4-4-2018

Analysis of Submerged Aquatic Vegetation Resources across the Northern Gulf of Mexico: Communities and Biomass

Eva R. Hillmann
Louisiana State University and Agricultural and Mechanical College, erhillmann@gmail.com

Recommended Citation

Hillmann, Eva R., "Analysis of Submerged Aquatic Vegetation Resources across the Northern Gulf of Mexico: Communities and Biomass" (2018). *LSU Doctoral Dissertations*. 4564.
https://digitalcommons.lsu.edu/gradschool_dissertations/4564

ANALYSIS OF SUBMERGED AQUATIC VEGETATION ACROSS THE NORTHERN GULF OF MEXICO: COMMUNITIES AND BIOMASS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

School of Renewable Natural Resources

by
Eva Rebecca Hillmann
B.A., Tulane University, 1997
M.S., Southeastern Louisiana University, 2011
May 2018

ACKNOWLEDGMENTS

I would like to start by thanking my entire Dissertation Committee. I would especially like to thank Dr. Megan La Peyre, the chairman of my committee, for the opportunity to work on such an exciting project, for her guidance and support. This has been an extraordinary experience. Thank you. I thank the rest of my committee, Dr. Andy Nyman, Dr. Victor Rivera-Monroy, Dr. Kyle Harms and Dr. William Kelso for their feedback from start to finish. It has been a pleasure. I thank Kristin DeMarco, my partner on this project. I couldn't image a better partner or person to see me through this entire experience. I thank Lindsey Schwarting, Gary Peterson, Bran Wagner, Katie Bowes and many student workers for their tireless work in the field and countless hours in the lab. I would also like to extend a special thanks to the faculty, staff and graduate students of the Louisiana State University Department of Renewable Natural Resources who made this journey so enjoyable. A special thanks belongs to Ms. Nedra Ghoram, for her unwavering patience with me.

This work was possible through funding from the U.S. Geological Surveys South Central Climate Science Center, the Gulf Coast Joint Venture, the Gulf Coast Prairie Landscape Conservation Cooperative, U.S. Fish and Wildlife Service, Region 2 and Region 4, and the U.S. Geological Survey. Many people were critical in helping to get this work done including staff at state and national wildlife refuges, private landowners, and non-profit land owners across the study area. Brady Couvillion and Holly Beck (U.S. Geological Survey) helped with site maps and site selection; Barry Wilson, Mike Brasher, Stephen DeMaso helped design the project, and acquire funding; Mike Poirrier, Andy Nyman, Joy Merino helped in initial planning of the project.

Nobody has been more important to me in the pursuit of this endeavor than my family. I would like to thank my parents and my children for providing unending inspiration. Finally, and most importantly, I need to thank my husband, whose support was invaluable and made this experience possible.

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ABSTRACT

Submerged aquatic vegetation (SAV) provides many critical ecosystem services, yet we lack basic information on SAV assemblages, biomass and diversity across expansive coasts such as the northern Gulf of Mexico (nGoM). This research investigated SAV along the nGoM from 2013-2015 examining (1) inter-annual variation in SAV assemblages and biomass across salinity zones and gulf coast eco-regions (Texas Mid-Coast, Texas/LA Chenier Plain, Louisiana Delta, MS/AL), (2) intra-annual variation in SAV assemblages and biomass across salinity zones, (3) response of two species, *Ruppia maritima* and *Myriophyllum spicatum*, to salinity and light regimes, and (4) estimated organic carbon stock and storage of SAV habitat soils across salinity zones. Coast wide, there was no variation among years, but significant differences in biomass and diversity within zones and regions were observed. Specifically, fresh zones and the Louisiana delta region had higher species diversity and contained more biomass than other zones and regions. Intra-annually, there were significant differences in SAV biomass and assemblages by salinity zone and month. Fresh/ intermediate zones contained more species and biomass than brackish/saline zones, and biomass was higher in summer months than winter months. Competitive relationships between co-occurring species were examined using *M. spicatum* and *R. maritima* growth response, under different salinity and light regimes. *M. spicatum* growth decreased with increasing salinity, while *R. maritima* growth was not impacted. *R. maritima* was also not impacted by light, while *M. spicatum* growth increased in high light. We observed strong competitive interactions; both species decreased in mixture and under no conditions was production in mixtures greater than monocultures. We estimated organic carbon stocks (C_{org}) within Mississippi River Delta Plain (MRDP) SAV habitat, out to the Chandeleur Islands, and found that MRDP SAV C_{org} did not differ across salinity zones, but was greater than Chandeleur SAV C_{org}. MRDP SAV habitat (159,609 ha) contains greater than $3.2 * 10^7$ Mg of C_{org}, representing an unaccounted for reservoir of “blue carbon,” particularly when extrapolated across the Gulf Coast. These new data provide a better understanding of factors controlling SAV spatial distribution, temporal variation and ecosystem services, which helps managers prepare for coastal changes.

