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Shifting Niche Space in Coastal Landscapes: Spatio-temporal Patterns Driving Submerged Aquatic Vegetation across the Northern Gulf of Mexico

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SHIFTING NICHE SPACE IN COASTAL LANDSCAPES: SPATIO-TEMPORAL PATTERNS DRIVING SUBMERGED AQUATIC VEGETATION ACROSS THE NORTHERN GULF OF MEXICO

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ABSTRACT

Identifying distributions of submerged aquatic vegetation (SAV) across the northern Gulf of Mexico (NGOM) coastal landscape necessitates describing ecological processes in estuarine gradients. SAV assemblages are ecological indicators of aquatic ecosystem health; spatial and temporal distributions are strongly correlated to environmental conditions. Many wildlife species, including waterfowl, are dependent on SAV and seeds in NGOM coastal marshes for food and habitat. To understand SAV distributions at multiple spatial and temporal scales a multi-tiered project was designed to collect SAV presence, species assemblage, and cover data, and cores to describe seed food. The first tier sampled inter-annually in the growing seasons 2013-2015 from Mobile Bay, Alabama to San Antonio Bay, Texas. The second tier sampled seasonally, every 6-8 weeks in 2015, in Barataria Basin, Louisiana. These data were used to characterize SAV distributions and to drive a spatial species distribution model (SDM) in coastal Louisiana.

Across the NGOM landscape, SAV presence, percent cover, species assemblages, and seed resources varied across marsh zones and regions. There was no temporal effect at this spatial scale. The patterns of food seed and SAV distributions were almost entirely driven by regionally specific patterns in environmental conditions (i.e., salinity and depth). The SDM linked SAV occurrence to environmental conditions and identified winter mean salinity, turbidity, and exposure as significant predictors for SAV occurrence. Increases in these parameters were evident in saline marsh zones, which had a low likelihood of SAV occurrence. The seasonal study in Barataria Basin showed a significant interaction between SAV and invasive water hyacinth, as water hyacinth increased in cover during the summer season, SAV cover declined. Results indicate that SAV presence, cover, and species assemblages are seasonally mediated and spatially differentiated by environmental conditions in estuaries. These ecological patterns in turn affect the availability of potential food resources across estuarine gradients. Understanding region and estuary-specific gradients over time and space defines the fundamental and realized ecological niche space for SAV assemblages. The identification of this space illustrates how ecological patterns may influence associated species within the community, and provides a benchmark to assess future changes in these critical habitats.

GENERAL INTRODUCTION

In ecological communities species-level responses are induced via the direct link from the environment to the organism. In coastal ecosystems, the environment to organism link is spatially and temporally dynamic, as eco-hydrological factors often shift rapidly and significantly in response to climate, habitat management, and anthropogenic activities (Timchenko 2016). As coastal ecosystems respond to changing environmental conditions, communities, all species that interact within an area, will be reorganized as shifts occur in species distributions and assemblages, and the outcomes of multi-species interactions change. Community-level change may be driven by the ecological response of one key species, and has the potential to alter the entire trophic structure of a coastal ecosystem (Harley et al., 2006). Habitats and the species that occupy them are inextricably connected. Understanding the processes that drive species-level response to changing habitat conditions can help to describe the state of the ecosystem, particularly across aquatic landscapes.

Within a coastal ecosystem, a variety of habitat types (marshes, tidal creeks, rivers, ponds, bays, etc.) exchange energy and support unique populations of wildlife. Shallow aquatic habitats that support vegetation in these ecosystems are especially unique; submerged aquatic vegetation (SAV) assemblages, different species that have similar ecological requirements, are at the interface between coastal emergent wetlands and coastal marine habitat. SAV exists in the ecotone between the land and the ocean, and responds rapidly to changes in the abiotic environment as hydrologic parameters are altered (Janauer 1998; Jennerjahn et al., 2012). Because of their physical location and tightly coupled relationship to the aquatic conditions, SAV distribution and species assemblages characterize the conditions of the habitat they occupy, and indicate the "health" of the ecosystem (Schneider et al., 2016; Søndergaard et al., 2010.

SAV spends the entirety of its life cycle, with the possible exception of flowering, beneath the surface of the water (Cronk & Fennesy, 2001), which is a growth habit that links SAV closely to hydrologic factors. SAV is widely distributed across the salinity gradient in northern Gulf of Mexico (NGOM) estuaries (Merino et al., 2005; Merino et al., 2009). The distribution and composition of SAV in estuarine habitats can be coarsely linked to the salinity regime over the growing season (Cho et al., 2016; Doering et al., 2002; Porrier et al., 2010). However, it is the interaction of spatial and temporal drivers, including light penetration, turbidity, water quality, and exposure to waves and currents within coastal estuaries that act in concert to locally define SAV presence, cover, and species assemblages (Cho & Porrier, 2005; Palinkas and Koch, 2012). As individual SAV species and assemblages respond differently to these environmental conditions, reflected as presence and cover, unique SAV distributions emerge across estuarine habitats.

The NGOM is composed of multiple ecological regions where hydrology, geology, and climate patterns are the result of spatially distinct processes (Omernik and Griffith, 2014; USEPA, 2013). The Mississippi River Delta is the largest, and most well-studied estuary in the NGOM, but is bounded by many other ecologically important estuaries. Estuaries are characterized by spatial gradients created by variable environmental conditions, largely related to salinity, turbidity, nutrients, and exposure to currents, tides, and waves (Cloern et al., 2014; Das et al., 2012; Moyle et al., 2010; Seers and Shears, 2015). Across the NGOM coastal landscape, marsh zone classifications determined from long-term emergent vegetation are generally used to describe wetland habitats (Chabreck, 1970; Penfound and Hathaway, 1938; Enwright et al., 2014; Sasser et al., 2014; Visser et al., 1998). In the absence of more specific habitat descriptions

of permanently flooded, aquatic habitats, SAV assemblages are generally grouped according to emergent marsh classification types. These distinctions are referred to hereafter as marsh zones (fresh, intermediate, brackish, and saline) to reflect this extension of the marsh type into aquatic habitats without long-term emergent vegetation.

Classifying coastal habitats has many practical applications in research and management, not the least of which is associating a habitat value to wildlife populations within each marsh zone. The coastal wetlands and aquatic habitats of the NGOM are critical to many different wildlife species (Castellanos and Rozas, 2001; Hitch et al., 2011; Kanouse et al., 2006), and are especially important to wintering waterfowl (Brasher et al., 2012). Coastal wetland managers actively manage water levels and salinity to maintain suitable conditions for SAV and other aquatic plants to maximize habitat and food availability for wintering waterfowl (Merino et al., 2005). Wintering waterfowl forage extensively on SAV roots, shoots, and seeds to increase carbohydrate stores during the stressful winter months (Anderson and Low, 1976; Chamberlain, 1959; Sponberg and Lodge, 2005; Walley, 2016). Habitat area objectives used by coastal wildlife and waterfowl managers to identify hectares needed to support waterfowl populations are largely based on the associated habitat value determined by biomass of potential food resources, or energy density. These values are assigned based on emergent marsh zone classifications for management purposes (Brasher et al., 2012). Spatial and temporal characterization of SAV and seed resources that reflects both emergent and submergent resources, extending estimates to marsh zones, will refine habitat value estimates for waterfowl.

As climate and landscape change alter the coastal landscape of the NGOM, the importance of SAV habitats becomes more significant. Although the precise rates of water level increase are uncertain, research is generally in agreement that sea levels will rise significantly in the future, likely up to1 meter above current water levels by 2100 (DeMarco et al., 2012). Sea level rise will inundate some coastal lands, and along with initiating wetland migration inland, will convert wetland habitat into open water, and expand the potential habitat for SAV establishment (CPRA, 2017; Sheets et al., 2012). Shallow aquatic habitats with SAV will provide enhanced ecosystem benefits when compared to bare benthic floor, and the protection and restoration of SAV beds will be increasingly valued in coastal restoration efforts. The refined identification of SAV assemblages and distribution within coastal marsh zones can be indicative of environmental change on multiple spatial and temporal scales.

This research is an effort to understand and describe SAV distribution across the NGOM. Once quantified, the SAV assemblages, presence, and cover can in turn describe the conditions unique across estuaries, and between regions across the coastal landscape. Because SAV are so closely tied to their environment, the identification of SAV patterns goes beyond a vegetation survey, and characterizes the nature of the aquatic habitat, and its associated value to the rest of the ecological community.

Questions/objectives for each chapter are described below:

Chapter 1: More than a marsh zone: How regional characteristics create unique estuarine gradients and submerged aquatic vegetation (SAV) habitats across the northern Gulf of Mexico

Question: Are there differences in SAV occurrence, percent cover, and species assemblages between years, regions, marsh zones across the NGOM? Where and when do these differences occur?

Chapter 2: Submerged aquatic vegetation mapping in coastal Louisiana through development of a spatial likelihood occurrence (SLOO) model

> *Objective: To create a predictive occurrence model for SAV across marsh zones in coastal Louisiana, specifically, identifying and quantifying primary environmental drivers of presence of SAV assemblages.*

Chapter 3: Seasonal and spatial interactions between submerged and floating aquatic vegetation (FAV) create distinctive differences in estuarine habitats in Barataria Basin, Louisiana

> *Question: Are there seasonal or spatial patterns in the occurrence, percent cover, and species assemblages of SAV in the Barataria Bay estuary? Are there significant spatio-temporal interactions between SAV and FAV?*

Chapter 4: Assessing waterfowl habitat value of seed forage in estuaries across multiple regional and temporal scales

> *Question: Are there spatio-temporal differences in seed biomass (total, waterfowl food, and SAV seeds) across years, seasons, marsh zones, or regions?*

Investigating these questions provides distribution and environmental data, and contributes to the field of aquatic ecology. Assessing the environmental conditions and species interactions that drive SAV distribution will define the niche space that the species assemblages can occupy. Although it is a shifting term in the ecological and biological sciences, the concept of niche refers to the suite of conditions, abiotic and biological, that a species or assemblage of species needs to survive and reproduce (Chase and Leibold, 2003). Niche space describes the specific place and time that a species exists with respect to these conditions, differing subtly from niche by referring to the multi-dimensional space as species exists in addition to the role it fulfills in the ecosystem. In this multi-dimensional space, different species are linked in communities, and changes in the niche space of one species can create community-wide changes in the resources and conditions necessary for species to exist, described here as the habitat for that species or assemblage of species. Since niche space is neither static in time or space, its' identification requires approaches to sampling and analysis that are spatially and temporally hierarchical. These efforts will define the niche space for SAV across the NGOM coastal landscape, identify how ecological patterns may influence associated species within the community, and illustrate the consequences of environmental change on these spaces.

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CHAPTER 1. MORE THAN A MARSH ZONE: HOW REGIONAL CHARACTERISTICS CREATE UNIQUE ESTUARINE GRADIENTS AND SUBMERGED AQUATIC VEGETATION (SAV) HABITATS ACROSS THE NORTHERN GULF OF MEXICO

Introduction

Identifying the distribution of species is a central theme in ecology. The foundation of ecological sciences was developed as pioneers in ecological research sought to understand why species occurred where they did (Hutchinson, 1957; MacArthur and Wilson, 1963; Whittaker, 1956). This fundamental question still guides much of the science, research, and management currently practiced today. As climate patterns are altered, and landscapes change, the collection of species distribution data has become increasingly relevant and necessary to both scientific research and management. Consistent and quantitative baseline data describing the geographic and timing of species distributions are critical for multitudes of natural resource management purposes including conservation, restoration, protection, eradication, and harvest.

Distribution data describing submerged aquatic vegetation (SAV) across estuarine gradients are particularly relevant to evaluate the effects of climate and landscape change on coastal ecosystems. Coastal SAV occupies ecotones that exchange energy between the land and the ocean, and are inextricably linked to changes in the abiotic environment as hydrologic parameters are altered (Short and Neckles, 1999; Koch, 2001; Madsen et al., 2001; Jennerjahn et al., 2012). SAV occurrence and species assemblages are influenced by some of the first environmental conditions altered by climate and landscape change (salinity patterns, sea-level rise, and pollution) and act as meaningful indicators to assess changes across estuarine gradients in coastal habitats.

Estuaries are characterized by variable physical and biological patterns which are largely driven by the salinity gradient (Cloern et al., 2017). Salinity plays a fundamental role in structuring nekton and both emergent and aquatic vegetation assemblages (Burgos-León et al., 2013; Lirman et al., 2008; Rodríguez-Gallego et al., 2015), but the actual patterns of SAV distribution across estuarine gradients are related to more than just salinity. Exposure to waves and currents, water clarity/light availability, sediment type, human activities, seasonality, and the variability of these factors as well as salinity have been identified as significant drivers of SAV occurrence and abundance across estuaries (Cho and Biber, 2016: Findlay et al., 2014; Koch, 2001; Martin and Valentine, 2012). These drivers of SAV are variable across landscapes, and distinctive to ecological and anthropogenic boundaries.

SAV distributions are variable temporally as well as spatially. Shifts in SAV presence and cover can be short term, related to inter-annual or seasonal variation (Cho and May, 2008; Lirman et al., 2008; Patrick and Weller, 2015), or long term, indicative of regime shifts to alternative ecological states in water bodies (Hilt et al., 2011; McCann, 2016; Rossi et al., 2016). Temporal changes in SAV distributions can be caused by changing water quality (Findlay et al., 2014; Moorman et al., 2017) or physical conditions (Berglund et al., 2002; Topuzović et al., 2015). Often, the presence and cover values of SAV are used as ecological indicators of aquatic ecosystem health, and changes in SAV distribution over time are strongly correlated to changing environmental conditions in a habitat (Schneider et al., 2016).

In the northern Gulf of Mexico (NGOM), SAV in estuaries creates highly productive habitats that provide significant ecological benefits. Coastal waters supporting SAV provide

multiple physical, chemical and ecological benefits to the ecosystem – increasing accretion, minimizing erosion, and buffering energy (Gracia et al., 2017; Västilä and Järvelä, 2017), aiding in nutrient cycling (Juston et al., 2013; Yan et al., 2016) and providing food and habitat for important species (Brasher et al., 2012; Hitch et al., 2011; La Peyre and Gordon, 2012; Pujol et al., 2012). Healthy SAV systems can also mitigate the effects of sea-level rise (SLR) on the NGOM ecosystem where water levels are predicted to inundate much of the coastal zone, altering estuarine gradients and increasing shallow open-water areas (Anderson et al., 2014; Sheets et al., 2012). As land becomes submerged, areas with SAV present will still provide benefits to both wildlife and the remaining coastal wetlands and newly flooded areas will become suitable for SAV establishment (Cho and Poirrier, 2005).

Despite extensive research on the role and importance of SAV, datasets describing SAV distribution baseline data across estuarine gradients over time are not widely available in the NGOM, particularly in interior shallow water marsh areas (Handley, 2005; Merino et al., 2009; Carter et al., 2009). Field studies dating back to 1938 (Penfound and Hathaway, 1938) noted differences in SAV species assemblages. Attempts to distinguish the drivers for SAV distribution and subsequent habitat value of SAV to waterfowl in coastal ponds across estuarine gradients have continued in earnest over the years (Chabreck, 1971; Joanen and Glasgow, 1965). Across the United States there have been more recent efforts to collect data on SAV occurrence via remote sensing and aerial imagery, with variable success (Carter et al., 2011; Vis, 2003; Watanabe et al., 2006). Consequently, there are no true estimates of SAV distribution coast-wide, nor are there recent data on the relative abundance or extent of SAV across different coastal marsh zones or how SAV resources vary across these zones.

In this study, a large-scale coastal dataset was developed describing SAV across the estuarine gradient. To delineate the estuarine gradient, marsh zones were used, derived from the classification of marsh types as defined by emergent vegetation, and extended into nearby aquatic habitats capable of supporting SAV (sensu Enwright et al., 2014; Visser et al., 2013). Patterns of SAV distribution and assemblage were assessed across the entire coastal landscape, across marsh zones and ecologically defined regions. The specific objectives were to quantify and compare SAV presence, percent cover, and species assemblages in the summer growing season (2013-2015), by marsh zone (fresh, intermediate, brackish, saline) and region across the NGOM. SAV species assemblages, presence, and percent cover will likely differ spatially between regions and across marsh zones, and temporally among years. Identifying patterns of distribution distinctive to marsh zones within regions can provide insight into drivers of SAV occurrence as they relate to unique environmental conditions within estuarine habitats.

Methods

Study Area

The study area focused on shallow aquatic habitats, estuaries, and coastal marshes of the NGOM from Mobile Bay, Alabama, to Nueces River, Texas. Regions were defined by the Gulf Coast Joint Venture (GCJV) Initiative areas, which adapted Omernik Level III Ecoregions (U.S. EPA, 2013) to include only the coastal marshes and plains (Ecoregions 34g, 34h, 73n, 73o, 75a, 75k) critical to waterbird habitat. Omernik ecoregions were developed using a hierarchical spatial framework to create boundaries for ecologically similar areas based on the analysis of patterns that were characteristic to an area (Omernik and Griffith, 2014). Initiative Areas of the

GCJV (Coastal Mississippi-Alabama – CMA, Mississippi River Coastal Wetlands – MRCW, CP – CP, and Texas Mid-Coast – TMC; Wilson et al., 2002) were used as they encompassed the estuarine gradient including multiple salinity regimes in the NGOM (Figure 1.1). Hyper-saline and marine habitats were excluded from the study area.
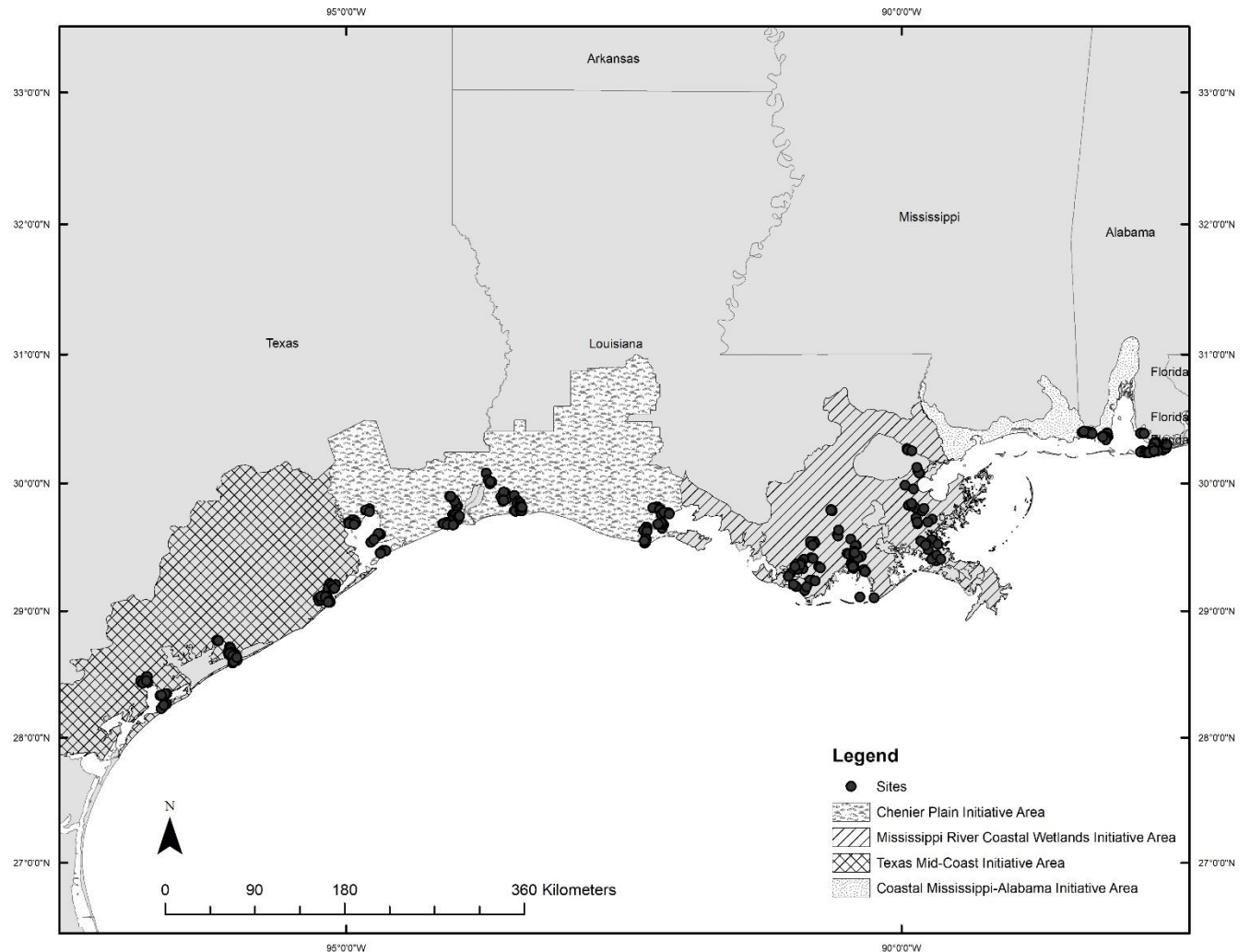
Figure 1.1. Regional boundaries as defined by Gulf Coast Joint Venture Initiative Areas. A total of 384 study sites were sampled in the summer of 2013, 2014, and 2015.

Sampling Design. The study area was divided into 43 subregions overlapping the GCJV ecoregions, spatially defined as rectangles oriented north-south and of equal east-west width. Twelve subregions were randomly selected, with the selection process forced to prevent the selection of adjacent subregions to increase spatial distribution of sites. The creation of subregions attempted to capture the full estuarine salinity gradient (fresh to saline salinity regimes) across multiple habitat types in the NGOM.

To define potential SAV habitat within each subregion, four separate methods were developed to create a contiguous spatial mask across the study area. The final output combined each of the methods into a single potential SAV habitat mask covering approximately 550,000 ha

across the study area. The first method stacked cloud-free Landsat satellite (1984-2011) images by path/row with a minimum of 48 and a maximum of 124 images for a given path/row. Erdas Imagine (2016) software was trained to automatically recognize a pre-defined SAV class, creating an "un-supervised" SAV identification technique. When SAV habitat was indicated in more than 10% of the stacked images the pixel was included as potential SAV habitat.

The second method used the stacked Landsat 8 remote sensing imagery and conducted a "supervised" classification of bands 3, 4, and 5 using the maximum zonal statistics tool in ArcGIS (ArcGIS v 10.5). The potential presence of SAV in water was identified by higher reflectivity in bands 4 and 5 in water bodies than water (B. Couvillon, USGS, personal communication). If a pixel was reflective in both band 4 and 5 for 10% of the available images, it was classified as potential SAV habitat and included in the final mask output.

The third approach used the National Land Cover Dataset (NLCD) for the years 1992, 2001, 2006 (NLCD, 2012) and the Coastal Change Analysis Program (C-CAP) datasets for the years 1996, 2001, 2005, and 2006 (C-CAP 2012). All the rooted vascular bed classes identified by both remotely sensed and field data in these datasets were selected to create a vascular bed spatial layer. The final approach used the same NCLD (2012) data, and was the only method that relied on habitat data instead of remote sensing data. Here, a spatial layer of interior coastal marsh ponds was created to target sampling in areas of potential waterfowl foraging habitat where SAV is likely to occur by excluding deep water, heavily traveled canals, upland habitats, dense emergent marsh, and water bodies >1295 ha. The land/water layer was generated in ArcGIS using the maximum extent of water, aquatic bed, and unconsolidated shore Areas identified as less than 0.1 ha were excluded as they represented individual pixels and were potentially not actual ponds. These four methods were combined to create a potential spatial SAV habitat layer in ArcGIS (v 10.5).

Eight sites per subregion were selected in fresh, intermediate, brackish, saline marsh zones (32 sites per subregion, 384 total sites). Sites were located on both private and public lands across the coast. Marsh zone designations were based on emergent marsh vegetation communities, which reflect long-term salinity patterns (Visser et al., 2013). The initial marsh zone designations used for sampling design were defined in Louisiana by Sasser et al. (2008), and for Mississippi, Alabama, and Texas by best professional judgment and early efforts by USGS to delineate coast-wide emergent vegetation types. Final marsh zone designations used in analyses were assigned using Sasser et al. (2013) in Louisiana and Enwright et al. (2014) emergent marsh vegetation zone dataset in the rest of the states. Marsh zone designations differed from Enwright et al. (2014) and Sasser et al. (2013) in that marsh type classifications were extended into the aquatic habitat where the site was located marsh zone was assigned based on the nearest pixel.

Data Collection. Data were collected once each summer growing season (1 June–15 September) in 2013, 2014, and 2015. Sites were accessed via mudboat or airboat, and in occasional instances, by walking if normal routes became dry. Water samples for turbidity testing (NTU-Hach 2100Q, Hach, CO) were collected upon arrival at the site before disturbing benthic sediments. Salinity and temperature were recorded (YSI Pro2030, YSI Incorporated, OH) at approximately half a meter under the water surface (when possible). Sites were all less than 2 m in depth.

After collecting the water quality data, a 0.25 m^2 quadrat was haphazardly thrown from the boat and anchored in place. If vegetation was present, either floating or submerged, percent

cover was estimated and identified to genus level. Triplicate percent cover were collected at each site. Percent cover and SAV species were assessed and recorded in the field. If necessary, plants were collected and brought back to the lab for identification.

Analyses. Environmental variables (salinity, temperature, turbidity, and dissolved oxygen) were summarized and presented by means and ranges to describe the discrete sampling conditions across the landscape. To assess SAV presence and cover a generalized linear model and a linear regression model, respectively, were used to test the main and interactive effects of year, marsh zone and region, and least squared means testing identified significant differences between groups (Russel, 2016). All analyses were performed in R (The R Group, 2016).

Species assemblages were described using the partitioning around mediods clustering algorithm, applying the gower distance method as it is most appropriate for evaluating the effect of both categorical (region and marsh zone) and numerical (salinity, turbidity, depth) variables (Kaufman and Rousseeuw, 1990). The gower distance formula expresses the similarity and dissimilarity between observations, where the distance between observations is the sum of all standardized variable-specific distances (Gower 1971). Partitioning around mediods assigned every observation to its closest mediod, the observation that serves as an exemplar for each cluster based on variables of interest (region, marsh zone, salinity, turbidity, depth), based on the gower distance matrix (Maechler et al., 2016). The optimal number of clusters was determined using the silhouette width validation metric, which aggregates how similar an observation is to its own cluster relative to its closest neighboring cluster. The highest silhouette value (-1 to 1) was used to determine the optimal number of clusters mediods and species assemblages within each cluster were identified. Only the observations with presence were evaluated in the cluster analysis.

Results

Environmental Variables

The environmental parameters were collected once per sampling event in each year, and were consequently applied primarily for descriptive purposes and in cluster analyses to describe species assemblages (Table 1.1). Salinity values ranged as expected within marsh zones, increasing in mean salinity as the estuarine gradient transitioned from fresh to saline. Turbidity ranged from 0 to 176.5 NTUs. Mean temperature varied little across marsh zones and regions, with mean temperature ranging from 30.2 °C to 33.8 °C across all marsh zones and regions. Dissolved oxygen was also similar across marsh zones and regions, ranging from 5.0 to 9.0 mg/L. Depth was greatest in fresh marsh across all regions except the CP (0.68 ± 0.03m), with greatest depth occurring in the fresh marsh zone of the MRCW (0.84 ± 0.05m). TMC and CP depth were lowest in depth across all marsh zones.

Table 1.1. Environmental parameters by region and marsh zone as mean, ± SE, and range.

	Salinity (PPT)	Turbidity (NTUs)	Temperature (°C)	DO (mg/L)	Depth (m)
Texas Mid-Coast (TMC)					
Fresh	1.9 (0.3) 0.3 -7.0	43.2 (11.3) 0 - 162.0	30.2 (6.6) 27.6 - 37.3	5.6 (1.0) 0.3 - 18.8	0.44 (0.05) 0.09 - 0.79
Intermediate	6.3 (1.2) 0.3 - 18.6	117.8 (22.2) 16.8 - 162.0	30.5 (0.5) 26.9 - 34.8	6.7 (0.6) 2.3 -17.2	0.46 (0.03) 0.23 - 0.81
Brackish	10.7 (3.3) 0.3 - 19.9	176.5 (49.7) 19.3 - 414.0	33.8 (1.0) 29.7 - 38.3	9.3 (1.7) 4.0 - 18.7	0.34 (0.05) 0.16 - 0.62
Saline	20.6 (0.7) 0.3 - 44.6	58.8 (6.6) 0 - 500.0	31.4 (0.2) 26.9 - 36.8	5.7 (0.1) 0 - 11.4	0.40 (0.01) 0.05 (1.01
Chenier Plain (CP)					
Fresh	2.0 (0.6) 0.1 - 17.7	37.3 (4.5) 2.5 - 144.0	31.1 (0.4) 21.2 - 35.4	4.8 (0.5) 0 - 17.4	0.60 (0.03) 0.23 - 1.08
Intermediate	3.8 (0.5) 0.1 - 21.6	77.5 (9.5) 0 - 551.0	31.0 (0.5) 0 -37.3	4.7 (0.3) 0 - 12.9	0.43 (0.02) 0.05 - 0.97
Brackish	10.0 (0.5) 0 - 25.0	78.4 (5.3) 8.6 - 766.0	31.7 (0.1) 27.4 - 37.3	5.0 (0.1) 0 - 11.4	0.40 (0.01) 0.06 -1.43
Saline	19.6 (1.3) 4.3 - 30.2	80.8 (10.9) 0 - 184.0	31.7 (0.4) 27.3 - 35.0	5.4 (0.4) 2.7 - 9.3	0.30 (0.03) 0.10 - 0.60
Mississippi River Coastal Wetlands (MRCW)					
Fresh	0.2 (<0.1) 0 - 0.5	26.1 (4.9) 1.1 - 198.0	31.0 (0.3) 25.1 - 37.2	4.5 (0.4) 0.6 - 10.27	0.84 (0.05) 0.15 - 1.88
Intermediate	1.1 (0.2) 0.1 - 6.5	22.0 (2.5) 1.7 - 98.6	31.3 (0.9) 25.6 - 36.9	5.3 (0.3) 0 - 10.8	0.50 (0.03) 0.08 - 1.02
Brackish	3.8 (0.3) 0.1 - 11.2	24.0 (2.2) 0 - 157.0	31.6 (0.2) 25.1 - 36.0	5.9 (0.2) 0 - 10.8	0.57 (0.02) 0.19 - 0.84
Saline	11.3 (0.5) 0.7 - 26.7	29.6 (1.3) 5.0 - 65.1	31.9 (0.2) 27.9 - 35.4	5.7 (0.1) 0 - 9.1	0.57 (0.02) 0.13 - 1.01
Coastal Mississippi-Alabama (CMA)					
Fresh	5.6 (1.4) 0 - 19.0	25.2 (14.4) 1.24 - 252.0	33.3 (0.6) 29.1 - 41.0	6.3 (0.7) 1.8 - 11.6	0.59 (0.05) 0.09 -1.09
Intermediate	6.4 (1.1) 0.9 - 13.6	11.8 (0.9) 6.6 - 16.2	31.6 (0.4) 29.5 - 33.0	6.7 (0.8) 1.0 - 12.9	0.69 (0.05) 0.31 -1.06
Brackish	13.3 (1.4) 0.6 - 32.3	10.1 (0.9) 0 - 24.4	31.5 (0.9) 29.9 - 35.4	5.5 (0.4) 1.0 - 10.8	0.59 (0.05) 0.34 - 1.53
Saline	13.1 (0.8) 0.2 - 34.0	22.7 (2.0) 0 - 178.0	30.9 (0.4) 28.0 - 35.4	5.2 (0.2) 0 - 12.5	0.59 (0.02) 0.20 -1.69

SAV Presence and Species Assemblages

Coast -wide, there were 15 species of SAV, and the patterns of presence across marsh zones different among regions (Chisq < 0.001; Table 1.2; Figure 1.2). There was no effect of year on presence of SAV in any of the marsh zones or regions, nor was there any interaction between year and marsh zone or year and region. Fresh, intermediate, and brackish marsh zones

in the MRCW region and fresh marsh zones of the TMC region supported similar SAV presence (~80%), and were the highest of all regions and marsh zones. Fresh marsh zones in the TMC and the CP regions supported significantly higher SAV presence than the other marsh zones within the region while in the CMA region fresh zones had the lowest (17%). The saline marsh zone in the MRCW was unique in that it had lower presence (9%) than saline marsh zones in other regions and was significantly different from the other marsh zones in the MRCW ($p < 0.001$). Percent presence was similar in the brackish and saline marsh zones of the CP and CMA regions.
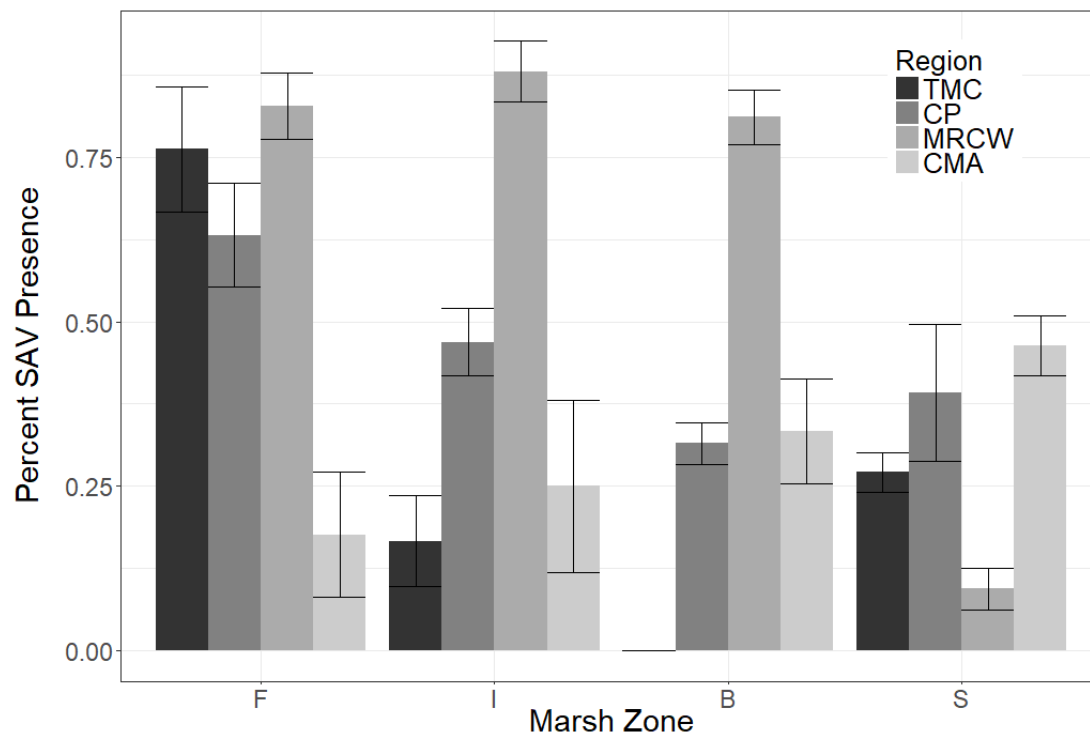
Figure 1.1. Percent presence ±SE at sample sites across regions and marsh zones. Regions and marsh zones: TMC = Texas Mid-Coast, CP = Texas Chenier Plain, MRCW = Mississippi River Coastal Wetlands, CMA = Coastal Mississippi-Alabama, F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone.

