.000	0.997
	2011-2013	1.000	1.000	1.000	1.000	0.837	1.000
	2012-2013	1.000	1.000	1.000	1.000	0.837	1.000

Table B9. Post hoc Tukey multiple comparison tests for seagrass percent cover change over time for each subregion in the Upper Laguna Madre (ULM) region (ULM-N = ULM North, ULM-NC = ULM North-Central, ULM-SC = ULM South-Central, ULM-S = ULM South). Significant differences ($\alpha = 0.05$) are denoted in bold.

Subregion	**Years**	**Total (All Species)**	***Halodule wrightii***	***Thalassia testudinum***	***Syringodium filiforme***	***Halophila engelmannii***	***Ruppia maritima***
ULM-N	2011-2012	**< 0.001**	**0.028**	1.000	0.912	**0.007**	1.000
	2011-2013	0.318	0.482	1.000	0.999	0.972	0.831
	2012-2013	**0.048**	0.922	1.000	0.535	0.143	0.831
ULM-NC	2011-2012	**< 0.001**	**0.011**	0.437	1.000	0.661	1.000
	2011-2013	0.790	**< 0.001**	0.437	**< 0.001**	**0.026**	0.985
	2012-2013	**< 0.001**	0.997	1.000	**< 0.001**	0.792	0.985
ULM-SC	2011-2012	**0.036**	**0.043**	1.000	1.000	0.872	1.000
	2011-2013	0.957	0.053	1.000	0.063	0.480	1.000
	2012-2013	0.455	1.000	1.000	0.096	0.999	1.000
ULM-S	2011-2012	**0.004**	**0.002**	1.000	1.000	1.000	**0.017**
	2011-2013	0.083	**0.043**	1.000	1.000	1.000	**< 0.001**
	2012-2013	0.983	0.984	1.000	1.000	1.000	0.888

Table B10. Post hoc Tukey multiple comparison tests for seagrass percent cover change over time for each subregion in the Lower Laguna Madre (LLM) region (LLM-N = LLM North, LLM-C = LLM Central, LLM-SW = LLM Southwest, LLM-SE = LLM Southeast). Significant differences (α = 0.05) are denoted in bold.

Subregion	**Years**	**Total (All Species)**	***Halodule wrightii***	***Thalassia testudinum***	***Syringodium filiforme***	***Halophila engelmannii***	***Ruppia maritima***
LLM-N	2011-2012	< **0.001**	< **0.001**	0.995	1.000	1.000	1.000
	2011-2013	< **0.001**	< **0.001**	0.886	1.000	0.822	1.000
	2012-2013	0.789	0.863	1.000	1.000	0.822	1.000
LLM-C	2011-2012	1.000	1.000	1.000	1.000	1.000	0.871
	2011-2013	0.421	0.074	1.000	1.000	1.000	**0.026**
	2012-2013	0.155	**0.028**	1.000	1.000	1.000	0.560
LLM-SW	2011-2012	0.987	0.825	1.000	1.000	1.000	0.997
	2011-2013	0.999	0.953	1.000	1.000	1.000	0.986
	2012-2013	1.000	1.000	1.000	1.000	1.000	1.000
LLM-SE	2011-2012	1.000	0.901	0.499	**0.026**	1.000	0.983
	2011-2013	0.393	0.638	< **0.001**	0.260	0.640	0.463
	2012-2013	0.196	1.000	0.147	< **0.001**	0.640	0.972

Table B11. Seagrass canopy height (cm) measurements for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.).

		Halodule wrightii			***Thalassia testudinum***			***Syringodium filiforme***			***Halophila engelmannii***		
Region		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
CB	x̄	18.76	20.53	16.03	32.57	35.29	33.93	34.79	39.24	30.72	7.00	---	3.48
	S.E.	0.74	0.84	0.87	1.19	1.31	1.03	5.79	2.97	3.27	---	---	0.49
	n	72	65	64	59	59	56	6	9	11	1	---	4
ULM	x̄	19.22	21.05	17.36	---	---	---	25.18	30.51	15.47	5.71	6.39	5.02
	S.E.	0.67	0.71	0.51	---	---	---	0.85	1.24	1.00	0.40	0.63	0.50
	n	152	152	158	---	---	---	61	53	28	15	14	7
LLM	x̄	10.76	14.24	14.20	24.32	24.60	19.73	27.69	27.26	19.33	---	---	4.20
	S.E.	0.41	0.46	0.44	1.08	0.96	0.67	1.16	1.94	1.40	---	---	1.07
	n	153	162	170	95	90	106	16	17	14	---	---	3

Table B11 (continued).

		Ruppia maritima		
Region		**2011**	**2012**	**2013**
CB	x̄	18.96	15.60	16.19
	S.E.	1.68	2.72	1.86
	n	12	9	15
ULM	x̄	12.68	4.86	8.65
	S.E.	1.55	1.09	0.64
	n	7	4	4
LLM	x̄	7.65	8.70	12.17
	S.E.	0.69	1.21	1.68
	n	16	9	4

Table B12. Repeated measures ANOVA table for the effect of year on seagrass canopy height for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences (α = 0.05) are denoted in bold.

	Halodule wrightii			*Thalassia testudinum*			*Syringodium filiforme*			*Halophila engelmannii*		
Region	**df**	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**
CB	2, 118	12.208	< **0.0001**	2, 106	2.549	0.0829	2, 9	3.442	0.0776	---	---	---
ULM	2, 295	20.299	< **0.001**	---	---	---	2, 73	47.469	< **0.0001**	2, 5	0.585	0.5912
LLM	2, 296	79.624	< **0.001**	2, 175	24.750	< **0.0001**	2, 23	13.305	< **0.001**	---	---	---

Table B12 (continued).

	Ruppia maritima		
Region	**df**	**F**	**P**
CB	2, 8	1.064	0.3891
ULM	2, 1	8.536	0.2352
LLM	2, 5	3.359	0.1189

Table B13. Post hoc Tukey multiple comparison tests for seagrass canopy height change over time for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences (α = 0.05) are denoted in bold.

Region	**Years**	***Halodule wrightii***	***Thalassia testudinum***	***Syringodium filiforme***	***Halophila engelmannii***	***Ruppia maritima***
CB	2011-2012	0.080	0.063	0.409	---	0.374
	2011-2013	**0.009**	0.429	0.562	---	0.424
	2012-2013	< **0.001**	0.578	**0.024**	---	0.954
ULM	2011-2012	**0.002**	---	<**0.001**	0.989	< **0.001**
	2011-2013	**0.007**	---	< **0.001**	0.622	0.132
	2012-2013	< **0.001**	---	< **0.001**	0.532	0.480
LLM	2011-2012	< **0.001**	0.804	0.930	---	0.668
	2011-2013	< **0.001**	< **0.001**	< **0.001**	---	**0.025**
	2012-2013	0.521	< **0.001**	< **0.001**	---	0.157

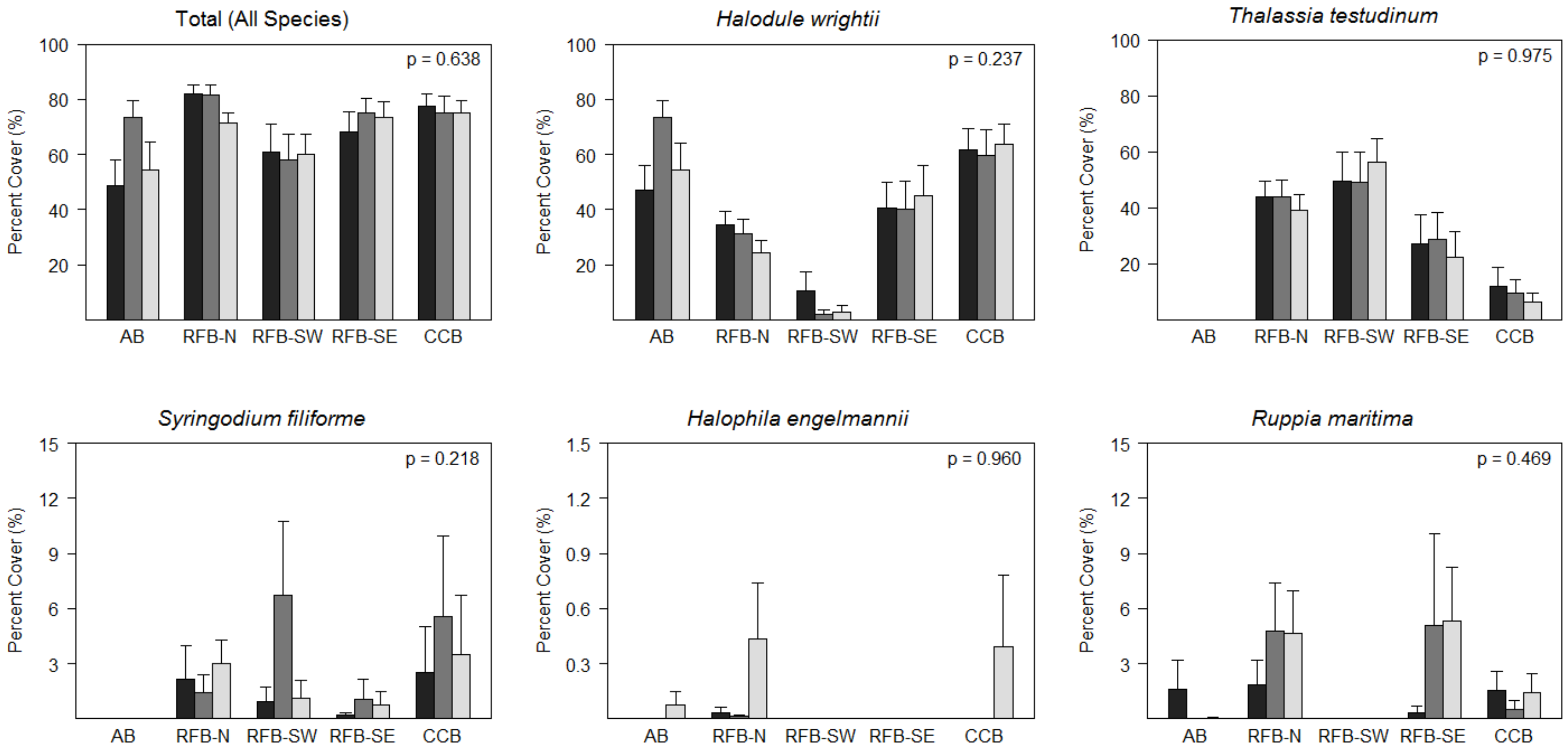

Figure B1. Seagrass percent cover (%; mean + standard error) for all subregions in the Coastal Bend (CB) region (AB = Aransas Bay, RFB-N = Redfish Bay North, RFB-SW = Redfish Bay Southwest, RFB-SE = Redfish Bay Southeast, CCB = Corpus Christi Bay) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs and Tukey multiple comparison tests were applied with subregion and year treated as fixed effects, and the interaction term is reported for each model. Significant differences from multiple comparison tests (α = 0.05) are listed (A, B, C) where present. Note the difference in y-axis ranges.