CHAPTER 1
GENERAL INTRODUCTION

Coastal ecosystems encompass a variety of habitats, which include mangrove forests, bald cypress-water tupelo swamps, fresh to saline marshes, seagrass meadows and non-marine submerged aquatic vegetation (SAV) beds. At the interface of terrestrial landscapes and oceans, SAV is dynamic and productive habitat, vulnerable to impacts (i.e. temperature) associated with global climate change.

Non-marine SAV and seagrasses (collectively called SAV) are vascular plants rooted to water bottom sediments and generally grow completely submerged in water under anaerobic conditions. Seagrasses grow in coastal marine waters, while non-marine SAV occur throughout the remaining salinity zones (fresh, intermediate, brackish, saline). Seagrasses first appeared in the geologic record about 100 million years before present in the sub-class *Alismatidae* and today (along with non-marine SAV) exhibit extremely low taxonomic diversity (~ 60 species, collectively) compared to terrestrial vascular plants (Les et al. 1997). This lack of species diversity may be due in part to specific growing conditions, largely controlled by high incident light requirements.

Geographic Distribution and Decline of SAV

The total global areal extent of SAV is currently unknown, in part because of a lack of data about the spatial distribution of non-marine SAV. Global research that has focused on the spatial distribution of SAV globally has focused specifically on seagrasses, and shows that these assemblages occur on all continents, except Antarctica, and occupy an estimated 300,000-600,000 km^2 of coastal aquatic habitats (Hemminga and Duarte 2000). Enhanced water clarity in marine systems improves the accuracy of seagrass meadows aerial estimation using remote sensing techniques (Meyer and Pu 2012; Thorhaug et al. 2006; Yuan and Zhang 2008), and therefore, their spatial distribution is better understood. However, only 177,000 km^2 of seagrass habitat is mapped because field assessments are geographically biased; most research occurring in the European Mediterranean Sea, Japan, and Australia and along the Atlantic and Gulf coast of North America (Mcleod et al. 2011). Overall, t seagrass habitats have declined approximately 29% globally since the 1870s (Waycott et al. 2009) while the rate of seagrass habitat loss has increased since the 1940;, from less than 1% per year to ~ 7% per year (Fourqurean et al. 2003; Waycott et al. 2009).

SAV Ecology

The term *ecosystem engineer* applies to organisms that alter the environment by modulating the available resources (i.e. nutrients) for other community members (Jones et al. 1994). Seagrasses are ecosystem engineers; they are ecologically important (see below), and also physically alter the environment through nutrient cycling, removing sediment from the water column and carbon sequestration and storage (Cuddington et al. 2009; Gutiérrez et al. 2011).Furthermore, the role of non-marine SAV as ecosystem engineers is less understood. Yet,, studies show that they provide many of the same services as true seagrasses, including foraging habitat and refuge for invertebrates and fish (La Peyre and Gordon 2012; Thom et al. 2004; King and Sheridan 2006; Blandon and zu Ermgassen 2014; Williams and Heck 2001), food for waterfowl (Bortolus et al. 1998; Miller et al. 1996; Plattner et al. 2010; Shaughnessy et al. 2012; Url et al. 1991), improvement of water quality (DeBusk et al. 2011; Dierberg et al. 2005, 2002; Knight et al. 2003; Kosten et al. 2009) and shoreline stabilization (Gutiérrez et al. 2011; Hemminga and Duarte 2000; Thayer et al. 1975).