Species assemblages were distinctive between regions and marsh zones as indicated by the gower distance (Figure 1.3), except in the CMA region, where there was no clear distinction among the zones. The most similar species were *M. spicatum* and *Ceratophyllum dermersum*, both located in the brackish marsh zone of the MRCW region. The fresh, intermediate, and brackish marsh zones of the MRCW and the CP regions were strongly dissimilar, represented by the large distance between clusters. The most dissimilar species were *H. verticillata* in the fresh marsh zone of the MRCW region, and *R. maritima* in the brackish marsh region of the CP region. The mediod species for brackish and saline marsh in the TMC, CP, and CMA regions was *R. maritima*, and *M. spicatum* in the MRCW (Table 3). *Ceratophyllum demersum* was the mediod species for the CP and MRCW fresh marsh zone, and in the TMC fresh zone it was *H. dubia*. The intermediate marsh zone mediod species was *P. pusillus* in the TMC, *M. spicatum* in the CP, and *V. americana* in the MRCW. Brackish marsh zones of the TMC region were not

included in the species assemblage cluster analysis due to the absence of SAV at those sites. Cluster analyses did not include year, as there was no effect on percent presence.

Ruppia maritima and *C. demersum* were the most widespread species found in all regions and in most marsh zones. *Ruppia maritima* was present in all marsh zones except fresh and dominated presence in the CP intermediate and brackish marsh zones, while *C. demersum* was found in most marsh zones except saline. *Stuckenia pectinata* was located primarily in the fresh and intermediate marsh zones of the TMC region, although some presence was observed in the CP and MRCW. *V. americana* was frequently present in the MRCW intermediate marsh zone.

Table 1.2. Mediod species associated categorical and environmental data for cluster analysis

	Salinity (PPT)	Turbidity (NTUs)	Depth (m)	Species Code
Texas Mid-Coast (TMC)				
Fresh	1.80	15.40	0.55	HEDU2
Intermediate	0.30	48.50	0.29	POPU7
Brackish	N/A	N/A	N/A	N/A
Saline	0.80	34.80	0.38	RUMA5
Chenier Plain (CP)				
Fresh	0.40	24.90	0.57	CEDE4
Intermediate	2.10	33.60	0.42	MYSP2
Brackish	14.40	61.40	0.33	RUMA5
Saline	4.30	79.50	0.31	RUMA5
Mississippi River Coastal Wetlands (MRCW)				
Fresh	0.20	5.97	0.87	CEDE4
Intermediate	0.20	13.70	0.46	VAAM3
Brackish	7.10	16.70	0.60	MYSP2
Saline	1.50	43.00	0.51	MYSP2
Coastal Mississippi-Alabama (CMA)				
Fresh	N/A	N/A	N/A	N/A
Intermediate	N/A	N/A	N/A	N/A
Brackish	1.80	15.40	0.60	RUMA5
Saline	7.70	24.20	0.50	RUMA5
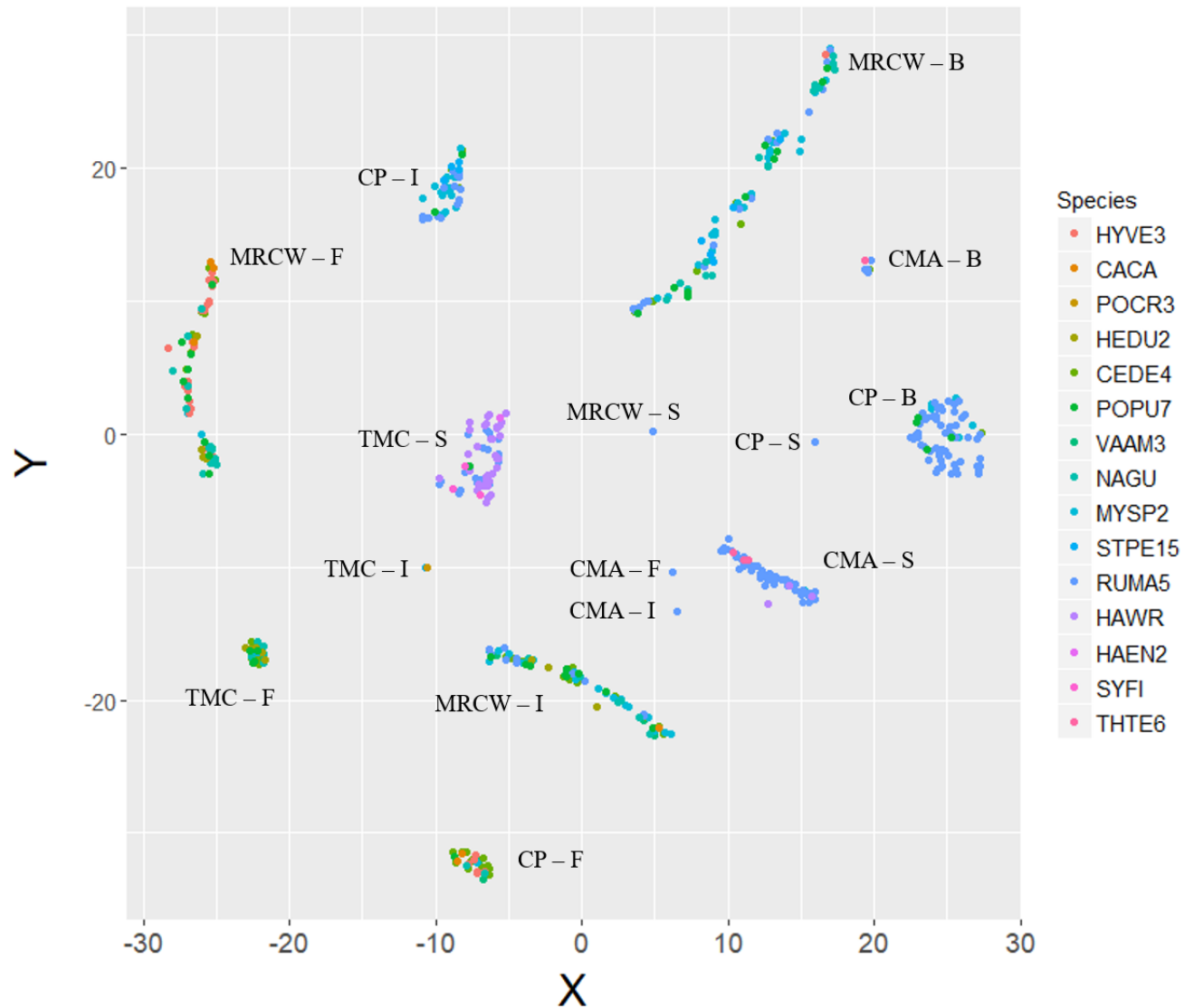
Figure 1.2. Cluster analysis of species assemblages using partitioning around mediods. XY axis represents the gower distance, or dissimilarity between clusters. Regions and marsh zones: TMC = Texas Mid-Coast, CP = Texas Chenier Plain, MRCW = Mississippi River Coastal Wetlands, CMA = Coastal Mississippi-Alabama, F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone. Species Codes: HYVE3 = *Hydrilla verticillata*, CACA = *Cabomba caroliniana*, POCR3 = *Potamogeton crispus*, HEDU4 = *Heteranthera dubia*, CEDE4 = *Ceratophyllum demersum*, POPU7 = *Potamogeton pusillus*, VAAM3 = *Vallisneria americana*, NAGU = *Najas guadalupensis*, MYSP2 = *Myriophyllum spicatum*, STPE15 = *Stuckenia pectinata*, RUMA5 = *Ruppia maritima*, HAWR = *Halodule wrightii*, SYFI = *Syringodium filiforme*, THTE6 = *Thalassia testidinum*.

Several species were distinctive to individual marsh zones: *Halodule wrightii*, *Syringodium filiforme*, and *Thalassia testidinum*, the only "true" seagrasses observed, were present only in saline marsh zones, while *Cabomba caroliniana* was found only in fresh marsh

zones. SAV assemblages were more diverse across fresh, intermediate, and brackish marsh zones in the MRCW region than other regions, with multiple species occurring in multiple marsh zones versus in other regions where they only occurred in one. The TMC region had largest species assemblage in the saline marsh zone, supporting both true seagrass species (*H. wrightii* and *S. filiforme*) and brackish SAV species (*P. pusillus* and *R. maritima*). *Ruppia maritima* dominated occurrence in all marsh zones of the CMA region. Floating aquatic vegetation (FAV) was present primarily in fresh and intermediate marsh zones, was completely absent in saline marsh zones of all regions, and was sparse in brackish marsh zones. FAV species included *Eichhornia crassipes*, *Alternanthera philoxeroides*, *Nelumbo lutea*, *Utricularia sp.*, *Lemna minor*, and *Salvinia* sp.

SAV Percent Cover

The patterns of SAV percent cover across marsh zones differed among regions as indicated by a significant interaction effect (F value = 10.861; $p < 0.001$; Table 1.3; Figure 1.4). There was no effect of year. The interaction was largely explained by the higher cover in the MRCW fresh marsh zone ($50 \pm 5\%$) and the lower cover in the MRCW saline marsh zone ($1 \pm 0.5\%$) than all other marsh zone and region combinations. The MRCW intermediate and brackish zones had the highest percent cover (I = $28 \pm 4\%$, and B = $23 \pm 3\%$ cover) of all regions in the same marsh zones, while the TMC and CMA regions had the highest cover in saline marsh zones ($15 \pm 2\%$ and $16 \pm 3\%$ cover respectively). Mean percent cover of individual species varied by species type in marsh zone by region (Figure 1.5).

Specifically, in the TMC region, there was an effect of year on percent cover of *H. wrightii* to *R. maritima*. From 2013 to 2015, percent cover of *R. maritima* increased, as percent cover of *H. wrightii* decreased (Figure 1.6).

Discussion

Findings indicate that SAV differs among marsh zones as defined by emergent marsh vegetation types, and suggest that the ecological processes may affect SAV differently than emergent vegetation in coastal landscapes. Across the NGOM, SAV presence, percent cover, and species assemblages varied across marsh zones and regions. These patterns were likely driven by regionally specific ecological processes influencing the environmental conditions (subsidence, sea-level rise, rainfall, and anthropogenic management) that assemble aquatic communities (Cho and Biber, 2016; Ejankowski and Lenard, 2015; Quiros et al., 2017; Sharpe and Baldwin, 2012). The interaction between region and marsh zones indicates that SAV within the same marsh zone differs among regions. This spatial variability influences key drivers of SAV presence, species assemblages and percent cover (i.e., salinity, water depth) and creates distinctive SAV habitat between regions and zones.
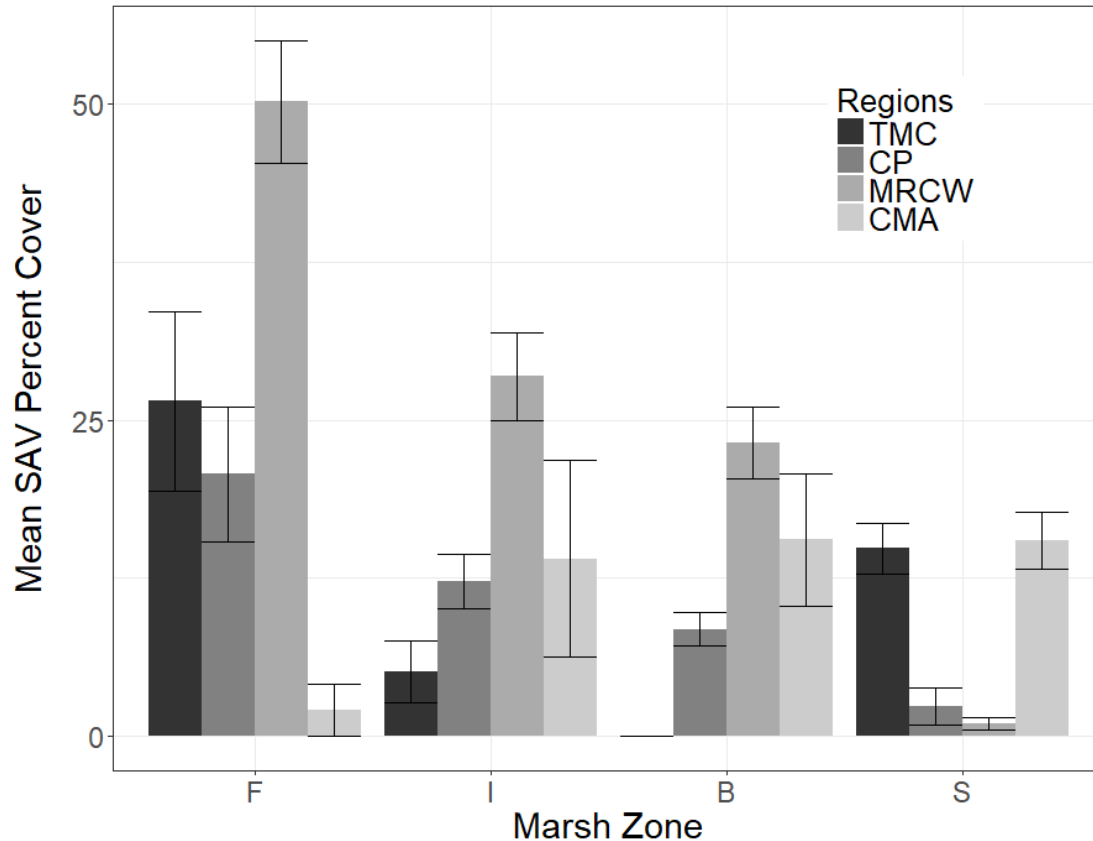
Figure 1.3: Mean percent total SAV cover (±SE) by region and marsh zone. Regions and marsh zones: TMC = Texas Mid-Coast, CP = Texas Chenier Plain, MRCW = Mississippi River Coastal Wetlands, CMA = Coastal Mississippi-Alabama, F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone.

Salinity and water depth were the primary environmental conditions characterizing marsh zones between regions distinguished in this study. The impacts on SAV were largely expressed between fresh and saline marsh zones, both within and between regions. In all regions, fresh marsh zones were fresher and deeper than saline marsh zones. The conditions in fresh marsh created habitats that were less stressed by salinity regimes, but potentially light limited, and vice versa in saline marsh zones. Across the study area, species able to grow rapidly to reach light will be characteristic in fresh habitats, while species able to tolerate stress will be characteristic in saline habitats.

Regional differences further distinguished the same marsh zones in different regions from one another. In particular, the saline marsh zone of the MRCW region was significantly different than all other regions and zones. Environmental conditions in the MRCW support fresher salinities when compared to other regions and zones, potentially preventing the establishment of true seagrass species found in the saline marsh zones of other regions. Seagrass species are sensitive to hypo-, hyper-, and variable salinity conditions (Hemminga and Duarte, 2000; Torquemada et al., 2005; Koch et al., 2006), all of which are characteristic of the MRCW region (Snedden and Steyer, 2013). Similarly, fresh marsh zones in the MRCW region were fresher (mean salinity 0.2± 0.01) and deeper (0.84± 0.05) than other regions. Although fresh marsh

coast-wide had the lowest salinity and the greatest depth these conditions distinguished MRCW fresh marsh from fresh marsh in other regions.

While differing SAV cover between the same marsh zones is at least partially an artifact of dissimilar salinity regimes between regions within the same zones, other environmental conditions are likely to influence SAV percent cover. Overall, the distinctive environmental conditions in fresh marsh zones (temperature, salinity, depth) promotes the establishment of species which can persist at deeper depths, germinating not necessarily from seed but from vegetative cloning (i.e., *H. verticillata* and *C. caroliniana)* (Cronk and Fennessy, 2001; Haller et al., 1976). The high sediment load deposited by the Mississippi River may have also impacted SAV distribution in the MRCW region. Sediment deposition can create high turbidity, and the characteristic soft, organic soils of the Mississippi River Delta can be easily mobilized, affecting water clarity and decreasing growth in many plant species (Booth et al., 2000; White and Visser, 2016). Specifically, seagrass species, which are particularly sensitive to water clarity, would be significantly limited in turbid saline marsh zones, namely the MRCW and the CP regions (Dunton 1994; Hemminga and Duarte, 2000; Kenworthy and Fonseca, 1996). The high salinity and water clarity of much of the TMC region and the eastern-most part of the CMA region produce conditions more amenable to the establishment and persistence of seagrass meadows, leading to higher presence and cover of SAV in saline marsh zones of these regions.

The species assemblage at specific marsh zones within regions could influence cover estimates. In fresh marsh zones, stress tolerance is traded for increased competitive ability (Grime 1977), and superior competitors exhibit rapid growth that in some cases will only be limited by space and morphological characteristics like thicker leaves and stems that prevent the establishment of other species (Kautsky, 1988). Species able to tolerate salinity stress in brackish and saline marsh zones, namely *R. maritima,* are less competitive in fresh marsh, and typically have a shorter and patchy growth habit (Kantrud, 1991) compared to fresh species like *H. verticillata* that typically create dense mats of complete cover over the benthic sediments (Rybicki and Carter, 2002), confounding cover estimates.

Environmental conditions in intermediate marsh zones contributed to a diverse assemblage of SAV species typically considered desirable for waterfowl. Specifically, intermediate marsh zones had high percent cover of native species versus high percent cover of invasive species found in fresh marsh zones, particularly in the MRCW region. Although the presence of exotic SAV may not directly cause the decline of higher trophic level predators such as waterfowl (Goecker et al., 2006), reduced foraging efficiency for macro-invertebrates has been documented in *H. verticillata* and *M. spicatum* SAV beds versus native species (Chaplin and Valentine, 2009; Valinoti et al., 2011). Exotic invasive SAV observed in the study area at high percent cover values include *H. verticillata* and *M. spicatum*, with *H. verticillata* primarily restricted to the fresh marsh zones (Sheilds et al., 2012). SAV species considered valuable to waterfowl, including *S. pectinata*, *V. americana*, and *R. maritima*, found in intermediate and brackish marsh zones, can exist in habitats that prevent establishment and growth of many of the exotic species limited to fresh water (Borgnis and Boyer, 2016; Rodríguez-Gallego et al., 2015; Shields and Moore, 2016).

Table 1.3. SAV presence, total percent cover, and percent cover by species Data are presented as mean (±SE). FAV = floating aquatic vegetation species, HYVE3 = Hydrilla verticillata, CACA = *Cabomba caroliniana*, POCR3 = Potamogeton crispus, HEDU4 = *Heteranthera dubia*, CEDE4 = *Ceratopyllum demersum*, POPU7 = *Potamogeton pusillus*, VAAM3 = *Vallisneria americana*, NAGU = *Najas guadalupensis,* MYSP2 = *Myriophyllum spicatum*, STPE15 = Stuckenia pectinata, RUMA5 = *Ruppia maritima*, HAWR = *Halodule wrightii*, SYFI = *Syringodium filiforme*, THTE6 = *Thalassia testidinum*.

	Absent	Present	SAV Cover	FAV	HYVE3	CACA	POCR3	HEDU2	CEDE4	POPU7	VAAM3	NAGU	MYSP2	STPE15	RUMA5	HAWR	HAEN2	SYFI	THTE6
Texas Mid-Coast																			
Fresh	23.8	76.2	26.5 (7.1)	4.7 (3.0)	0.0	0.0	0.0	5.8 (4.6)	10.1 (4.6)	2.1 (1.2)	1.5 (1.5)	2.8 (1.4)	0.0	5.8 (3.5)	0.0	0.0	0.0	0.0	0.0
Intermediat	83.3	16.7	5.07 (2.4)	0.0	0.0	0.0	0.0	1.1 (0.2)	0.2 (0.2)	1.1 (1.1)	0.0	1.1 (1.1)	0.0	2.0 (1.5)	0.4 (0.3)	0.0	0.0	0.0	0.0
Brackish	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Saline	73.2	26.8	14.9 (2.0)	0.0	0.2 (0.2)	0.0	0.0	0.0	0.0	0.2 (0.2)	0.0	0.0	0.0	0.0	5.3 (1.3)	9.1 (1.7)	<0.1	0.2 (0.1)	0.0
Chenier Plain																			
Fresh	38.5	61.5	20.7 (5.3)	1.8 (0.6)	4.0 (1.2)	0.8 (0.8)	0.0	0.0	14.2 (4.2)	0.4 (0.4)	< 0.1	1.2 (1.0)	<0.1	0.0	0.0	0.0	0.0	0.0	0.0
Intermediat	55.9	44.1	12.3 (2.2)	3.1 (0.1)	0.0	0.0	0.0	0.0	1.7 (0.7)	0.8 (0.7)	0.0	0.0	4.1 (1.3)	2.3 (1.2)	3.3 (1.1)	0.0	0.0	0.0	0.0
Brackish	68.9	31.1	8.4 (1.3	0.2 (0.1)	0.0	0.0	0.0	0.0	<0.1	0.7 (0.4)	0.0	<0.1	0.4 (0.3)	0.0	7.3 (1.2)	0.0	0.0	0.0	0.0
Saline	62.5	37.5	2.4 (1.4)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4 (1.4)	0.0	0.0	0.0	0.0
Mississippi River Coastal Wetlands																			
Fresh	18.3	81.7	50.2 (4.8)	6.1 (1.8)	25.0 (4.3)	0.4 (0.3)	0.0	1.2 (1.0)	14.1 (2.3)	2.4 (0.9)	1.2 (0.8)	5.4 (1.8)	1.7 (1.1)	0.0	0.0	0.0	0.0	0.0	0.0
Intermediat	11.8	88.2	28.4 (3.5)	1.1 (0.5)	0.0	0.0	0.0	0.9 (0.8)	10.2 (2.3)	1.6 (0.8)	4.7 (2.1)	1.8 (0.8)	11.4 (2.2)	0.0	2.5 (1.6)	0.0	0.0	0.0	0.0
Brackish	18.9	81.1	23.2 (2.8)	0.6 (0.3)	0.3 (0.3)	0.0	0.0	0.0	4.5 (1.1)	0.9 (0.4)	0.7 (0.4)	3.0 (1.2)	10.0 (1.9)	0.3 (0.2)	4.2 (1.2)	0.0	0.0	0.0	0.0
Saline	90.8	9.2	1.0 (0.5)	0.0	0.0	0.0	0.0	0.0	0.3 (0.3)	0.0	0.0	0.0	0.3 (0.2)	0.0	0.4 (0.2)	0.0	0.0	0.0	0.0
Coastal Mississippi-Alabama																			
Fresh	83.3	16.7	2.5 (2.1)	5.0 (2.8)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1 (2.1)	0.0	0.0	0.0	0.0
Intermediat	75.0	25.0	14.0 (7.8)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.0 (7.8)	0.0	0.0	0.0	0.0
Brackish	66.7	33.3	15.9 (5.2)	0.0	0.0	0.0	0.0	0.0	0.3 (0.2)	0.0	0.2 (0.2)	0.0	0.0	0.0	15.3 (5.2)	0.0	0.0	0.0	0.0
Saline	54.0	46.0	15.5 (2.3)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<0.1	0.0	13.0 (2.1)	1.1 (0.7)	0.0	0.0	1.3 (0.8)

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Further limiting the quality of habitat in fresh marsh is the depth, as waterfowl are less likely to forage in deep water (Lantz et al., 2010), which is characteristic of many of the fresh marsh zones across the NGOM landscape. Additionally, analyses describing SAV in the brackish marsh zones of the TMC region may have limited statistical power. Sampling in brackish marsh zones of the TMC region was restricted to only 3 sites as there was limited habitat identified as brackish marsh by Enwright et al. (2014), with approximately 170 hectares out of 8,000 hectares total.

Although not explicitly an objective of this study, SAV patterns across marsh zones between regions appeared more spatially variable in heavily managed coastal landscapes. In all regions except CMA, most of the sites in fresh and intermediate marsh zones were located on actively managed property, either public, as national wildlife refuges, wildlife management areas, and state parks, or private. Water level management, salinity manipulation through freshwater introduction, levee construction and maintenance, and biological control of species are typical to the public and private lands sampled in this study. These management techniques can create steep salinity and depth gradients, particularly inside and across water management units, where managers attempt to control water input and output (personal observation). The only region where most of the sites in fresh and intermediate marsh zones were not actively managed was the CMA region. Here, the cluster analysis and environmental parameter description showed the least separation between marsh zones, indicating more similar conditions across the region. SAV in the CMA region was dominated by one species according to the cluster analysis, *R. maritima*, a species adapted to both stress and disturbance (Kantrud, 1991). This dominance by a species tolerant to variable conditions subject to frequent disturbance may demonstrate the ecological effects of intense management in other areas, usually to encourage freshwater and create stable conditions, versus conditions in the natural environment, higher salinities, more variable conditions, and less habitat stability. Patterns of SAV distribution and occurrence in this area could provide insight into environmental conditions in un-managed versus un-managed submerged habitats across estuarine gradients.

Human activities can further influence environmental conditions via pollution, shoreline development, and navigation. Sites in Galveston Bay, Texas, part of the CP region, had very little presence, cover, and only one species (*R. martima*) observed. Pulich and White (1991) reported a significant decline in SAV presence and cover in Galveston Bay, attributing it to both natural (storm) and anthropogenic (development, pollution, dredging) causes. Months before the 2014 sampling season of this study, a large oil spill occurred in Galveston Bay near to several sites in the saline marsh zone (https://gis1.harcresearch.org/oilspill/). Similarly, the Deepwater Horizon oil spill in 2011 may have impacted large areas in the brackish and saline marsh zones of the MRCW region (https://response.restoration.noaa.gov/sites/default/files/erma-deepwater-gulf-response-surface-and-shoreline-oiling_noaa.png). The effects of these pollution events on SAV are largely unknown, but have the potential to impact SAV populations in those areas.
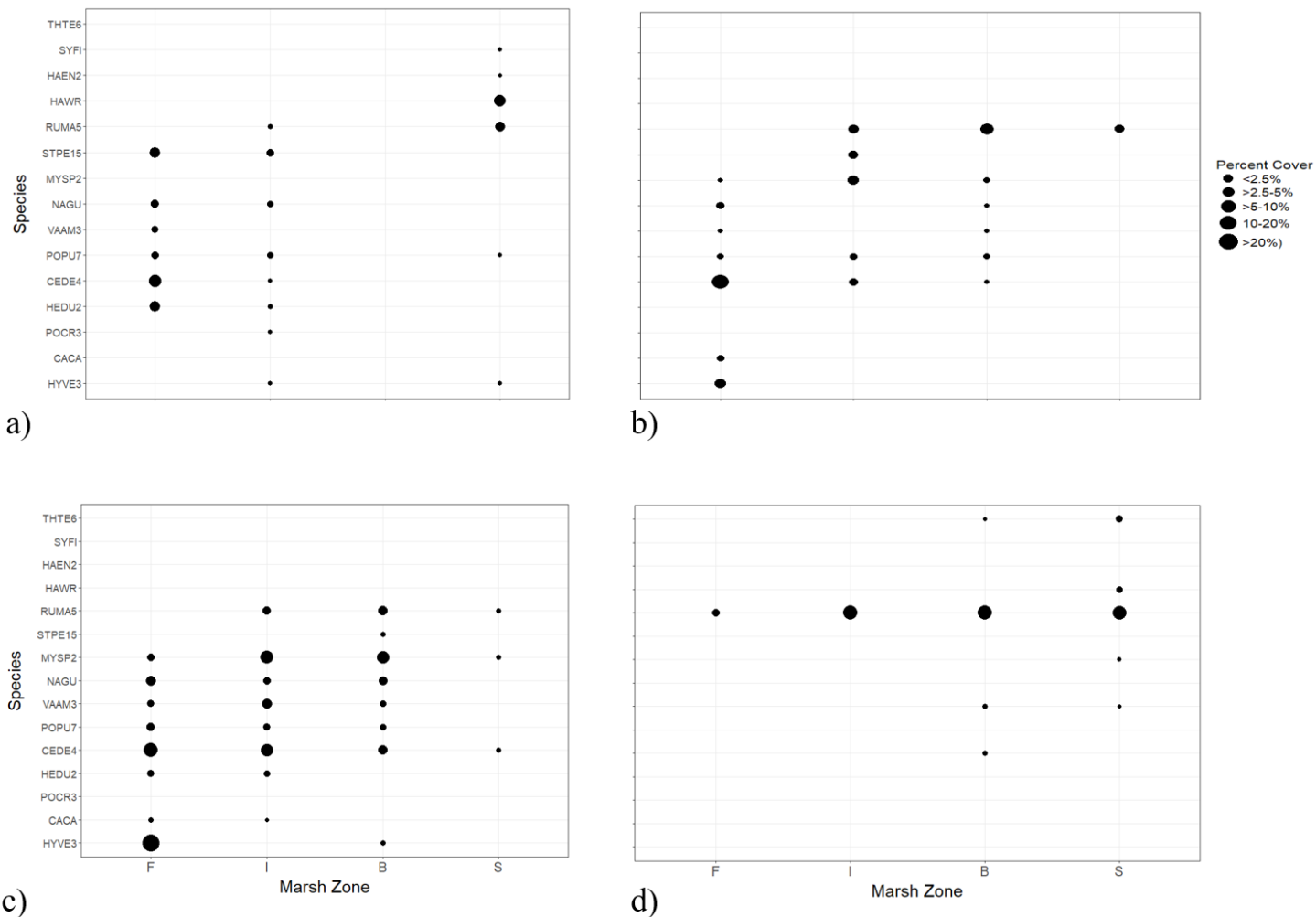
Figure 1.4. SAV species percent cover and presence by region and marsh zone. a) Texas Mid-Coast, b) Texas Chenier Plain, c) Mississippi River Coastal Wetlands, and d) Coastal Mississippi-Alabama. HYVE3 = *Hydrilla verticillata*, CACA = *Cabomba caroliniana*, POCR3 = *Potamogeton crispus*, HEDU4 = *Heteranthera dubia*, CEDE4 = *Ceratophyllum demersum*, POPU7 = *Potamogeton pusillus*, VAAM3 = *Vallisneria americana*, NAGU = *Najas guadalupensis*, MYSP2 = *Myriophyllum spicatum*, STPE15 = *Stuckenia pectinata*, RUMA5 = *Ruppia maritima*, HAWR = *Halodule wrightii*, SYFI = *Syringodium filiforme*, THTE6 = *Thalassia testidinum*.

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Although total SAV cover did not differ among years, there was a temporal shift in dominant species. Shifts towards *R. maritima* dominated SAV cover in 2015, from *H. wrightii* dominated in 2013, could be an ephemeral response of a disturbance adapted species to temporarily optimum conditions, or, indicative of long-term habitat alterations including changing salinity (decreasing in mean or increasing in variability), decreasing water clarity, or increasing organic content in sediment (Cho et al., 2009; La Peyre and Rowe, 2003; Palinkas and Koch, 2012). In 2013 the central and southern Texas coast experienced an extreme drought, with improving conditions and increasing rain until 2015, when most of the rivers and estuaries in the eastern portion of the TMC region were experiencing flood conditions (http://www.twdb.texas.gov/surfacewater/conditions/report/index.asp). The increased rainfall and subsequent sediment discharge may have produced species shifts that could be temporary or long-term. This indicates that the lack of a temporal effect on SAV cover may be the result of grouping SAV into species assemblages, or caused by the spatial scale of the analysis. It is possible that a temporal effect may have been significant within regions, with different regional boundaries, or among specific species.