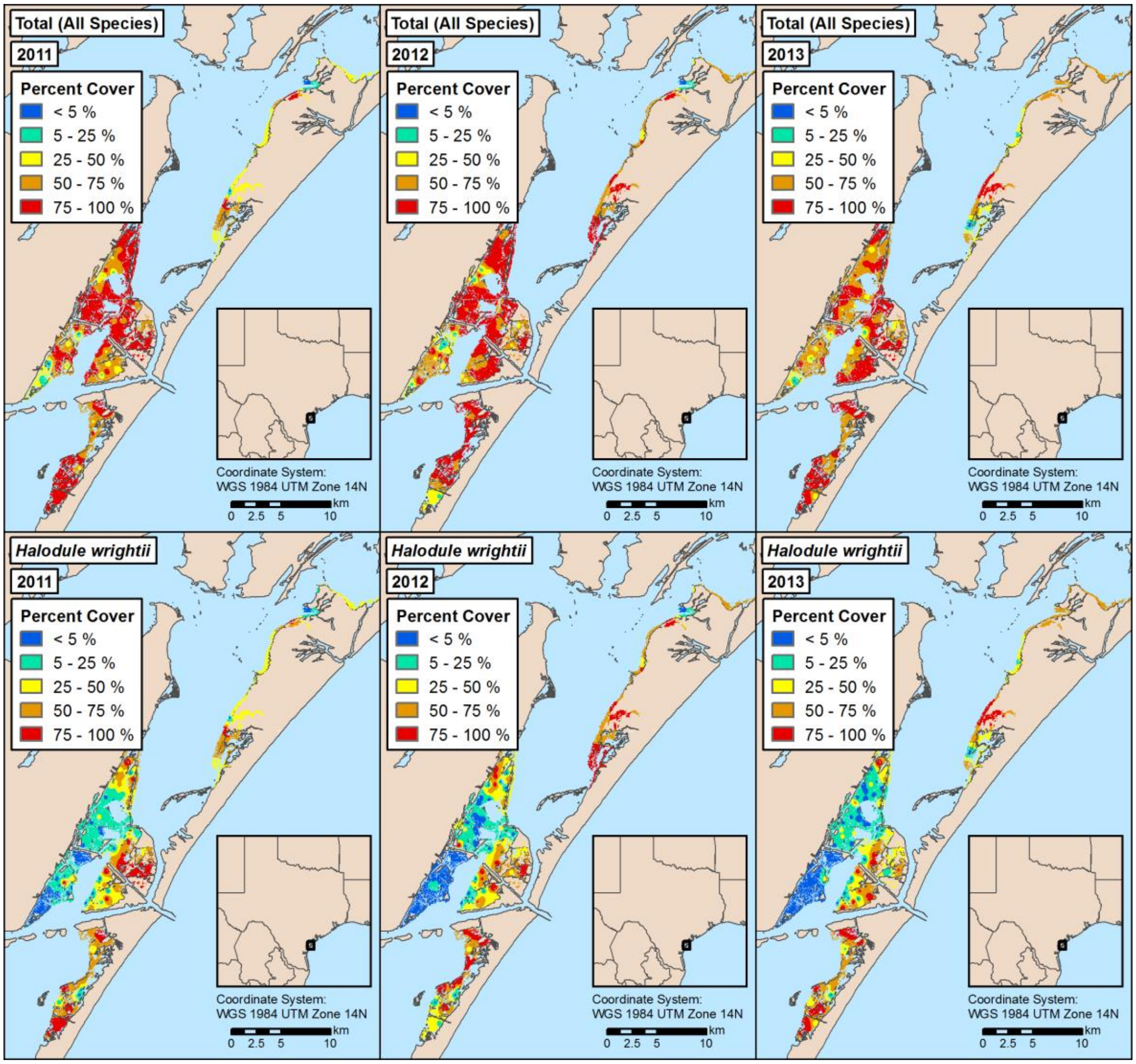

Figure B2. Seagrass percent cover in the Coastal Bend from 2011-2013 for total (all species) seagrass and *Halodule wrightii*.

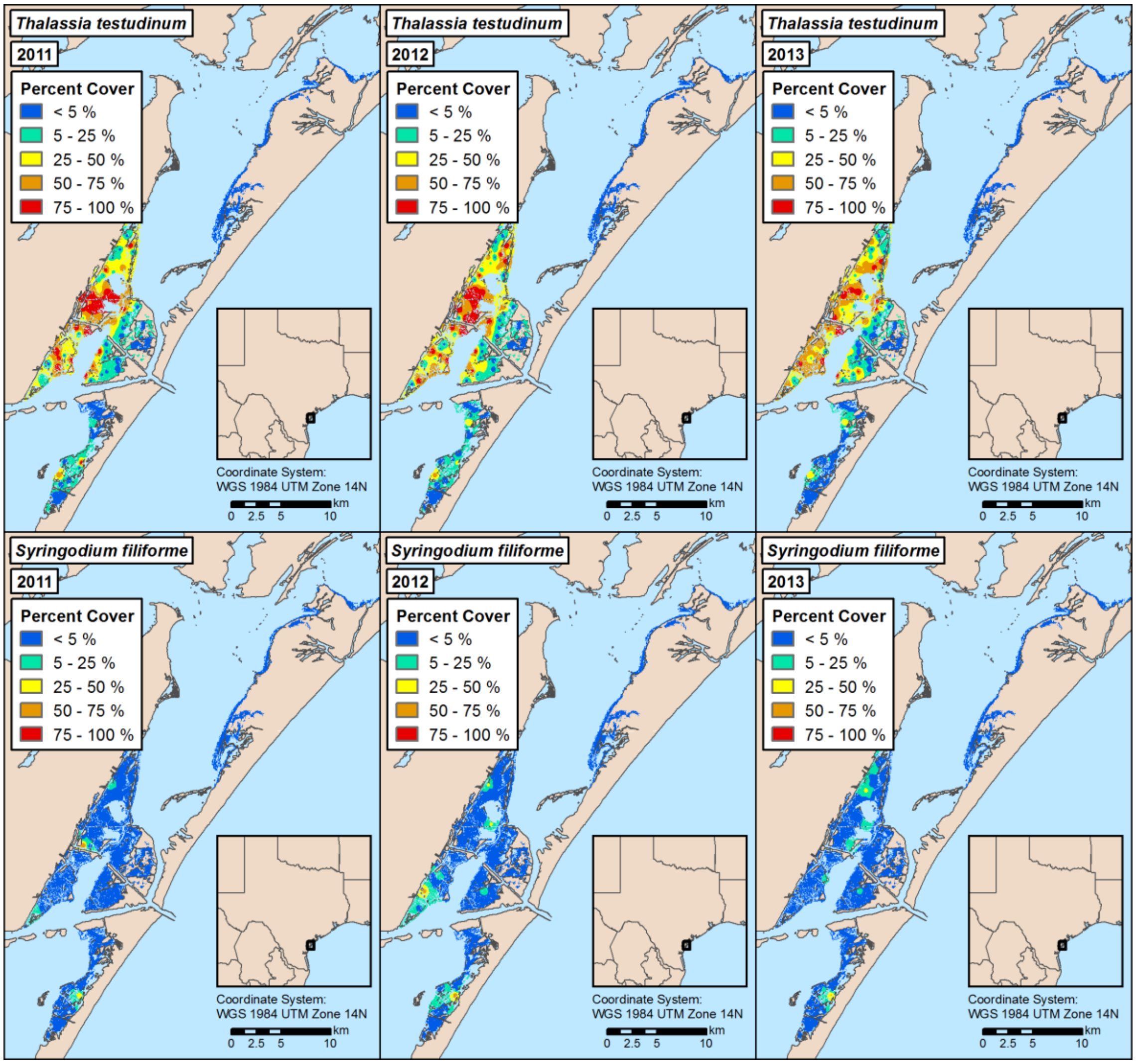

Figure B3. Seagrass percent cover in the Coastal Bend from 2011-2013 for *Thalassia testudinum* and *Syringodium filiforme*.

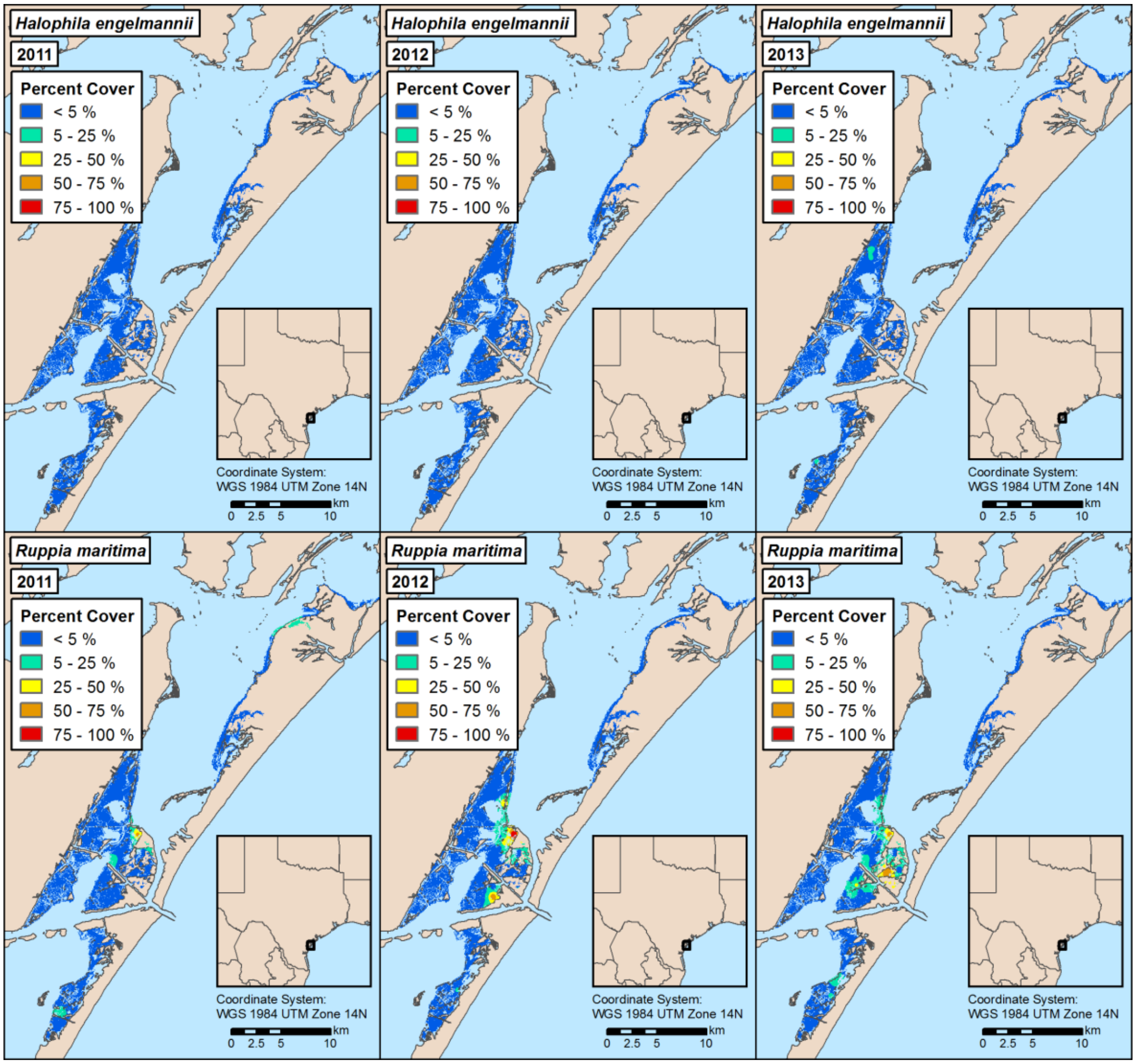

Figure B4. Seagrass percent cover in the Coastal Bend from 2011-2013 for *Halophila engelmannii* and *Ruppia maritima*.

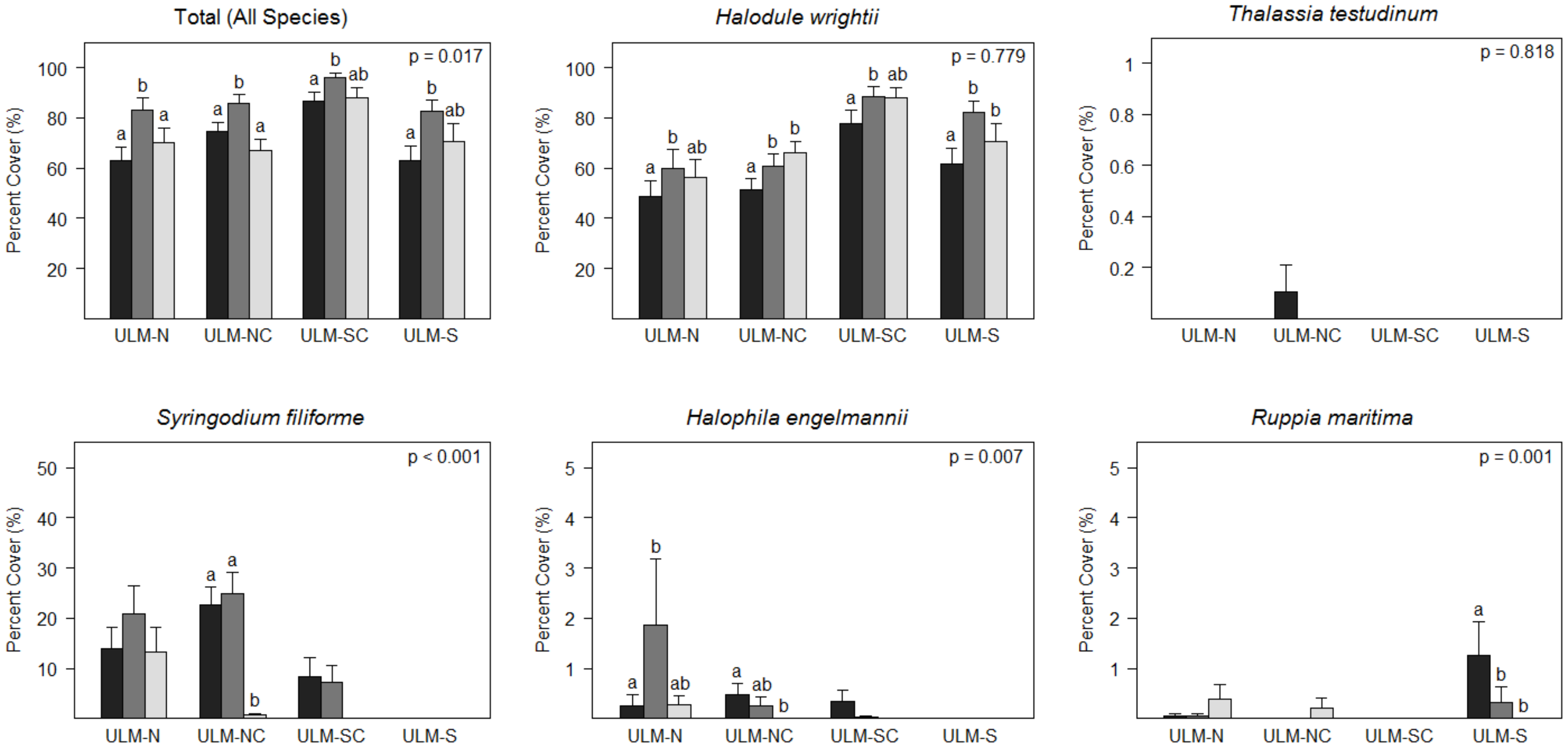

Figure B5. Seagrass percent cover (%; mean + standard error) for all subregions in the Upper Laguna Madre (ULM) region (ULM-N = ULM North, ULM-NC = ULM North-Central, ULM-SC = ULM South-Central, ULM-S = ULM South) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs and Tukey multiple comparison tests were applied with subregion and year treated as fixed effects, and the interaction term is reported for each model. Significant differences from multiple comparison tests ($\alpha = 0.05$) are listed (A, B, C) where present. Note the difference in y-axis ranges.