Several environmental factors are used as predictors of SAV presence/absence, although they do not explain why SAV are absent in areas suitable for SAV colonization. Light attenuation values are co-related to water depth and clarity, and are recognized as the primary factor controlling SAV presence/absence (Kemp et al., 2004). SAV require 10-20% of incident light at the leaf surface for growth and develop, compared to 0.5-2% for terrestrial plants and 0.5-3% for benthic macro algae (Dennison et al. 1993). Species-specific SAV distribution and range are apparently largely dependent on latitude (Short et al. 2007) and salinity (Lirman et al. 2008), and therefore are expected to be affected by global climate change.

Global Climate Change Impacts on SAV

Global climate change refers to an increase in the concentration of greenhouse gases in the atmosphere, including carbon dioxide (CO_2) and methane (CH_4). Since the Industrial Revolution, the concentration of CO_2 in the atmosphere has increased from 280 to 400 parts per million (ppm) (Mcleod et al. 2011). Both CO_2 and CH_4 concentrations increase the trapping efficiency of energy in the atmosphere by deflecting thermal energy from the Earth's surface back towards Earth, thereby increasing mean atmospheric temperature over time (Short and Neckles, 1999). Secondary impacts of climate change include sea level rise, higher ocean surface water temperature, increase in regional precipitation, and variable surface water salinity (IPCC 2013).

The 5th Assessment of the International Panel on Climate Change (IPCC) states that mean atmospheric temperatures are *most likely* to increase in the *range* of 1.1 and 6.4^{o}C by the end of the 21st century, with a variability ranging from 1.8 to 4.0°C (IPCC 2013). This temperature increase is assumed to impact the distribution and function of most of the Earth's ecosystems; terrestrial, coastal and oceanic. Increasing atmospheric temperature is associated with an increase in water temperature. For instance, ocean water temperatures have increased since 1850, especially in the northern hemisphere (IPCC 2013). Climate change is also expected to have a variable effect on surface water salinity. With increased precipitation, systems dominated by fresh water input may become fresher and coastal systems dominated by sea water may become more saline (IPCC 2013).As a result the distribution of SAV assemblages and overall standing stocks could be impacted, especially in intermediate-brackish habitats, though exactly how is unknown.

Carbon Storage in SAV Habitats

It is expected that soil organic carbon stocks and storage (blue carbon), one of the least investigated ecosystem services provided by SAV, will be impacted by climate change, although it is not clear how as we lack any current baseline information of organic carbon stocks in non-seagrass SAV habitat soils. In coastal systems, blue carbon research has focused on cypress-tupelo swamps, mangrove forests, marshes (Drake and Read 1981) and seagrasses habitats (Duarte et al. 2013; Fourqurean et al. 2012; Mcleod et al. 2011), but is lacking in SAV soils. Seagrass habitats efficiently store carbon because of low decomposition rates, high primary production and turnover rates, long term accumulation of detrital material and the external contribution of laterally imported organic matter. The long-term accumulation of detrital and imported organic matter contributes to the net reduction of CO_2 and CH_4 in the atmosphere (DeLaune and Lindau, 1987). Despite the limited number of studies, it is estimated that seagrass carbon burial ranged from 45-190 g C m^{-2} yr^{-1}, equivalent to 48-112 Tg C yr^{-1} globally. Although seagrasses occupy only 2% of the world's oceans, this habitat can sequesters as much carbon as mangrove forests and salt marshes, widely present at different latitudes (Mcleod et al. 2011). Long term carbon burial in non-marine SAV is currently unknown, and seagrass habitat estimates underscore the need to examine the potential magnitude of carbon stocks and storage in non-marine SAV.