SAV assemblages are potentially more sensitive to temporal changes in macroclimatic drivers like precipitation and temperature than emergent vegetation species. Osland et al. (2016) describe several "zones of instability" across the NGOM where coastal wetlands are especially sensitive to other macroclimatic drivers as rainfall and temperature patterns are altered over time. A large portion of the south and central Texas coast, including the entire TMC region and much of the CP region, was identified as a rainfall-driven zone of instability where small changes in freshwater availability could result in comparatively large changes in the coverage of wetland plants. A study evaluating the effects of drought in brackish marsh zones of this region found that SAV response was significantly greater than emergent plant communities, even though the severity of the drought, measured as increased salinity, was spatially uniform across the study site (Kinney et al., 2014). This sensitivity is likely to differ across marsh zones, and SAV response to changes in large scale environmental conditions will vary accordingly.

Conclusion

Describing spatial gradients that drive SAV distribution across the NGOM provides valuable information about the environmental conditions and habitat available in aquatic ecosystems. The use of categorical features including marsh zone and region to distinguish patterns in environmental conditions leading to species composition and distribution may be more useful across large spatial scales than continuous variables, depending on data availability. Effects of landscape scale climate processes (sea level rise, precipitation changes), characteristics distinctive to individual estuaries, and human activities (management activities, dredging, boat traffic, and pollution) created spatial gradients determining SAV distributions and assemblages unique to marsh zones and regions.
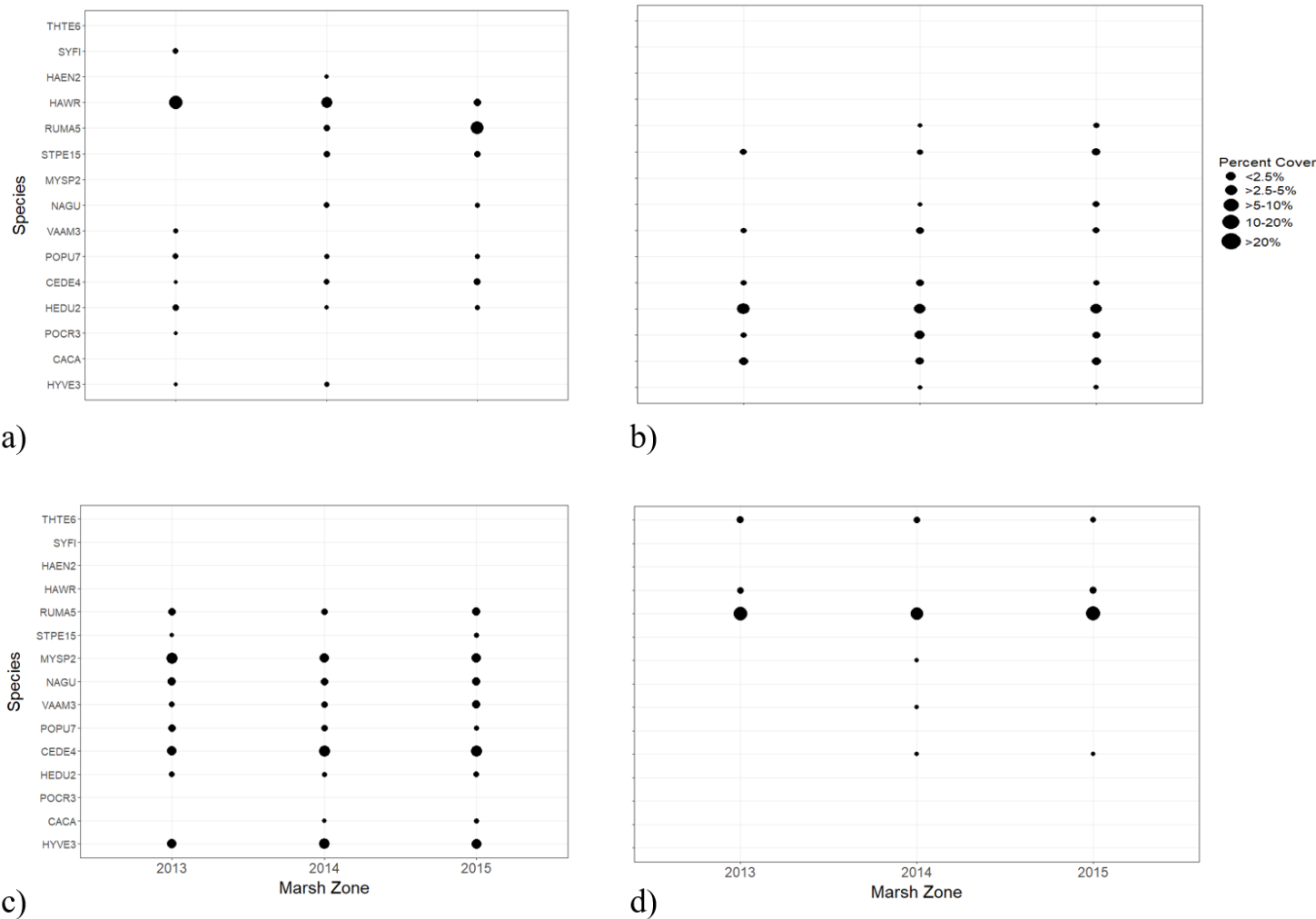
Figure 1.5. SAV species percent cover and presence by year. Species Codes: HYVE3 = *Hydrilla verticillata*, CACA = *Cabomba caroliniana*, POCR3 = *Potamogeton crispus*, HEDU4 = *Heteranthera dubia*, CEDE4 = *Ceratophyllum demersum*, POPU7 = *Potamogeton pusillus*, VAAM3 = *Vallisneria americana*, NAGU = *Najas guadalupensis*, MYSP2 = *Myriophyllum spicatum*, STPE15 = *Stuckenia pectinata*, RUMA5 = *Ruppia maritima*, HAWR = *Halodule wrightii*, SYFI = *Syringodium filiforme*, THTE6 = *Thalassia testidinum*. There was a significant effect of year on RUMA5 and HAWR in the TMC region.

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Consideration of species assemblages across regions and marsh zones is equally essential to describing habitat quality for waterfowl. All SAV species do not provide equal habitat value or ecological services to associated communities and ecosystems. Research indicates that exotic and native SAV species have significantly different value as food and habitat resources, and that the presence of exotic SAV can change the structure of the plant community (Santos et al., 2011). Incorporating species assemblage, estuarine gradient, and regional environmental data estimates is critical to fully describing aquatic habitats, both in terms of understanding ecological processes and estimating habitat value to wildlife species.

This description of spatial patterns in SAV distribution supplies valuable information about a critical habitat type. The presence, cover, and species of SAV in an aquatic habitat is indicative of water quality, physical conditions, and, in many cases, the overall effect of human activities in an area. Incorporating descriptions of submerged vegetation communities into marsh zone designations would both assist in fully characterizing estuarine habitats as well as offer insight into underlying abiotic processes affecting coastal wetlands across large landscapes. In particular, salinity patterns in estuaries and water bodies, exposure to wave energy, shoreline type (natural, bulkhead, channelized, etc.), water body size, and sediment type have shown to be useful parameters to describe SAV habitat in coastal estuaries (Cho and Biber, 2016; DeMarco et al., in press; Palinkas and Koch, 2012). Collating these data into meaningful distinctions that include both emergent wetlands and aquatic habitats will be increasingly necessary as coastal landscapes are subjected to sea-level rise, changing precipitation patterns, and coastal development.

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CHAPTER 2. SUBMERGED AQUATIC VEGETATION MAPPING IN COASTAL LOUISIANA THROUGH DEVELOPMENT OF A SPATIAL LIKELIHOOD OCCURRENCE (SLOO) MODEL

Introduction

Submerged aquatic vegetation (SAV) communities occur extensively in shallow coastal waters in the northern Gulf of Mexico (NGOM) (Carter et al., 2011; Merino et al., 2009). SAV is a vital coastal resource for fish and wildlife (Heck et al., 2003; Hitch et al., 2011; Kanouse et al., 2006; La Peyre and Gordon, 2011) and can mitigate the effects of erosion on the adjacent marsh shoreline (Christianen et al., 2013; Gurbisz et al., 2016; Nowacki et al., 2017; Robbins and Bell, 2000). Despite the valuable ecological role SAV plays in estuaries, relatively few studies have examined drivers of presence and distribution across the estuarine gradient (Cho and Biber, 2016; Estes et al., 2015), and this knowledge gap has limited attempts to map and predict SAV distribution across estuarine gradients. Distribution mapping is particularly challenging in coastal Louisiana where the use of remote sensing and aerial photography is problematic due to high turbidity (Carter et al., 2009; Merino et al., 2009; Vis et al., 2003), while field surveys remain logistically difficult and expensive.

Species distribution models (SDMs) characterize the distributions of species, and can have strong predictive power when supported by field data (Elith and Leathwick, 2009). SDMs are particularly useful in coastal landscapes where large areas of potential habitat are inaccessible and/or difficult to view remotely (Anderson et al., 2014; Cho and Biber, 2016; Guisan et al., 2005; Menuz et al., 2015). SDMs predict the likelihood of occurrence across potential habitats based on relationships between functionally relevant drivers for presence and the species or assemblage of species of interest (Beale and Lennon, 2012; Peterson and Li, 2015; Mendoza-González et al., 2013). Linking habitat studies with spatial data via SDMs can provide valuable datasets to support maps across large landscapes which can inform research, management, and restoration (Adams et al., 2016; Kotta et al., 2014; Wenger and Freeman, 2008).

The primary environmental conditions driving SAV presence or absence are light availability, physical disturbance from wind and waves (exposure), and salinity (Bornette and Puijalon, 2011; Kemp et al., 2004; Koch, 2001; Martin and Valentine, 2012; Santos et al., 2011). Multiple parameters may alter light availability to SAV including water depth, total suspended solids, turbidity, epiphytes, and as such are typically used as the proxy for light penetration. Generally, as light availability decreases or exposure increases, the ability for SAV species to colonize and persist decreases (Barrat-Segretain, 2001; Fonseca and Bell, 1998; Gurbisz et al., 2015; Robbins and Bell, 2000; Strand and Weisner, 2001). For example, Cho and Poirrier (2005a) found that in Lake Pontchartrain the likelihood of successful colonization of two brackish species *(Ruppia maritima* and *Vallisneria americana*) decreased due to reduced light availability as depth increased. Exposure can also affect SAV indirectly by decreasing light availability (i.e., increased turbidity due to resuspension of sediments), or, directly through drag exerted on the plants themselves, breaking shoots and leaves (decreasing plant biomass) or tearing the plant from the sediments by the roots and removing the entire plant (Koch, 2001; Martin and Valentine, 2012).

Ecological communities can be distinctive across estuarine gradients as individual species tolerance to salinity patterns structure plant assemblages into groups largely dictated by salinity

patterns (Burgos-León et al., 2013; Lirman et al., 2008; Rodríguez-Gallego et al., 2015). Salinity acts as an environmental filter, where fresh species with increased competitive abilities are unable to tolerate salinity stress, and salt tolerant saline species are competitively excluded from fresh habitats (Grime 1979; Kautsky 1988; Snedden and Steyer, 2013). Assemblages of SAV (different species that share similar ecological requirements) are relatively predictably organized across estuarine gradients in the northern Gulf of Mexico (NGOM), sorted by fresh (0-3.0 ppt), intermediate (>3.0-10 ppt), brackish (>10-20 ppt), and saline (>20 ppt) (Chabreck 1970; Louisiana Department of Wildlife and Fisheries, accessed December 2017; Penfound and Hathaway, 1938) Extreme conditions (i.e. drought, floods) that alter salinity patterns can influence SAV assemblages (Kinney et al., 2014). Additionally, light requirements have been found to be lower in fresh and intermediate SAV communities as compared to brackish and saline SAV communities in the Chesapeake Bay, VA (Kemp et al., 2004), suggesting a potential interaction between salinity tolerance and light requirements.

While salinity regimes are typically described by mean values they can be further differentiated by salinity variability, or deviation from mean values. In wetlands, salinity patterns function as a layer in an "environmental sieve", preventing the colonization of species unable to adapt to the environmental conditions while creating conditions for species better adapted to those conditions (Snedden and Steyer, 2013; Van der Valk, 1981). However, the effects of salinity variation on the likelihood of SAV occurrence are less clear. Increased salinity fluctuations in a greenhouse setting significantly decreased growth for a key brackish SAV species, *Ruppia maritma* (La Peyre and Rowe, 2003). Similarly, survival and biomass of *R. maritima* seedlings and adults decreased significantly at sites with large salinity fluctuations in the Florida Everglades ecotone (Strazisar et al., 2015), supporting earlier work showing that for every 3% increase in salinity standard deviation, SAV biomass decreased by an order of magnitude (Montague and Ley, 1993). Salinity variability may directly influence SAV presence by essentially acting as a benthic disturbance (van Diggelen and Montagna, 2016), and generally has been found to decrease SAV growth.

The need to describe SAV occurrence across the salinity gradient in relation to environmental conditions in coastal Louisiana is pressing as marsh loss rates remain high (Couvillion et al., 2017). Marsh loss can alter hydrologic and exposure conditions in aquatic habitats, and potentially create new SAV habitat. Further, ongoing and planned restoration efforts, including large scale sediment diversions, are predicted to impact coastal isohalines and sediment input (CPRA, 2014). Sea-level rise (SLR) and subsidence impacts much of the Louisiana coastal zone, altering salinity regimes, and changes the location and extent of shallow open-water areas suitable to SAV (Anderson et al., 2014; CPRA, 2017; Sheets et al., 2012). As wetland loss occurs, areas maintaining healthy SAV beds can continue to provide benefits to both wildlife and the remaining coastal wetlands (Brasher et al., 2012; Castellanos and Rozas, 2001; Petrie et al., 2011; Wilson et al., 2002), while newly inundated areas may become suitable for SAV establishment (Cho and Poirrier, 2005a). As SAV habitat changes across the coast will predicting the likelihood of SAV occurrence will be increasingly useful, as a coast with healthy SAV habitat provides valuable ecosystem services and can mitigate some of the effects of SLR.

To map SAV in coastal Louisiana, we developed a spatial species distribution model describing the SAV likelihood of occurrence (SLOO), and projected the model spatially. The primary objectives of this study were to 1) define the key drivers for SAV presence and absence across the salinity gradient in estuarine coastal Louisiana, 2) develop a predictive occurrence model to determine probability of SAV occurrence given a set of environmental conditions in

shallow aquatic habitats, and to 3) project the predictive occurrence model into geographic space, creating a map depicting the probability of SAV occurrence.

Methods

Study Area

The study area encompasses the coastal zone of Louisiana as defined by the Coastal Wetland Planning, Protection and Restoration Act (CWPPRA) basins (LA CWPPRA, 2011). The study area was further restricted to water bodies persistently present during the 2012-2015 period of observation (Couvillion et al., 2017). Additionally, only water bodies that were less than 2 m deep based on 2015 bathymetry data (USGS, 2015) were included in the analysis, because SAV species were not typically located at depths greater than 2 m in Louisiana coastal waters (Cho and Poirrier, 2005a; Merino et al., 2009). Offshore, marine areas (i.e., Chandeleur Islands) were excluded from this analysis as field data were not available. The study area included the full range of salinities within the Louisiana coastal zone, with sites stratified across fresh, intermediate, brackish, and saline marsh zones (Table 2.1; Sasser et al., 2014).

SAV Presence/Absence Data

Presence and absence data for SAV from two sources were used to develop the SDM (Figure 2.1). Both sources of data, referred to as (1) survey data, and (2) Wetland Value Assessments (WVA) data, include observations of SAV presence-absence collected during the summer growing season (June 1-September 15th) over a 3 year period (2013-2015), and have been previously described as noted below.

Survey data

Survey data from 158 sites for a coast-wide survey of SAV across the estuarine salinity gradient were used to inform the SLOO (DeMarco et al., 2016; Hillmann et al., 2016, La Peyre et al., 2017). Sites were randomly selected from shallow aquatic habitats across the salinity gradient. The study area included the full range of salinities within the Louisiana coastal zone, with sites stratified across fresh, intermediate, brackish, and saline marsh zones (Table 2.1; Sasser et al., 2014). Due to logistical restrictions (physically accessing site, obtaining landowner permission to access site) there were fewer sites sampled in fresh marsh (n = 27) than the other zones (intermediate = 42, brackish = 59, and saline n = 51). To determine presence or absence at each site, a quarter meter quadrat was thrown from the boat three times and presence or absence was assessed by collecting SAV from within the quadrat. If SAV was present in one quadrat, the site was considered to have SAV present. The same sites were visited in 2013, 2014, and 2015, resulting in 462 individual observations.

Wetland Value Assessments (WVA) data

SAV presence and absence data were collected in wetland value assessments (WVA) surveys by the Coastal Wetlands Planning, Protection, and Restoration Act (CWPPRA)

Environmental Workgroup (Roy, 2012; Appendix A), were also used for model calibrations. Presence or absence of SAV was determined at 60 sites over the time period by visual assessment or by rake sampling when visual assessment was impossible due to turbidity along transects across the proposed restoration project area.

Environmental parameters and spatial layer development

We compiled, analyzed and tested spatial datasets of environmental parameters known to be associated with SAV presence-absence. These datasets included data from continuous data recorders, remotely sensed satellite imagery, and bathymetry datasets (Couvillion et al., 2017; USGS, 2015).

Salinity, temperature, and water level. Continuously recorded hydrographic (salinity and water level) data from the Coast-wide Reference Monitoring System (CRMS; https://lacoast.gov/crms2/home.aspx) recorders were used to develop spatial layers for salinity and water levels. These data described spatial and temporal variation in temperature, salinity, and water level trends for the Louisiana coastal zone from October 2012 through October 2016 (Table 1). Daily means were used for the mean values in the analyses, and standard deviations of these daily means were used to assess salinity variability.

Table 2.1. Number of sites (N) across marsh zones and salinity values (PPT).

	Fresh	Intermediate	Brackish	Saline
N	27	42	59	51
Mean	1.38	3.63	5.58	13.24
Standard Error	0.13	0.13	0.16	0.26
Range	0.02 - 10.64	0.23 - 19.39	0.02 - 25.59	0.53 - 31.87

To assess the potential effect of seasonal conditions on summer SAV presence and growth, we separated hydrologic data into seasons using CRMS water temperature data. Seasons were delineated as: Summer = May 15 – September 14 (daily mean temperature $\geq 25°C$), Fall = September 15 – November 14 (daily mean temperature range = 24°C–16°C), Winter = November 15 – February 14 (daily mean temperature $\leq 15°C$), and Spring = February 15 – May 14 (daily mean temperature range = 16°C – 24°C). Temperature was only incorporated to define seasons for this model, and was not included as an environmental parameter elsewhere as temperature did not vary substantially across sites within the study area.

Daily averaged data from approximately 390 CRMS sites were interpolated in ArcGIS to create a raster surface for the salinity and water level data using hydrographic barriers to prevent interpolation across boundaries. The resulting daily interpolated data sets were used to calculate seasonal means and standard deviation, as an indicator of salinity and water level variability, and hereafter referred to as variability.
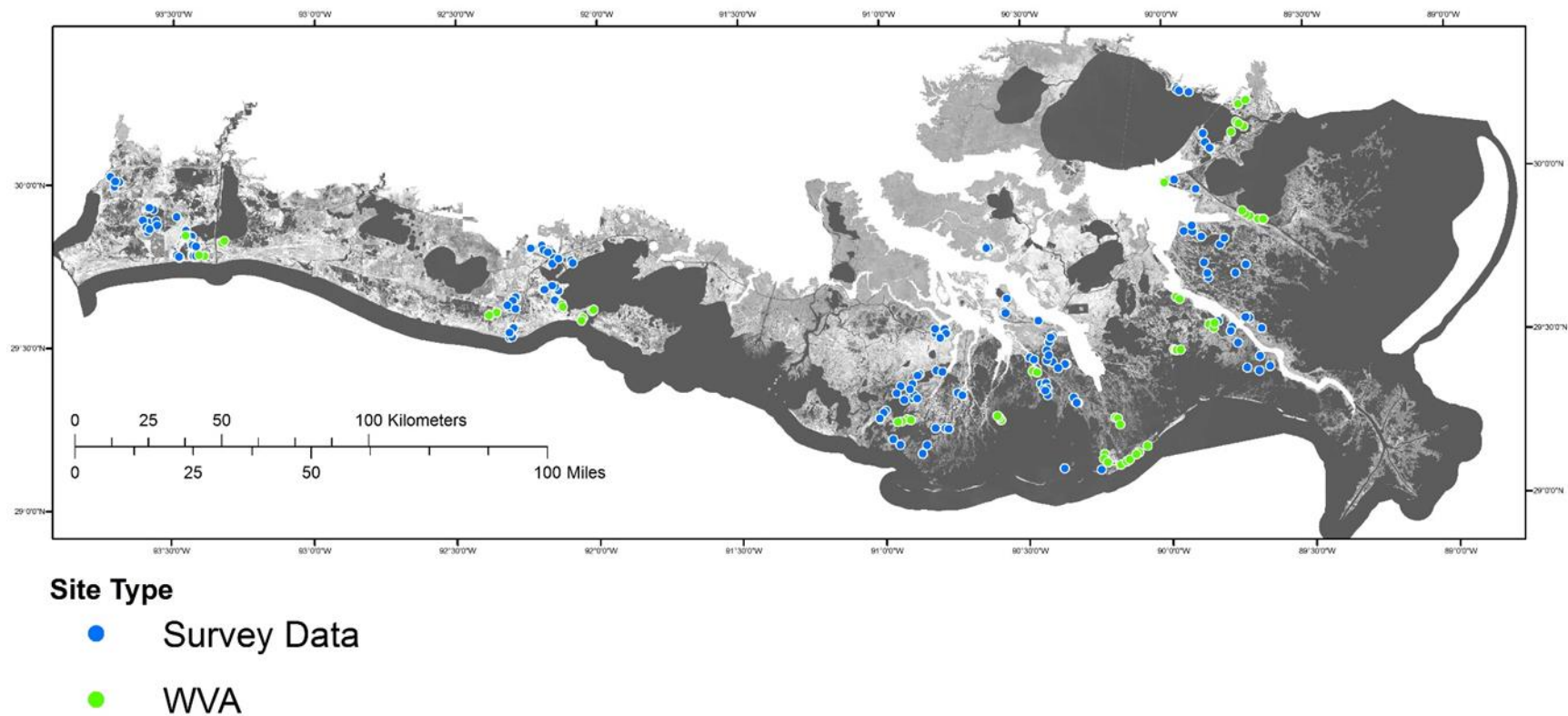
Figure 2.1. Map of field observed presence-absence sites. Survey data (blue) had 3 observations for each year sampled (2013, 2014 and 2015). Wetland Value Assessment (WVA) sites (green) had 1 observation in the year it was sampled (one year each, between 2013 and 2015).

The interpolation was performed in ArcGIS v. 10.3, using the spline with barriers interpolation technique to create daily datasets. Barriers consisted of levees, impoundments, and basin boundaries that confine hydrologic flow. These daily values were used to calculate seasonal averages and standard deviations, on a per-pixel basis (30 m pixels). Spatial layers were clipped to a 2 m depth, as this was the depth cut off point for the field sampling data.

Exposure and turbidity spatial layer development. Exposure and turbidity were not separated by seasons due to data limitations and are unitless parameters associated with an average over the study period at each location. Exposure values are an index reflecting maximum fetch, and reflectance values are a proxy for turbidity.

Exposure Index. The relative exposure (as a function of potential wave energy) of a site was considered as a potential parameter affecting the probability of SAV occurrence. This exposure index was developed using an average 2013-2015 landscape configuration (Couvillion et al., 2017). A relative exposure index was developed based upon the maximum potential fetch in 16 compass directions (every 22.5 degrees). The maximum potential fetch for the 16 compass directions was calculated in ArcGIS (v. 10.3) and an omni-directional, maximum fetch raster spatial layer was developed. This omni-directional fetch raster was then reclassified on a scale of 0-100 based upon a 2 standard deviation stretch of all values in coastal Louisiana. This measure did not account for directionality of dominant winds or waves and is essentially a measure of the relative "open-ness" of the water body.

Turbidity.To investigate the relationship between light and SAV occurrence in coastal Louisiana, we developed a spatial layer to approximate turbidity. The turbidity layer was developed using reflectance values from the Landsat 8 Operational Land Imager (OLI) in the red wavelengths of visible light, which is covered by Band 4 (0.636 - 0.673 micrometers) of the sensor. Red wavelengths of light have been shown to be highly correlated with turbidity and/or total suspended solids (TSS) in other studies around the world (Chen et al., 2007; Fritz et al., 2017; Hadjimitsis et al., 2006; Misbari and Hashim, 2016; Quang et al., 2017). The values in this layer represent an average of all cloud-free dates of imagery from 2012-2015 and is a relative measure of the average turbidity over the entire time period. The reflectance imagery is based off of satellite imagery (Landsat 8 OLI) which has a revisit period of 16 days. Cloudy conditions in coastal Louisiana often lead to cloud-contaminated images and an inability to observe turbidity for long periods of time (sometime more than 3 months). As such, we were unable to differentiate turbidity into seasons, and the resulting layer represents average turbidity conditions. There are currently insufficient field data to correlate the reflectance values to TSS, so this measure is unitless. Reflectance is hereafter referred to as turbidity.

Model development

A generalized linear model (GLM) was selected as the statistical modeling method most appropriate for the presence-absence dataset (n = 522, 462 from survey data, 60 from WVA data). The model was developed using field data sites with observations of SAV presence and absence. Field observations were intersected with the spatial layers describing seasonal mean salinity, seasonal salinity variability, seasonal water level mean, seasonal water level variability, exposure to wind, and reflectance as a proxy for turbidity at each geographic location (Table

2.2). Potential environmental variables were evaluated for model inclusion using stepwise analysis in both directions of the binomial regression model including all possible variables and post-hoc Tukey HSD tests to determine significant differences. All statistical analyses were conducted in R (The R Core Team 2016).

The final variables included in the SLOO model were selected via stepwise selection (both directions) of both single and interactive effects. To choose the most appropriate model we compared AIC scores, Wald tests, and likelihood ratio tests to assess the predictive power of the full model, a reduced model, and a null model. A probability threshold of 50% likelihood of occurrence was selected as presence (SAV = 1), and anything below that threshold was considered absence (SAV = 0). The GLM for the final SLOO Model generated a logit function to predict the probability of presence spatially for each cell in the 2017 land/water USGS coastal map (Couvillion et al., 2017). The model was developed with field data sites with observations of SAV presence and absence (n = 522). The model development tool in ArcGIS version 10.4 (ESRI, 2015) spatially projected the logit function in each pixel, creating continuous spatial layer that quantified the probability of SAV occurrence across the Louisiana coastal landscape. A confusion matrix, a table used to evaluate model performance by comparing known observations to predicted observations, was used to evaluate model performance (Lewis and Brown, 2010; Tinoco et al., 2017). The confusion matrix calculated the actual observations versus predicted SAV presence and included other performance measures such as model sensitivity and specificity.

Results

SAV presence/absence

SAV species observed included *Ceratophyllum demersum*, *Hydrilla verticillata*, *Cabomba caroliniana*, *Myriophyllum spicatum*, *Vallisneria americana*, *Potamogeton pusillus*, *Najas guadalupensis*, *Stuckenia pectinata*, and *Ruppia maritima*, and ranged from fresh to saline marsh zones and salinities All species are submerged and rooted, excluding *C. demersum*, which is rootless and primarily found floating at the top of the water column. Although other species of floating aquatic vegetation were observed, they were not included in this analysis. There was no significant difference in presence or absence in field collected data between years; SAV was present at 109 sites (n = 179) in 2013, 96 sites in 2014 (n = 170), and 97 sites in 2015 (n = 173).

Salinity and water level

Salinity ranged from 0.02 – 31.86 across all sites and seasons (Table 2.2). Mean seasonal salinity in the fall was higher (9.22± 0.3) than the other seasons. Mean salinity was similar across the other seasons, ranging from 5.47 to 6.16 (Figure 2.2a). Fall (1.61± 0.05) and spring (1.64± 0.06) salinity standard deviation were similar, with winter (2.14± 0.09) and summer (1.84± 0.06) salinity variance higher (Figure 2.2b). Mean water level was significantly different across all seasons with lowest levels in the winter (1.72± 0.04 m), and steadily and significantly increased into the fall (mean = 2.12± 0.04 m) season across the year (Figure 2.2c). Standard deviation in water level was significantly lower in the fall (0.35± 0.01 m), and similar across the other seasons (Figure 2.2d). Water level data were ultimately removed from the model as attempts to spatially reconcile the CRMS recorded depth and bathymetric elevation data were

unsuccessful. This was not entirely unexpected, as bathymetry data in Louisiana is known to have very high error rates (Couvillion, personal communication).

Exposure index and turbidity

Exposure index values ranged from 15 to 79, with a mean value of 16.67 (± 0.27), with the majority of exposure values between 15 and 18 (Table 2.2). There were very few instances of exposure values above 50 (n = 9); highest exposure index value incorporated into the model was 79. Higher exposure numbers reflect potentially higher wave/wind energy at the site. Turbidity values ranged from 6098 to 8557, with a mean value of 7061 (± 20). The highest turbidity values were located near freshwater outflows of the Atchafalaya River and the Mississippi River Delta, indicating low water clarity.

Model

Both the AIC scores and ANOVA for the variables in the full model indicated that the reduced model was better (Full model AIC = 575.87; Reduced model AIC = 567.01; df = 521). The ANOVA tests for the full model showed that winter mean salinity and turbidity were significant ($p < 0.05$) predictors of SAV presence. Exposure was included in a stepwise (both directions) reduced model from all of the evaluated predictor variables ($p < 0.07$). The inclusion of an interaction effect did not improve model performance, and was removed from the final model. Model comparison tests indicate that there was no significant difference between the reduced and the full models, so the reduced model was chosen for the final analyses and included winter mean salinity, turbidity, and exposure (Figure 2.2). Significant predictors were winter mean salinity ($p < 0.00001$), and reflectance ($p = 0.002129$), with exposure included in the final model ($p = 0.068871$).

The binomial logistic regression equation for the final SLOO Model is:

$$Logit(Presence) = 6.6330 - 0.2068(WinterM) - 0.0007(REFL) - 0.0277(EPO)$$

Where Logit (Presence) is the logit function for the likelihood of presence, *WinterM* is mean winter salinity, *REFL* is reflectance, and *EPO* is exposure.

The corresponding logit function for the SLOO is:

$$P(SAV = 1) = \frac{[\exp(6.6630 - 0.2068(WinterM) - 0.0007(REFL) - 0.0277(EPO)]}{[1 + \exp(6.6630 - 0.2068(WinterM) - 0.0007(REFL) - 0.0277(EPO)]}$$

Table 2.2. Mean seasonal (± SE) salinity, salinity variance, mean water depth (m), water depth variance, exposure index, and reflectance values for observed sites (n = 522) 2013 - 2015. Reflectance and exposure values are not seasonally differentiated due to data limitations, and are represented as a mean value over the period of study.

Explanatory Variable	Winter	Spring	Summer	Fall
Mean Salinity (ppt)	6.1 (0.27)	5.47 (0.26)	6.16 (0.24)	9.22 (0.30)
Mean Salinity Minimum (ppt)	0.02	0.02	0.04	0.02
Mean Salinity Maximum (ppt)	31.86	26.14	26.96	31.13
Salinity Variance (ppt)	2.14 (0.07)	1.64 (0.07)	1.85 (0.07)	1.61 (0.05)
Salinity Variance Minimum (ppt)	0.01	0.01	0.01	0.01
Salinity Variance Maximum (ppt)	7.38	6.86	8.14	8.53
Mean Depth (m)	1.17 (0.04)	1.86 (0.04)	1.98 (0.04)	2.13 (0.04)
Mean Depth Minimum (m)	-0.79	-0.56	-0.36	-0.34
Mean Depth Maximum (m)	6.33	6.19	6.13	6.42
Depth Variance (m)	0.38 (0.01)	0.40 (0.01)	0.40 (0.01)	0.35 (0.01)
Depth Variance Minimum (m)	0.07	0.08	0.14	0.07
Depth Variance Maximum (m)	1.38	1.10	1.60	1.77
Reflectance Mean*	7059 (20)	7059 (20)	7059 (20)	7059 (20)
Reflectance Minimum	6098	6098	6098	6098
Reflectance Maximum	8557	8557	8557	8557
Exposure Mean*	16.67 (0.27)	16.67 (0.27)	16.67 (0.27)	16.67 (0.27)
Exposure Minimum	15	15	15	15
Exposure Maximum	79	79	79	79

The logit function was attached to the value for the environmental data derived from CRMS recorders depicting mean winter salinity, exposure, and turbidity at each pixel to develop a continuous spatial layer describing probability of SAV occurrence across the Louisiana coastal landscape (Figure 2.3).