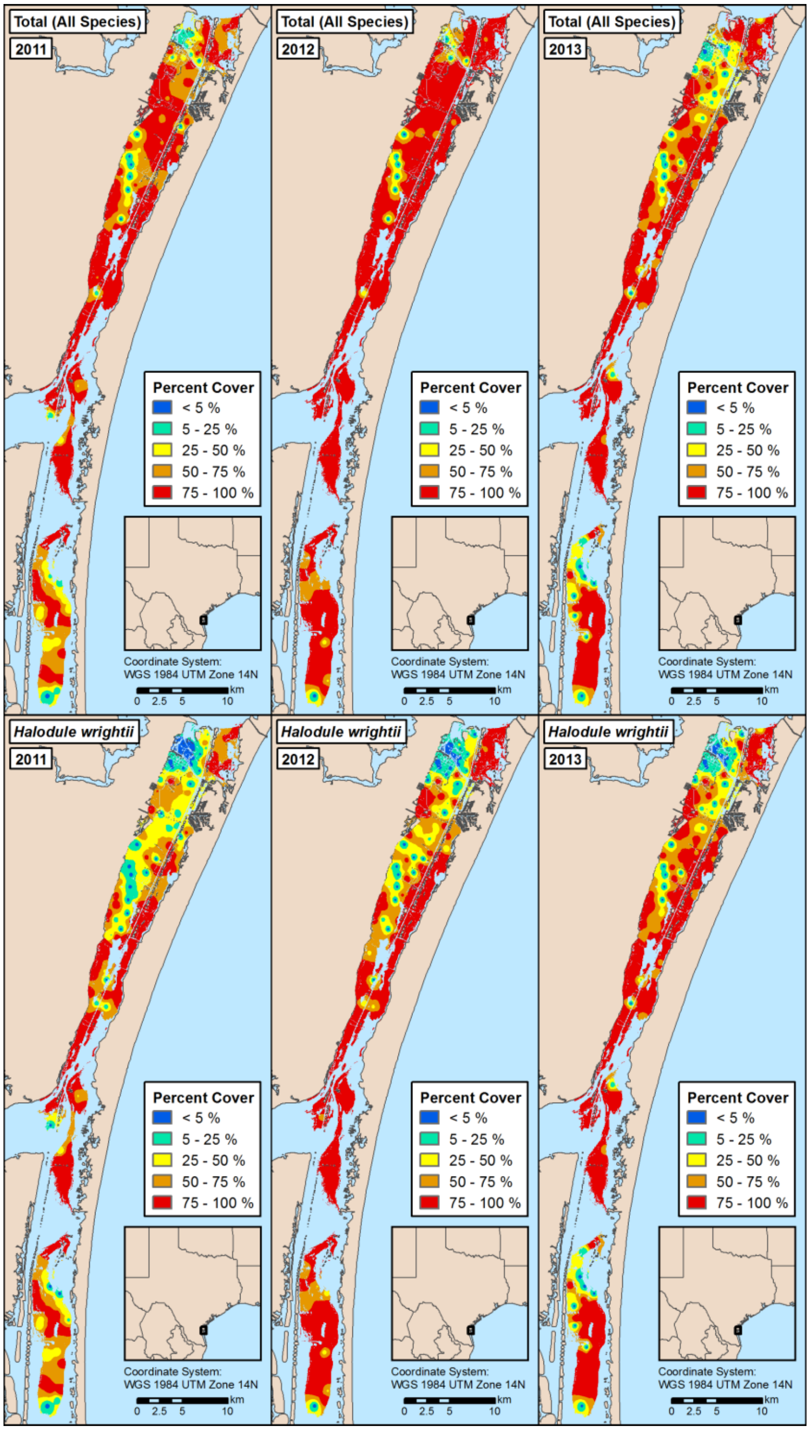

Figure B6. Seagrass percent cover in the Upper Laguna Madre from 2011-2013 for total (all species) seagrass and *Halodule wrightii*.

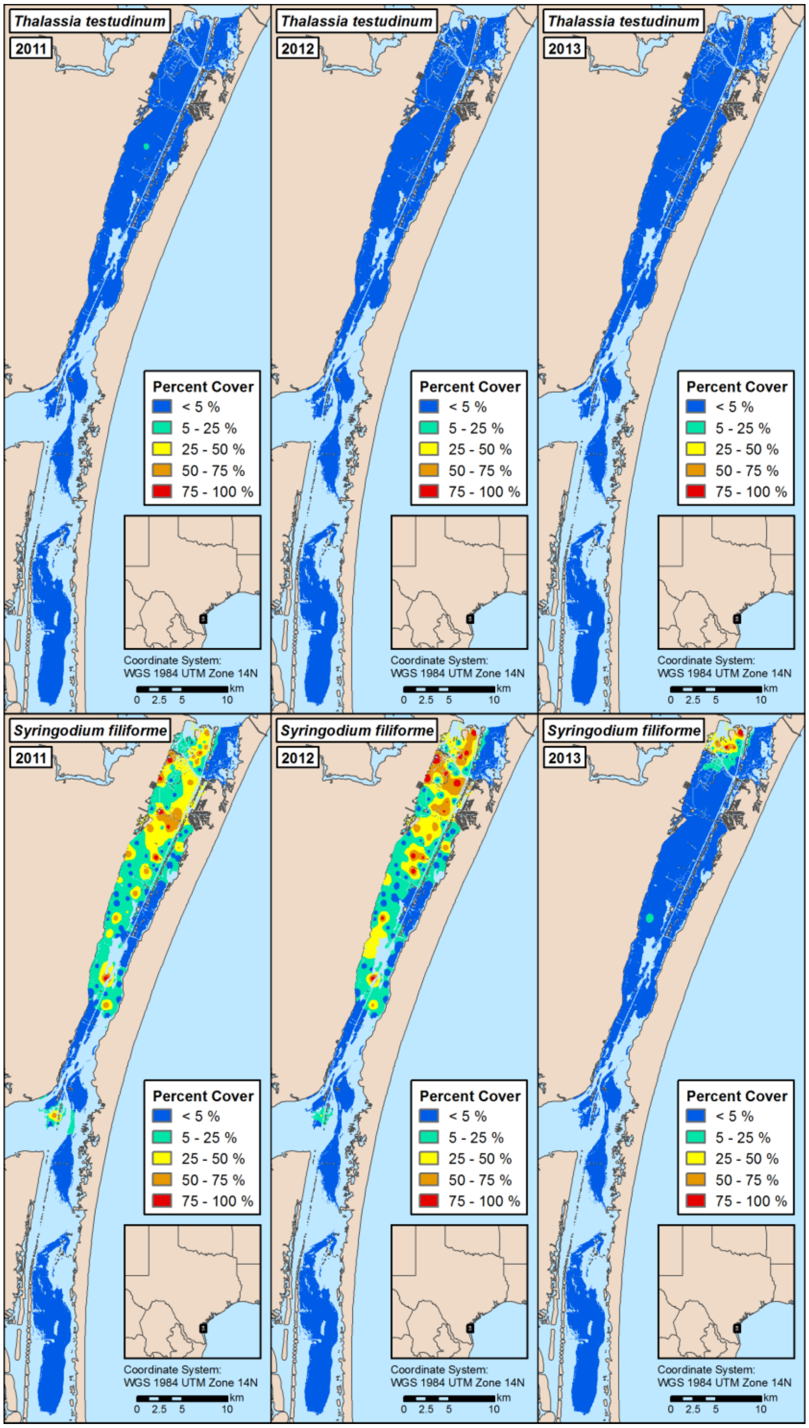

Figure B7. Seagrass percent cover in the Upper Laguna Madre from 2011-2013 for *Thalassia testudinum* and *Syringodium filiforme*.

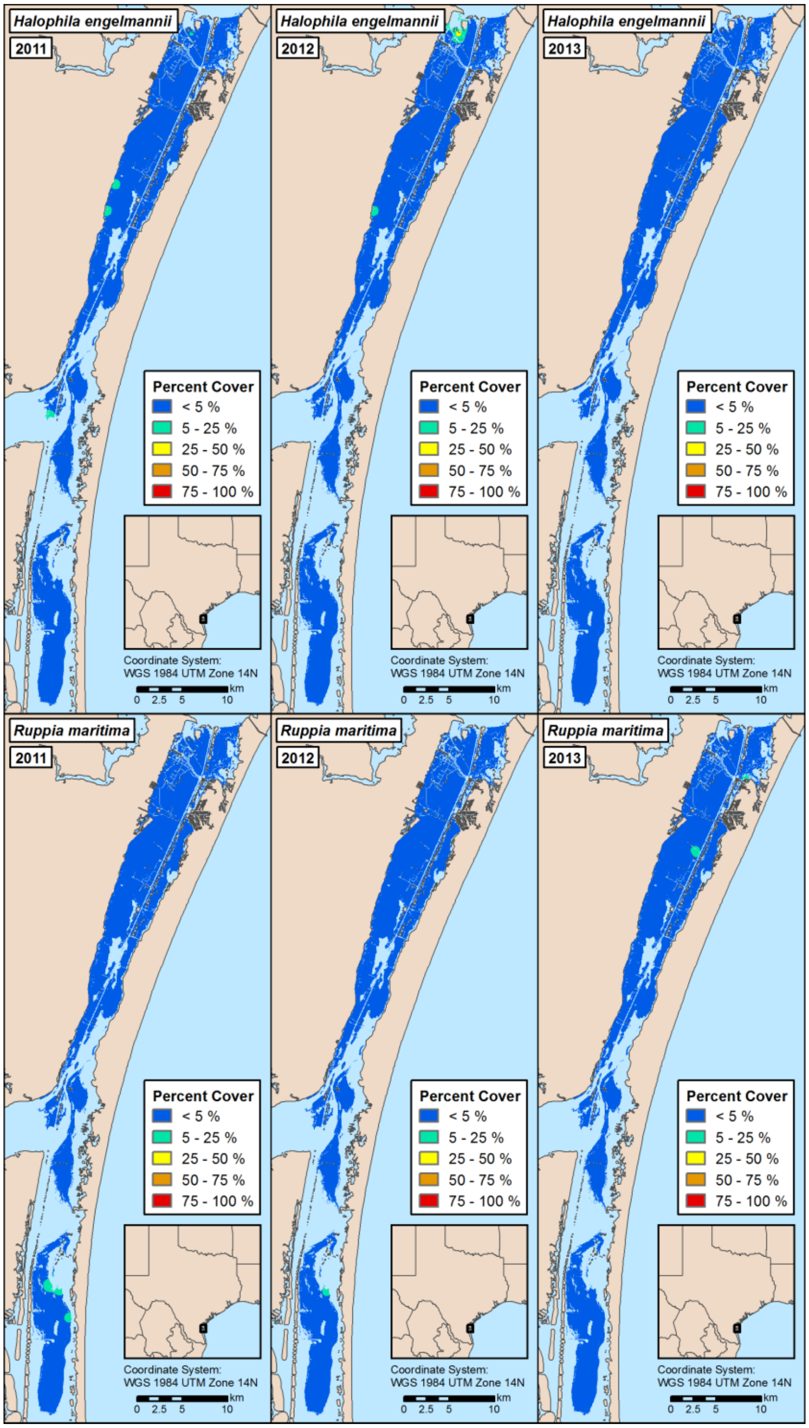

Figure B8. Seagrass percent cover in the Upper Laguna Madre from 2011-2013 for *Halophila engelmannii* and *Ruppia maritima*.