SAV along the Northern Gulf of Mexico

Coastal ecosystems are the cultural, economic and ecological backbone of the northern Gulf of Mexico (nGoM). SAV assemblages along this coastal region represent a significant and valuable habitat type extending inland in some areas over 200 km along a salinity gradient running from freshwater to saline environments. Understanding changes in SAV assemblages, production and spatial distribution are of great interest to natural resource managers and researchers. Even as this habitat is an important food source for waterfowl and habitat for fish, and subsequently an important economic resource across the coast, few SAV coast wide spatial and temporal surveys have been conducted. Some research gaps include a lack of information on SAV presence, standing stock, assemblages, and carbon storage,. For example, along the nGoM, only one study has evaluated organic carbon stock in non-marine SAV habitats. This study examined above and below-ground organic carbon content of SAV tissue in brackish marshes in the Lower Neches Wildlife Management Area near Port Arthur, Texas. Results from this work shows that SAV captured less carbon (100-300 g m^{-2}) than adjacent emergent marsh vegetation (200-1,700 g m^{-2}), although the study did not measure soil organic carbon stocks and laterally imported organic matter into soil pools (Madrid et al. 2012).

Similar to global studies, the majority of SAV research studies along the nGoM have focused mainly on seagrass assemblages. Research has documented the factors controlling seagrass assemblages, distribution and growth in meadows along the Texas coast, which are patchily dispersed and dominated by *Halodule wrightii* and *Thallasium testudinum* (Dunton 1994; Kaldy et al. 2004; Lee and Dunton 1997; Tomasko and Dunton 1995). *H. wrightii* net primary production in coastal Texas ranges between 100-500 g m^{-2} yr^{-1} and growth rates are 4-7 mm a day during the peak growing season (May-mid June).This production is controlled by light attenuation, and photosynthetically active radiation (PAR), as shown in three different Texas estuaries.

Along the Mississippi/Alabama coast, Heck and others (2008) documented seagrass resilience after Hurricanes Ivan and Katrina and noted an increase in *Ruppia maritima* abundance. The role of seagrasses in coastal trophic interactions and food webs has also been investigated, and suggests that herbivory may be an important factor influencing SAV assemblages along this coastal region (Williams and Heck 2001; Heck et al. 2008; Heck and Valentine 2006; Valentine and Heck 1999).

In southeast Louisiana, east of the Mississippi River, research has identified the environmental drivers (hurricanes, salinity) behind shifts in SAV assemblages in Lake Pontchartrain, from *Vallisnaria americana* dominance to *R. maritima* prevalence (Cho and Poirrier 2005). *R. maritima* in Lake Pontchartrain has two biomass production peaks throughout the growing season as a result of high surface water temperature and little competition (light, space, nutrients) from other species. *R. maritima* peak biomass from May-November ranges from 155 to 489 gdw m^{-2} (roots and shoots). However, winter and summer storms (exposure) inhibit *R. maritima* production rates. Poirrier and others (2007, 2009) have also documented changes in species assemblages and seagrass abundance landward of the Chandeleur Islands; the only area in coastal Louisiana with true seagrasses.

Overall, information about the structural and functional properties of SAV west of the Mississippi River to Texas is lacking. Field surveys that focused on non-marine SAV distribution (Carter et al. 2009; Merino et al. 2009), did not report or discuss SAV biomass data, while research that documented SAV biomass were performed on small regional scales. Merino et al. (2009) sampled across four salinity zones (fresh, intermediate, brackish and saline) from south Florida to Texas and documented 20 different SAV and macro-algae species, 14 of which were observed more than once throughout the study (Merino et al. 2009). Merino et al. (2009) and Carter et al. (2009) did not sample interior marsh ponds, which are important SAV/waterfowl foraging habitat and an essential fish refuge. Thus, they may have underestimated SAV presence and/or density. Winslow (2003) documented SAV biomass in interior marsh ponds in Texas and Louisiana, but only in fresh water habitat. SAV biomass estimates in freshwater ponds are 262.3 ± 95.0 kg per ha^{-1}, thus exceeding the 50 kg per ha^{-1} value of SAV biomass availability required to meet minimum waterfowl food requirements (Winslow 2003).