The SLOO model performed satisfactorily to predict the presence of SAV in the Louisiana coastal zone, with a correct classification rate of 0.738 (Table 2.3). As indicated by a very high sensitivity rate (or true positive) of 0.868, and a moderate specificity rate (true negative) of 0.557. The model is strongly influenced by changes in winter mean salinity, turbidity, and exposure.

a)   b)   c)
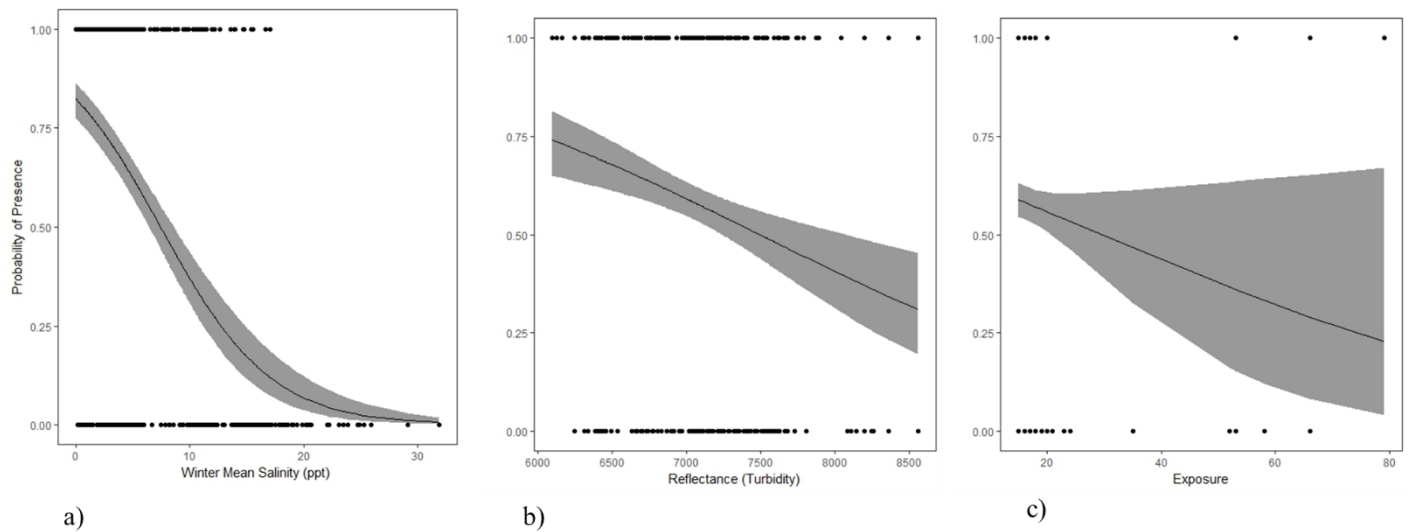
Figure 2.2. Contour plots for effect of significant predictors on the likelihood of submerged aquatic vegetation (SAV) presence in the spatial likelihood of occurrence (SLOO) model. a) Winter Mean Salinity vs probability of presence, b) Reflectance vs. probability of presence, and c) Exposure vs. probability of presence.

Table 2.3. Measured error rates for the submerged aquatic vegetation (SAV) likelihood of occurrence model (SLOO). A confusion matrix was designed with presence/SAV = 1 and absence/no SAV = 0. If a cell was given a probability of 50% or greater likelihood of presence, it was coded as present = 1.

Measure	Error Rate
Correct Classification Rate	0.736
Misclassification Rate	0.264
Sensitivity (true positive rate)	0.861
Specificity (true negative rate)	0.564
False Positive Rate	0.436
False Negative Rate	0.139

Discussion

The model accurately predicts SAV presence 74% of the time across the Louisiana study area. The SLOO model identifies three primary drivers for SAV occurrence across Louisiana, mean winter salinity, turbidity, and exposure. Increases in mean winter salinity, turbidity, and exposure decreased the likelihood for SAV presence during the summer growing season coast-wide. These results indicate that SAV occurrence across large landscapes can be predicted based on a few key environmental parameters, providing a means to both estimate current SAV habitat and to predict future changes to SAV habitat availability. Moreover, the use of imagery data to approximate turbidity as a proxy for light availability is the first application of this method in coastal Louisiana.

The strong response of SAV occurrence to winter salinity is likely driven by the species specific adaptations and competitive abilities of dominant species. In Louisiana, coast-wide species occurrence was dominated by *H. verticillata*, *C. demersum*, and *M. spicatum*, with other species (*N. guadalupensis*, *V.americana*, and *R. maritima*) found much less frequently (Hillmann et al., 2016). Each of these SAV species are known for being "winter-hardy" as they overwinter in the benthos as roots, tubers, or winter buds (or turions) and regenerate vegetatively instead of from seed (Cho and Poirrier, 2005b; Cronk and Fennessy, 2001; Nichols and Shaw, 1986; Van den Berg et al., 2003). In this region, as soon as temperatures increase above 15° C plants can begin to germinate, and SAV shoots are able to grow rapidly to form canopies (Haller et al., 1976; Jarvis and Moore, 2008; Rybicki and Carter, 2002). These SAV species are dominant in shallow aquatic habitats in the fresh marsh zones of coastal Louisiana (Hillmann et al., 2016) but are sensitive to increased salinities. Consequently, increased salinities during early growth (i.e. winter) negatively impact their likelihood of occurrence.

The absence of SAV in the coastal marshes adjacent to the open Gulf of Mexico, particularly in the bays proximate to the Mississippi River (Figure 2.3) of the study area may be due to the inability of the salt-tolerant species (i.e., *R. maritima*) to colonize and germinate under exposure to high wave and wind energy. Reviews of somewhat limited data for non-marine SAV species indicated that fresher SAV, while unable to persist in high current or wave conditions, may be more tolerant to lower light levels as compared to more salt tolerant SAV (Koch, 2001, and references therein). Declines of SAV as the result of physical disturbances have been well documented in other locations (Fonseca and Bell, 1998; Gurbisz et al., 2016; Pulich and White, 1991; Robbins and Bell, 200; Santos et al., 2011) and in specific species (Barrat-Segretain, 2001; Martin and Valentine, 2012; Strand and Weisner, 2001). In particular, SAV species in Louisiana that are able to persist in brackish salinities and high turbidities (*R. maritima* and *M. spicatum*) have a low tolerance to physical disturbance (Cho and Poirrier, 2005b; Martin and Valentine, 2012). Although the relationship between exposure and presence is the most uncertain of the significant environmental drivers identified (Figure 2.2c), it is likely due to the coarseness of the exposure index itself. An exposure index with a finer resolution that accounts for wave and wind orientation may improve model predictions by more accurately capturing the linkage between SAV presence-absence and exposure, particularly if seasonal exposure can be calculated based on dominant wind direction and speed.

Past work on SAV has identified light to be a dominant factor influencing SAV occurrence (Koch, 2001; Kemp et al., 2004; Poirrier et al., 2009). The SLOO model corroborates this work,
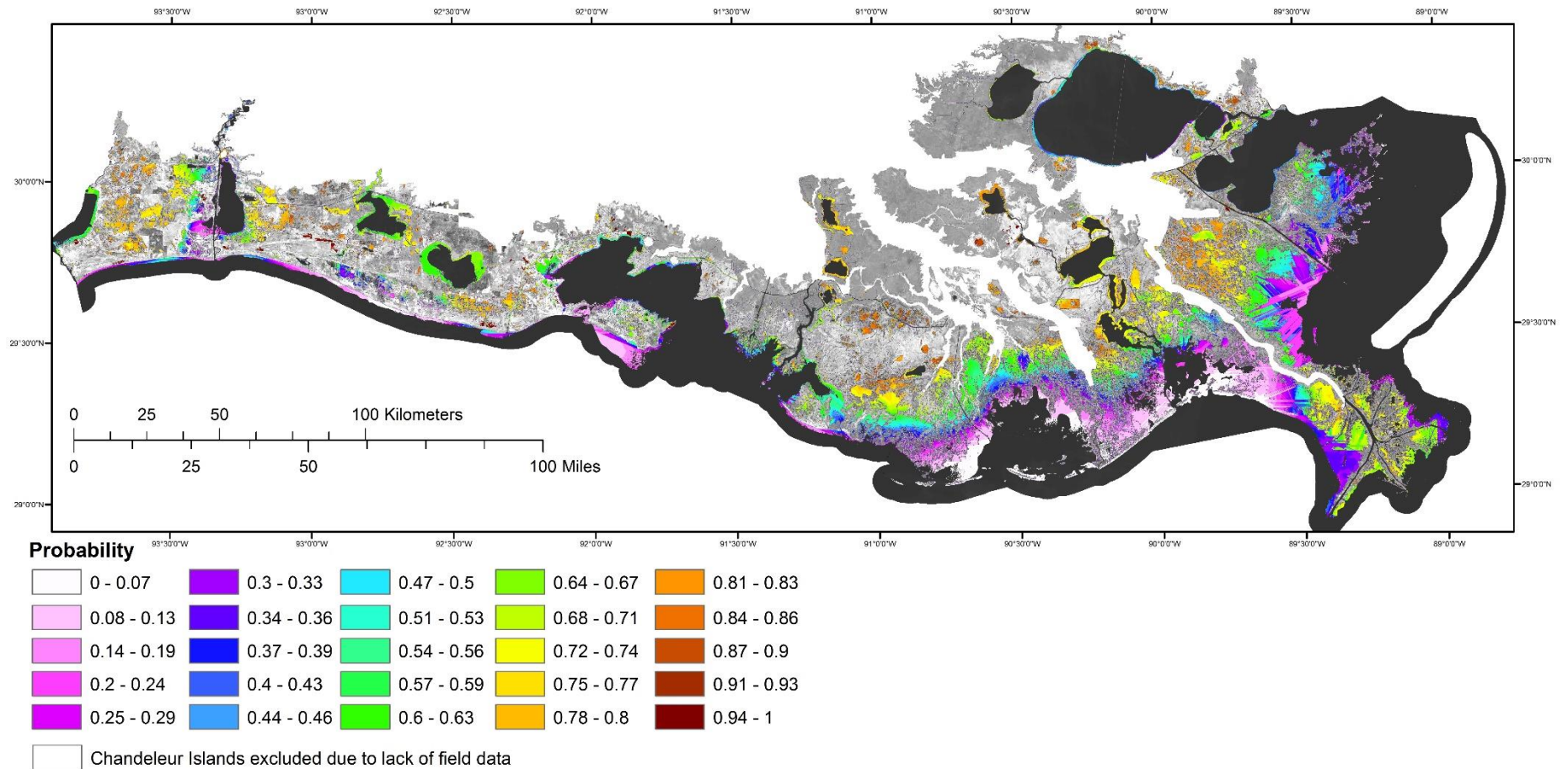
Figure 2.3. Probability of submerged aquatic vegetation (SAV) occurrence across coastal Louisiana (2013 – 2015)

as the probability of SAV presence decreased linearly as turbidity increased. Presumably, turbidity wouldhave a strongerffect on SAV occurrence if seasonal turbidity was identified, as light availability has been shown to have a greater impact on seedling plants than adults (Cho and Poirrier, 2005a; Cho and Poirrier, 2005b; Fourqurean et al., 2003).

The SLOO model tended to over-predict presence and under-predict absence. The errors in prediction are concentrated in areas where (1) brackish and saline marsh zones converge, (2) areas with high freshwater outflow, and (3) intensive human management activities affecting water level and salinity occur (Figure 2.4). There are several possible reasons for this: 1) the timing of sampling fails to capture the full growing season and thus probability of presence, 2) the lack of directionality and seasonality in exposure and turbidity does not accurately reflect field conditions, 3) anthropogenic activities which significantly impact local conditions, and/or 4) there is an interaction effect missing in the model.

The focus on a summer growing season in coastal Louisiana may not capture the full influence of seasonal environmental conditions on the probability of presence. In the continental United States, the growing season of SAV is loosely defined as the summer months, when temperatures and light availability are high enough for growth (Dennison et al., 1993; Rybicki and Landwehr, 2007; Stevenson et al., 1993; Vis et al., 2003). However, the subtropical climate of Louisiana is characterized by mild winters (https://www.ncdc.noaa.gov/climatenormals/clim60/states/Clim_LA_01.pdf), with average air temperature in January (the coldest month) at 45°F, and even milder water temperatures averaging 60°F. Further, Cho and Poirrier (2005b) identified two separate growing seasons for SAV in Lake Pontchartrain, Louisiana, finding high percent cover of SAV species in the summer and fall seasons. An intra-annual study in one Louisiana basin identified high SAV biomass in May and July, with a low in December (Hillmann et al., in review), and further differentiated by marsh vegetation zone. A field sampling designed to match the seasonal growth of SAV and corresponding environmental conditions may be more reflective of patterns of occurrence.

The incorporation of orientation into exposure to capture dominant winds, and the identification of seasonal trends in both exposure and turbidity have the potential to provide significantly greater predictive capacity. SAV in the northern Gulf of Mexico are known to persist in sheltered areas of open bays and in areas protected from wind/waves in relatively large water bodies (Hillmann et al., 2016). Including directionality and orientation spatially as well as seasonally into the exposure index would more accurately reflect existing seasonal wind patterns in the field (Allison et al., 2016; Feng and Li, 2010; Walker and Hammack, 2000). Turbidity patterns are similarly seasonal as they are influenced by seasonal (spring) riverine flooding, winter cold fronts, and summer storm events (hurricanes). The effects of increased exposure and/or turbidity have a greater influence on SAV species during the seedling stage (Doyle and Smart, 2001; Jarvis and Moore, 2008; Strazisar et al., 2013) as seedlings are more sensitive than adult plants to fluctuating salinity, decreased light in the water column, and water movement. The effects of and interactions among exposure and turbidity could be seasonally significant, and a better resolution of these drivers would improve model performance and representation of SAV occurrence.
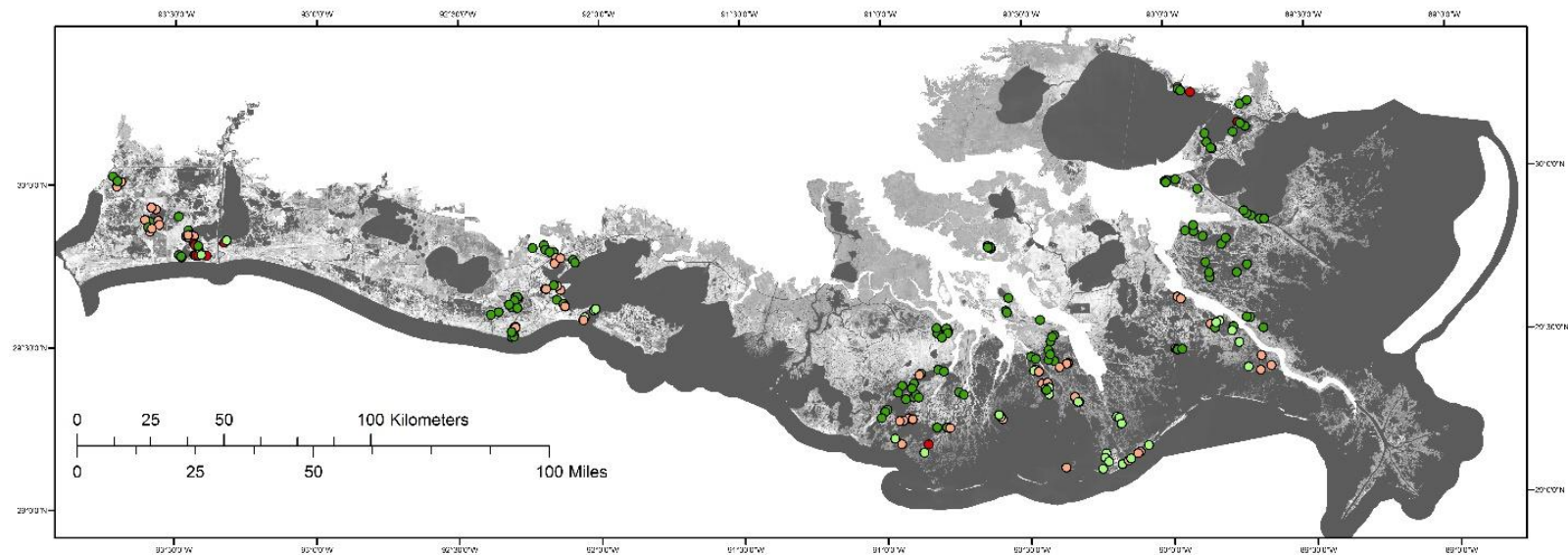
Spatial Model Occurrence vs. Field Confirmed Occurrence

- ○ Correct - Field = Absence / Model = Absence
- ● Correct - Field = Presence / Model = Presence
- ● Incorrect - Field = Absence / Model = Presence
- ● Incorrect - Field = Presence / Model = Absence

Figure 2.4. Areas of error between observed and predicted presence-absence at sampled sites.

Louisiana's coast is largely privately owned and as such is intensely managed for various natural use efforts, creating highly dynamic and variable environmental conditions (Merino et al., 2005; Snedden and Steyer, 2013; Syvitski et al., 2009) that can in turn have abrupt and localized effects on the SAV community. Anthropogenic influences are inherently difficult to parameterize for model applications and include commercial and recreational boating, commercial fishing, chemical industries, navigation, and water level management activities – all of which can significantly influence the ability for SAV to colonize and germinate in the immediate vicinity. In fact, high error in western Louisiana, near the Sabine National Wildlife Refuge could potentially indicate human management activities in this area, although the results of these efforts remain somewhat unclear (https://www.fws.gov/refuge/Sabine/what_we_do/resource_management.html). This influence of human management, along with the active natural processes in the coast complicate our ability to model and predict environmental conditions (CPRA, 2012; Keddy et al., 2006; Snedden and Steyer, 2013; White and Visser, 2016). Incorporating the regional activities and natural processes may improve model accuracy that while difficult to evaluate on a large scale, may be testable as a local, site specific study.

Although the inclusion of an interaction effect decreased overall model performance, future improvements might incorporate the interaction of salinity with exposure and turbidity. The strong salinity response is spatially distinctive, and marsh vegetation zones (Sasser et al., 2014) and SAV may respond uniquely to these interactions. The physiological tolerances to hydrologic stressors of an assemblage of species as they are organized by salinity patterns could be dictating the presence of SAV across large landscapes (Koch, 2001; Lhotsky et al., 2016; Patrick and Weller, 2015). The creation of submerged habitat zones based on salinity patterns and exposure and the development of models specific to these spatial zones will reflect natural separations between species assemblages, resulting in more accurate predictive models.

Conclusion

Across the NGOM coast, SAV communities are known to exist across a wide range of salinity, water clarity, and exposure conditions (DeMarco et al., 2016; Hillmann et al., 2016; Merino et al., 2009). However, this large-scale analysis identified hotspots for SAV and areas less likely to support SAV communities. Specifically, there was marked SAV absence in the saline and brackish marsh areas located in the more exposed, down-estuary regions in the Louisiana coastal landscape. In contrast, interior estuarine habitats with lower salinity, turbidity, and/or exposure were found to have a high likelihood of SAV occurrence. It is probable that the combined salinity and turbidity patterns in these areas are only suitable for SAV species that, while tolerant of brackish to saline salinities and low water clarity, are unable to colonize or persist in high exposure habitats, preventing the occurrence of any SAV in down-estuary coastal waters.

Development of the SLOO model relied heavily on the field collection of presence/absence data to create a SDM modeling tool that can quantify drivers of SAV occurrence, represent these drivers spatially, and inform coastal restoration and management. Coastal restoration projects Louisiana wetlands may significantly alter environmental and hydrologic conditions (Allison and Meselhe, 2010; CPRA, 2017; Kemp et al., 2016; Snedden et al., 2007; White and Visser, 2016) and ultimately the extent and location of SAV communities by changing salinity, water clarity, and exposure patterns. It may be advantageous to consider

both changes in the annual and the seasonal patterns to predict SAV response to restoration efforts. Incorporation of the SLOO model and map into coastal management and restoration strategies provides a useful predictive tool to ensure healthy aquatic ecosystems and robust SAV habitat in future coastal landscapes.

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CHAPTER 3. SEASONAL AND SPATIAL INTERACTIONS BETWEEN SUBMERGED AND FLOATING AQUATIC VEGETATION CREATE DISTINCTIVE DIFFERENCES IN ESTUARINE HABITATS IN BARATARIA BASIN, LOUISIANA

Introduction

Submerged aquatic vegetation (SAV) are ecologically important in shallow aquatic habitats, supporting critical fish and wildlife and improving water quality (Orth et al., 2016). SAV leaves, roots, and shoots are important food resources for many waterfowl species (Chabreck et al., 1989; Wilson et al., 2002), particularly in the winter, and provide both food and habitat structure to nekton assemblages (Bakker et al., 2016; Hitch et al., 2011; Kanouse et al., 2007). Areas supporting SAV can provide different ecological services compared to bare benthic bottoms, and are considered desirable in coastal landscapes. Across the northern Gulf of Mexico, SAV exists across estuarine gradients (Merino et al., 2009) and seasons (Cho and Poirrier, 2005a), but interactions across season and estuarine gradients remain largely unknown.

SAV occurrence and coverage vary spatially and temporally in coastal habitats (Findlay et al., 2014; Hillmann et al., 2016; Merino et al. 2005). Environmental drivers such as salinity regimes, exposure to wind and waves, light availability, and temperature affect each species differently (Biber and Cho, 2016; Bornette and Puijalon, 2011; Patrick and Weller, 2015), and often vary across estuarine gradients (Hillmann et al., 2016; Merino et al., 2009). Past studies have shown that individual SAV species exhibit different peaks of biomass and growth at different times (Cho and Poirrier, 2005a; Santos et al., 2010), and that seasonal changes in species' distribution are influenced by salinity and exposure regimes (Berglund et al., 2002; Lirman et al., 2008).

Seasonal shifts in species composition are common in SAV assemblages (Burgos-León et al., 2013; Shields et al., 2016). SAV species dominance is related to salinity, light, and temperature, and will change as the environmental conditions change with each species responding with growth or decay. Competition is generally highest in fresh marsh habitats where, in the absence of stress, competitive abilities lead to dominance by a few rapidly growing species (Grime, 1977). In the absence of disturbance, inferior competitors are unlikely to experience any "release" from competition. Seasonal variation can induce changes in environmental conditions that will in turn affect SAV growth, granting limited resources to species that would otherwise be unable to persist (Berglund et al., 2002; Kaldy et al., 2015; Rybicki and Carter, 2001).

In submerged habitats the most valuable resource is light (Barko et al., 1986; Doyle and Smart, 2001; Kemp et al., 2001). As floating aquatic vegetation (FAV) always occupies the prime position for light acquisition (van Gerven et al., 2015), the formation of dense FAV canopies changes the structure of aquatic ecosystems, preventing the growth of submerged species and altering ecological functioning of these habits. In some cases, environmental conditions (climate, nutrients, depth, water body size) can increase FAV cover significantly and prevent the establishment of any SAV assemblages in the ecosystem. This may initiate a regime shift in aquatic habitats from SAV dominated habitats with high water clarity to FAV dominated with turbid conditions (Scheffer et al., 2003; Scheffer and van Nes, 2007). This is particularly concerning in sub-tropical habitats of the Louisiana Mississippi River Delta, which have seen a massive increase in invasive water hyacinth presence and cover since its introduction in the late

1800s (Penfound and Earle, 1948). To better understand the spatial and temporal patterns of SAV in this area, it is useful to evaluate its relationship to FAV.

Understanding seasonal and spatial SAV patterns may help to guide management and restoration in estuaries. SAV is a valuable coastal resource found in much of south Louisiana, an area that is currently undergoing one of the most massive coastal restoration and flood protection endeavors in the United States (CPRA, 2017). Moreover, Louisiana contains a variety of salinity regimes, creating a dynamic ecosystem undergoing both rapid natural and anthropogenic spatial and temporal changes. Within estuaries, salinity gradients, hydrodynamics, and geomorphology shape distinct coastal habitats (Cloern et al., 2014; Seers and Shears, 2015), that can be described by long-term vegetation communities, representing fresh (F), intermediate (I), brackish (B), and saline (S) marsh zones (Penfound and Hathaway, 1938; Visser et al., 1998).

The objectives of this study were to 1) understand how patterns in SAV and FAV presence and cover vary seasonally and across an estuarine gradient, and 2) identify relationships between SAV and FAV. SAV and FAV are expected to respond spatially and temporally to changes in environmental drivers, such as salinity, temperature and light availability. Furthermore, FAV is expected to impact SAV where they co-occur. Understand how environmental conditions and interactions between FAV and SAV among marsh zones and seasons will broaden the understanding of aquatic ecosystem functioning in estuaries.

Methods

Study Area

The study was conducted within shallow waters (USGS, 2015) in the Barataria Basin estuary in southeast Louisiana, with explicit boundaries defined by US Geological Survey hydrologic unit codes (HUC 08090301). Barataria Basin is a semi-enclosed estuarine bay situated along the western side of the Mississippi River with wide expanses of emergent marshes, punctuated by forested swamp, marsh ponds, shallow bays, and industrial canals. Barataria Basin contains several freshwater diversions and many other wetland restoration projects including marsh creation and shoreline protection (http://coastal.la.gov/our-plan/annual-plan/).

Site Selection and Sampling Design

Within Barataria Basin, 4 sites were selected from fresh (F), intermediate (I), brackish (B), and saline (S) marsh vegetation zones, as identified in Sasser et al. (2014), totaling 16 sampling sites across the basin (Figure 3.1). Potential areas for site selection were first identified via aerial imagery, and final locations for sites for repeated sampling were determined in the field. As one of the primary project goals was to evaluate intra-annual changes in SAV assemblages, sites supporting, or deemed likely to support, SAV at the first field visit were specifically targeted. Final sites selected were all less than 2 m deep. Each site was visited every 6-8 weeks in 2015, beginning February 1st and ending December 10th. Sampling seasons were defined as early spring (ERLY_Spring; February-March), late spring (April; LT_Spring), early summer (May-June; ERLY_Summer), late summer (August; LT_Summer), fall (September-October; Fall), early winter (December; ERLY_Winter), and late winter (February; LT_Winter).
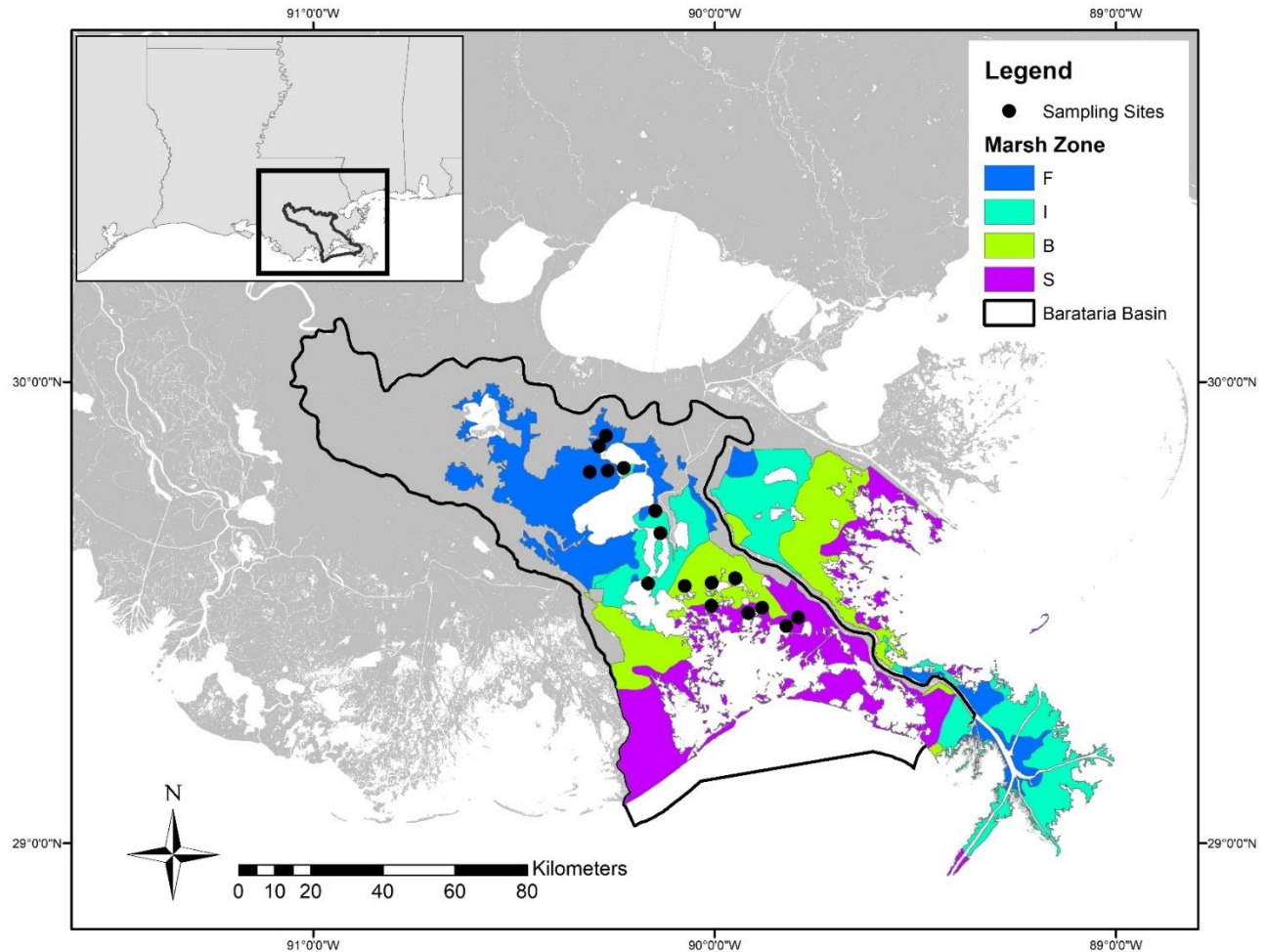
Figure 3.1. Sampling sites located in Barataria Basin, Louisiana. Samples were collected every 6-8 weeks in 2015. F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone.

Data Collection

Presence-Absence. Two transects were sampled by boat at each field site, with the two transects run at right angles to one another, forming a "T". Each transect was approximately 50 meters long, and included 10 rake sample points per transect. A drop rake sample was collected approximately every 5 meters, and recorded depth, presence or absence of SAV, presence or absence of FAV, and species (if present). This method covered a larger area than discrete sampling methods. These data were used to calculate a species-specific percent occurrence value, which was the number of times a species was observed in a transect, divided by the total number of transects within each season and a marsh zone (4 per marsh zone).

Percent Cover. Sites were accessed via mudboat or airboat, and in occasional instances, by walking in if normal routes became dry. Water samples for turbidity testing (NTU-Hach 2100Q, Hach, CO.) were collected upon arrival at the site before disturbing benthic sediments.

Salinity and temperature were recorded (YSI Pro2030, YSI Incorporated, OH.) at approximately half a meter under the water surface (when possible).

After collecting the water quality data, a 0.25 m² quadrat was haphazardly thrown from the boat and anchored in place. If vegetation was present in the quadrat, either floating or submerged, it was identified to the species level, and percent cover was assessed from within the quadrat. Triplicate percent cover estimates were collected at each site, and mean values of the three replicates were used for analyses.

Data Analyses

Environmental variables. Salinity, turbidity, depth, and temperature were evaluated for significant differences using ANOVA testing by marsh zone, season, and interactions between marsh zone and season. The threshold for significance for all analyses was identified as $p < 0.05$ unless indicated otherwise.

SAV percent occurrence, presence/absence and species assemblages. SAV percent occurrence was used for describing species assemblages among marsh zones only, and described the number of times a species of SAV was observed in a marsh zone, divided by the total transects sampled in a marsh zone. A binomial generalized logistic model described the effect of marsh zone and season on SAV and FAV presence/absence, and two-way ANOVA tests compared SAV presence/absence among marsh zones and seasons. FAV was separated into a native and invasive FAV groups. Post-hoc tests using Tukey's honest significant difference (HSD) described strength of differences between presence/absence across groups (The R Group 2016). Species assemblages and presence/absence were assessed and described using transect data only.

Percent Cover. Percent cover was analyzed using the discrete quadrat data. A linear regression model was created to assess the response of SAV percent cover to the single and interactive effects of FAV cover, marsh zone and season. An additional linear regression model was created to evaluate the effects of marsh zone and season on FAV cover alone. Two-way ANOVA tests, accounting for repeated measures, evaluated the effects of marsh zone and season on SAV and FAV percent cover, and Tukey's HSD and least squared means tests using the lsmeans program (Russel, 2016) compared differences in cover across groups.

Results

Environmental variables

Seasonal patterns in salinity different among the marsh zones as indicated by a significant interaction effect (F value = 6.825; $p < 0.0001$) (Table 1; Figure 3.2a). Salinity in saline marsh zones in early (13.95± 1.19) and late winter (13.10± 1.60) washigher than all other marsh zone and season combinations. Salinity in fresh marsh zones across all seasons (0.15 – 0.2) except early winter was lower than saline in all seasons, and different from brackish in all seasons except early summer.

Depth differed among marsh zones and seasons independently of one another. Depth was different across all marsh zones (F value = 18.214; p < 0.001) except between brackish and intermediate marsh zones (Table 3.1; Figure 3.2b). Mean depth ranged from 0.87 ± 0.08 in fresh marsh zones to 0.45± 0.03 in saline marsh zones. Seasonal depth was lower in late winter from the other seasons (F value = 5.490; p < 0.001), when mean water depth (0.36± 0.04) was lower than all the other seasons in all marsh zones.

Seasonal patterns in water temperature differed among marsh zones and seasons. There was an interaction of marsh zone and season for temperature (F value = 2.208; p = 0.008). Differences were largely driven by low temperatures in the fresh marsh zone in late winter (16.4°C) (Table 3.1; Figure 3.2c). Turbidity (25.9 – 36.6 NTUs) did not differ among marsh zones or seasons (Table 3.1: Figure 3.2d).

*S*AV and FAV presence

SAV presence differed among marsh zones (Chisq p < 0.001), but not among seasons, nor was there any interaction between season and marsh zone. Fresh, intermediate, and brackish were all similar in terms of SAV presence and significantly greater as compared to saline (Figure 3.3). Presence was highest in intermediate marsh zones (96%), followed by fresh (79%) and brackish (67%) and was lowest in the saline marsh zone (26%).