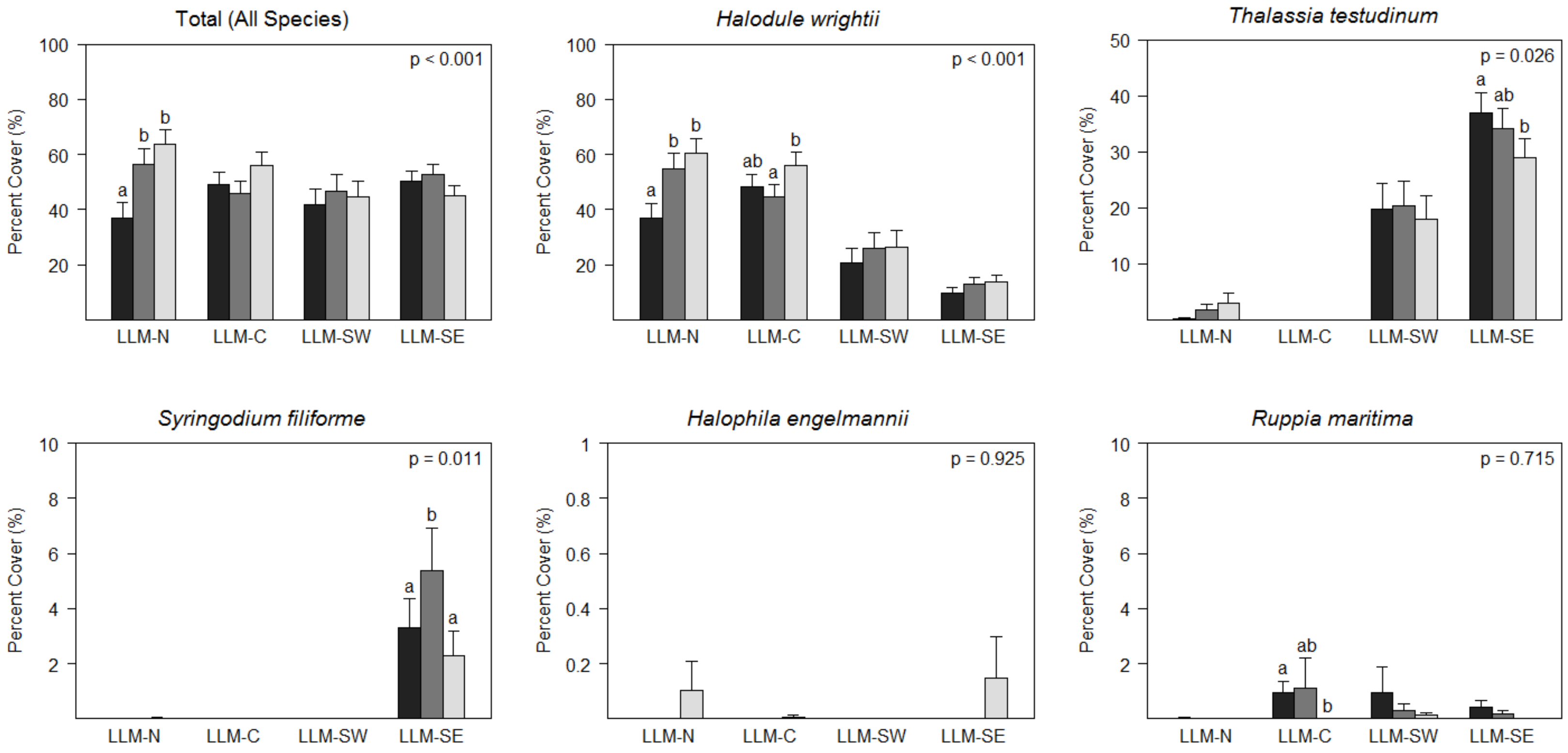

Figure B9. Seagrass percent cover (%; mean + standard error) for all subregions in the Lower Laguna Madre (LLM) region (LLM-N = LLM North, LLM-C = LLM Central, LLM-SW = LLM Southwest, LLM-SE = LLM Southeast) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs and Tukey multiple comparison tests were applied with subregion and year treated as fixed effects, and the interaction term is reported for each model. Significant differences from multiple comparison tests (α = 0.05) are listed (A, B, C) where present. Note the difference in y-axis ranges.

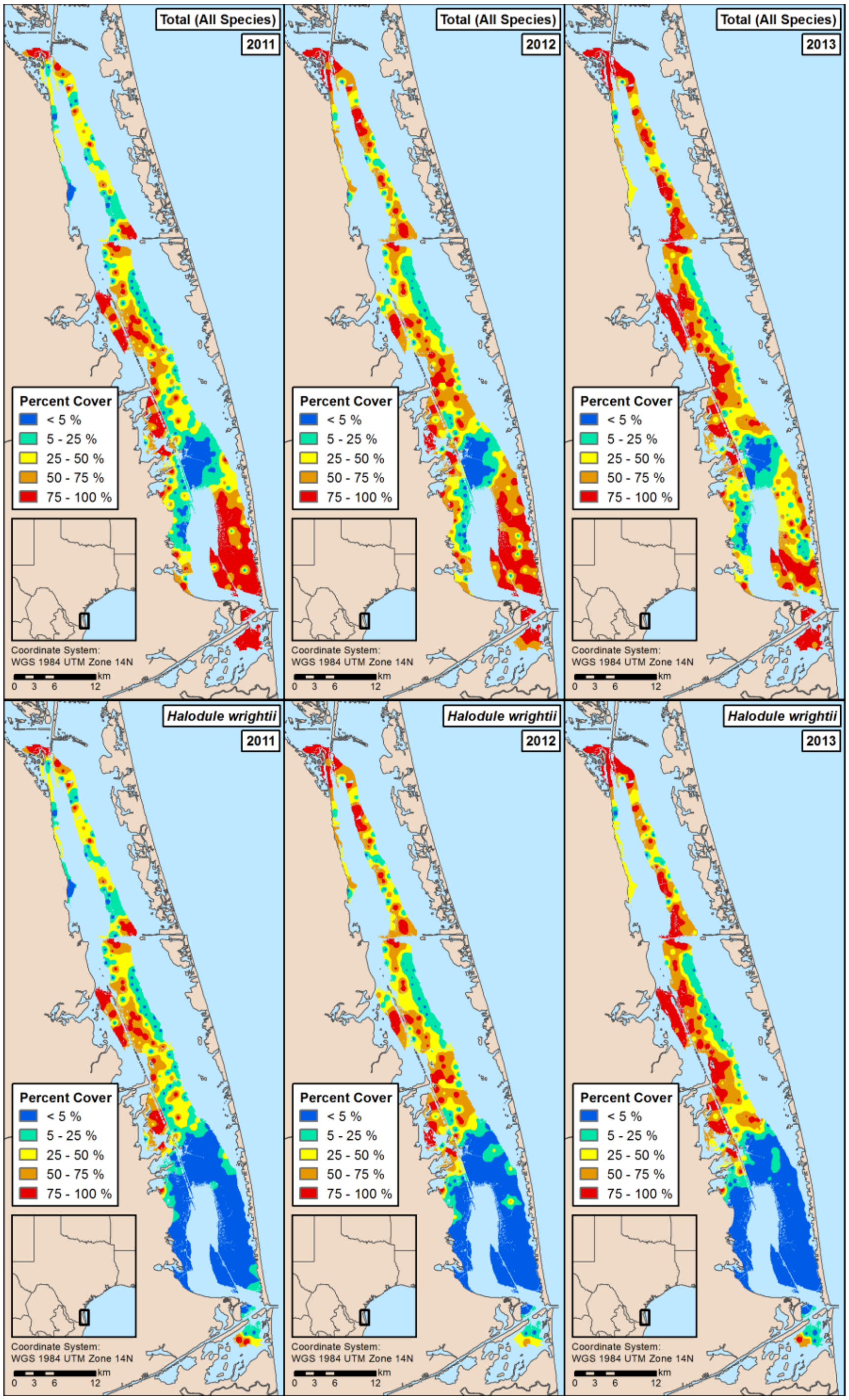

Figure B10. Seagrass percent cover in the Lower Laguna Madre from 2011-2013 for total (all species) seagrass and *Halodule wrightii*.

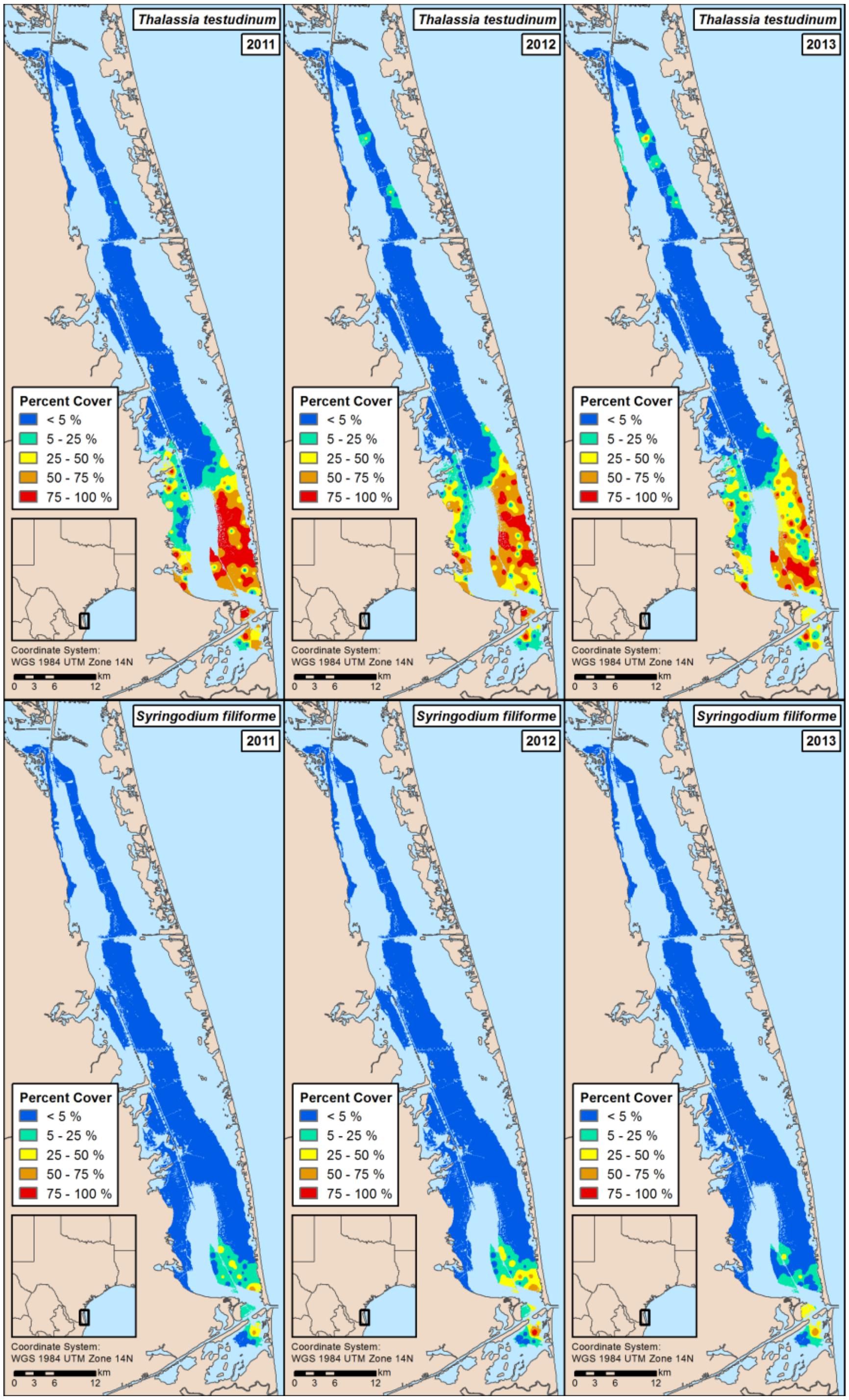

Figure B11. Seagrass percent cover in the Lower Laguna Madre from 2011-2013 for *Thalassia testudinum* and *Syringodium filiforme*.

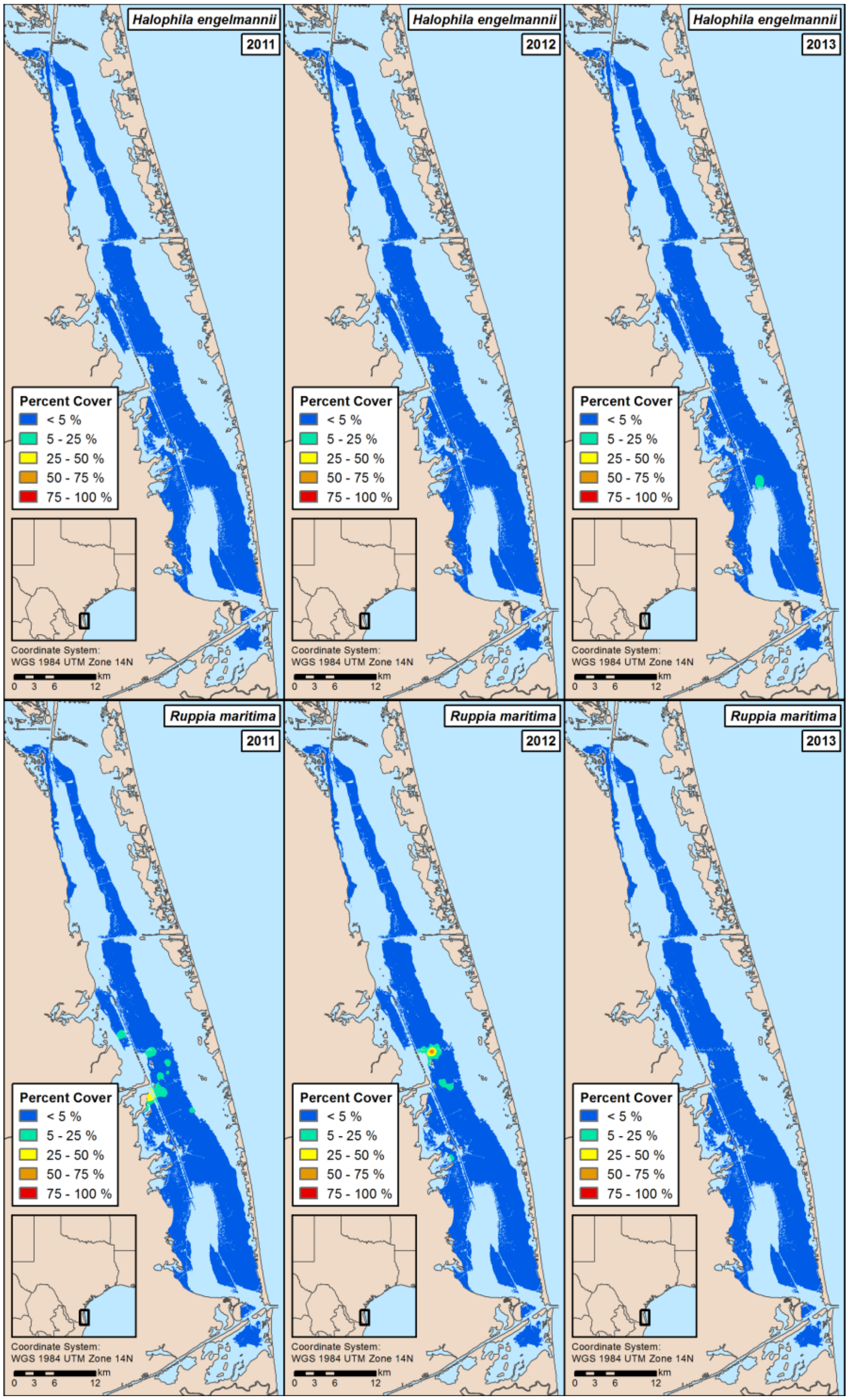

Figure B12. Seagrass percent cover in the Lower Laguna Madre from 2011-2013 for *Halophila engelmannii* and *Ruppia maritima*.

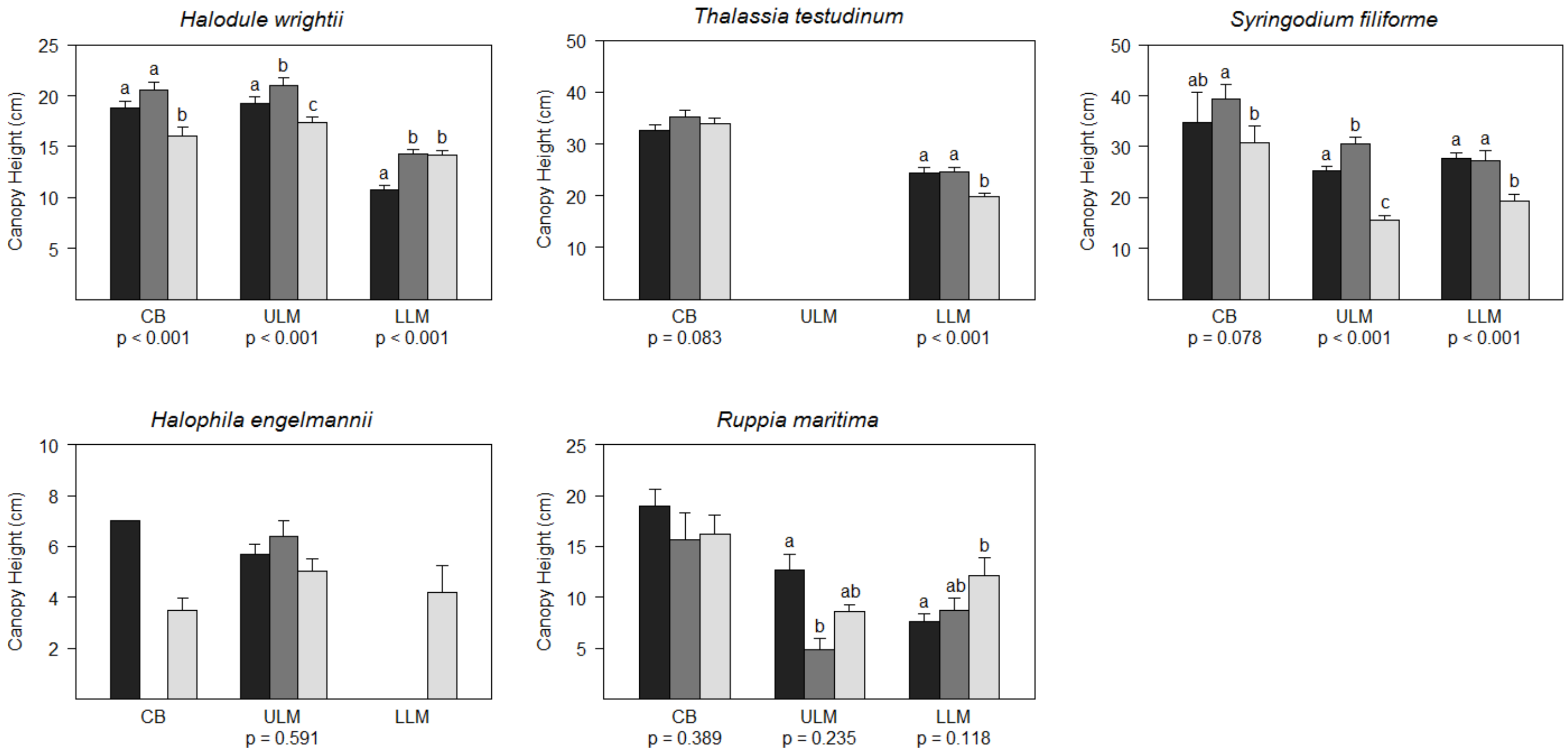

Figure B13. Seagrass canopy height (cm; mean + standard error) for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs testing the effect of year and Tukey multiple comparison tests were applied within each region for each species. Results from RM ANOVAs are listed below each region, and significant differences from multiple comparison tests ($\alpha = 0.05$) are listed (A, B, C) where present. Note the difference in y-axis ranges.

Appendix C – Tissue Elemental Composition and Stable Isotope Signatures

Table C1. Seagrass C:N:P molar ratios for *Halodule wrightii* in each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.).

		C:N			**C:P**			**N:P**			**$\delta^{13}C$**		
Region		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
CB	x̄	20.38	20.73	21.80	596.43	501.37	564.14	29.47	24.17	25.89	-10.42	-10.86	-10.24
	S.E.	0.27	0.37	0.38	13.93	23.39	23.25	0.70	0.97	0.99	0.14	0.25	0.24
	n	68	45	36	66	43	36	66	43	36	68	45	36
ULM	x̄	20.39	22.51	22.25	844.79	729.22	702.21	41.38	32.47	31.84	-11.07	-10.21	-11.00
	S.E.	0.23	0.31	0.22	19.76	23.20	19.02	0.85	0.99	0.95	0.12	0.14	0.15
	n	151	82	79	145	79	77	145	79	77	151	82	79
LLM	x̄	18.45	19.75	20.58	872.47	665.40	895.99	47.06	33.38	42.91	-9.66	-8.95	-9.39
	S.E.	0.19	0.26	0.34	20.17	24.80	36.69	0.92	1.05	1.35	0.11	0.13	0.15
	n	145	77	70	137	74	69	137	74	69	145	77	70

Table C1 (continued).

			$\delta^{15}N$	
Region		**2011**	**2012**	**2013**
CB	x̄	1.13	1.44	1.64
	S.E.	0.20	0.33	0.27
	n	68	45	36
ULM	x̄	1.38	2.56	2.25
	S.E.	0.11	0.13	0.14
	n	151	82	79
LLM	x̄	1.44	3.00	3.12
	S.E.	0.20	0.25	0.26
	n	145	77	70

Table C2. Seagrass C:N:P molar ratios for *Thalassia testudinum* in each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011, 2012 and 2013. Values are x̄ (mean) and standard error (S.E.).

		C:N			**C:P**			**N:P**			**δ^{13}C**		
Region		**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
CB	x̄	17.34	17.02	16.42	584.00	475.00	435.04	33.68	27.86	26.35	-8.60	-9.00	-8.74
	S.E.	0.23	0.29	0.28	19.94	14.21	22.65	1.04	0.61	1.03	0.23	0.21	0.20
	n	27	27	27	27	27	26	27	27	26	27	27	27
ULM	x̄	---	---	---	---	---	---	---	---	---	---	---	---
	S.E.	---	---	---	---	---	---	---	---	---	---	---	---
	n	---	---	---	---	---	---	---	---	---	---	---	---
LLM	x̄	18.47	17.70	16.75	671.11	631.25	657.27	36.28	35.56	38.90	-8.54	-8.48	-8.58
	S.E.	0.26	0.37	0.27	26.42	27.75	24.36	1.31	1.37	1.12	0.13	0.12	0.13
	n	64	65	65	64	65	64	64	65	64	64	65	65

Table C2 (continued).

			$\delta^{15}N$	
Region		**2011**	**2012**	**2013**
CB	x̄	3.15	3.33	3.77
	S.E.	0.26	0.19	0.20
	n	27	27	27
ULM	x̄	---	---	---
	S.E.	---	---	---
	n	---	---	---
LLM	x̄	2.73	2.75	3.08
	S.E.	0.24	0.17	0.20
	n	64	65	65

Table C3. Repeated measures ANOVA table for the effect of year on seagrass C:N:P molar ratios and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) signatures for *Halodule wrightii* in each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences ($\alpha = 0.05$) are denoted in bold.

	C:N			**C:P**			**N:P**			**$\delta^{13}C$**		
Region	**df**	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**
CB	2, 79	4.48	**0.0144**	2, 77	8.86	**0.0003**	2, 77	12.78	< **0.0001**	2, 79	4.16	**0.0191**
ULM	2, 158	24.43	< **0.0001**	2, 151	23.02	< **0.0001**	2, 151	55.80	< **0.0001**	2, 158	21.93	< **0.0001**
LLM	2, 145	30.54	< **0.0001**	2, 137	58.36	< **0.0001**	2, 137	77.55	< **0.0001**	2, 145	26.88	< **0.0001**

Table C3 (continued).

	$\delta^{15}N$		
Region	**df**	**F**	**p**
CB	2, 79	3.94	**0.0233**
ULM	2, 158	30.32	< **0.0001**
LLM	2, 145	51.39	< **0.0001**

Table C4. Repeated measures ANOVA table for the effect of year on seagrass C:N:P molar ratios and stable isotope (δ^{13}C and δ^{15}N) signatures for *Thalassia testudinum* in each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences ($\alpha = 0.05$) are denoted in bold.

	C:N			**C:P**			**N:P**			**δ^{13}C**		
Region	**df**	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**
CB	2, 52	3.40	**0.0410**	2, 51	18.58	**< 0.0001**	2, 51	18.76	**< 0.0001**	2, 52	2.18	0.1229
ULM	---	---	---	---	---	---	---	---	---	---	---	---
LLM	2, 122	11.39	**< 0.0001**	2, 121	2.90	0.0591	2, 121	6.72	**0.0017**	2, 122	0.55	0.5808

Table C4 (continued).

	δ^{15}N		
Region	**df**	**F**	**p**
CB	2, 52	4.48	**0.0161**
ULM	---	---	---
LLM	2, 122	2.36	0.0985

Table C5. Post hoc Tukey multiple comparison tests for seagrass C:N:P molar ratio and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) signature changes in *Halodule wrightii* over time for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences ($\alpha = 0.05$) are denoted in bold.

		C:N	**C:P**	**N:P**	**$\delta^{13}C$**	**$\delta^{15}N$**
CB	2011-2012	0.707	< **0.001**	< **0.001**	0.084	0.395
	2011-2013	**0.008**	0.325	**0.006**	0.647	**0.014**
	2012-2013	0.098	**0.049**	0.335	**0.017**	0.263
ULM	2011-2012	< **0.001**	< **0.001**	< **0.001**	< **0.001**	< **0.001**
	2011-2013	< **0.001**	< **0.001**	< **0.001**	0.945	< **0.001**
	2012-2013	0.745	0.670	0.839	< **0.001**	0.054
LLM	2011-2012	< **0.001**	< **0.001**	< **0.001**	< **0.001**	< **0.001**
	2011-2013	< **0.001**	0.534	**0.002**	**0.004**	< **0.001**
	2012-2013	**0.029**	< **0.001**	< **0.001**	< **0.001**	0.991

Table C6. Post hoc Tukey multiple comparison tests for seagrass C:N:P molar ratio and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) signature changes in *Thalassia testudinum* over time for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre). Significant differences ($\alpha = 0.05$) are denoted in bold.