There was a significant effect of season (Chisq = 0.018) and marsh zone (Chisq p <0.001) on invasive FAV presence, but no interaction between season and marsh zone. Invasive FAV occurred in the fresh and intermediate marsh zones only and was less present in the early spring. Native FAV species differed among marsh zones (Chisq < 0.001), but there was no effect of season or interaction between season and marsh zone. Native FAV also only occurred in the fresh and intermediate marsh zones.
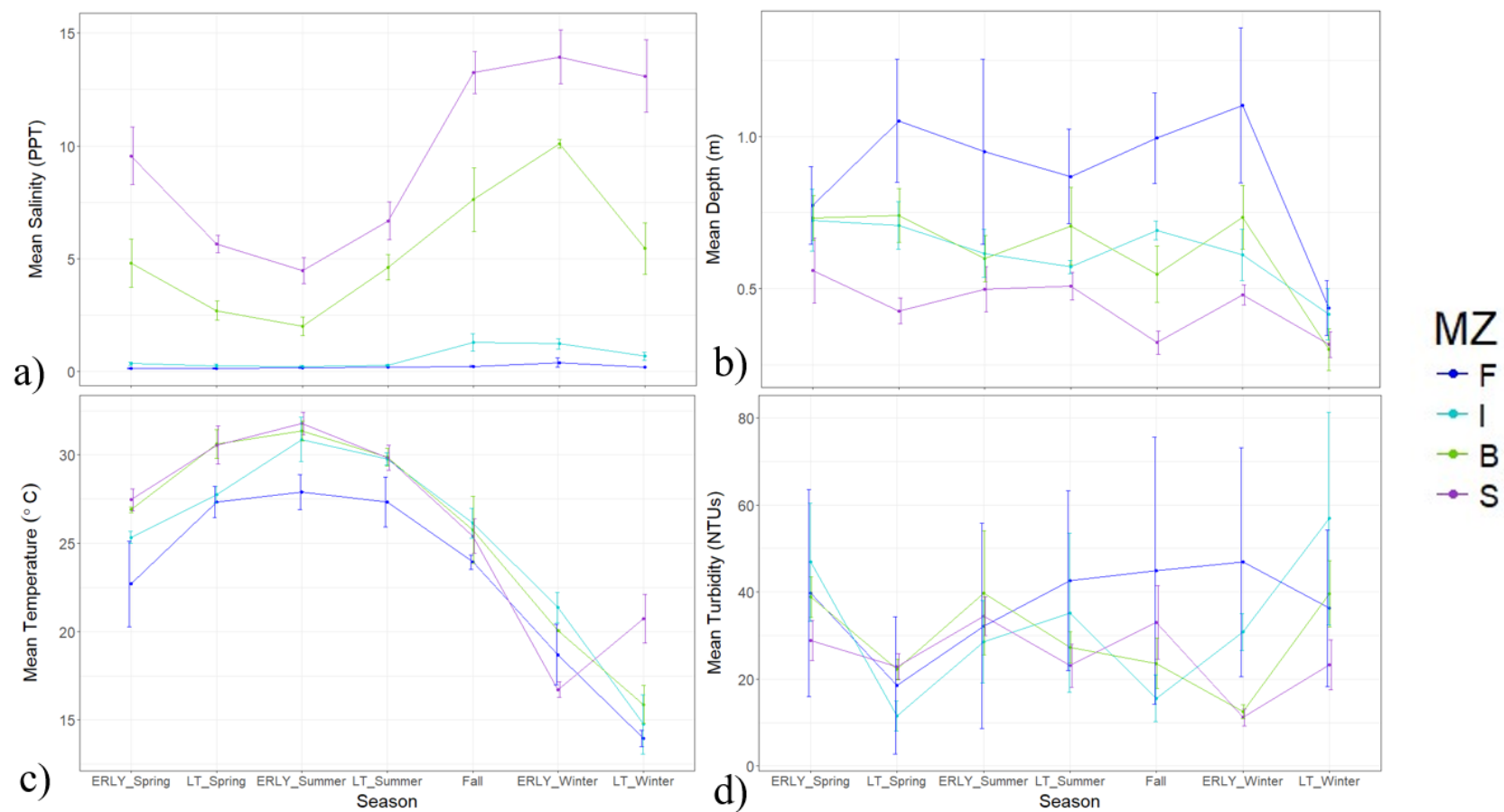
Figure 3.2. Environmental variables across season by marsh zone. a) Mean salinity (PPT) ± SE, b) mean depth (m) ± SE, c) mean water temperature (°C) ± SE, and d) mean turbidity (NTUs) ± SE. MZ = marsh zone, F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone.

[1]Table 3.1. Environmental variables by marsh zone and season. Mean (± SE) and range are reported.

	Salinity (PPT)	Turbidity (NTUs)	Temperature (°C)	Depth (m)
		Overall		
Fresh	0.21 (0.03) 0.1 - 0.8	36.6 (7.5) 1.5 - 111.0	22.7 (2.4) 16.4 - 27.7	0.87 (0.08) 0.25 - 1.6
Intermediate	0.61 (0.1) 0.1 - 1.9	32.2 (5.3) 4.8 - 126.0	25.3 (0.3) 24.6 - 25.9	0.62 (0.03) 0.23 - 1.01
Brackish	4.86 (0.53) 0.7 - 10.3	30.1 (3.1) 11.0 - 96.7	26.9 (0.2) 26.6 - 27.3	0.62 (0.04) 0.15 - 1.12
Saline	9.36 (0.76) 3.3 - 16.4	25.9 (2.1) 7.3 - 57.7	24.5 (0.62) 25.4 - 28.7	0.45 (0.03) 0.19 - 0.97
		Early Spring		
Fresh	0.15 (0.03) 0.1 - 0.2	39.8 (23.8) 10.0 -111.0	22.7 (2.4) 16.4 - 27.7	0.77 (0.13) 0.49 - 1.03
Intermediate	6.3 (1.2) 0.3 - 18.6	48.9 (13.6) 14.1 - 80.5	25.3 (0.3) 24.6 - 25.9	0.72 (0.10) 0.55 - 1.01
Brackish	4.80 (1.07) 2.3 - 7.5	38. 9 (4.6) 30.7 - 52.1	26.9 (0.2) 26.6 - 27.3	0.73 (0.07) 0.63 - 0.95
Saline	9.56 (1.26) 6.6 - 13.3	28.9 (4.57) 17.4 - 39.9	24.5 (0.62) 25.4 - 28.7	0.56 (0.11) 0.39 - 0.97
		Late Spring		
Fresh	0.15 (0.03) 0.1 - 0.2	18.5 (15.7) 1.5 - 65.7	37.3 (0.9) 25.0 - 28.8	1.05 (0.20) 0.28 - 1.60
Intermediate	3.8 (0.5) 0.1 - 21.6	11.5 (3.5) 5.22 - 21.2	27.8 (0.5) 27.0 - 29.1	0.71 (0.08) 0.56 - 0.93
Brackish	2.70 (0.43) 1.7 - 3.7	22.2 (2.3) 18.2 - 29.7	30.6 (0.8) 30.2 - 32.9	0.60 (0.09) 0.43 - 0.97
Saline	5.65 (0.38) 4.9 - 6.3	22.9 (3.0) 18.9 - 31.7	31.78 (1.08) 30.5 - 33.9	0.43 (0.04) 0.35 - 0.55
		Early Summer		
Fresh	0.17 (0.03) 0.1 -0.2	32.2 (23.6) 5.6 - 79.1	27.9 (1.0) 26.2 - 29.6	0.95 (0.30) 0.5 - 1.53
Intermediate	1.1 (0.2) 0.1 - 6.5	28.6 (9.4) 8.3 - 52.8	30.9 (1.3) 28.7 - 34.4	0.62 (0.08) 0.47 - 0.84
Brackish	2.00 (0.42) 0.7 - 2.7	39.8 (14.3) 22.7 - 96.7	31.4 (0.5) 29.1 - 31.8	0.60 (0.08) 0.45 - 0.87
Saline	4.48 (0.58) 3.3 - 6.5	34.4 (4.4) 21.3 - 48.5	31.78 (0.63) 30.5 - 33.9	0.51 (0.07) 0.35 -0.76
		Late Summer		
Fresh	0.2 (<0.1) 0.2 - 0.2	42.6 (20.7) 5.1 - 76.4	27.3 (1.4) 25.6 - 30.1	0.87 (0.16) 0.57 - 1.09
Intermediate	6.4 (1.1) 0.9 - 13.6	35.2 (18.2) 9.0 -88.6	29.8 (0.4) 29.0 - 30.6	0.57 (0.02) 0.51 - 0.60

table cont'd

	Salinity (PPT)	Turbidity (NTUs)	Temperature (°C)	Depth (m)
		Overall		
Brackish	4.62 (0.56) 3.4 - 6.7	27.3 (3.6) 17.2- 39.6	29.9 (0.5) 29.1 - 31.8	0.70 (0.13) 0.35 -1.12)
Saline	6.68 (0.84) 4.6 - 9.0	23.1 (4.9) 19.2 -57.7	29.84 (0.69) 28.1 - 31.6	0.51 (0.05) 0.37 -0.64
		Fall		
Fresh	0.23 (0.03) 0.2 - 0.3	44.9 (30.6) 10.5 - 106.0	23.9 (0.4) 23.2 - 24.6	0.99 (0.15) 0.76 - 1.27
Intermediate	6.4 (1.1) 0.9 - 13.6	15.5 (5.4) 4.8 - 25.2	29.8 (0.9) 23.8 - 27.8	0.69 (0.03) 0.62 - 0.75
Brackish	7.62 (1.42) 2.0 - 9.6	23.6 (5.8) 13.0 - 46.0	25.8 (1.9) 20.7 - 30.9	0.55 (0.09) 0.32 - 0.83
Saline	13.25 (0.93) 11.1 - 15.6	33.0 (8.5) 19.2 - 57.7	25.4 (0.98) 23.0 - 27.0	0.32 (0.04) 0.25 -0.43
		Early Winter		
Fresh	0.4 (0.2) 0.2 - 0.8	46.9 (26.3) 4.8 - 95.2	18.7 (0.5) 15.3 -20.7	1.10 (0.25) 0.61 - 1.47
Intermediate	6.4 (1.1) 0.9 - 13.6	30.9 (4.2) 25.2 - 43.1	21.4 (0.9) 19.7 - 23.7	0.69 (0.08) 0.46 - 0.85
Brackish	10.10 (0.20) 3.4 - 8.4	12.6 (1.6) 11.0 - 14.1	20.1 (0.1) 20.0 - 20.1	0.74 (0.10) 0.63 - 0.84
Saline	13.95 (1.19) 11.2 - 16.4	11.17 (2.0) 7.3 - 15.3	16.72 (0.45) 15.6 -22.9	0.48 (0.03) 0.23 - 0.37
		Late Winter		
Fresh	0.2 (<0.01) 0.2 - 0.2	36.2 (18.1) 7.1 - 89.0	14.0 (0.5) 12.7 - 14.8	0.44 (0.09) 0.25 - 0.63
Intermediate	6.4 (1.1) 0.9 - 13.6	56.9 (24.4) 14.3 - 126.0	14.8 (1.7) 10.6 - 18.0	0.42 (0.08) 0.23 - 0.34
Brackish	5.45 (1.13) 3.4 - 8.4	39.6 (7.6) 17.2 - 51.4	15.9 (1.1) 13.4 - 18.5	0.30 (0.07) 0.15 - 0.42
Saline	13.1 (1.60) 11.3 - 16.3	23.2 (5.7) 15.7 - 34.5	20.73 (1.37) 18.2 - 22.9	0.32 (0.04) 0.23 - 0.37

Percent occurrence and species assemblages

Fresh marsh SAV assemblages were dominated by *Cabomba caroliniana*, *Ceratophyllum demersum*, and *Hydrilla verticillata*, each having over 50% occurrence during all seasons (Figure 3.4a). In fresh marsh, invasive FAV occurred during every season at greater than 75% occurrence except the early spring. Native FAV occurred at 50% or greater in every season except the early winter in fresh marsh. Native FAV species included *Utricularia vulgaris*, *Nuphar lutea*, *Nelumbo lutea*, and *Lemna minor*, invasive species dominated by *E. crassipes*, with *Althernathera philoxerioides*, *Salvinia molesta*, and *S. minima* occurring in much smaller amounts.
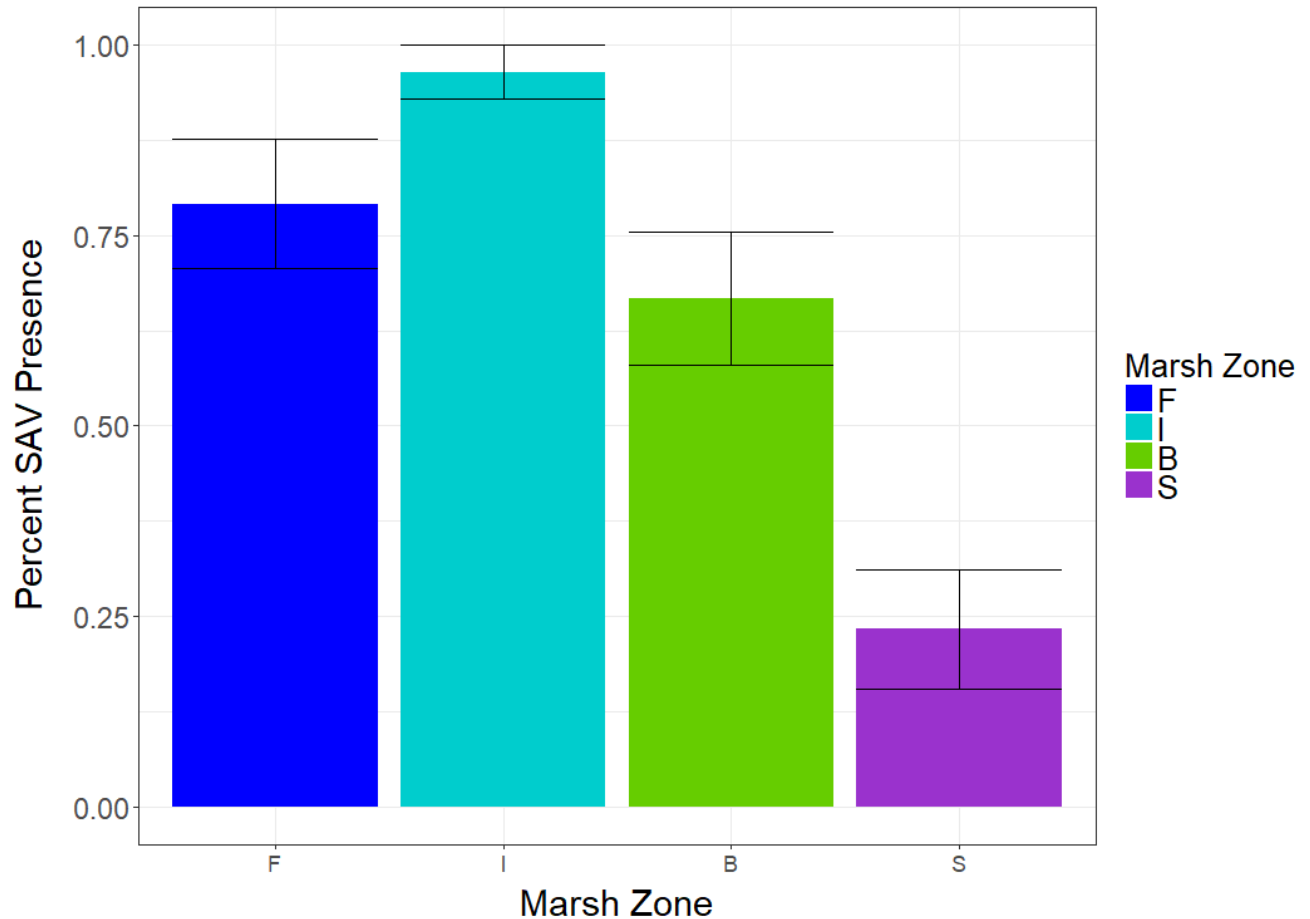
Figure 3.3. Percent SAV presence across marsh zones. Presence was similar between fresh, intermediate, and brackish marsh zones, and was significantly lower in saline marsh zones. MZ = marsh zone, F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone.

SAV assemblages were more seasonally variable than the other marsh zones (Figure 3.4b). *C. demersum* (≥50% occurrence), *N. guadalupensis* (≥50% occurrence), *Vallisneria americana* (≥50% occurrence), *M. spicatum* (≥25% occurrence), occurred in all seasons, *C. caroliniana* occurred in all but the fall and early winter seasons, and *Zanichellia palustris* occurred solely in the early and late spring seasons. In intermediate marsh, invasive and native FAV occurred 50% or less of the time in all seasons.

Brackish marsh contained fewer species than fresh and intermediate (Figure 3.4c); *Ruppia maritima* and *M. spicatum* occurred ≥50% of the time during all seasons, *C. demersum* occurred in all seasons except early and late winter, and *P. pusillus* appeared only in the late summer season. Saline marsh zones supported sparsely occurring (< 25% occurrence) *R. maritima* during all seasons except late winter, and *M. spicatum* in the early spring only (Figure 3.4d).
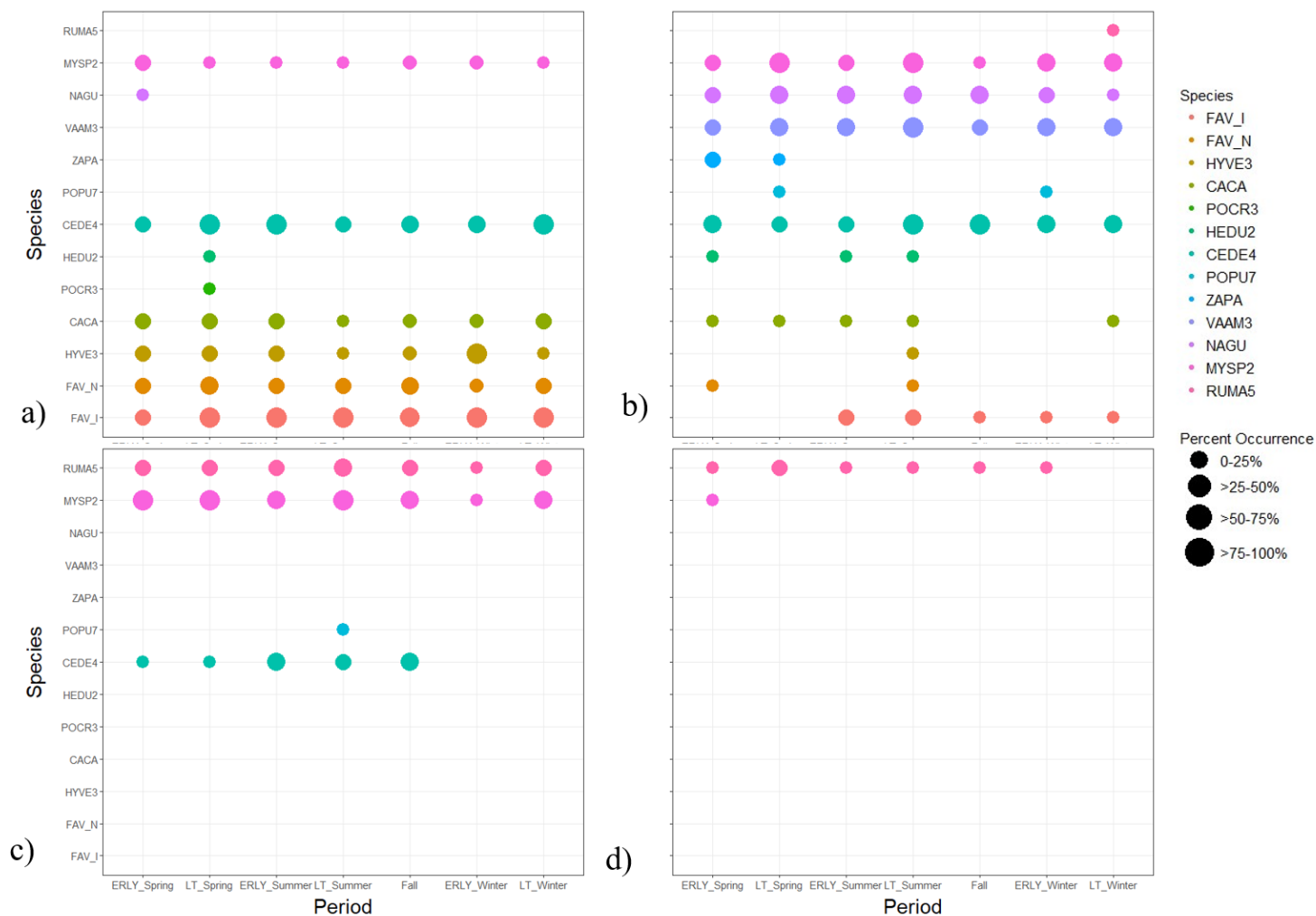
Figure 3.4. Percent occurrence by species per season in a) fresh, b) intermediate, c) brackish, and c) saline marsh zones. Percent occurrence is the number of times a species was observed across transect samples divided by total number of observations within each season and a marsh zone. FAV_I = invasive FAV species, FAV_N = native FAV species, HYVE3 = *Hydrilla verticillata*, CACA = *Cabomba caroliniana*, POCR3 = *Potamogeton crispus*, HEDU2 = *Heteranthera dubia*, CEDE4 = *Ceratophyllum demersum*, POPU7 = *Potamogeton pusillus*, ZAPA = *Zannichellia palustris*, VAAM3 = *Vallisneria americana*, NAGU = *Najas guadalupensis*, MYSP2 = *Myriophyllum spicatum*, RUMA5 = *Ruppia maritima*.

Percent Cover

SAV percent cover differed among marsh zones (F value = 13.456; p < 0.0001) (Figure 3.5), with fresh with intermediate marshes supporting more cover than brackish and saline (Table 3.2). Mean SAV cover was similar between fresh (38± 7%) and intermediate (41± 6%) marsh, and between brackish (11± 3%) and saline marsh (9± 4%) cover. SAV cover did not differ among seasons nor was there an interaction between season and marsh zones.

Invasive FAV cover differed among seasons and marsh zones (F value = 3.855; p < 0.001). Invasive FAV cover was absent in the brackish and saline marsh zones, and was higher in the late summer (66.7± 26.2%) and fall (63.3± 25.2%) than all the other seasons (5-36.7%) (Figure 3.6). Native FAV cover differed among marsh zones, as it was only present in the fresh marsh zone only in the quadrat samples (but was observed in transect data in intermediate marsh). Native FAV cover did not differ among seasons nor was there an interactions between marsh zones and seasons.

There was no effect of FAV cover, invasive, native, or combined, on SAV cover. However, as most of the FAV cover was located in fresh marsh zones only additional analyses in fresh marsh zones were performed. Season had a significant effect on invasive FAV cover (F value = 3.524; p = 0.0188), where FAV cover was significantly different in the late summer and fall seasons than the other season. Invasive FAV cover and season had aninteractive effect on SAV cover in fresh marsh zones (F value = 7.987; p = 0.0130), and SAV cover in fresh marsh responded differently to FAV invasive FAV cover among the seasons. As invasive FAV cover increased in the summer and fall, SAV cover decreased significantly, in fresh marsh zone (Figure 3.7).

Discussion

The environmental conditions of each marsh zone presumably drove the differing seasonal ecological responses of the aquatic community. Specifically, SAV assemblages, FAV cover, and interspecific species interactions were driven by seasonal processes that created environmental conditions that were distinct to each marsh zone. Fresh marsh largely drove seasonal and spatial differences in SAV patterns; an effect of the low salinity, water depth, cooler temperatures, and generally more stable conditions. While mean salinities were similar between fresh and intermediate zones, the salinity range differed, with intermediate marsh exhibiting higher salinities during the fall and early winter seasons. Shallower water depths, and higher salinities described brackish and saline marsh zone conditions, with increasing salinity and decreasing depth in saline marsh zones. The effect of season on aquatic vegetation in this estuary differed among marsh zones, and can reasonably be attributed to the environmental conditions representative of each marsh zone.

Table 3.2. Mean SAV cover (%) by marsh zone (± SE) collected within quadrat samples. FAV = FAV species, CACA = *Cabomba caroliniana*, CEDE4 = *Ceratophyllum demersum*, HYVE3 = *Hydrilla verticillata*, MYSP2 = *Myriophyllum spicatum*, RUMA5 = *Ruppia maritima*, VAAM3 = *Vallisneria americana*, NAGU = *Najas guadalupensis*, ZAPA = *Zannichellia palustris*, POPU7 = *Potamogeton pusillus*, HEDU4 = *Heteranthera dubia*.

	All SAV	All FAV	CACA	CEDE4	MYSP2	RUMA5	VAAM3	NAGU	HYVE3	ZAPA	HEDU2
Fresh	38.2 (6.0)	38.0 (7.1)	9.6 (2.8)	15.9 (3.1)	0.8 (0.4)	0.00	0.0	0.0	10.2 (0.4)	0.0	0.0
Intermediate	41.2 (5.8)	0.7 (0.4)	0.4 (0.3)	4.0 (1.4)	11.6 (3.2)	0.00	13.4 (3.4)	10.6 (3.5)	0.0	0.5 (0.5)	0.6 (0.6)
Brackish	10.6 (2.6)	0.0	0.0	0.4 (0.2)	5.6 (1.7)	4.0 (1.9)	0.0	0.0	0.0	0.0	0.0
Saline	8.3 (3.6)	0.0	0.0	0.0	0.5 (0.5)	7.8 (3.4)	0.0	0.0	0.0	0.0	0.0
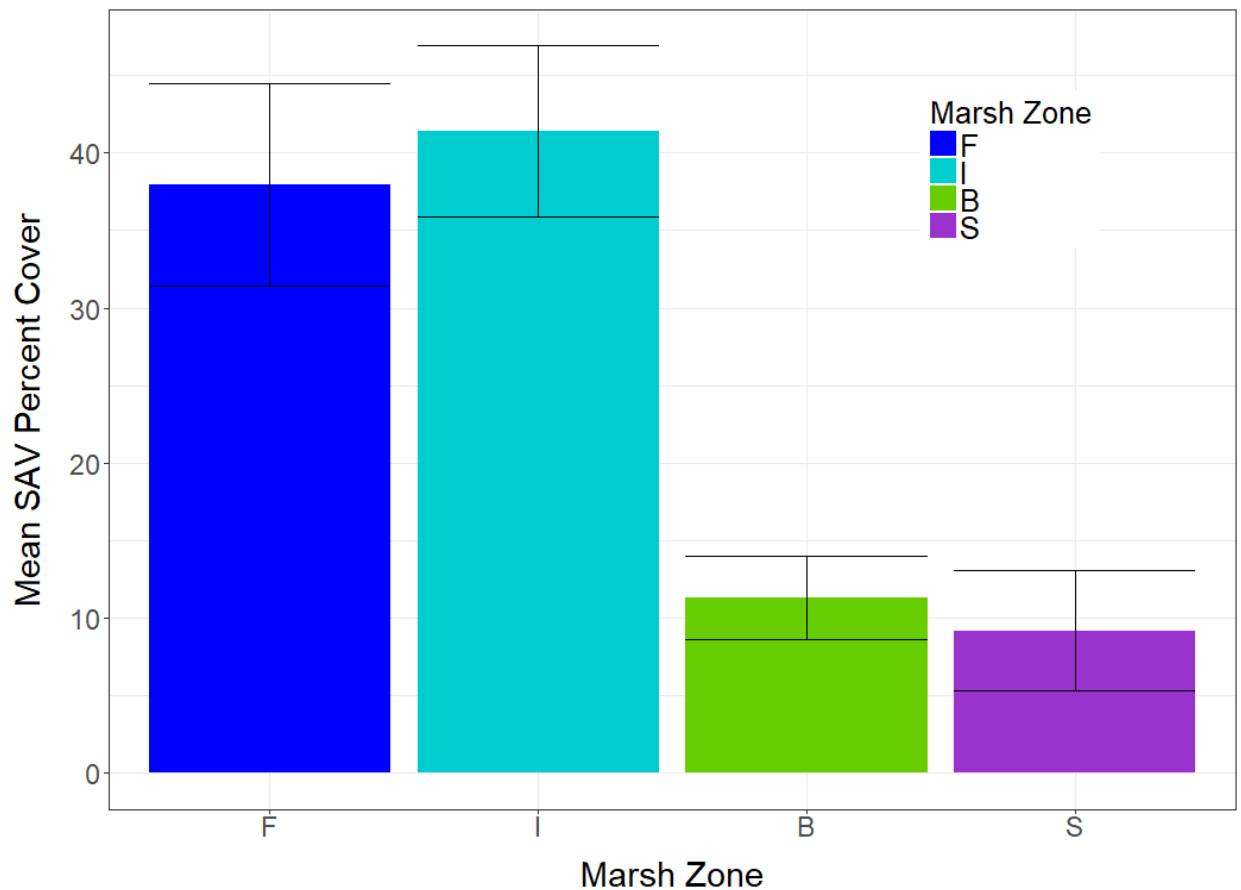
Figure 3.5. Percent SAV cover by marsh zone. Fresh and brackish marsh zones were significantly different from brackish and intermediate marsh zones. MZ = marsh zone, F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone.

The similarity across fresh, intermediate, and brackish marsh zones of SAV species presence suggests that salinity alone is not a limiting factor for SAV presence, although percent cover and assemblages were affected. There were obvious differences in species assemblages, with the highest number of species in intermediate marsh zones, and the lowest in saline marsh zones. The stable conditions and low salinity in the fresh marsh zone encourages the presence of highly competitive SAV species, including *H. verticillata* and *C. caroliniana*, and consequently reduced the number of species relative to intermediate marsh. The superior competitive ability of many of the species in fresh marsh enables them to produce rapidly in favorable conditions (Kautsky 1988). As salinity increases in intermediate marsh zones, the competitive advantage of these species is lessened (Bornette and Puijalon, 2011), and additional species (*Z. palustris*, *V. Americana*, *N. guadalupensis*, and *M. spicatum*) are able to establish, increasing the number of species. While SAV in brackish marsh zones were limited to 2 species (*Ruppia maritima*, and *M. spicatum*), these species were ubiquitous, resulting in similar percent presence to fresh and intermediate marsh zones. The significant reduction in presence in saline marsh zones indicates that stress from salinity and exposure interacted to limit presence to a single species, namely *R.*

maritima, a species adapted to both disturbance and variable salinities (Cho and Poirrier, 2005b; Cho et al., 2009; Martin and Valentine, 2012).
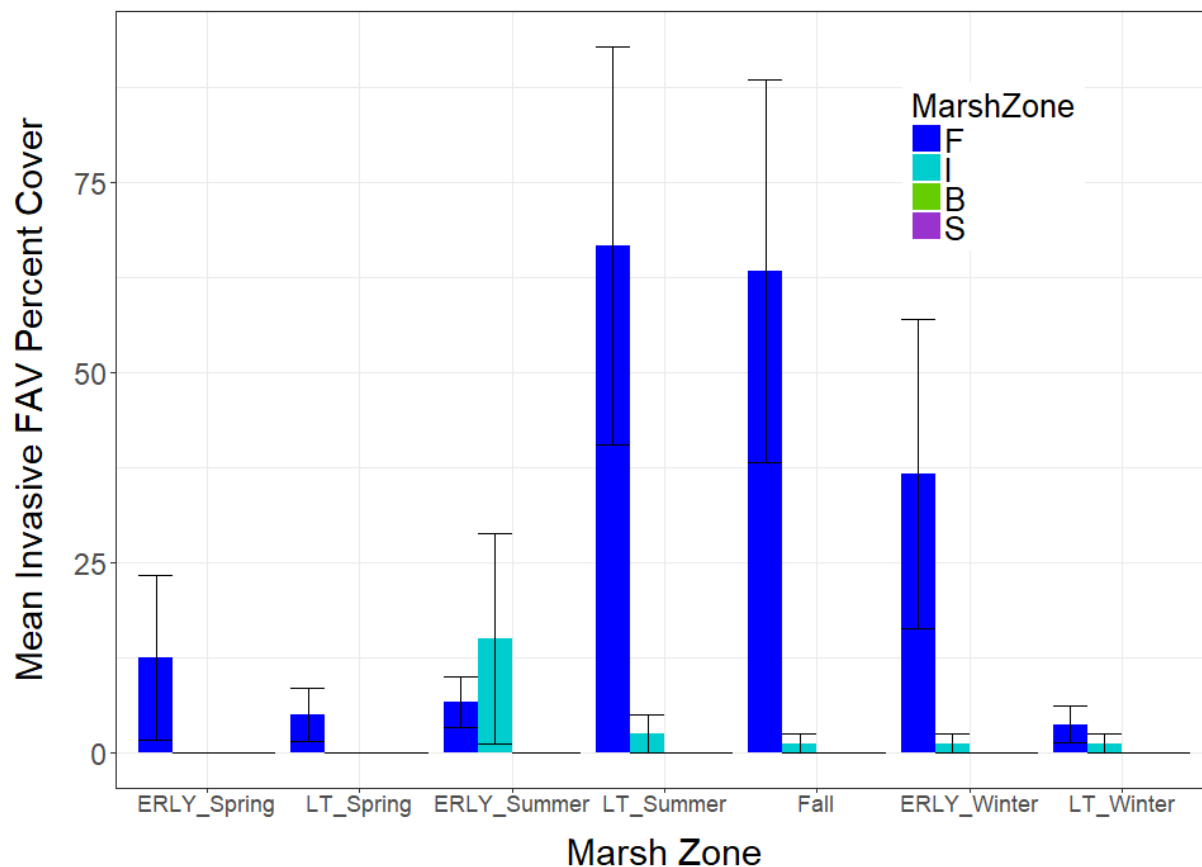
Figure 3.6. Percent invasive FAV cover by marsh zone. There was a significant interaction effect of marsh zone and season on invasive FAV cover. MZ = marsh zone, F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone

Variation in species assemblages across the seasons highlight the short-lived, and ephemeral nature of many of these species. *Zanichellia palustris*, the most seasonally variable species in this study, can be classified as a ruderal SAV species as it is able to complete its reproductive life cycle in a short period of time in optimal conditions (Grime 1977; Kautsky 1988). This species also known is to prefer cool water and spring conditions (Greenwood and DeBowy 2005; Haramis and Carter. 1983), and would have been unobserved completely if not for the seasonal sampling. *Vallisneria americana*, a species adapted to variable salinities (Frazer et al., 1974; Jarvis and Moore, 2008) was only present in intermediate marsh zones, but was present during each season, suggesting that this species may specialize in areas where salinity means are low, but is tolerant of variation in salinity, and short periods of higher salinities. The seasonal and ephemeral occurrence of individual species highlights the need to sample through the year to fully capture SAV and FAV community dynamics.
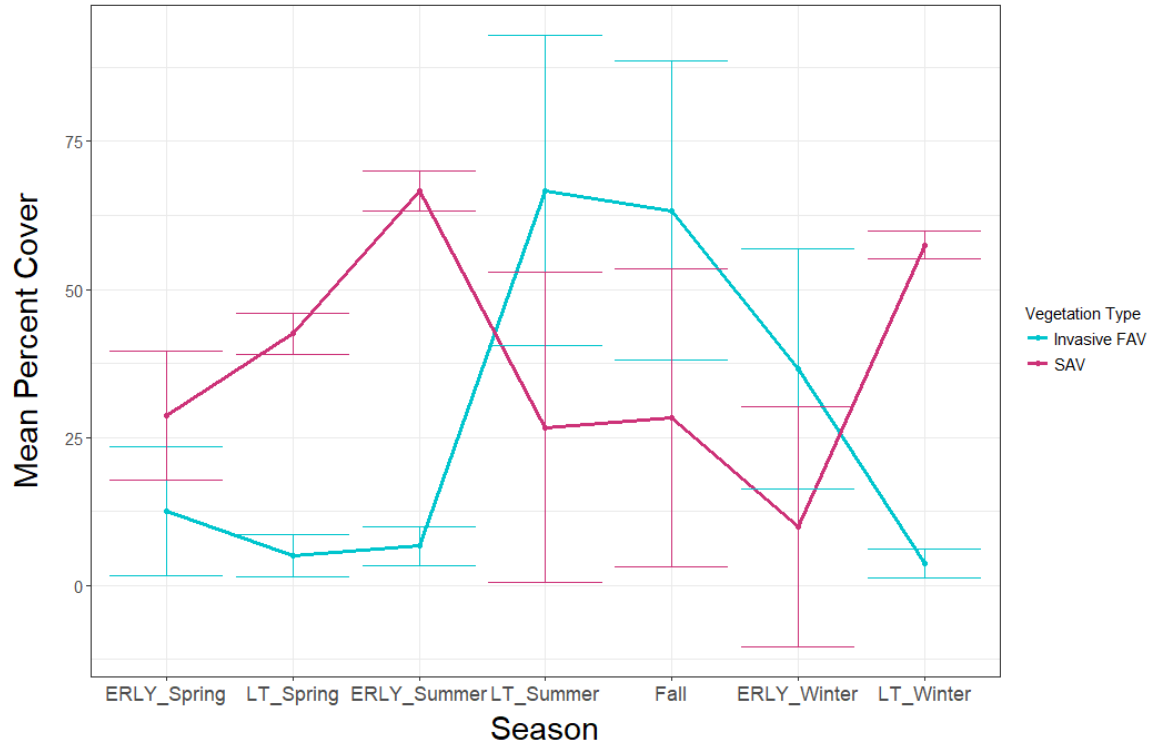
Figure 3.7. SAV (blue) and invasive FAV (red) percent cover in fresh marsh across seasons. Invasive FAV cover and season had a significant interactive effect on SAV cover in fresh marsh zones.