		C:N	**C:P**	**N:P**	**$\delta^{13}C$**	**$\delta^{15}N$**
CB	2011-2012	0.647	< **0.001**	< **0.001**	0.094	0.675
	2011-2013	**0.028**	< **0.001**	< **0.001**	0.671	**0.010**
	2012-2013	0.214	0.111	0.259	0.437	0.098
ULM	2011-2012	---	---	---	---	---
	2011-2013	---	---	---	---	---
	2012-2013	---	---	---	---	---
LLM	2011-2012	0.095	0.052	0.746	0.737	1.000
	2011-2013	< **0.001**	0.807	**0.016**	0.962	0.145
	2012-2013	**0.022**	0.199	**0.002**	0.570	0.147

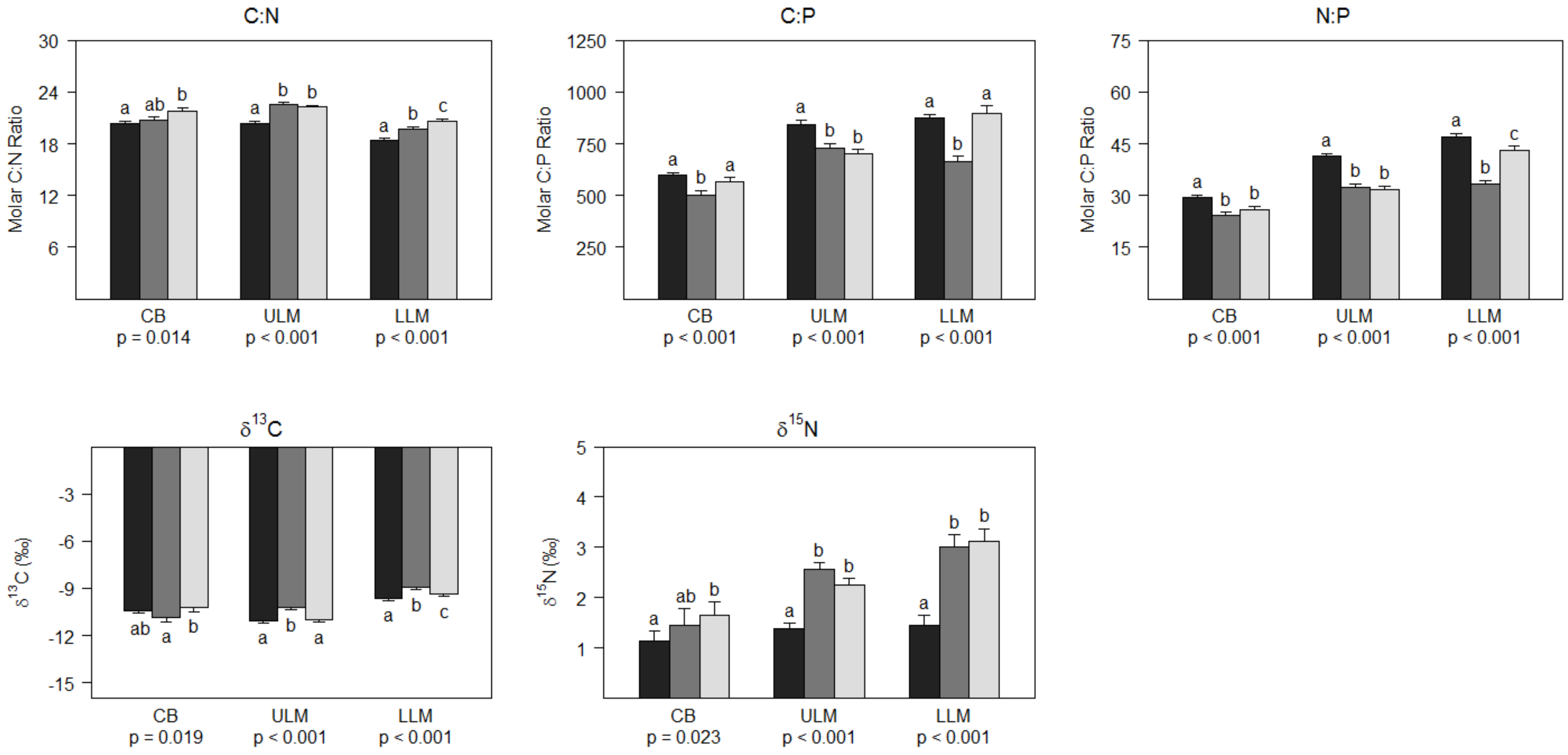

Figure C1. *Halodule wrightii* leaf C:N, C:P, and N:P molar ratios and δ^{13}C and δ^{15}N signatures (‰; mean + standard error) for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs testing the effect of year and Tukey multiple comparison tests were applied within each region for each species. Results from RM ANOVAs are listed below each region, and significant differences from multiple comparison tests ($\alpha = 0.05$) are listed (A, B, C) where present. Note the difference in y-axis ranges.

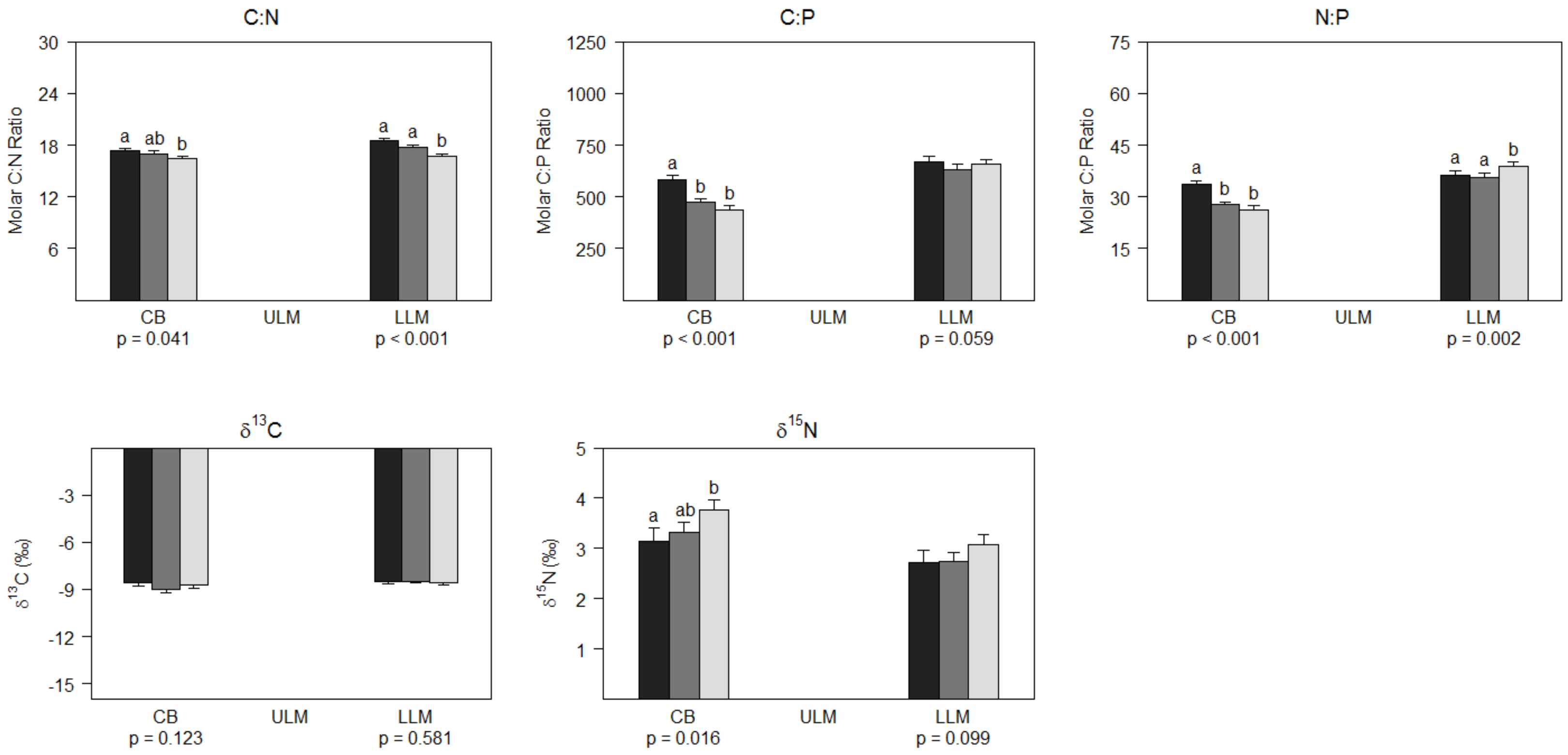

Figure C2. *Thalassia testudinum* leaf C:N, C:P, and N:P molar ratios and δ^{13}C and δ^{15}N signatures (‰; mean + standard error) for each region (CB = Coastal Bend, ULM = Upper Laguna Madre, LLM = Lower Laguna Madre) in 2011 (dark gray), 2012 (medium gray), and 2013 (light gray). RM ANOVAs testing the effect of year and Tukey multiple comparison tests were applied within each region for each species. Results from RM ANOVAs are listed below each region, and significant differences from multiple comparison tests ($\alpha = 0.05$) are listed (A, B, C) where present. Note the difference in y-axis ranges.

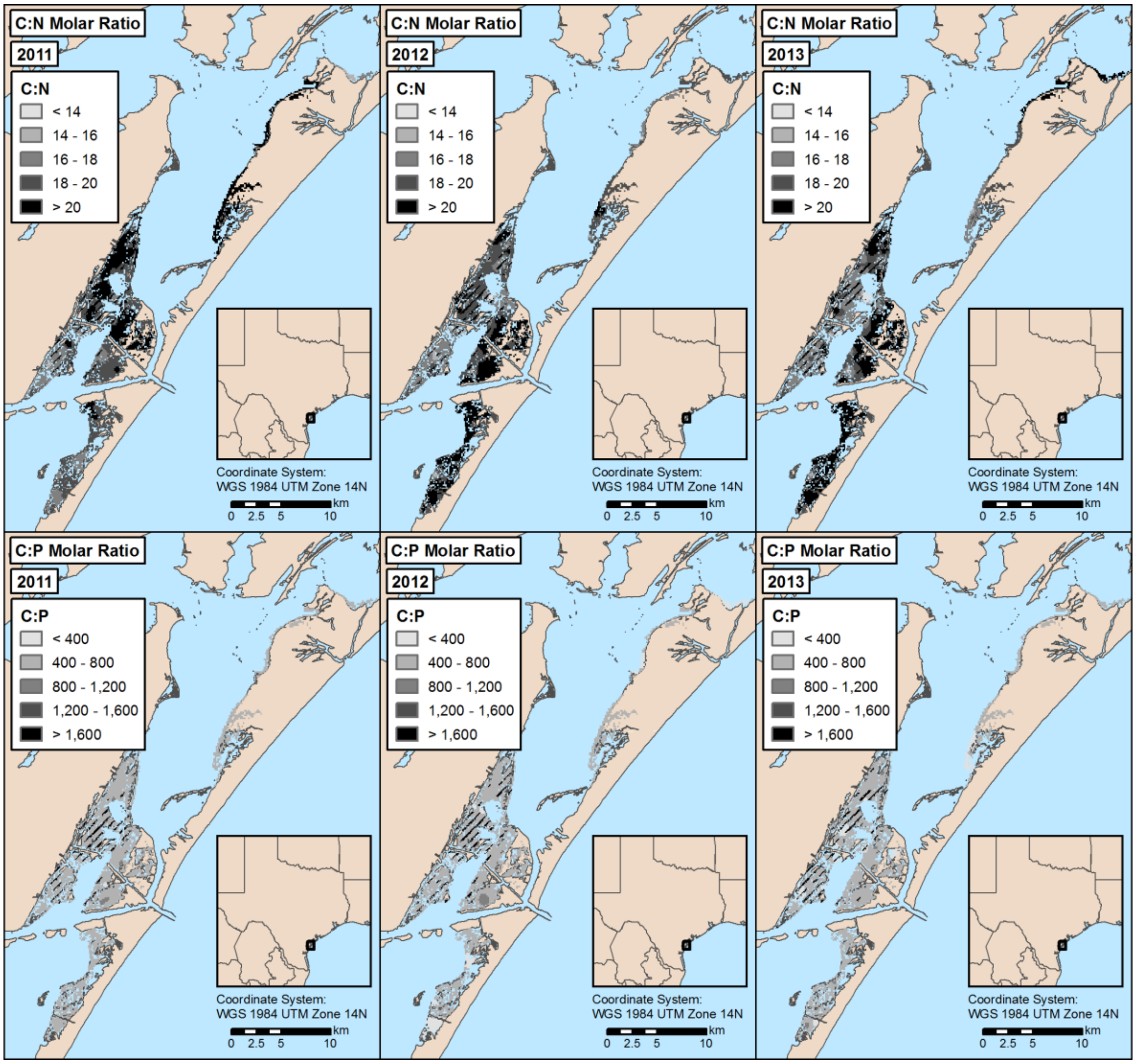

Figure C3. C:N and C:P molar ratios for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in the Coastal Bend from 2011-2013.

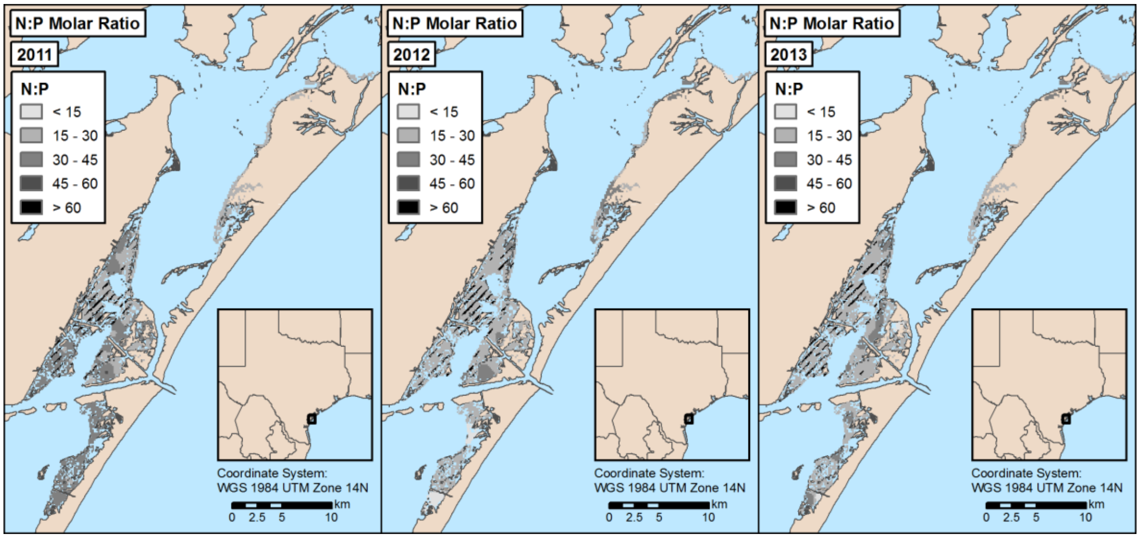

Figure C4. N:P molar ratios for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in the Coastal Bend from 2011-2013.

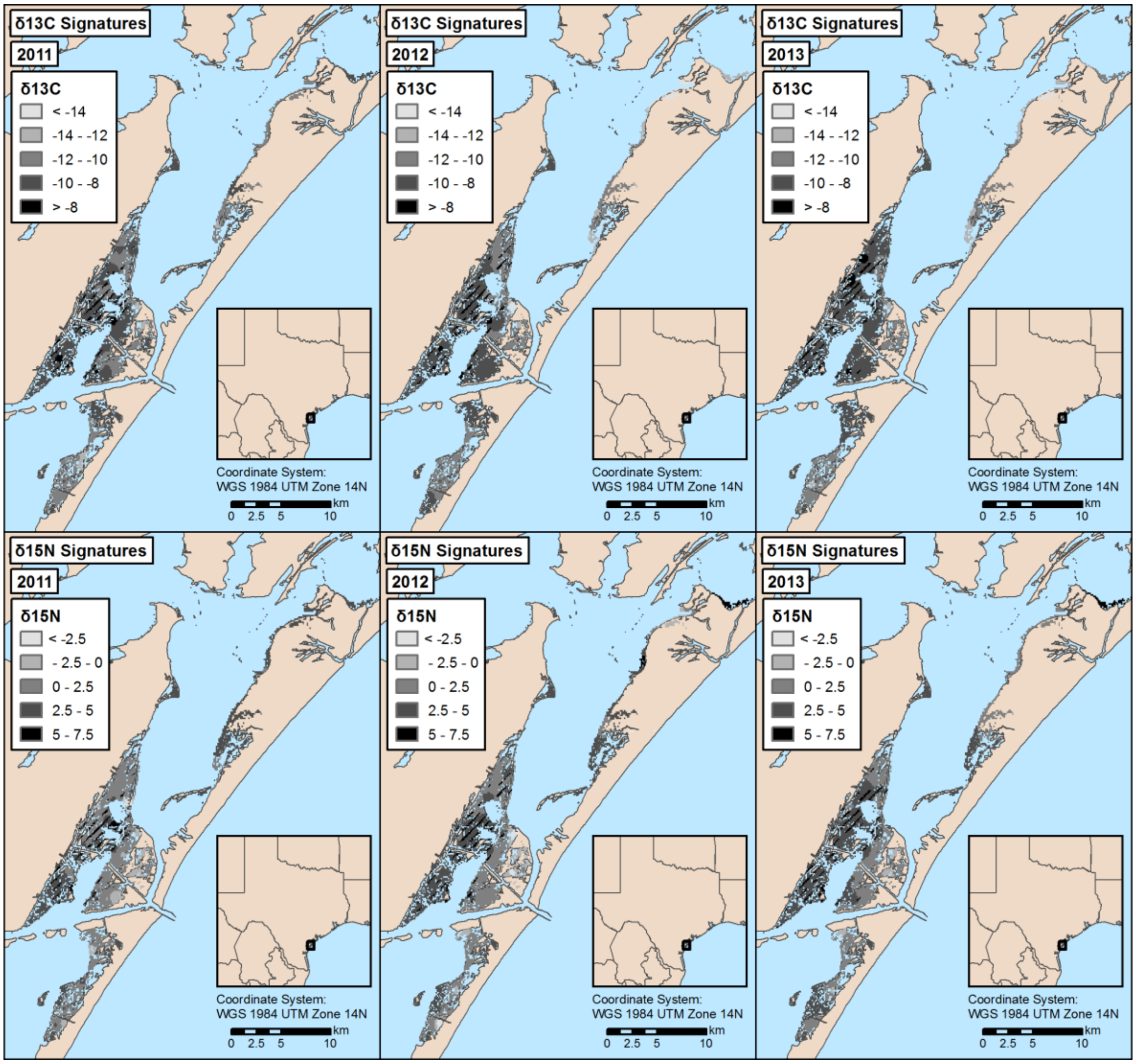

Figure C5. δ^{13}C signatures and δ^{15}N signatures for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in the Coastal Bend from 2011-2013.

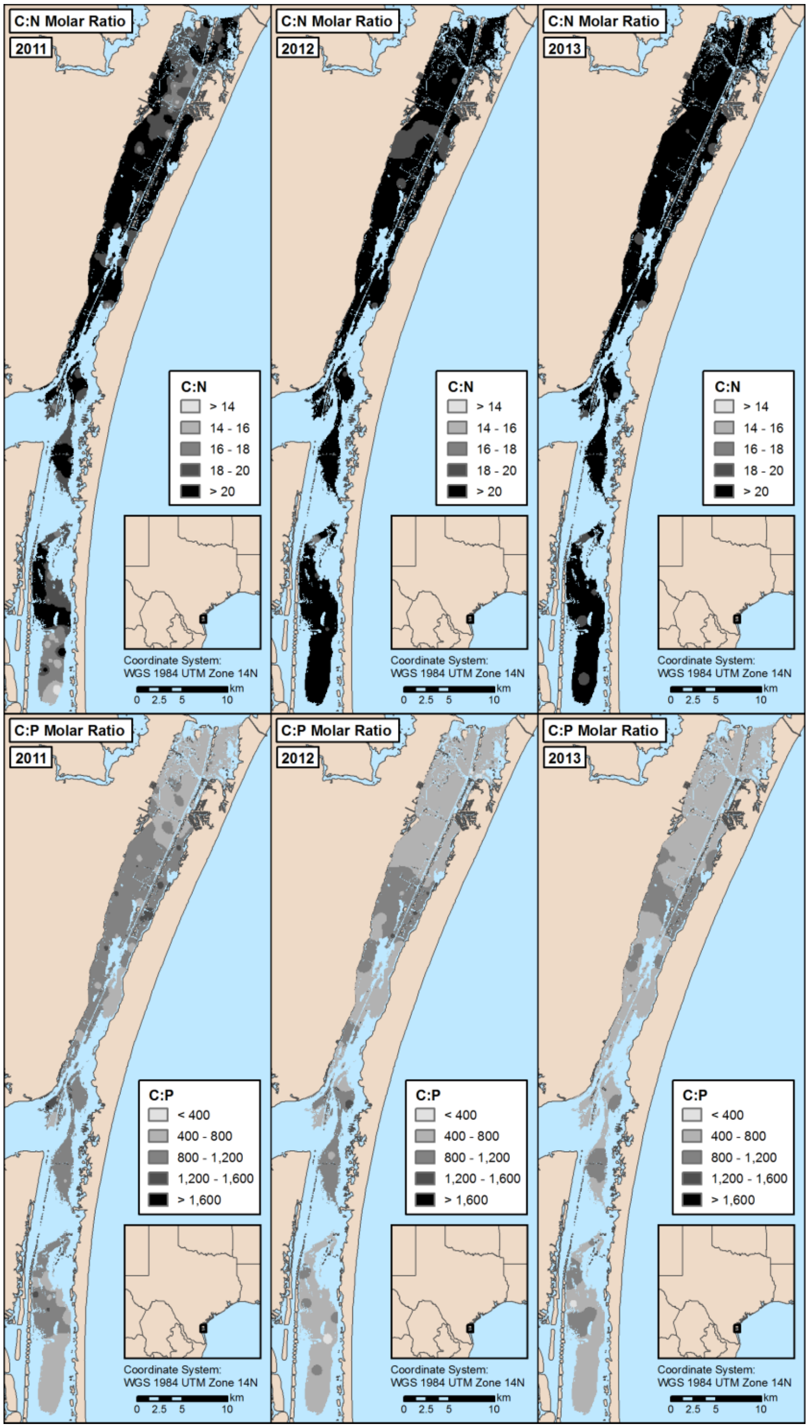

Figure C6. C:N and C:P molar ratios for *Halodule wrightii* in Upper Laguna Madre from 2011-2013.

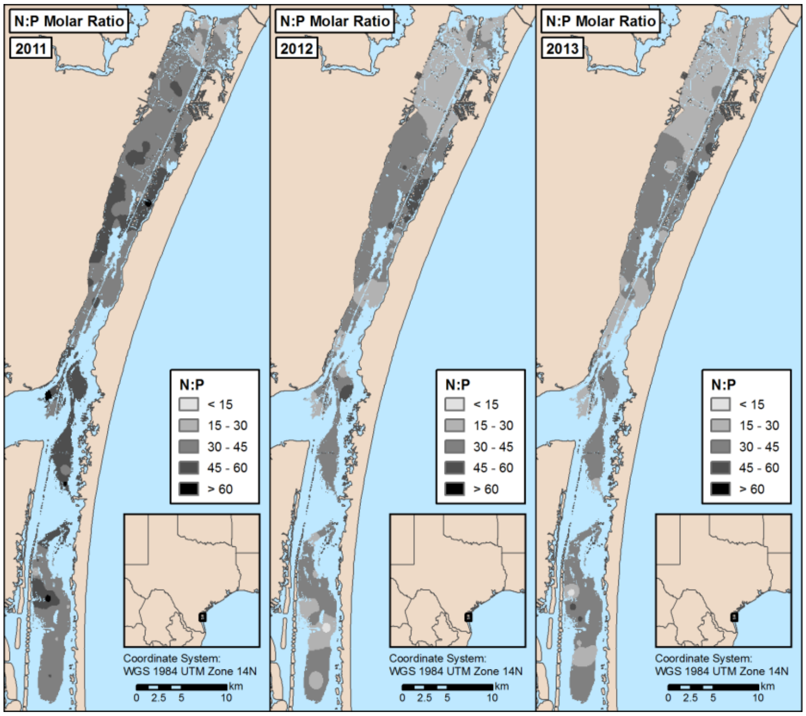

Figure C7. N:P molar ratios for *Halodule wrightii* in Upper Laguna Madre from 2011-2013.