If abiotic conditions and biotic interactions are unique to individual marsh zones across the estuary, it can be assumed that the distribution of SAV in this habitat is the result of these effects. The physiological tolerances of individual species to environmental conditions of each marsh zone can create spatially distinctive patterns of vegetative growth. Increasing mean salinity and salinity variability (Boustany et al., 2014; Sheilds et al., 2012; Strazisar et al., 2013; Van Diggelen and Montagna, 2016), decreasing light availability (Bickel and Schooler, 2015; Rybicki and Carter, 2001), and increased water movement (Madsen et al., 2001; Martin and Valentine, 2012) decrease growth rates for many of the species observed in this study. The cumulative growth response of the SAV assemblages across marsh zones was the effect of the environmental conditions in each of the habitats. Similar SAV presence and cover between fresh and intermediate marsh zones, but differing species assemblages, indicate conditions were optimal for many different SAV species to establish and grow. The similar percent cover but lower presence of SAV in saline marsh zones compared to brackish indicates that although the establishment of SAV (*R. maritima*) was limited, when it was able to colonize, growth was not significantly restricted.

The interaction between invasive FAV and SAV cover in fresh marsh zones highlights the indirect effect of season on SAV cover. Indirect interactions dominate ecological communities (Wooten, 1994), and are particularly pronounced in plant communities via resource competition (Tilman, 1997), which in turn is particularly pronounced in low stress aquatic habitats (Kautsky, 1988). Higher salinities limit the growth of water hyacinth, the dominant invasive FAV in this study (Haller et al., 1974), as shown by limited growth of FAV.

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Intermediate salinity regimes (0.1 – 1.9 ppt) appear to limit the growth of FAV compared to fresh marsh (0.1 – 0.8 ppt). Additionally, water hyacinth is killed directly or exhibits pronounced growth declines when exposed to freezing or near-freezing air temperatures (<5°C) for prolonged season of time (Owens and Madsen, 1995). Several SAV species that co-occurred with invasive FAV in fresh marsh (*C. demersum*, *C. caroliniana*, *H. verticillata*, and *M. spicatum*) overwinter in the benthos as roots, tubers or winter buds, and regenerate vegetatively instead of from seed (Cho and Poirrier, 2005a; Cronk and Fennessy, 2001; Nichols and Shaw, 1986; van den Berg et al., 2003). As soon as water temperatures increase above 15° C plants can germinate, and SAV shoots are able to grow rapidly and form canopies (Haller et al., 1976; Jarvis and Moore, 2008; Rybicki and Carter, 2001). Low winter air temperatures presumably decreased FAV cover, ultimately providing a release from competition for light, leading to increased growth of SAV in the winter and spring seasons.

Including additional environmental conditions to the description of marsh zones would be valuable in attempting to characterize aquatic and wetland habitats (Timchenko et al., 2016). Although nutrient concentrations were not collected for this study, it is possible that nutrients from the Mississippi River water, in addition to optimal salinity conditions, may have contributed to the high occurrence of FAV presence in fresh marsh. The Davis Pond freshwater river diversion released a large amount of nutrient rich Mississippi River water near the fresh marsh zones of the study area in March of 2015 (http://coastal.la.gov/diversion-operations/; https://nwis.waterdata.usgs.gov/usa/nwis/uv). Many FAV species exhibit rapid growth in response to increased nutrient levels (Gopal and Goel, 1993; Reddy and DeBusk, 1984; van Gerven et al., 2015), and this freshwater release in 2015 may have contributed to FAV occurrence in fresh marsh. Sediment type has also been shown to impact growth of many species (Barko et al., 1988; Koch et al., 2001), and the characterization of sediments may further develop aquatic habitat descriptions.

Conclusion

Distinctive aquatic habitats across estuarine gradients are the product of abiotic and biotic interactions that go beyond the effects of salinity, and can be represented spatially with good confidence by marsh zone. To fully assess the habitat quality of these shallow water areas more detailed descriptions of physical factors (hydrology, sediment patterns, bathymetry, etc.) and biological interactions in the aquatic community can be useful to quantify ecological benefits across estuaries. Specifically, incorporating parameters representing the ecological hydrology of aquatic habitats (i.e., currents, exposure conditions, physical properties of benthic sediment, sediment in the water column) could more fully characterize the wetland as an ecosystem – linking the shallow water to the emergent marsh. The spatial and seasonal conditions across this estuary created unique aquatic vegetation communities, and in turn create habitats that are heterogeneous across time and space. Specifically, marsh zones supported differing cover and assemblages of SAV species considered to be desirable food resources (ie. *V. americana*, *N. guadalupensis*, *Z. palustris*) for waterfowl (Hansson et al., 2010; Sponberg and Lodge, 2005), with intermediate marsh zones containing the most diverse and valuable (in terms of habitat quality) SAV species in this study.

The effects of changing environmental conditions as a result of climate change (i.e., increasing temperatures and salinity) have the potential to significantly alter patterns in SAV

presence, cover, and assemblages. While in some regions, temperature increases may expand the distribution and range of SAV (Hossain et al., 2016; Kotta et al., 2010), this pattern can also vastly increase the presence and cover of invasive aquatic species, particularly the water hyacinth. Reduced low temperatures in the winter may further encourage the spread and growth of many of these species (Ehrenfeld, 2010; Santos et al., 2011). In coastal Louisiana, it is likely that the spatial and seasonal extent of water hyacinth will increase in the future, preventing establishment and growth of SAV in fresh marsh zones. This has far reaching implications for the presence of winter wildlife species, notably wintering waterfowl (Hagy, 2010; Brasher et al., 2012). In this event, the protection and conservation of intermediate and brackish marsh zones, or intensifying management of fresh marsh habitats, will be essential to maintaining adequate habitat for many wildlife species.

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CHAPTER 4. ASSESSING WATERFOWL HABITAT VALUE OF SEED FORAGE IN ESTUARIES ACROSS REGIONAL AND TEMPORAL SCALES

Introduction

Seed banks are critical food resources for waterfowl populations, directly, as food for wildlife; but also indirectly, as they contribute to future vegetation communities. While seed banks have long been investigated in upland and emergent wetland areas (Harper, 1977; van der Valk, 1981), less is known about seed banks in submerged aquatic habitats. Seeds in permanently flooded habitats are subject to high and variable rates of import and export due to waves and currents, which also act as ecological filters for seed dispersal, persistence, and germination (Koch et al., 2010; Myers and Harms, 2009). These conditions create seed banks composed of emergent and submergent vegetation species (DeMarco et al., 2015). Within aquatic habitats, seed bank composition may influence plant communities, which in turn, affects relative habitat quality for wildlife (Collins et al., 2013; Hölzel and Otte, 2004; Poiani and Dixon, 1995).

In the northern Gulf of Mexico (NGOM), wintering waterfowl rely heavily on interior coastal marshes and associated SAV for foraging habitat. The carbohydrate rich roots, shoots, and seeds of SAV account for a valuable portion of waterfowl forage in the winter months when the energy costs of molting, pair formation, migration, and thermoregulation are high (Prince, 1979, Wilson et al., 2002). Waterfowl numbers generally increase in response to the presence of submerged aquatic vegetation (SAV) (Hansson et al., 2010). In coastal wetland habitats, several waterfowl species are dependent on SAV and seeds for food during the winter months, particularly in the NGOM region (Sponberg and Lodge, 2005; Wilson et al., 2002). Seed bank composition (species, density, and biomass) in permanently inundated coastal habitats may provide critical important waterfowl food resources, as well as contribute to habitat resilience, through their potential contributions to future vegetative communities.

The distribution of SAV and seeds across coastal landscapes in aquatic habitats influences the carrying capacity of coastal marshes to support wintering waterfowl. SAV beds occur across the salinity gradient in estuaries, providing habitat for wildlife across large coastal landscapes (Hagy et al., 2012; Hitch et al., 2011). Coastal wildlife and waterfowl managers develop objectives based on food availability in coastal marshes including SAV and seed biomass (Petrie et al., 2011). These objectives are calculated by estimating the energy density of available food, measured as biomass and extrapolated spatially across coastal landscapes (Williams et al., 2014; Winslow, 2003; Stafford, 2004).

Food for wintering waterfowl from SAV and seeds in aquatic coastal habitats is presumed to vary across the salinity gradient in terms of both abundance and quality of food, resulting in marsh zone (fresh, intermediate, brackish, saline) specific resource estimates (Brasher et al., 2012). Environmental conditions determining SAV distribution are primarily related to hydrology and salinity. These conditions drive seed production, seed germination, vegetation species assemblages, and percent cover of both emergent and submergent aquatic vegetation (Bournette and Puijalon; Kemp et al., 2004; Koch et al., 2001). SAV percent cover, biomass, and species assemblages differ among marsh zones (Carter et al., 2009; Hillmann et al., 2016; Merino et al., 2009), and are generally grouped with emergent marsh zone classification methods to develop estimates of SAV and seeds within coastal habitats. In-situ seed production from SAV beds, and the ability for SAV beds to slow sediment (and potentially seeds) transport

and increase sediment and seed deposition (Gracia et al., 2017; Gurbisz et al., 2016) could contribute additional value beyond direct food value in marsh zones estimates of habitat value.

Waterfowl can respond to changes in resource availability across multiple spatial and temporal scales. Understanding how seed banks may vary through time and space helps to estimate and predict habitat value to waterfowl across time and space. For some SAV species, sexual reproduction from seed is critical to maintaining vegetation populations in habitats that experience disturbance, occurring as storms, floods, salinity changes, and predation in aquatic systems (Bornis et al., 1995; Sponberg and Lodge, 2005; Tabacchi et al., 1998). Seed production may be seasonal and/or episodic, as species respond to environmental conditions (Thompson and Grime, 1979; Grime, 1977; Kautsky, 1988; van der Valk, 1981). Numerous SAV species have well documented seasonal and annual fluctuations with annual and climatic cycles controlling many of the environmental conditions dictating SAV distribution and seed production (Cho and Poirrier, 2005, Carter et al., 2009). Quantifying SAV and seed resource variability over large temporal and spatial scales increases the reliability in assessing contributions of coastal marsh landscapes to waterfowl populations.

Despite the importance of shallow coastal waters as a food resource for waterfowl, few datasets exist to quantify the spatial and temporal variability, distribution, and abundance of SAV and seeds in permanently submerged areas. As a result, managers make assumptions regarding the wildlife habitat values of shallow waters in coastal marshes. Foraging values are assigned to marsh zones based largely on limited empirical data (Winslow, 2003) and relative abundance of waterfowl among marsh vegetation zones (Brasher et al., 2012). Because estuarine gradients are created by multiple interacting environmental factors, including salinity patterns, hydrology, sediment input and type, regional geomorphology, nutrient regimes, and weather (Cloern et al., 2017; Crain et al., 2004; Morais et al., 2015; Piehler and Smyth, 2011), empirical data are needed from all coastal marsh zones and temporal variation of seeds in these areas should be better described to fully represent patterns over space and time.

This study (1) describes and quantifies SAV percent cover and the shallow (< 20 cm) seed bank across the estuarine gradient in shallow water habitats from Mobile Bay, AL to Nueces River, TX over three years (hereinafter "inter-annual landscape study"), and (2) describes and quantifies the SAV percent cover and the shallow (< 20 cm) seed bank across the estuarine gradient in Barataria Basin, Louisiana over a full calendar year (hereinafter "seasonal estuarine study").

Methods

This study quantified and described the seedbank, and SAV percent cover at two different spatial and temporal scales. The first scale was inter-annual and large-scale, evaluating submergent habitats across the NGOM from Mobile Bay, Alabama, to Nueces River, Texas. The second scale was seasonal and estuary specific, focusing on the Barataria Basin in southeast Louisiana. For both scales the study focused on shallow aquatic habitats and coastal marshes. Sites were located on private and public lands.

To identify shallow coastal waters capable of supporting SAV for both the inter-annual and seasonal studies, four separate approaches were developed and compiled to create a contiguous spatial mask covering approximately 550,000 ha across the study area. The first approach used cloud-free Landsat satellite (1984-2011) images stacked by path/row with a minimum of 48 and a maximum of 124 images for a given path/row. Erdas Imagine software

was trained to automatically recognize a pre-defined SAV class. When SAV habitat was indicated in more than 10% of the stacked images the pixel was included as potential SAV habitat.

The second approach stacked Landsat 8 remote sensing imagery and using the maximum zonal statistics tool in ArcGIS (ArcGIS v 10.5) conducted an unsupervised classification of bands 3, 4, and 5 based on possible past presence of SAV in an individual pixel. The potential presence of SAV in water was identified by higher reflectivity in bands 4 and 5 in water bodies than water (B. Couvillon, USGS, personal communication). If a pixel was reflective in both band 4 and 5 for 10% of the available images, it was classified as possibly containing SAV and was included in the final mask output.

The third approach developed a spatial layer of interior coastal marsh ponds to target sampling in areas of potential waterfowl foraging habitat where SAV is likely to occur. This approach excluded deep water, heavily traveled canals, upland habitats, dense emergent marsh, and water bodies >1295 ha. A land/water layer was generated in ArcGIS using the maximum extent of water, aquatic bed, and unconsolidated shore from the National Land Cover Dataset (NLCD) for the years 1992, 2001, 2006 (NLCD 2012) and the Coastal Change Analysis Program (C-CAP) datasets for the years 1996, 2001, 2005, and 2006 (C-CAP 2012). Areas identified as less than 0.1 ha were excluded as they represented individual pixels and were typically not actual ponds. The same NCLD (2012) and C-CAP (2012) datasets were also used to create a final spatial layer containing all of the rooted vascular bed classes identified.

To delineate marsh zones, long term emergent wetland vegetation type classifications were used. The initial marsh designations used for sampling design were defined in Louisiana by Sasser et al. (2008), and for Mississippi, Alabama, and Texas by best professional judgment and early efforts by USGS to delineate coast-wide emergent vegetation types. Final marsh zone designations used in analyses were assigned using Sasser et al. (2014) in Louisiana and Enwright et al. (2014) emergent marsh vegetation zone dataset in the rest of the states. Sasser et al. (2008) marsh type boundaries extended into shallow waters, while Enwright et al. (2010) occasionally did not. In this case the closest pixel was used to assign marsh zone to the individual site. The term marsh zone is used hereafter to include the aquatic habitat, extending beyond the boundaries of the emergent marsh type classification.

Inter-annual landscape study sampling design

This study sampled a total of 384 sites from Mobile Bay, AL to Nueces River, Texas, annually, over a period of three years. Regions were defined by the GCJV Initiative areas, which adapted Omernik Level III Ecoregions (U.S. EPA 2013) to include only the coastal marshes and plains (Ecoregions 34g, 34h, 73n, 73o, 75a, 75k) critical to waterbird habitat. Omernik ecoregions were developed using a hierarchical spatial framework to create boundaries for ecologically similar areas based on the analysis of patterns that were characteristic to an area (Omernik and Griffith, 2014). For this study, we used the initiative areas of the Gulf Coast Joint Venture to define regions (GCJV: Coastal Mississippi-Alabama – CMA, Mississippi River Coastal Wetlands – MRCW, Chenier Plain – CP, and Texas Mid-Coast – TMC; Wilson et al. 2002) which were largely based on the ecoregions, and included the estuarine gradient in the NGOM (Figure 4.1). All sites were sampled once annually, with data collected during the summer growing season (1 June–15 September), over a 3 year period in 2013, 2014, and 2015. Site selection, described below, was stratified by GCJV regions (CMA, MRCW, CP, TMC), and

the salinity gradient, as defined by marsh zones (Visser et al. 2013; fresh, intermediate, brackish, and saline).
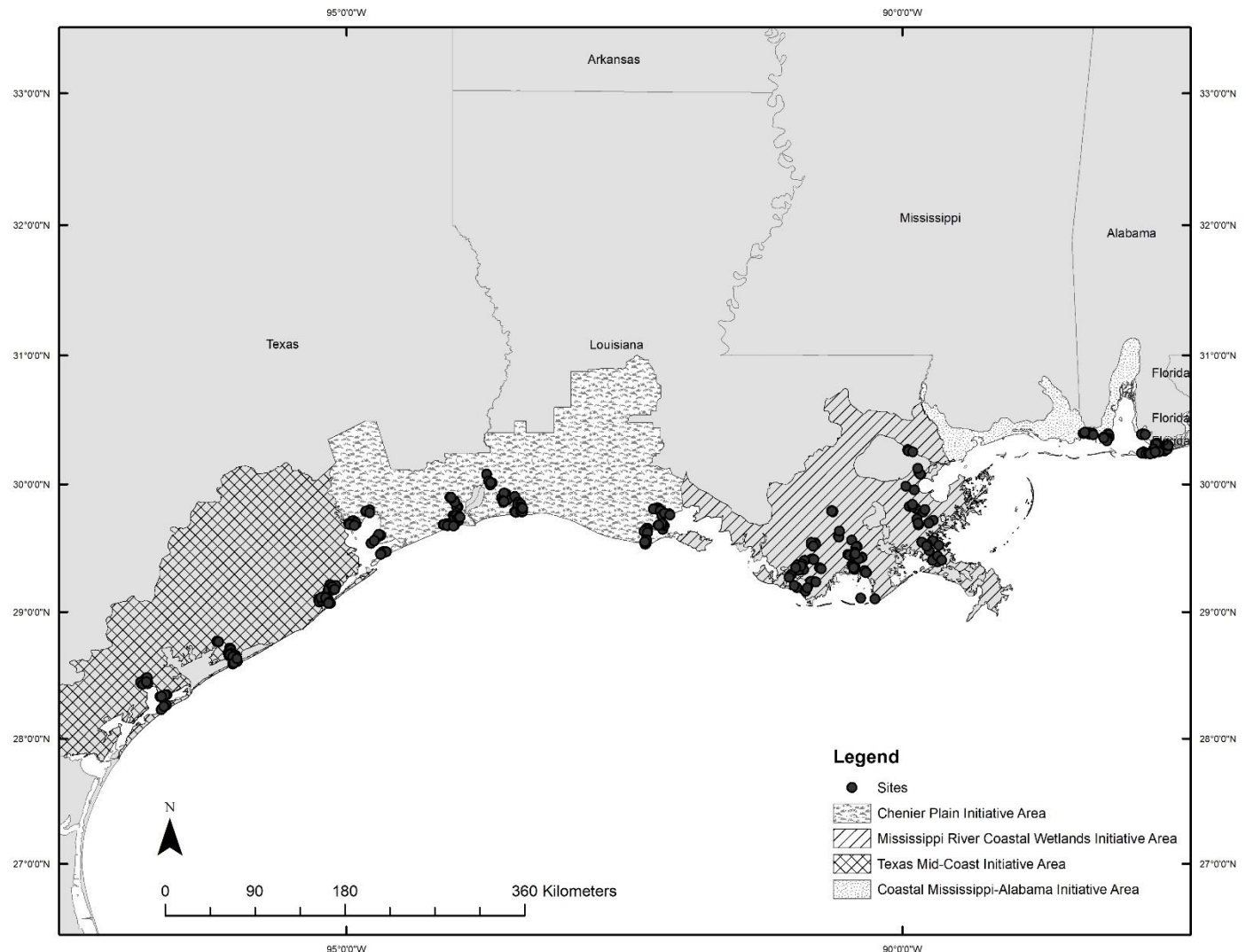
Figure 40.1. Inter-annual dataset study area and sample sites with regions as defined by the Gulf Coast Joint Venture Initiative areas.

From within the GCJV regions, the study area was divided into 43 subregions, spatially defined as rectangles oriented north-south and of equal east-west width. Using a random number generator, 12 subregions were selected out of the full suite, with the selection process forced to prevent the selection of adjacent subregions to ensure coverage of multiple habitats in the NGOM, and stratified to distribute sites evenly across GCJV areas.

To evaluate SAV and seed resources across an estuarine gradient, site selection was also forced to create equal numbers of sites per marsh zone; 8 sites per subregion in fresh, intermediate, brackish, saline marsh zones (32 sites per subregion, 384 total sites). Marsh zone designations were based on emergent marsh vegetation community types, which reflect long-term salinity patterns (Visser et al., 2013).

Seasonal estuarine study sampling design

The area investigated included all shallow waters (USGS 2015) within Barataria Bay in southeast Louisiana, with explicit boundaries defined by US Geological Survey hydrologic unit codes (HUC 08090301). Barataria Basin is a semi-enclosed fresh to saline bay situated along the western side of the Mississippi River with wide expanses of emergent marshes, punctuated by forested swamp, marsh ponds, shallow bays, and industrial canals. Barataria Basin contains several freshwater diversions, and many other wetland restoration projects including marsh creation and shoreline protection (http://coastal.la.gov/our-plan/annual-plan/).

Within Barataria Basin, 4 sites were selected from fresh (F), intermediate (I), brackish (B), and saline (S) marsh vegetation zones, as identified in Sasser et al. (2014), totaling 16 sampling sites across the basin (Figure 4.2). Potential areas for site selection were first identified via aerial imagery, and final locations for sites for repeated sampling were determined in the field. As one of the primary project goals was to evaluate intra-annual changes in SAV and seed resources, sites supporting, or deemed likely to support, SAV at the first field visit were specifically targeted. Final sites selected were all less than 2 meters in depth.

This study sampled a set of 16 sites stratified along the estuarine gradient (4 sites each: fresh, intermediate, brackish, saline), every 6-8 weeks in 2015, beginning February 1st and ending December 10th. Sampling seasons describing seasons were defined as early spring (ERLY_Spring; February-March), late spring (April; LT_Spring), early summer (May-June; ERLY_Summer), late summer (August; LT_Summer), fall (September-October; Fall), early winter (December; ERLY_Winter), and late winter (February; LT_Winter).

Field and Laboratory Data Collection and Processing

Sites were accessed via mudboat or airboat, and in occasional instances, by walking in if normal routes became dry. Water samples for turbidity testing (NTU-Hach 2100Q, Hach, CO) were collected upon arrival at the site before disturbing benthic sediments. Salinity and temperature were recorded (YSI Pro2030, YSI Incorporated, OH) at approximately half a meter under the water surface (when possible). Sites were all less than 2 m in depth.

After collecting the water quality data, a 0.25 m^2 quadrat was haphazardly thrown from the boat and anchored in place. If vegetation was present, either floating or submerged, percent cover was estimated and identified to genus level. One seed core (5 cm diameter, 20 cm depth) was collected adjacent to the quadrat, placed in a labeled plastic bag, and returned to the lab for processing. Field testing indicated that a core depth any less than 20 cm was typically too short to collect the upper portion of soil profile, as many of the soils in our study area were extremely soft and unconsolidated in the uppermost 5–10 cm. Triplicate percent cover and seed cores were collected at each site.

Seed cores were refrigerated (20°C) and processed within one week if possible, or frozen (0°C) if they could not, and then thawed before processing. Cores were washed with hydrogen peroxide and baking soda prior to rinsing to dissolve bound clays and mineral sediments (Kross et al., 2008; Marty 2013). Treated seed core samples were rinsed through two sieves, 1.0 mm (#18) and 0.5 mm (#35), and all material retained in each sieve was air dried and kept for analysis. Seeds were separated from organic debris, identified to the lowest possible taxonomic level, dried at 60°C to a constant mass (±0.001 g), and weighed.
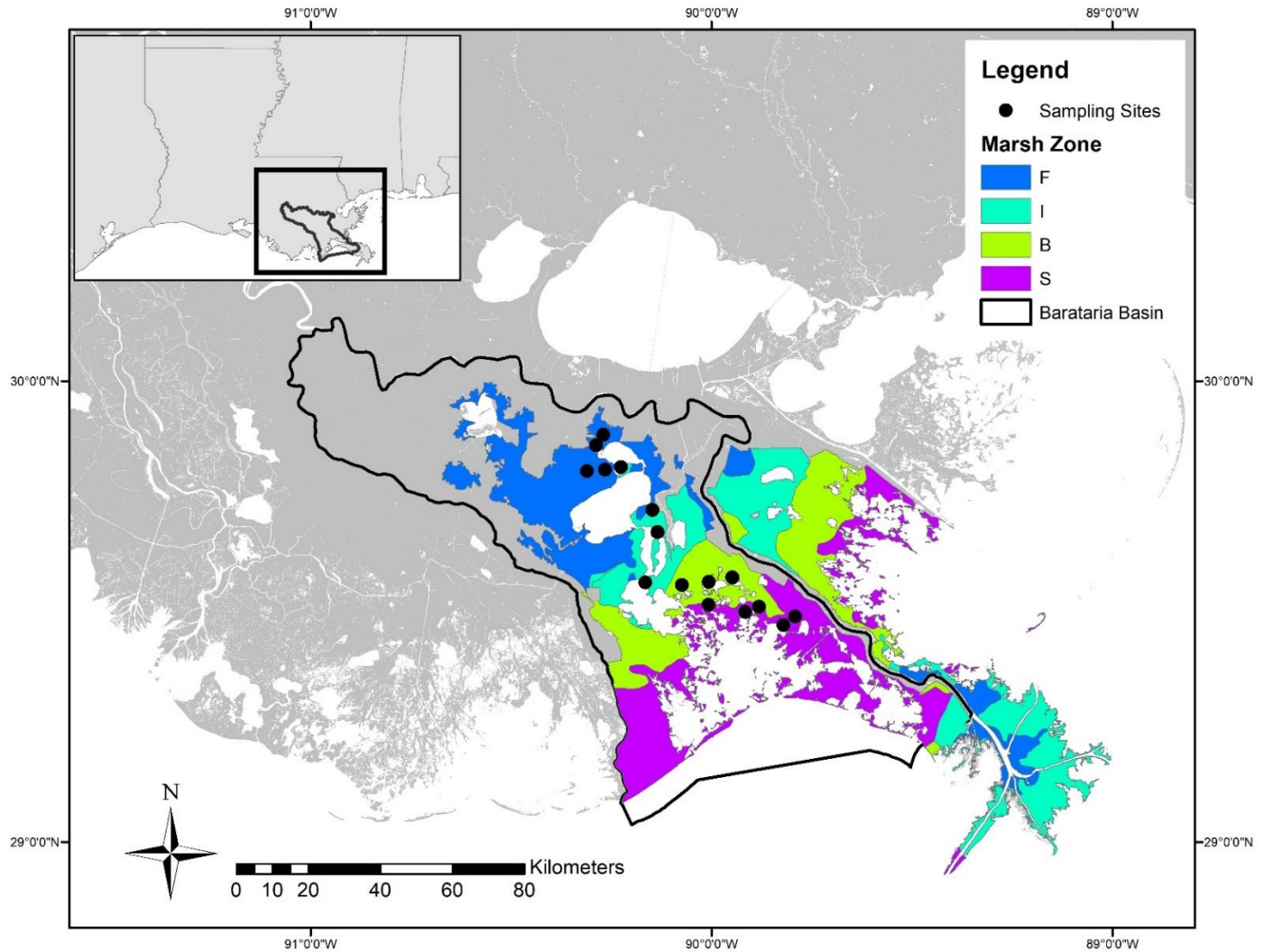
Figure 40.2. Study area and sample sites for the seasonal dataset in Barataria Bay, Louisiana. F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone.

Statistical Analyses

The inter-annual landscape and the seasonal estuarine study were analyzed separately, but using similar approaches. Environmental variables (salinity, temperature, turbidity, temperature, and dissolved oxygen) were summarized and presented by means and ranges to describe the discrete sampling conditions in the inter-annual landscape study, and were statistically analyzed to characterize marsh zone characteristics in the seasonal estuarine study. Multivariate ANOVA analyses using Tukey's honest significant difference (HSD) and least squared means (Russel, 2016) tests compared biomass of all seeds, food seeds, and SAV seeds among region, marsh zone and year (large-scale study), or marsh zones and seasons (estuarine study) (The R Group 2016). Seed groups were separated into food versus non-food seed species, with respect to waterfowl, determined from previous research by Winslow (2003) and Hagy and Kaminski

(2012). Species and genus of seed groups were identified when possible. Correlation between SAV cover as an assemblage and food seed and SAV seed biomass groups, and between individual cover and seed species were evaluated using a linear model and ANOVA testing. The threshold for significance was defined as $p \leq 0.05$ unless noted otherwise.

Results

Inter-annual landscape study

Environmental Variables. Because the environmental parameters were only collected once per sampling event in each year, they were consequently applied primarily for descriptive purposes and in cluster analyses to describe species assemblages (Table 4.1). Salinity values ranged as expected within marsh zones, increasing in mean salinity as the estuarine gradient transitioned from fresh to saline. Turbidity ranged from 0 to 176.5 NTUs. Mean temperature varied little across marsh zones and regions, with mean temperature ranging from 30.2 °C to 33.8 °C across all marsh zones and regions. Dissolved oxygen was also similar across marsh zones and regions, ranging from 5.0 to 9.0 mg/L. Overall, water depth was greatest in fresh marsh.

Total Seeds. There were over 60 genera of seeds identified (Table 4.2). Seeds were broadly classified for analyses into the following groups as Cyperaceae, SAV, floating aquatic vegetation (FAV), *Cladium jamaicense*, Poaceae, Polygonaceae, and other seeds. *Cladium jamaicense* was placed in a separate group from the rest of the Cyperaceae family group due to its large biomass and frequency of occurrence. Coast-wide, *C. jamaicense* had the highest seed biomass in each marsh zone, excluding *N. lutea* from the fresh marsh zone. Schoenoplectus seed sp. composed the second largest biomass across fresh, intermediate, and brackish marsh zones, with all the species together in the Cyperaceae group generally constituting a large portion of the biomass in most marsh zones. A single site from year 2014 was omitted from analyses, because unusually high biomass of *Nelumbo lutea* seeds identified this site as an outlier. There was a significant correlation between SAV cover and total seed biomass ($p < 0.001$).

Seed biomass patterns differed among marsh zones and regions as indicated by an interaction effect (F value = 5.562; $p < 0.0001$; Table 4.3, Figure 4.3). There was no effect of year. The significant interaction was primarily driven by high total seed biomass in the intermediate marsh zones of the CP region (9.40 ± 1.76 g m^{-2}) and the low total seed biomass in the saline marsh zones of the CMA (0.79 ± 0.39) and TMC regions (0.79 ± 0.18 g m^{-2}). Overall, fresh and intermediate marsh zones had the highest total seed biomass (Table 4.3; Figure 4.3a) in all regions, primarily due to high biomass of *C. jamaicense* in both zones, high seed biomass from the Cyperaceae group in the intermediate zone, and *N. lutea* in fresh marsh zone.

Food Seeds. Biomass of food seeds differed among marsh zones and regions as indicated by a interaction effect. (F value = 3.412; $p < 0.0001$; Table 4.3; Figure 4.3b). There was no effect of year. Differences in biomass among marsh zone and region were driven by high food seed biomass in the fresh marsh zones of the TMC, CP, and CMA regions and the intermediate marsh zone of the MRCW region. Food seed biomass was higher in the saline marsh zones of the MRCW and CMA regions than in the other saline marsh zones, and food seed biomass in brackish marsh zones was highest in the CP and MRCW region.

Table 4.1: Environmental data for inter-annual sampling dataset with mean values, ±SE, and range. Collected at each site during sampling events in 2013, 2014, and 2015.

	Salinity (PPT)	Turbidity (NTUs)	Temperature (°C)	DO (mg/L)	Depth (m)
Texas Mid-Coast (TMC)					
Fresh	1.9 (0.3) 0.3 -7.0	43.2 (11.3) 0 - 162.0	30.2 (6.6) 27.6 - 37.3	5.6 (1.0) 0.3 - 18.8	0.44 (0.05) 0.09 - 0.79
Intermediate	6.3 (1.2) 0.3 - 18.6	117.8 (22.2) 16.8 - 162.0	30.5 (0.5) 26.9 - 34.8	6.7 (0.6) 2.3 -17.2	0.46 (0.03) 0.23 - 0.81
Brackish	10.7 (3.3) 0.3 - 19.9	176.5 (49.7) 19.3 - 414.0	33.8 (1.0) 29.7 - 38.3	9.3 (1.7) 4.0 - 18.7	0.34 (0.05) 0.16 - 0.62
Saline	20.6 (0.7) 0.3 - 44.6	58.8 (6.6) 0 - 500.0	31.4 (0.2) 26.9 - 36.8	5.7 (0.1) 0 - 11.4	0.40 (0.01) 0.05 (1.01
Chenier Plain (CP)					
Fresh	2.0 (0.6) 0.1 - 17.7	37.3 (4.5) 2.5 - 144.0	31.1 (0.4) 21.2 - 35.4	4.8 (0.5) 0 - 17.4	0.60 (0.03) 0.23 - 1.08
Intermediate	3.8 (0.5) 0.1 - 21.6	77.5 (9.5) 0 - 551.0	31.0 (0.5) 0 -37.3	4.7 (0.3) 0 - 12.9	0.43 (0.02) 0.05 - 0.97
Brackish	10.0 (0.5) 0 - 25.0	78.4 (5.3) 8.6 - 766.0	31.7 (0.1) 27.4 - 37.3	5.0 (0.1) 0 - 11.4	0.40 (0.01) 0.06 -1.43
Saline	19.6 (1.3) 4.3 - 30.2	80.8 (10.9) 0 - 184.0	31.7 (0.4) 27.3 - 35.0	5.4 (0.4) 2.7 - 9.3	0.30 (0.03) 0.10 - 0.60
Mississippi River Coastal Wetlands (MRCW)					
Fresh	0.2 (<0.1) 0 - 0.5	26.1 (4.9) 1.1 - 198.0	31.0 (0.3) 25.1 - 37.2	4.5 (0.4) 0.6 - 10.27	0.84 (0.05) 0.15 - 1.88
Intermediate	1.1 (0.2) 0.1 - 6.5	22.0 (2.5) 1.7 - 98.6	31.3 (0.9) 25.6 - 36.9	5.3 (0.3) 0 - 10.8	0.50 (0.03) 0.08 - 1.02
Brackish	3.8 (0.3) 0.1 - 11.2	24.0 (2.2) 0 - 157.0	31.6 (0.2) 25.1 - 36.0	5.9 (0.2) 0 - 10.8	0.57 (0.02) 0.19 - 0.84
Saline	11.3 (0.5) 0.7 - 26.7	29.6 (1.3) 5.0 - 65.1	31.9 (0.2) 27.9 - 35.4	5.7 (0.1) 0 - 9.1	0.57 (0.02) 0.13 - 1.01
Mississippi-Alabama Coastal Wetlands (MACW)					
Fresh	5.6 (1.4) 0 - 19.0	25.2 (14.4) 1.24 - 252.0	33.3 (0.6) 29.1 - 41.0	6.3 (0.7) 1.8 - 11.6	0.59 (0.05) 0.09 -1.09
Intermediate	6.4 (1.1) 0.9 - 13.6	11.8 (0.9) 6.6 - 16.2	31.6 (0.4) 29.5 - 33.0	6.7 (0.8) 1.0 - 12.9	0.69 (0.05) 0.31 -1.06
Brackish	13.3 (1.4) 0.6 - 32.3	10.1 (0.9) 0 - 24.4	31.5 (0.9) 29.9 - 35.4	5.5 (0.4) 1.0 - 10.8	0.59 (0.05) 0.34 - 1.53
Saline	13.1 (0.8) 0.2 - 34.0	22.7 (2.0) 0 - 178.0	30.9 (0.4) 28.0 - 35.4	5.2 (0.2) 0 - 12.5	0.59 (0.02) 0.20 -1.69

[2]Table 4.2. Coast-wide seed biomass (g m-2) ±SE from inter-annual dataset.

Species, Genus, or Family name	Taxonomic code	Fresh	Intermediate	Brackish	Saline
Food					
Cyperaceae Group					
Eleocharis R. Br.	ELEOC	0.016 (0.004)	0.013 (0.006)	0.072 (0.051)	0.008 (0.002)
Bolboschoenus robustus (Pursh) Soják	BORO5	0.011 (0.004)	0.082 (0.037)	0.057 (0.011)	0.041 (0.012)
Schoenoplectus (Rchb.) Palla	SCHOE6	0.454 (0.98)	1.100 (0.164)	0.531 (0.081)	0.081 (0.015)
Fimbristylis Vahl	FIMBR	0.043 (0.031)	0.015 (0.007)	0.025 (0.008)	0.024 (0.006)
Rhynchospora Vahl	RHYNC3	0.017 (0.011)	0.008 (0.005)	0.006 (0.002)	0.008 (0.003)
Cyperus L.	CYPER	0.005 (0.003)	0.004 (0.001)	0.004 (0.002)	<0.001
Juncus L.	JUNCU	0.021 (0.013)	0.004 (0.001)	0.005 (0.002)	0.012 (0.006
Oxycaryum cubense (Poepp. & Kunth) Lye	OXCU2	0.002 (0.002)	< 0.001	< 0.001	0
Scleria baldwinii (Torr.) Steud.	SCBA2	0.007 (0.007)	< 0.001	< 0.001	0
Typha L.	TYPHA	<0.001	< 0.001	< 0.001	< 0.001
SAV Seed Group					
Potamogeton L.	POTAM	0.209 (0.060)	0.031 (0.008)	0.015 (0.004)	0.008 (0.003)
Ruppia maritima L.	RUMA5	0.043 (0.018)	0.062 (0.015)	0.142 (0.032)	0.052 (0.007)
Najas guadalupensis (Spreng.) Magnus	NAGU	0.006 (0.002)	0.003 (0.001)	<0.001	< 0.001
Ceratophyllum demersum L.	CEDE4	0.091 (0.026)	0	0.009 (0.005)	< 0.001
Vallisneria americana Michx.	VAAM3	<0.001	<0.001	< 0.001	< 0.002
Myriophyllum spicatum L.	MYSP2	0.009 (0.006)	0.012 (0.005)	0.005 (0.002)	< 0.001
Cabomba caroliniana A. Gray	CACA	0.001 (0.001)	<0.001	0	< 0.001
Halodule wrightii Asch.	HAWR	0.006 (0.004)	0.002 (0.002)	<0.001	0.003 (0.001)
Heteranthera dubia (Jacq.) MacMill.	HEDU2	<0.001	<0.001	0.002 (0.002)	<0.001
Zostera marina L.	ZOMA	0	0	0.040 (0.040)	<0.001
Polygonaceae Group					
Polygonum L.	POLYG4	0.175 (0.33)	0.072 (0.012)	0.027 (0.006)	0.017 (0.006)
Carex L.	CAREX	< 0.001	0.004 (0.002)	0.009 (0.007)	< 0.001
Rumex L.	RUMEX	0.024 (0.018)	0.005 (0.001)	0.003 (0.001)	0.10 (0.004)
FAV Group					
*Brasenia schreberi J.*F. Gmel.	BRSC	0.153 (0.142)	0.001 (0.001)	0	0.001 (0.001)
Nymphaea L.	NYMPH	0.174 (0.083)	0.033 (0.009)	0.22 (0.010)	0.001 (0.001)
Nymphoides Hill	NYMPH2	<0.001	<0.001	<0.001	<0.001
Poaceae Group					
Distichlis spicata (L.) Greene	DISP	0.001 (0.001)	0.15 (0.006)	0.005 (0.001)	0.004 (0.001)
Panicum L.	PANIC	0.095 (0.088)	0.012 (0.005)	0.004 (0.001)	<0.001
Paspalum L.	PASPA2	0.001 (0.001)	0.007 (0.003)	0.002 (0.001)	<0.001
Sorghum halepense (L.) Pers.	SOHA	<0.001	<0.001	<0.001	0
Echinochloa P. Beauv.	ECHIN4	<0.001	<0.001	<0.001	0
Leersia hexandra Sw.	LEHE	0.013 (0.012)	<0.001	<0.001	<0.001

table cont'd

Species, Genus, or Family name	Taxonomic code	Fresh	Intermediate	Brackish	Saline
Other Group					
Heliotropium L.	HELIO3	0.007 (0.0014)	0.041 (0.025)	0.011 (0.007)	0.007 (0.003)
Sagittaria L.	SAGIT	< 0.001	< 0.001	0.001 (0.001)	0
Croton L.	CROTO	0.20 (0.009)	0.004 (0.004)	0.001 (0.001)	0.005 (0.003)
Non-Food					
Cladum jamaicense					
Cladium mariscus (L.) Pohl ssp. jamaicense (Crantz) Kük.	CLMAJ	0.940 (0.341)	4.696 (0.914)	1.364 (0.305)	0.305 (0.083)
FAV Group					
Eichhornia crassipes (Mart.) Solms	EICR	0.004 (0.002)	0.001 (0.001)	< 0.001	<0.001
Ranunculus L.	RANUN	<0.001	<0.001	0.003 (0.002)	<0.001
Utricularia macrorhiza Leconte	UTMA	0.001 (0.001)	<0.001	< 0.001	<0.002
Hydrocotyle L.	HYDRO2	0.055 (0.21)	0.050 (0.014)	0.007 (0.004)	0.003 (0.001)
Centella erecta (L. f.) Fernald	CEER2	0.004 (0.002)	0.001 (0.001)	0.002 (0.002)	< 0.001
Nelumbo lutea Willd.	NELU	2.808 (2.040)	0.062 (0.047)	0.042 (0.019)	0.013 (0.009)
Poaceae Group					
Zizaniopsis miliacea (Michx.) Döll & Asch.	ZIMI	0.015 (0.006)	0.012 (0.012)	0.001 (0.001)	0.001 (0.001)
Other Group					
Amaranthus australis (A. Gray) Sauer	AMAU	0.006 (0.004)	0.004 (0.001)	0.003 (0.001)	<0.001
Echinodorus cordifolius (L.) Griseb.	ECCO3	<0.001	<0.001	< 0.001	0
Cuscuta L.	CUSCU	0.008 (0.005)	0.010 (0.009)	0.007 (0.003)	0.011 (0.004)
Salicornia biglovii Torr.	SABI	< 0.001	<0.001	< 0.001	< 0.001
Chenopodium L.	CHENO	<0.001	<0.001	0.001 (0.001)	< 0.001
Borrichia frutescens (L.) DC.	BOFR	<0.001	<0.001	<0.001	0
Ludwigia L.	LUDWI	0.017 (0.017)	<0.001	<0.001	<0.001
Kosteletzkya virginica (L.) C. Presl ex A. Gray	KOVI	0.018 (0.009)	0.027 (0.024)	<0.001	0.001 (0.001)
Ipomoea L.	IPOMO	0.001 (0.001)	0	0.006 (0.005)	0.006 (0.003)
Baccharis halimifolia L.	BAHA	<0.001	0	0	0
Ambrosia artemisiifolia L.	AMAR2	0.003 (0.002)	0.004 (0.002	0.003 (0.002)	0.005 (0.003)
Cephalanthus occidentalis L.	CEOC2	0	0	< 0.001	0.015 (0.015)
Iva frutescens L.	IVFR	0	0.072 (0.058)	0.002 (0.001)	0.045 (0.025)
Morella cerifera (L.) Small	MOCE2	0.020 (0.015)	0.048 (0.027)	0.036 (0.018)	0.054 (0.030)
Ilex vomitoria Aiton	ILVO	0.065 (0.050)	0.008 (0.005)	0.004 (0.002)	0.008 (0.003)
Sesbania herbacea (Mill.) McVaugh	SEHE8	0.016 (0.016)	0	0.006 (0.005)	0
Avicennia germinans (L.) L.	AVGE	0	0	0.011 (0.011)	0
Nyssa sylvatica Marshall	NYSY	0.197 (0.113)	0	0	0.003 (0.002)
Nyssa aquatica L.	NYAQ2	0.266 (0.216)	0	0	0
Taxodium distichum (L.) Rich.	TADI2	0	0.001 (0.001)	0.005 (0.005)	0.002 (0.001)
Unknown		0.033 (0.081)	0.009 (0.003)	0.214 (0.051)	0.004 (0.001)

There was a positive correlation between food seed biomass and SAV cover (p < 0.0001). This correlation held in all marsh zones and all regions.

SAV Seeds. Biomass of SAV seeds differed among marsh zones and regions as indicated by an interaction (F value = 3.416; p = 0.0004; Table 4.3 Figure 4.3c). There was no effect of year on SAV seed biomass. The interaction was largely driven by the high SAV seed biomass in the fresh marsh zone of the TMC region (0.89± 0.28 g m^{-2}), due largely to high biomass of *Potamogeton* seeds (Table 4.3), and high SAV seed biomass in the MRCW fresh marsh zone (0.43± 0.15 g m^{-2}).

There was a positive correlation between SAV percent cover and SAV seed biomass (p < 0.0001). There was a correlation (p < 0.0001) for SAV cover and SAV seed biomass for *R. maritima*, *Potamogeton* species (*Potamogeton* seeds were all grouped together for biomass, and included *S. pectinata*), and *C. demersum*, there was no correlation between any other SAV species and seed of the same species, or seeds of other SAV species.

Seasonal estuarine study

Environmental variables. Salinity patterns different among marsh zones and season as indicated by an interaction (F value = 6.825; p < 0.0001; Table 4.4; Figure 4.4a), Mean salinity in saline marsh zones in early (13.95± 1.19) and late winter (13.10± 1.60) was higher than all other marsh zone and season combinations. Mean salinity in fresh marsh zones across all seasons (0.15 – 0.2) except early winter was lower than saline in all seasons, and different from brackish in all seasons except early summer.

Depth differed among marsh zones and seasons (Table 4.4; Figure 4.4b) Depth differed across all marsh zones (F = 18.215; p < 0.001) except between brackish and intermediate marsh zones. Mean depth ranged from 0.87± 0.08m in fresh marsh zones to 0.45± 0.03m in saline marsh zones. Depth was different among seasons (F value = 5.490; p < 0.0001), largely driven by low mean late winter depth (0.36± 0.04) compared to the other seasons.

Temperature patterns differed among marsh zones and seasons as indicated by an interaction (F value = 2.208; p = 0.008; Table 4.4; Figure 4.4c), driven largely by low temperatures in the fresh marsh zone in the winter season (14.0± 0.5°C). Across seasons, mean temperatures varied as expected, increasing in the summer and decreasing in the winter, and were lowest in late winter (16.4°C) and increased to peak in early summer (30.8°C). Turbidity (25.9 – 36.6 NTUs) was not different across marsh zones or seasons (Figure 4.4d).

Total Seeds. Total seed biomass differed among marsh zones (F value = 12.746; p < 0.0001). There was no effect of season, or any interaction between season and marsh zone on total seed biomass. Marsh zone differences were largely driven by high seed biomass in the intermediate marsh zone (Table 4.5; Table 4.6; Figure 4.5a). Seed biomass from one intermediate site was omitted from the final seed analyses as unusually high biomass values were determined to be an outlier for this dataset. *Nelumbo lutea* seeds were also identified as significant outliers due to high biomass of individual seeds, and were omitted from final seed analyses.

Food Seeds. Food seed biomass differed among marsh zones (F value = 17.809; p < 0.0001). There was no effect of season, or any interaction between marsh zone and season.

Differences were largely driven by the intermediate marsh zone which supported significantly higher food seed biomass than all other marsh zones (Table 4.6; Figure 4.5b). There was no correlation between food seed biomass and SAV cover.

SAV Seeds. SAV seed biomass did not differ by marsh zone or season, nor was there any interaction between marsh zone and season (Table 4.6; Figure 4.5c). SAV seed biomass was largely composed of *C. caroliniana* (64%) and *M. spicatum* (22%) seeds. There was no correlation between SAV percent cover and SAV seed biomass, either as an assemblages of cover and seeds or by species.

Discussion

The availability of potential food resources varied spatially across estuarine gradients, and was further distinguished across regions. This spatial variation across region and within estuaries is likely related to salinity, hydrology, bathymetry, and exposure conditions across the coastal landscape. While fresh and intermediate marsh zones statistically supported the highest food seed biomass across the entire landscape, this was not true for all regions. Food seed biomass in the fresh marsh zone in the TMC region was significantly higher than other zones in the same region. In contrast, the fresh, intermediate, and brackish marsh zones in the CP region had similar food seed biomass values. Depth, seed characteristics of dominant vegetation species (submergent or emergent), and habitat type (open bays, canals, creeks, ponds, etc.) may be necessary qualifiers to incorporate in describing seed bank and subsequent habitat value by marsh zone. Ecological filtering of seeds can occur as the environmental conditions of each marsh zone and region act to select seeds based on individual species physiology, encouraging or discouraging accumulation of seeds in submerged habitats (Myers and Harms, 2009).

Table 4.3: Grouped seed biomass (g m^{-2}) ±SE for inter-annual dataset in each region.

	Total	Food	SAV	Cyperaceae	Cladium	FAV	Poaceae	Polygonaceae	Other
Texas Mid-Coast									
Fresh	4.01 (1.96)	2.34 (0.64)	0.89 (0.28)	0.80 (0.25)	1.39 (1.39)	0.13 (0.04)	0.62 (0.56)	0.02 (0.02)	0.16 (0.08)
Intermediate	1.32 (0.39)	0.73 (0.16)	0.11 (0.04)	0.25 (0.07)	0.02 (0.01)	0.0	0.10 (0.04)	0.02 (0.01)	0.82 (0.38)
Brackish	0.22 (0.08)	0.22 (0.08)	0.04 (0.02)	0.08 (0.03)	0.0	<0.01	0.0	0.02 (0.02)	0.11 (0.08)
Saline	0.39 (0.06)	0.25 (0.03)	0.10 (0.02)	0.11 (0.02)	0.03 (0.02)	0.02 (0.02)	0.01 (<0.01)	0.01 (0.01)	0.11 (0.04)
Chenier Plain									
Fresh	5.91 (1.83)	1.92 (0.61)	0.05 (0.02)	1.04 (0.29)	0.78 (0.25)	9.11 (7.72)	0.07 (0.04)	0.29 (0.11)	2.17 (0.93)
Intermediate	9.40 (1.76)	1.45 (0.22)	0.13 (0.03)	1.14 (0.21)	7.72 (1.70)	0.18 (0.05)	0.18 (0.05)	0.08 (0.02)	0.07 (0.05)
Brackish	1.83 (0.35)	1.2 (0.17)	0.31 (0.08)	0.85 (0.14)	0.50 (0.30)	0.03 (0.02)	0.03 (0.02)	0.02 (0.01)	0.13 (0.04)
Saline	0.65 (0.18)	0.58 (0.17)	0.10 (0.04)	0.42 (0.15)	0.01 (<0.01)	0.06 (0.05)	0.06 (0.05)	<0.01	0.03 (0.02)
Mississippi River Coastal Wetlands									
Fresh	2.28 (0.67)	1.10 (0.20)	0.43 (0.15)	0.32 (0.10)	0.09 (0.05)	0.93 (0.63)	0.02 (0.01)	0.21 (0.05)	0.28 (0.10)
Intermediate	5.06 (0.98)	2.50 (0.48)	0.11 (0.03)	2.25 (0.46)	2.20 (0.62)	0.21 (0.16)	0.01 (<0.01)	0.11 (0.02)	0.17 (0.09)
Brackish	4.91 (0.94)	0.86 (0.15)	0.08 (0.02)	0.68 (0.14)	3.92 (0.89)	0.06 (0.04)	0.01 (0.01)	0.05 (0.01)	0.09 (0.03)
Saline	1.81 (0.43)	0.53 (0.09)	0.03 (0.02)	0.44 (0.09)	1.25 (0.42)	0.01 (0.01)	<0.01	0.06 (0.03)	0.02 (0.01)
Coastal Mississippi-Alabama									
Fresh	6.94 (2.46)	1.15 (0.43)	0.21 (0.08)	0.13 (0.07)	3.65 (1.94)	1.19 (0.68)	0.0	0.17 (0.07)	1.58 (1.02)
Intermediate	3.15 (1.39)	0.12 (0.07)	0.01 (0.01)	0.04 (0.03)	2.81 (1.39)	0.0	<0.01	0.0	0.29 (0.15)
Brackish	1.10 (0.36)	0.35 (0.15)	0.03 (0.02)	0.10 (0.02)	0.47 (0.14)	0.36 (0.19)	<0.01	0.06 (0.04)	0.08 (0.04)
Saline	0.79 (0.18)	0.11 (0.02)	0.02 (<0.01)	0.05 (0.01)	0.21 (0.05)	0.02 (0.01)	<0.01	0.03 (0.02)	0.46 (0.16)
Coast-wide									
Fresh	4.17 (0.75)	1.54 (0.23)	0.37 (0.08)	1.7 (0.36)	0.90 (0.34)	2.89 (2.04)	0.31 (0.10)	<0.01	2.96 (0.46)
Intermediate	6.55 (0.96)	1.53 (0.18)	0.11 (0.02)	5.86 (0.96)	4.7 (0.91)	0.14 (0.05)	0.10 (0.01)	0.07 (0.06)	1.8 (0.19)
Brackish	2.51 (0.33)	1.0 (0.11)	0.21 (0.05)	1.96 (0.32)	1.36 (0.31)	0.06 (0.02)	0.04 (0.01)	<0.01	1.33 (0.15)
Saline	0.78 (0.1)	0.29 (0.03)	0.06 (0.01)	0.44 (0.09)	0.31 (0.08)	0.02 (0.01)	0.03 (0.01)	0.06 (0.03)	0.48 (0.05)

Figure 4.3. Mean seed biomass for inter-annual landscape dataset. a) Total seed ±SE, b) food seed ±SE, and c) submerged aquatic vegetation (SAV) seed biomass ±S) for inter-annual dataset by marsh zone and region. Regions and marsh zones: TMC = Texas Mid-Coast, CP = Texas Chenier Plain, MRCW = Mississippi River Coastal Wetlands, CMA = Coastal Mississippi-Alabama, F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone

Figure 4.4. Environmental variables for seasonal estuarine dataset. a) Mean salinity (PPT) ±SE, b) mean depth (m) ±SE, c) mean temperature (°C) ±SE, and d) mean turbidity (NTUs) ±SE. MZ = marsh zone, F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone

[3]Table 4.4. Environmental variables for the seasonal dataset with mean values, ±SE, and range. Collected every 6-8 weeks in Barataria Basin, Louisiana for one calendar year (2015).

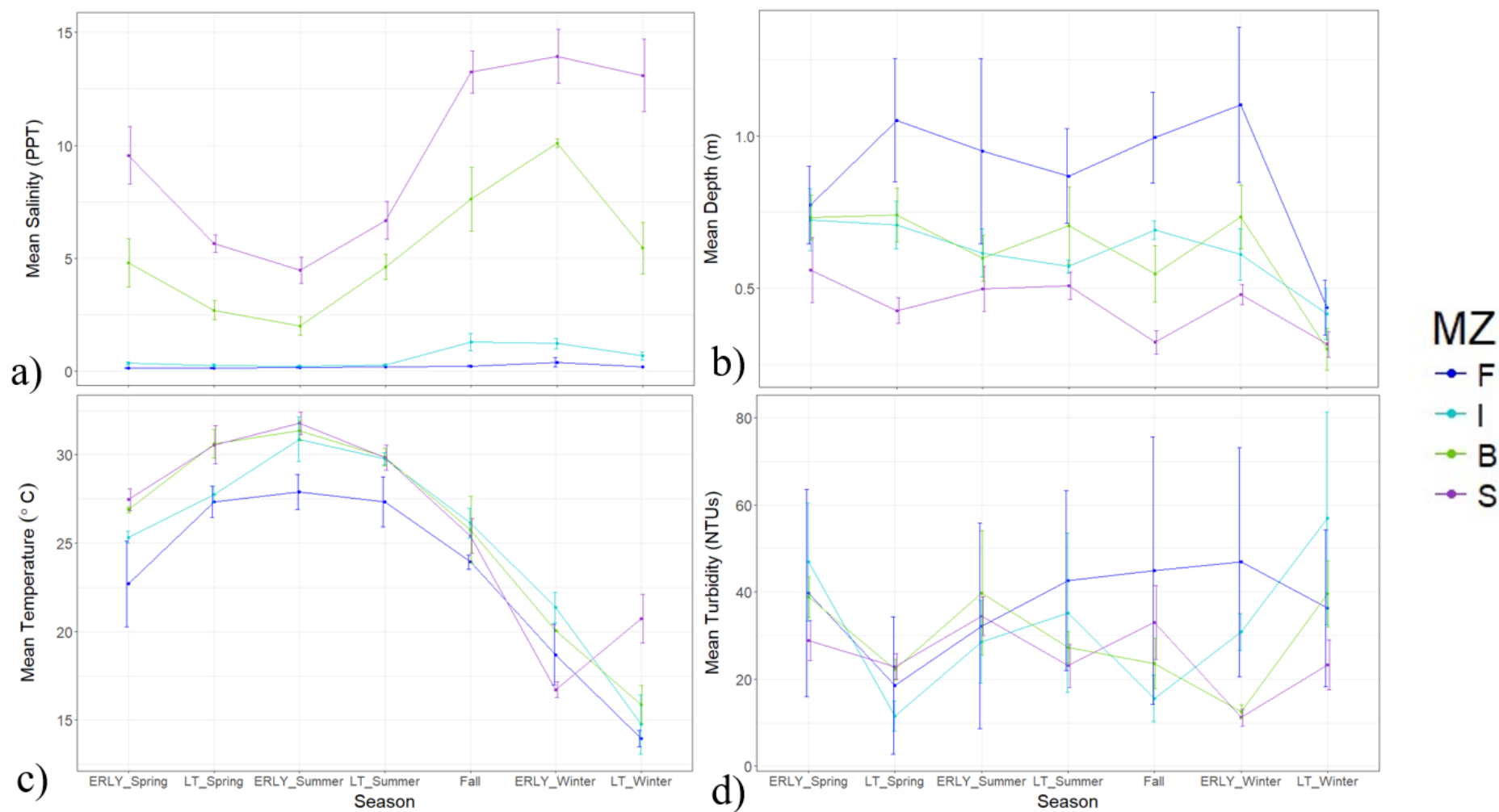|	Salinity (PPT)	Turbidity (NTUs)	Temperature (°C)	Depth (m)
	Overall			
Fresh	0.21 (0.03) 0.1 - 0.8	36.6 (7.5) 1.5 - 111.0	22.7 (2.4) 16.4 - 27.7	0.87 (0.08) 0.25 - 1.6
Intermediate	0.61 (0.1) 0.1 - 1.9	32.2 (5.3) 4.8 - 126.0	25.3 (0.3) 24.6 - 25.9	0.62 (0.03) 0.23 - 1.01
Brackish	4.86 (0.53) 0.7 - 10.3	30.1 (3.1) 11.0 - 96.7	26.9 (0.2) 26.6 - 27.3	0.62 (0.04) 0.15 - 1.12
Saline	9.36 (0.76) 3.3 - 16.4	25.9 (2.1) 7.3 - 57.7	24.5 (0.62) 25.4 - 28.7	0.45 (0.03) 0.19 - 0.97
	Early Spring			
Fresh	0.15 (0.03) 0.1 - 0.2	39.8 (23.8) 10.0 -111.0	22.7 (2.4) 16.4 - 27.7	0.77 (0.13) 0.49 - 1.03
Intermediate	0.35 (0.06) 0.2 - 0.5	48.9 (13.6) 14.1 - 80.5	25.3 (0.3) 24.6 - 25.9	0.72 (0.10) 0.55 - 1.01
Brackish	4.80 (1.07) 2.3 - 7.5	38. 9 (4.6) 30.7 - 52.1	26.9 (0.2) 26.6 - 27.3	0.73 (0.07) 0.63 - 0.95
Saline	9.56 (1.26) 6.6 - 13.3	28.9 (4.57) 17.4 - 39.9	24.5 (0.62) 25.4 - 28.7	0.56 (0.11) 0.39 - 0.97
	Late Spring			
Fresh	0.15 (0.03) 0.1 - 0.2	18.5 (15.7) 1.5 - 65.7	37.3 (0.9) 25.0 - 28.8	1.05 (0.20) 0.28 - 1.60
Intermediate	0.25 (0.09) (0.1 - 0.5)	11.5 (3.5) 5.22 - 21.2	27.8 (0.5) 27.0 - 29.1	0.71 (0.08) 0.56 - 0.93
Brackish	2.70 (0.43) 1.7 - 3.7	22.2 (2.3) 18.2 - 29.7	30.6 (0.8) 30.2 - 32.9	0.60 (0.09) 0.43 - 0.97
Saline	5.65 (0.38) 4.9 - 6.3	22.9 (3.0) 18.9 - 31.7	31.78 (1.08) 30.5 - 33.9	0.43 (0.04) 0.35 - 0.55
	Early Summer			
Fresh	0.17 (0.03) 0.1 -0.2	32.2 (23.6) 5.6 - 79.1	27.9 (1.0) 26.2 - 29.6	0.95 (0.30) 0.5 - 1.53
Intermediate	0.22 (0.06) 0.1 - 0.5	28.6 (9.4) 8.3 - 52.8	30.9 (1.3) 28.7 - 34.4	0.62 (0.08) 0.47 - 0.84
Brackish	2.00 (0.42) 0.7 - 2.7	39.8 (14.3) 22.7 - 96.7	31.4 (0.5) 29.1 - 31.8	0.60 (0.08) 0.45 - 0.87
Saline	4.48 (0.58) 3.3 - 6.5	34.4 (4.4) 21.3 - 48.5	31.78 (0.63) 30.5 - 33.9	0.51 (0.07) 0.35 -0.76
	Late Summer			
Fresh	0.2 (<0.1) 0.2 - 0.2	42.6 (20.7) 5.1 - 76.4	27.3 (1.4) 25.6 - 30.1	0.87 (0.16) 0.57 - 1.09
Intermediate	0.28 (0.02) 0.2 - 0.3	35.2 (18.2) 9.0 -88.6	29.8 (0.4) 29.0 - 30.6	0.57 (0.02) 0.51 - 0.60