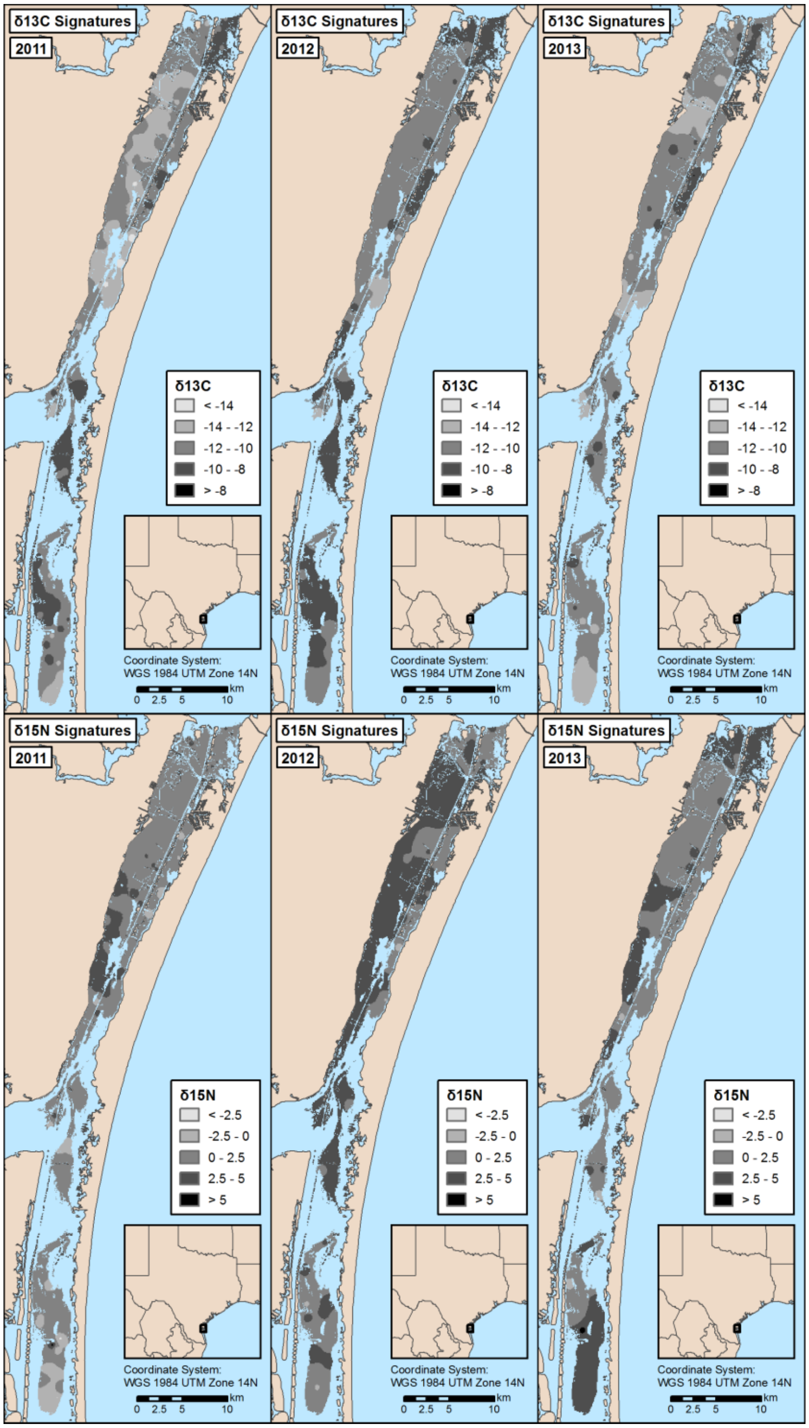

Figure C8. $\delta^{13}C$ and $\delta^{15}N$ signatures for *Halodule wrightii* in Upper Laguna Madre from 2011-2013.

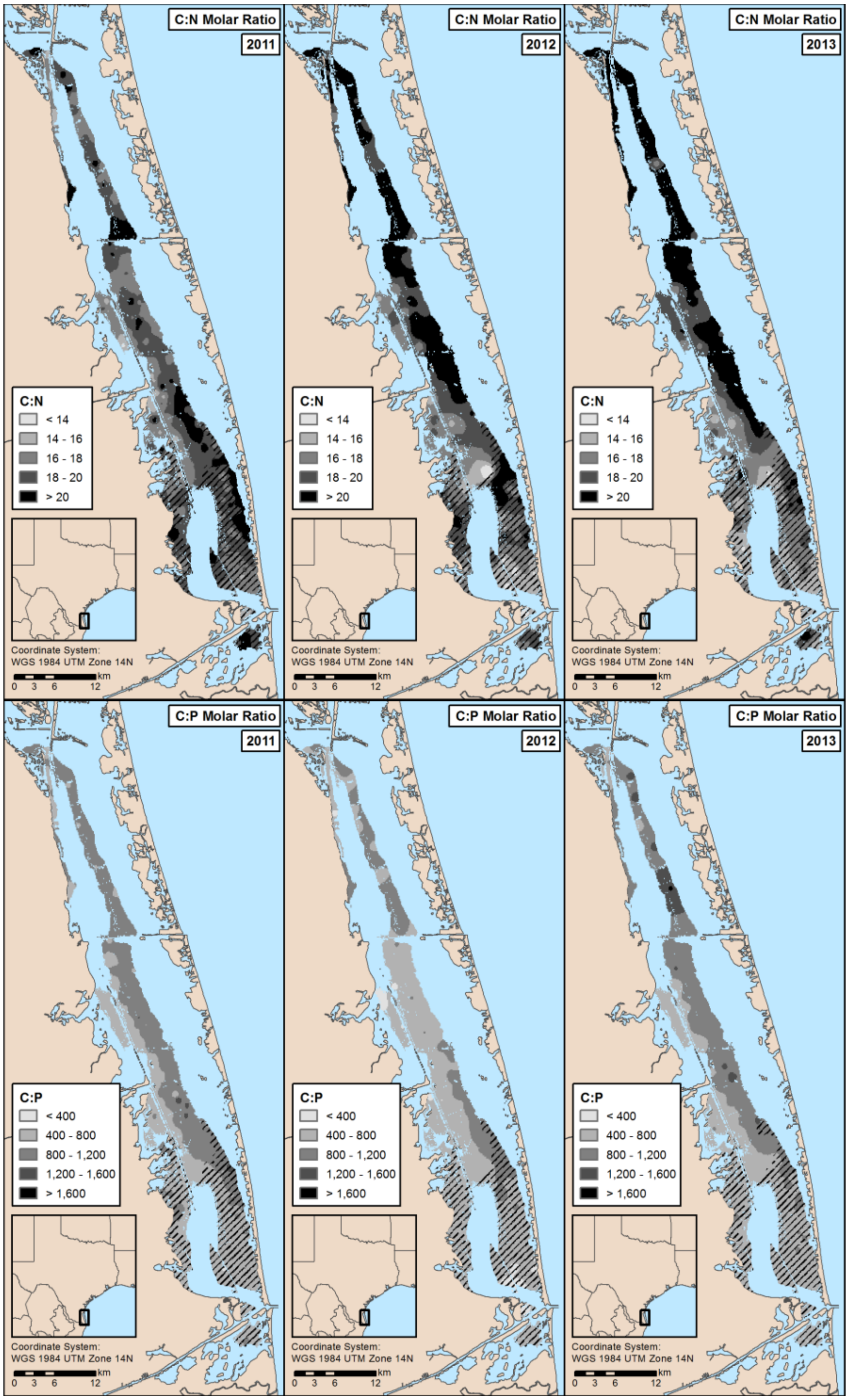

Figure C9. C:N and C:P signatures for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in Lower Laguna Madre from 2011-2013.

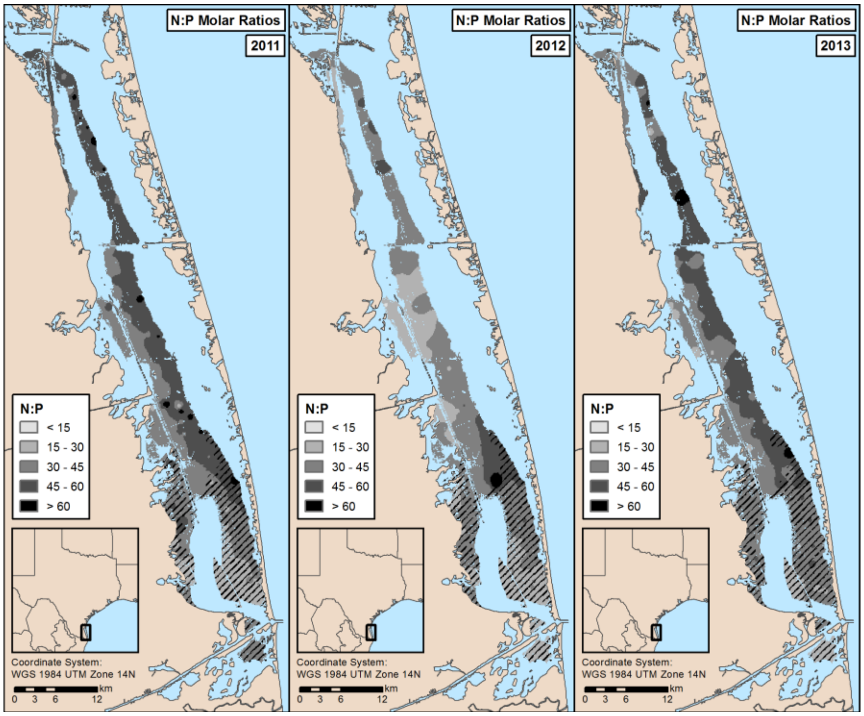

Figure C10. N:P molar ratios for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in Lower Laguna Madre from 2011-2013.

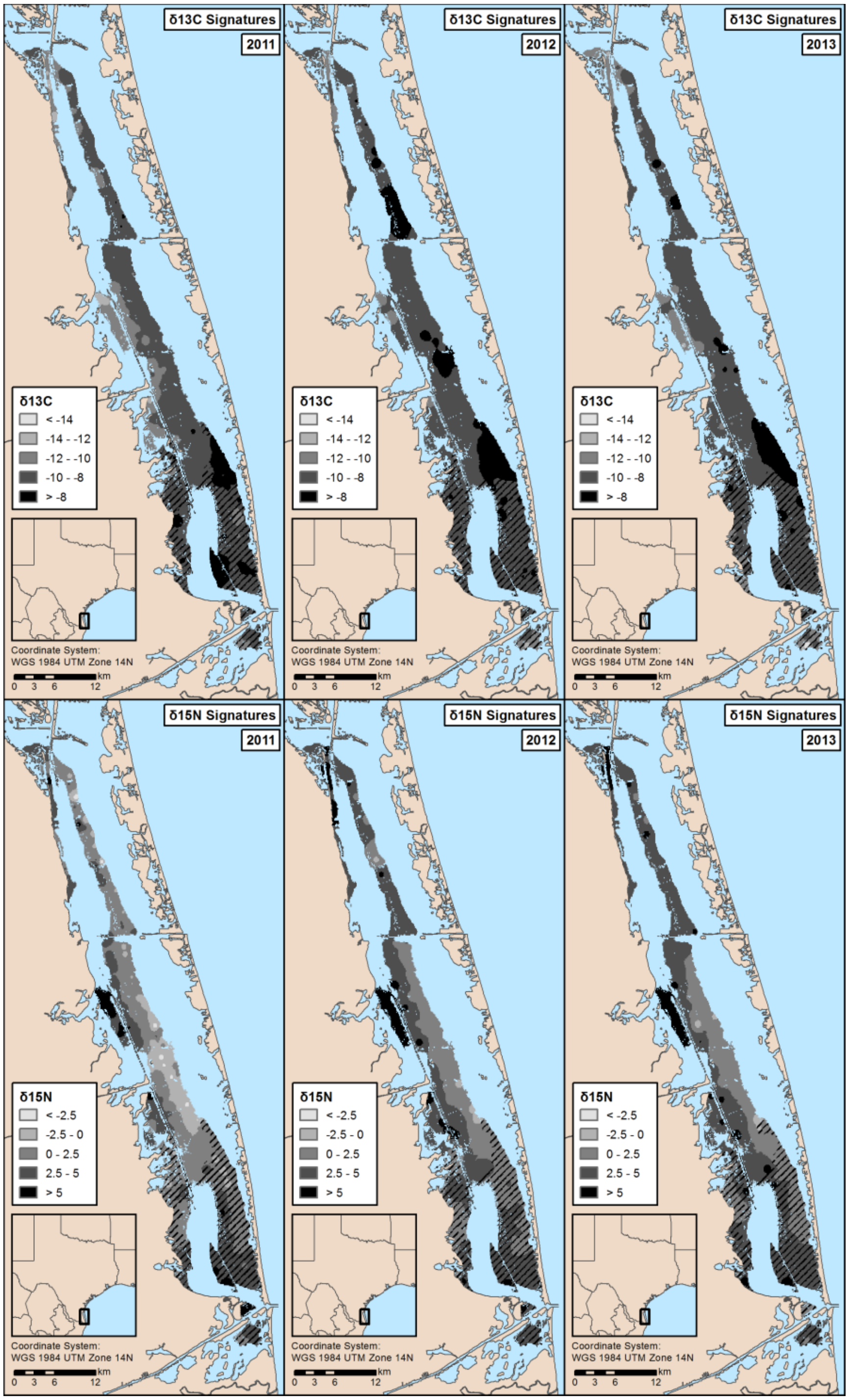

Figure C11: δ^{13}C and δ^{15}N signatures for *Halodule wrightii* and *Thalassia testudinum* (indicated with diagonal lines) in Lower Laguna Madre from 2011-2013.

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