table cont'd

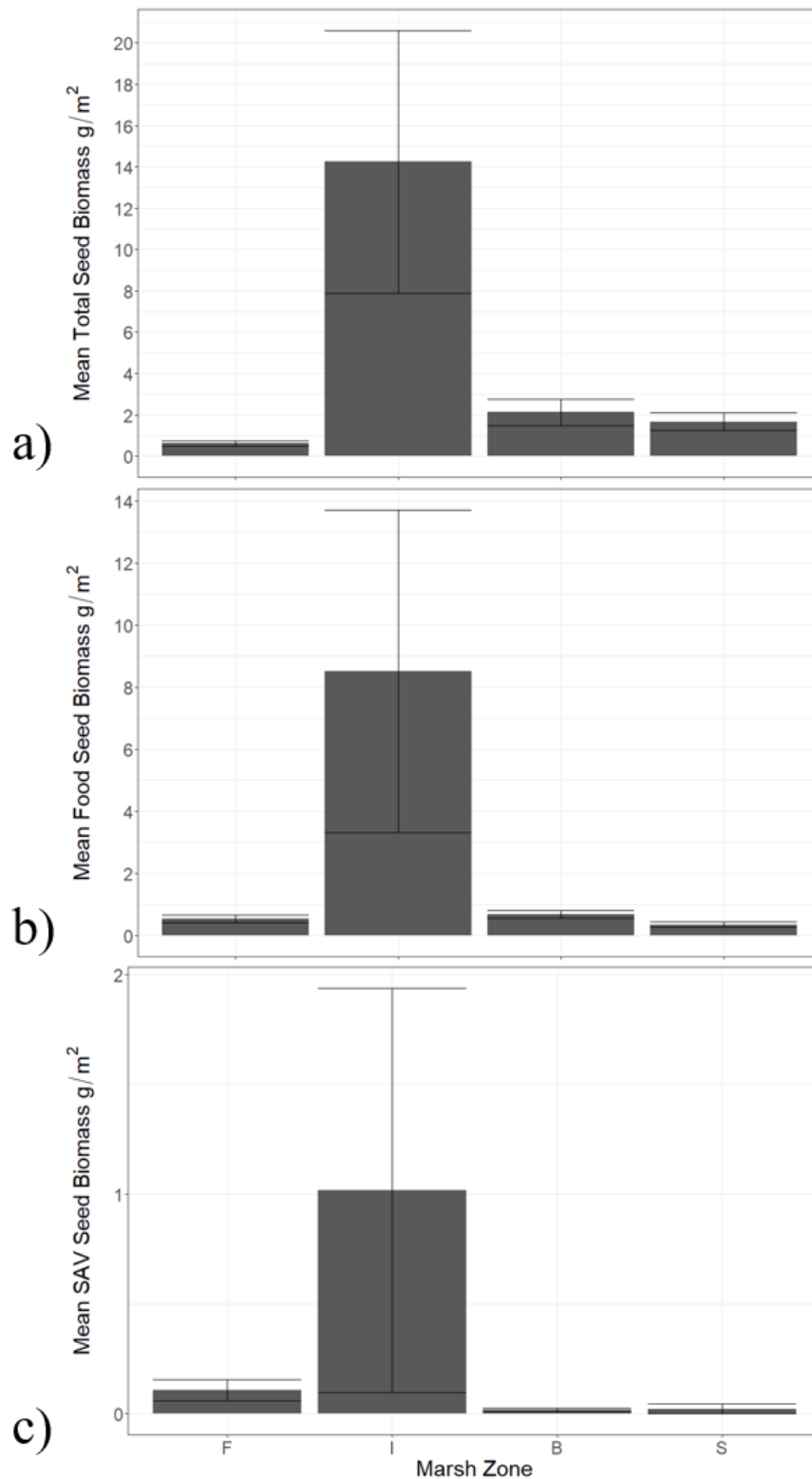|	Salinity (PPT)	Turbidity (NTUs)	Temperature (°C)	Depth (m)
		Overall		
Brackish	4.62 (0.56) 3.4 - 6.7	27.3 (3.6) 17.2- 39.6	29.9 (0.5) 29.1 - 31.8	0.70 (0.13) 0.35 -1.12)
Saline	6.68 (0.84) 4.6 - 9.0	23.1 (4.9) 19.2 -57.7	29.84 (0.69) 28.1 - 31.6	0.51 (0.05) 0.37 -0.64
		Fall		
Fresh	0.23 (0.03) 0.2 - 0.3	44.9 (30.6) 10.5 - 106.0	23.9 (0.4) 23.2 - 24.6	0.99 (0.15) 0.76 - 1.27
Intermediate	1.3 (0.39) 0.2 - 1.9	15.5 (5.4) 4.8 - 25.2	29.8 (0.9) 23.8 - 27.8	0.69 (0.03) 0.62 - 0.75
Brackish	7.62 (1.42) 2.0 - 9.6	23.6 (5.8) 13.0 - 46.0	25.8 (1.9) 20.7 - 30.9	0.55 (0.09) 0.32 - 0.83
Saline	13.25 (0.93) 11.1 - 15.6	33.0 (8.5) 19.2 - 57.7	25.4 (0.98) 23.0 - 27.0	0.32 (0.04) 0.25 -0.43
		Early Winter		
Fresh	0.4 (0.2) 0.2 - 0.8	46.9 (26.3) 4.8 - 95.2	18.7 (0.5) 15.3 -20.7	1.10 (0.25) 0.61 - 1.47
Intermediate	1.23 (0.23) 0.7 - 1.8	30.9 (4.2) 25.2 - 43.1	21.4 (0.9) 19.7 - 23.7	0.69 (0.08) 0.46 - 0.85
Brackish	10.10 (0.20) 3.4 - 8.4	12.6 (1.6) 11.0 - 14.1	20.1 (0.1) 20.0 - 20.1	0.74 (0.10) 0.63 - 0.84
Saline	13.95 (1.19) 11.2 - 16.4	11.17 (2.0) 7.3 - 15.3	16.72 (0.45) 15.6 -22.9	0.48 (0.03) 0.23 - 0.37
		Late Winter		
Fresh	0.2 (<0.01) 0.2 - 0.2	36.2 (18.1) 7.1 - 89.0	14.0 (0.5) 12.7 - 14.8	0.44 (0.09) 0.25 - 0.63
Intermediate	0.68 (0.17) 0.2 - 1.0	56.9 (24.4) 14.3 - 126.0	14.8 (1.7) 10.6 - 18.0	0.42 (0.08) 0.23 - 0.34
Brackish	5.45 (1.13) 3.4 - 8.4	39.6 (7.6) 17.2 - 51.4	15.9 (1.1) 13.4 - 18.5	0.30 (0.07) 0.15 - 0.42
Saline	13.1 (1.60) 11.3 - 16.3	23.2 (5.7) 15.7 - 34.5	20.73 (1.37) 18.2 - 22.9	0.32 (0.04) 0.23 - 0.37

Figure 4.5. Mean seed biomass ±SE by marsh zone for seasonal dataset in Barataria Bay, Louisiana. a) Total seed biomass, b) food seed biomass, and c) SAV seed biomass. Marsh zones: F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone.

There was no temporal trend in seed bank biomass, likely due to the high variability recorded across years, and seasons in this study. The absence of any seasonal or inter-annual patterns in seed density is likely related to 1) the variability of seed density in submerged habitats, and 2) the reproductive strategies of aquatic plants. For many seed species or groups, the standard error was 50% or greater than the total mean. This variability is expected, as wetland seeds are propagules randomly dispersed across large landscapes (Lui et al., 2006; Peterson and Baldwin, 2004), and exist in varying stages of deterioration depending on the age of the seed when it entered the water (if emergent) or was created (if submergent). Contributing to variability, many aquatic plants produce seeds in irregular events, responding to environmental conditions (Strazisar et al., 2016; Jarvis and Moore, 2008). During periods of stress of suboptimal conditions many aquatic and wetland plants will reproduce asexually, via cloning or propagules (Barko et al., 1986; Combroux and Gudrun, 2004). These reproductive events may or may not be seasonally mediated, and will be highly variable both locally and regionally as a result of spatial and estuarine gradients. A targeted approach to sampling during "optimal conditions" may provide insight into temporal trends of seed production for a single species, but on a landscape scale high seed biomass variability is typical, albeit problematic for managers (Hagy et al., 2014).

Although seeds were present in > 95% of samples and species identified were widely dispersed, both SAV seed and food seed biomass were positively correlated with SAV percent cover in the large inter-annual dataset. Moreover, there was significant correlation between SAV cover species and seed bank species. This is in contrast to emergent wetland habitats, where there is little relationship between above ground cover and seed banks (Hölzel and Otte, 2004; van der Valk and Rosburg, 1997), although there is a wide overlap of species located in the seed bank across the landscape (Baldwin et al., 1996). Aquatic vegetation seeds are widely dispersed by currents and wildlife (Mueller and van der Valk, 2002; Santamaria 2002; Soons et al., 2016), and as the NGOM is home to numerous highly mobile waterfowl species, the overlap of seed species across the landscape is not surprising. At the same time, some seed species were primarily located within SAV beds of the same species (i.e., *C. demersum*, *S. pectinata* and *R. maritima*). *Stuckenia pectinata* and *R. maritima* seeds were identified as having a rapid settling velocity by Koch et al. (2010), and are therefore likely limited by dispersal from currents and waves. This supports the theory that species seed morphology and physiology influences the dispersal of vegetation species, in turn controlling the distribution of seeds and recruitment of vegetation.

Table 4.5. Grouped seed biomass (g m^{-2}) ±SE for inter-annual dataset in each region.

	Total	Food	SAV	Cyperaceae	Cladium	FAV	Poaceae	Polygonaceae	Other
				Texas Mid-Coast (TMC)					
Fresh	4.01 (1.96)	2.34 (0.64)	0.89 (0.28)	0.80 (0.25)	1.39 (1.39)	0.13 (0.04)	0.62 (0.56)	0.02 (0.02)	0.16 (0.08)
Intermediate	1.32 (0.39)	0.73 (0.16)	0.11 (0.04)	0.25 (0.07)	0.02 (0.01)	0.0	0.10 (0.04)	0.02 (0.01)	0.82 (0.38)
Brackish	0.22 (0.08)	0.22 (0.08)	0.04 (0.02)	0.08 (0.03)	0.0	<0.01	0.0	0.02 (0.02)	0.11 (0.08)
Saline	0.39 (0.06)	0.25 (0.03)	0.10 (0.02)	0.11 (0.02)	0.03 (0.02)	0.02 (0.02)	0.01 (<0.01)	0.01 (0.01)	0.11 (0.04)
				Chenier Plain (CP)					
Fresh	5.91 (1.83)	1.92 (0.61)	0.05 (0.02)	1.04 (0.29)	0.78 (0.25)	9.11 (7.72)	0.07 (0.04)	0.29 (0.11)	2.17 (0.93)
Intermediate	9.40 (1.76)	1.45 (0.22)	0.13 (0.03)	1.14 (0.21)	7.72 (1.70)	0.18 (0.05)	0.18 (0.05)	0.08 (0.02)	0.07 (0.05)
Brackish	1.83 (0.35)	1.2 (0.17)	0.31 (0.08)	0.85 (0.14)	0.50 (0.30)	0.03 (0.02)	0.03 (0.02)	0.02 (0.01)	0.13 (0.04)
Saline	0.65 (0.18)	0.58 (0.17)	0.10 (0.04)	0.42 (0.15)	0.01 (<0.01)	0.06 (0.05)	0.06 (0.05)	<0.01	0.03 (0.02)
				Mississippi River Coastal Wetlands (MRCW)					
Fresh	2.28 (0.67)	1.10 (0.20)	0.43 (0.15)	0.32 (0.10)	0.09 (0.05)	0.93 (0.63)	0.02 (0.01)	0.21 (0.05)	0.28 (0.10)
Intermediate	5.06 (0.98)	2.50 (0.48)	0.11 (0.03)	2.25 (0.46)	2.20 (0.62)	0.21 (0.16)	0.01 (<0.01)	0.11 (0.02)	0.17 (0.09)
Brackish	4.91 (0.94)	0.86 (0.15)	0.08 (0.02)	0.68 (0.14)	3.92 (0.89)	0.06 (0.04)	0.01 (0.01)	0.05 (0.01)	0.09 (0.03)
Saline	1.81 (0.43)	0.53 (0.09)	0.03 (0.02)	0.44 (0.09)	1.25 (0.42)	0.01 (0.01)	<0.01	0.06 (0.03)	0.02 (0.01)
				Coastal Mississippi-Alabama (CMA)					
Fresh	6.94 (2.46)	1.15 (0.43)	0.21 (0.08)	0.13 (0.07)	3.65 (1.94)	1.19 (0.68)	0.0	0.17 (0.07)	1.58 (1.02)
Intermediate	3.15 (1.39)	0.12 (0.07)	0.01 (0.01)	0.04 (0.03)	2.81 (1.39)	0.0	<0.01	0.0	0.29 (0.15)
Brackish	1.10 (0.36)	0.35 (0.15)	0.03 (0.02)	0.10 (0.02)	0.47 (0.14)	0.36 (0.19)	<0.01	0.06 (0.04)	0.08 (0.04)
Saline	0.79 (0.18)	0.11 (0.02)	0.02 (<0.01)	0.05 (0.01)	0.21 (0.05)	0.02 (0.01)	<0.01	0.03 (0.02)	0.46 (0.16)
				Coast-wide					
Fresh	4.17 (0.75)	1.54 (0.23)	0.37 (0.08)	1.7 (0.36)	0.90 (0.34)	2.89 (2.04)	0.31 (0.10)	<0.01	2.96 (0.46)
Intermediate	6.55 (0.96)	1.53 (0.18)	0.11 (0.02)	5.86 (0.96)	4.7 (0.91)	0.14 (0.05)	0.10 (0.01)	0.07 (0.06)	1.8 (0.19)
Brackish	2.51 (0.33)	1.0 (0.11)	0.21 (0.05)	1.96 (0.32)	1.36 (0.31)	0.06 (0.02)	0.04 (0.01)	<0.01	1.33 (0.15)
Saline	0.78 (0.1)	0.29 (0.03)	0.06 (0.01)	0.44 (0.09)	0.31 (0.08)	0.02 (0.01)	0.03 (0.01)	0.06 (0.03)	0.48 (0.05)

[4]Table 4.5. Seed biomass (g m^{-2}) ±SE by species identified for seasonal dataset.

Species, Genus, or Family name	Taxonomic code	Fresh	Intermediate	Brackish	Saline
Food					
Cyperaceae Group					
Eleocharis R. Br.	ELEOC	0.038 (0.031)	0.546 (0.233)	0.137 (0.043)	0.126 (0.044)
Bolboschoenus robustus (Pursh) Soják	BORO5	0	0.0278 (0.016)	0.049 (0.021)	0.001 (0.001)
Schoenoplectus (Rchb.) Palla	SCHOE6	0.211 (0.043)	1.947 (0.405)	0.212 (0.059)	0.053 (0.021)
Fimbristylis Vahl	FIMBR	0.002 (0.002)	0.002 (0.002)	0.010 (0.007)	0.063 (0.018)
Rhynchospora Vahl	RHYNC3	0	0.112 (0.054)	0	0
Cyperus L.	CYPER	< 0.001	0.001 (0.001)	0.001 (0.001)	0.002 (0.001)
Juncus L.	JUNCU	0.002 (0.001)	0.006 (0.003)	0.005 (0.004)	< 0.001
Oxycaryum cubense (Poepp. & Kunth) Lye	OXCU2	0.095 (0.033)	< 0.001	< 0.001	0
SAV Seed Group					
Potamogeton L.	POTAM	0.003 (0.002)	0.005 (0.004)	0.008 (0.005)	< 0.001
Ruppia maritima L.	RUMA5	0	0	0.002 (0.002)	< 0.001
Najas guadalupensis (Spreng.) Magnus	NAGU	0.001 (0.001)	0.001 (0.001)	0	< 0.001
Ceratophyllum demersum L.	CEDE4	0.007 (0.007)	0	0.003 (0.003)	0
Vallisneria americana Michx.	VAAM3	0	0.001 (0.001)	< 0.001	0
Myriophyllum spicatum L.	MYSP2	< 0.001	0.040 (0.016)	0.005 (0.005)	< 0.001
Cabomba caroliniana A. Gray	CACA	0.096 (0.049)	0.012 (0.008)	0	0.022 (0.022)
Polygonaceae Group					
Polygonum L.	POLYG4	0.030 (0.013)	0.189 (0.040)	0.186 (0.061)	0.083 (0.37)
Carex L.	CAREX	< 0.001	< 0.001	0.002 (0.002)	< 0.001
Rumex L.	RUMEX	0.001 (0.001)	0	0.010 (0.005)	0.003 (0.003)
FAV Group					
Brasenia schreberi J.F. Gmel.	BRSC	0.002 (0.002)	0	0	0
Nymphaea L.	NYMPH	0.001 (0.001)	0	0	0
Poaceae Group					
Distichlis spicata (L.) Greene	DISP	0	0	< 0.001	0
Panicum L.	PANIC	0.025 (0.013)	0.001 (<0.001)	< 0.001	0.002 (0.002)
Other Group					
Heliotropium L.	HELIO3	< 0.001	<0.001	0.001 (0.001)	0
Sagittaria L.	SAGIT	0	< 0.001	0	0
Non-Food					
Cladum jamaicense					
Cladium mariscus (L.) Pohl ssp. jamaicense (Crantz) Kük.	CLMAJ	0.012 (0.007)	1.533 (0.502)	1.313 (0.584)	1.108 (0.369)
FAV Group					
Eichhornia crassipes (Mart.) Solms	EICR	<0.001	0.001 (0.001)	< 0.001	0
Ranunculus L.	RANUN	0	0.025 (0.014)	0.025 (0.014)	0.004 (0.004)

table cont'd

Species, Genus, or Family name	Taxonomic code	Fresh	Intermediate	Brackish	Saline
Utricularia macrorhiza Leconte	UTMA	0	0	< 0.001	0
Limnobium spongia (Bosc) Rich. ex Steud.	LISP2	0.009	0	< 0.001	0
Hydrocotyle L.	HYDRO2	0.0303 (0.013)	0.013 (0.006)	< 0.001	0.006 (0.004)
Centella erecta (L. f.) Fernald	CEER2	< 0.001	0.003 (0.002)	0	< 0.001
Poaceae Group					
Zizaniopsis miliacea (Michx.) Döll & Asch.	ZIMI	0.004 (0.004)	0.009 (0.009)	< 0.001	< 0.001
Other Group					
Proserpinaca palustris L.	PRPA3	0	0.009 (0.009)	0	< 0.001
Amaranthus australis (A. Gray) Sauer	AMAU	< 0.001	0.002 (0.002)	0.002	0.004 (0.003)
Echinodorus cordifolius (L.) Griseb.	ECCO3	0	0	< 0.001	< 0.001
Cuscuta L.	CUSCU	< 0.001	0	0	< 0.001
Salicornia biglovii Torr.	SABI	< 0.001	0	0	< 0.001
Aster L.	ASTER	0	0	< 0.001	0
Phytolacca americana L.	PHAM4	0	0.002 (0.002)	0	0
Iva frutescens L.	IVFR	0	< 0.001	< 0.001	0
Morella cerifera (L.) Small	MOCE2	0.020 (0.015)	1.002 (0.419)	0.056 (0.023)	0.210 (0.114)
Ilex vomitoria Aiton	ILVO	0	0.001 (0.001)	0	0
Sesbania herbacea (Mill.) McVaugh	SEHE8	0.025 (0.025)	0	0	0
Acer rubrum L.	ACRU	0	0	0.015 (0.15)	0

Table 4.6. Grouped biomass (g m^{-2}) ±SE by species identified for seasonal dataset.

	Total	Food	SAV	Cyperaceae	Cladium	FAV	Poaceae	Polygonaceae	Other
Fresh	0.62 (0.13)	0.55 (0.12)	0.11 (0.05)	0.35 (0.06)	0.01 (0.01)	0.04 (0.02)	0.03 (0.01)	0.03 (0.01)	0.04 (0.03)
Intermediate	5.74 (0.76)	2.94 (0.59)	0.08 (0.02)	2.64 (0.58)	1.53 (0.50)	0.31 (0.27)	0.01 (0.01)	0.19 (0.04)	1.0 (0.42)
Brackish	2.04 (0.68)	0.66 (0.14)	0.06 (0.01)	0.43 (0.09)	1.31 (0.58)	0.03 (0.01)	0	0.19 (0.06)	0.07 (0.03)
Saline	1.73 (0.42)	0.36 (0.09)	0.02 (0.02)	0.24 (0.06)	1.14 (0.38)	0.01 (0.01)	0	0.09 (0.04)	0.22 (0.12)

The lack of a correlation between food and SAV seed biomass to SAV cover in the Barataria dataset could be related to 1) the environmental conditions of the basin, or 2) the type of SAV species located in the basin. On the landscape scale, the MRCW region in all marsh zones had deeper water than other regions (Table 4.1), with the fresh marsh zone in Barataria Basin having significantly deeper waters, potentially limiting seed accumulation. Furthermore, SAV species common to this region (see Chapter 3) include *Hydrilla verticillata*, *Cabomba caroliniana*, *and Ceratophyllum demersum*, which do not typically produce high biomass of seeds, preferentially exhibiting asexual reproduction to save energy (Kautsky 1988). Sexual reproduction in aquatic plants is often considered a "luxury investment" of valuable plant resources (Li, 2014), and is not necessary, nor typical, for many species of SAV. Producing seeds takes a great deal of energy, and with relatively low chance of success in aquatic habitats (Cronk and Fennessy, 2001), asexual reproduction is critical to both emergent and submerged plants.

The potential for coastal waters supporting SAV to increase waterfowl habitat value relative to un-vegetated coastal waters could extend beyond the structural and nutritional benefits of the vegetation alone. While seed bank and germination studies of aquatic vegetation have shown spatially and seasonally distinctive patterns (Lui et al., 2006; Miao and Zou, 2009) there is generally poor correlation between vegetation cover and seed bank species (Holzel and Otte, 2004; van der Valk and Rosburg, 1997). This was not the case for SAV cover and seeds across the coastal landscape. The significant positive correlation between SAV cover and both food and SAV seed biomass suggests that areas supporting SAV beds provide additional foraging benefits. SAV may function to capture seeds as they are carried through currents in the water column, in turn increasing seed density through in-situ seed production and via seed capture of other species. Waterfowl may select habitats based on SAV presence and can adjust migratory routes to forage in areas with high water clarity and SAV cover (Anderson and Low, 1976, Paulus, 1982, Hansson et al., 2010). They may further be selecting habitats with SAV cover due to increased seed density, particularly in the winter months in the sub-tropical coastal wetlands of the NGOM, where SAV beds are persistent year round. It is also possible that increased seed density in SAV beds is the result of higher concentrations of waterfowl – as waterfowl feed on SAV roots and shoots, undigested seeds pass through the digestive track (Soons et al., 2016) and are deposited in the SAV bed. The additional benefit of increased seed biomass at habitats with SAV versus without, could be a useful tool to manage wildlife populations in wetlands depending on viability and metabolic energy contained in the seed.

Although estimates of seed bank biomass within the shallow water coastal habitats across the NGOM showed widespread, but low seed biomass, the energy from seed biomass potentially only represents a portion of the value of these habitats to waterfowl. Waterfowl managers generally use a threshold value of 5 g m^{-2}, or 50 kg/ha, for seed biomass as the giving up density below which waterfowl foraging is no longer energetically profitable (Loesch et al., 1994). Although there is some evidence that the threshold at which waterfowl give up foraging in an area is related to more than food density (Hagy and Kaminski, 2015), mean food seed biomass was less than this threshold (< 2.5 g m^{-2}) in all zones and regions for the inter-annual dataset, and was above this threshold only in the intermediate zone of the seasonal dataset (~ 8.5 g m^{-2}). However, as waterfowl are continually associated with SAV habitats (Hansson et al., 2010; Rybicki and Landwher, 2007), the aboveground vegetation and the structured habitat provided by SAV may increase the occurrence of other food resources (invertebrates, algae) for waterfowl and other bird species (Hitch et al., 2016; Kanouse et al., 2006; Lantz et al., 2007; Valinoti et al., 2011). Beyond providing food, SAV modifies the environmental conditions as well as adding structural habitat to aquatic systems (Madsen et al., 2001; Findlay et al., 2014), potentially providing benefits to wildlife species and the ecosystem as a whole, that are more difficult to quantify than biomass. At the same time, the shallow water seed bank, composed of emergent, submergent and upland seed species may provide some resiliency and adaptability to a region undergoing rapid habitat shifts (Hopfensperger, 2007; Inglish, 2000; Parker and Leck, 1985; van der Valk et al., 2009).

Estimates of food seed biomass would increase considerably if *C. jamaicense* were considered a waterfowl food. Although *C. jamaicense* was considered a valuable waterfowl food resource in the 1950s (Chamberlain 1959; Kimble and Esnminger, 1959), it is generally not considered to be energetically viable, despite limited research. *Cladium jamaicense* once dominated the fresh and intermediate marsh zones of coastal Louisiana (Chabreck, 1970) and much of the gulf coast (Conner et al., 1989), but its extent was significantly reduced by changing

environmental conditions (Day et al., 2000). *Cladium jamaicense* seeds are persistent in soils for long periods of time, and, although they are still frequently found in gizzard contents in large volumes (personal observation), are believed to be used as grit and not a food species due to the presumed age of the seeds. If *C. jamaicense* is not a food resource, it may yet provide habitat benefits to waterfowl species. Further research into energy content and waterfowl use of *C. jamaicense* seeds would be informative to assessing food seed biomass in NGOM habitats.

Conclusion

Due to regional differences in marsh zones, results indicate that quantifying biomass of seed food is more complex than assigning a value, or range of values, to a habitat type coast-wide. Environmental conditions unique to regions create distinctive aquatic habitats, associated vegetation communities, and seed banks. Over time, the seeds still present in the seed bank, particularly in submergent habitats, are likely those most resistant to these environmental conditions, namely, continuous inundation, salinity, and currents (Koch et al., 2010; van der Valk, 1981). This resistance is the product of the interaction between individual species seed physiology and the relative stress of the habitat on the seed – the seed will either persist in the seed bank, or decay. Each estuary and group of estuaries within a region is characterized by distinctive environmental conditions related to hydrology, geology, wildlife populations, and human activities. Although salinity gradients within estuaries follow similar patterns across large coastal landscapes, a given marsh zone in one region is likely to be strongly dissimilar to the same marsh zone in another region due to the influence of spatial gradients.

Across the NGOM, shallow coastal waters contain significant seed bank resources, providing support for wildlife populations. The ability of shallow water habitats to provide wildlife forage as seed biomass is influenced by spatial variability across local estuarine gradients and is further distinguished by regional conditions. SAV specifically functions as ecological indicators in aquatic habitats, responding rapidly to changing environmental conditions (Dennison et al., 1993; Moorman et al., 2017; Schneider et al., 2016) and may be some of the first areas be effected by climate and landscape changes. New climate regimes driving abiotic processes and biotic interaction within estuaries can result in different distributions of wetland vegetation, changing patterns of reproduction in aquatic plants, and shifting densities of seeds in both emergent and submerged habitats. These spatial relationships are critical to understand as coastal resource managers develop restoration and conservation strategies to optimize ecosystem function and services across aquatic landscapes.

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GENERAL CONCLUSION

The distribution of SAV in the NGOM coastal wetlands is the product of individual species' physiological tolerance to environmental conditions and the biological interactions within communities. This pattern is certainly not unique to SAV, and many species distributions can be understood and predicted by relating observations to environmental conditions (Elith and Leathwick, 2009). SAV are affected, often rapidly, by chemical, physical, and hydrological conditions (Schneider et al., 2016), and variations of and between these conditions will result in distinctive SAV species distributions and assemblages. By describing spatial and temporal patterns in SAV, it is also possible to characterize the habitat they occupy.

In the NGOM, the potential habitat for SAV covers an expansive coastal landscape with multiple and distinctive estuaries across regions. It could be assumed that the regional differences observed across the study area here are caused by different conditions in estuaries that result from regional processes. Estuaries are dynamic, and productive ecosystems ecosystems that are characterized by multiple and interacting environmental gradients and a variety of potential disturbance types. An estuarine gradient is a spatially delineated combination of abiotic conditions that influence ecological communities and processes therein. Across an estuary, salinity, turbidity, elevation, nutrient, temperature, and hydrologic gradients exist and interact (Cloern et al., 2017; Crain et al., 2004; Das et al., 2012; Seers and Shears, 2015), forming vegetation assemblages (Sasser et al., 2014). At the same time, estuaries are subject to a range of disturbances which can act as a stress or a subsidy depending on the species (Odum 1985; McClenachan, 2016). The combined effects of these individual environmental gradients and disturbance regimes create a regional gradient in the NGOM where estuaries may be distinguished from one another, providing a range of habitat for SAV distributions and assemblages. In identifying the SAV distribution and species assemblages over this landscape, the habitat was similarly characterized by understanding the individual species tolerances to environmental conditions. Essentially, identifying SAV in an estuary may act as a proxy for more detailed data on environmental conditions.

Regional gradients create conditions where the same marsh zones, as described by long-term emergent vegetation communities, in different regions, may not be equal in their ability to support SAV. The ecological responses of emergent and submergent vegetation assemblages to environmental conditions are not necessarily equivalent (Kinney et al., 2014), and although marsh zones across regions support similar emergent vegetation communities, SAV presence, assemblages, and cover can be significantly dissimilar. In particular, the combined results of this study indicate that fresh and saline marsh zones will support significantly different SAV populations in different regions, likely an effect of the estuary-specific gradients. Within individual estuaries, the environmental gradients produced spatially differentiated patterns in SAV presence, cover, and species assemblages. As individual species tolerance to conditions and stress structured species assemblages, they are particularly necessary to describe the habitat.

While the observations of SAV described the realized niche for SAV (Chapter 1), understanding how the environmental conditions of estuarine habitats drove SAV presence described described components of the fundamental niche for SAV species assemblages across the NGOM (Chapter 2). The fundamental niche of a species is the period of time and location where its ecological requirements are met (Chase and Leibold, 2003). Connecting Louisiana's abundant environmental data in the coastal zone

(https://www.lacoast.gov/crms_viewer2/Default.aspx) to the field observations of SAV presence created a statistically meaningful species distribution model (Elith and Leathwick, 2009). The spatial application of this model projected the potetnial distribution of SAV onto the coastal landscape, visually representing the differences between marsh zones in a region. The incorporation of environmental conditions not measured in the field study, namely exposure, helped to explain the patterns of SAV presence and cover. The saline marsh zone of Louisiana appears to have limited realized niche habitat for SAV assemblages.

Application of the niche concept to SAV distributions was similarly relevant by incorporating biological interactions between species and environmental variability over time. The interspecific interactions between SAV and FAV identified a seasonally variable, realized niche, for SAV assemblages in the fresh marsh zone of Barataria Basin. The realized or actual niche is the part of the fundamental niche a species is able to occupy in the presence of other species (Hutchinson 1957). The cold winter temperatures eliminated the niche for water hyacinth in fresh marsh, and in turn opened up a realized niche for SAV assemblages. Although interactions surely existed in the other marsh zones, the ability of SAV species to exist in these habitats appeared to be more closely related to abiotic conditions than interspecies competition. These patterns underpin the foundations of niche theory in aquatic ecosystems, and provide quantitative data on the potential for warming temperatures to have non-linear spatial effects in coastal habitats.

The ability of NGOM coastal marshes and aquatic habitat to provide foraging habitat for wintering waterfowl is related to the SAV and food seed distribution therein (Brasher et al., 2012). Coast-wide, there was a positive relationship between SAV cover and food seed biomass, showing that areas with SAV create forage habitat not only by directly providing food (as vegetation, roots, and seeds) but also by trapping seeds in the water column. Additionally, integrating the results from the landscape and estuarine -scale studies suggest that while food seed biomass in natural aquatic habitats may be lowered compared to managed coastal ponds areas (Winslow 2003), areas supporting SAV have additional habitat benefits beyond food biomass estimates. Trapping a diverse community of seeds able to germinate underwater may increase resiliency of the community in the event of rapid changes.

Incorporating species assemblage data into SAV cover estimates of NGOM aquatic valuation efforts is necessary to fully describe the habitat quality. Although results from the biomass portion of this study show that fresh marsh zones had the highest SAV biomass (Hillmann 2018), many of the species composing that biomass are less valuable to waterfowl (Valinoti et al., 2011). SAV assemblage data suggest that the value of fresh marsh habitats to waterfowl and other wildlife may be lowered in comparison to intermediate or brackish marsh zones, depending on the specific region. The food seed biomass in the fresh marsh zones of Barataria Basin in particular was significantly lower than intermediate marsh. Again, it is the estuary- and environmental gradient- specific conditions that drive both the accumulation of seeds and the species assemblages in an area over time.

The summation of this information is greater than the sum of its parts – the combined understanding of both estuary-specific gradients, niche habitat of SAV, and seed food densies across the NGOM coast provides a quantitative description of one of the most ecologically valuable coastal landscapes in the world. Characterizing these estuarine habitats by describing SAV distributions and assemblages across the landscape has implications for the application of niche theory, spatial predictive modeling, climate change impacts to aquatic communities, and the ability for coastal landscapes to support desirable wildlife communities. As the NGOM

coastal landscape becomes increasingly exposed to the effects of climate change and other anthropogenic activities, the potential for rapid ecological change grows. These data and patterns are both a contribution to the field of aquatic ecology as well as a benchmark from which to evaluate patterns of coastal change in the future.

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VITA

Kristin DeMarco was raised in Chatham County, North Carolina, and was introduced to coastal ecology as a young woman on fishing trips to the Outer Banks. She attended the University of North Carolina at Asheville, where she studied wetlands, majoring in Environmental Studies and minoring in Biology. After graduation, she moved to Charleston, South Carolina, working part time as a genius waitress and as a naturalist on Kiawah Island. This experience emboldened her interest in coastal ecology and led her back to school. She attended the Nicholas School of the Environment at Duke University, obtaining her Masters of Environmental Management in a dual concentration, Coastal Environmental Management and Global Environmental Change. After a short time consulting post-graduation, she moved to Baton Rouge, Louisiana, and worked as a coastal resources scientist for the Coastal Protection and Restoration Authority of Louisiana from 2010-2013. Again, she ended up back in school, understanding that a research and teaching career was where she wanted to be, entering into a PhD program at the Louisiana State University Agricultural Center's School for Renewable Resources. Following the completion of her PhD, Kristin hopes to stay in a university environment and continue research on aquatic ecosystems and teach.