In addition, in west Louisiana several studies investigated the relationship between SAV biomass and fish density. A study of brackish interior marsh ponds at the Rockefeller State Wildlife Refuge and the Sabine National Wildlife Refuge, LA *,* reported that locations with high SAV biomass supported higher fish population density (4x) than unvegetated marsh ponds (La Peyre and Gordon 2012). Kanouse et al. (2006) also found that fish density was positively related to SAV presence in brackish interior marsh ponds in Marsh Island, LA, while Hitch et al.

(2011) documented higher fish density with SAV presence in fragmented intermediate and brackish marsh ponds at Mandalay National Wildlife Refuge in southeast LA. Other studies have shown that hydrologically managed marsh ponds contained more SAV biomass than unmanaged ponds (17.2 g m^{-2} vs. 4.1 g m^{-2}). These results suggest that water depth controlled SAV biomass; making SAV habitat suitable for management (Merino et al. 2005).

Although these studies have provided critical information about SAV spatial distribution, there is still a lack of understanding about the environmental factors responsible for SAV presence and biomass at larger scales. Light, water depth and clarity (transparency) are identified as factors controlling SAV presence, assembly, and spatial distribution (Kemp et al. 2004; Koch 2001; Xu et al. 2011). Additionally, the interactions among light, salinity and temperature and their impact on SAV abundance and productivity have also been demonstrated (Bintz et al. 2003; Doering et al. 2001; Fey and Cottingham 2012; French and Moore 2003; Lee et al. 2007; Lirman and Cropper 2003; Shields et al. 2011; Thorhaug et al. 2006). Coastal waters along Mississippi, Alabama and southern Texas are dominated by tidal creeks and bays clear enough to sustain true seagrasses, while coastal Louisiana contains a large, shallow, subsiding coastal zone. West of the Mississippi River, up to eastern Texas, sediment in open water from rivers and coastal erosion reduces water clarity, likely precluding seagrasses in LA saline areas.

Climate change is expected to have an acute impact on coastal habitats along the nGoM (Karl et al. 2009; Mitsch et al. 2013). Rising sea level and shifting isohalines are assumed to be the most consequential factors affecting aquatic habitats along the coast. SAV assemblages are particularly vulnerable (Neckles et al. 1997; Short and Neckles 1999). Climate change impacts (i.e. increased precipitation, frequency of disturbance, rising sea level, increased runoff, changes in salinity and temperature) will affect the environmental drivers (light, depth, salinity, temperature, water quality) of SAV assemblages and their spatial distribution. Specifically how is unknown. Only a few studies have tested these variables in manipulative experiments and they focused on seagrasses, specifically. Olsen et al. (2012) investigated biomass production of *Posidonia oceanica* and *Cymodocea nodosa* in relation to increasing water temperature (increased from 27 to 32 ^{o}C for both species), and found both inter- and intraspecies variability in biomass production and allocation. *C. nodosa* above and belowground biomass production increased from 28 to 31^{o}C, and then decreased at 32^{o}C, while *P. oceanica* aboveground biomass was not significantly affected by increasing water temperature. Bintz et al. (2003) also tested temperature and found decreasing *Zostera marina* density and biomass with increasing temperature and nutrient loading. Studies like these show that seagrasses are impacted by subtle shifts along environmental gradients; non-marine SAV may respond similarly although we need data to confirm this assumption.

In Louisiana and across the nGoM, species specific biomass and its spatial distribution is of particular importance because of the complex, varied functions SAV species perform. An understanding of baseline species specific and regional biomass data, related to environmental variables will help in understanding SAV spatial distribution patterns, and enable predictive modeling of climate change and management impacts on SAV.

Research Objectives

This project proposes to

- (1) characterize SAV along salinity gradients, quantify SAV biomass and describe spatial and inter-annual variation in SAV across the nGoM
- (2) describe important environmental drivers and SAV intra-annual variation in Barataria Basin, LA
- (3) examine competitive interactions between two ubiquitous nGoM SAV species (*Ruppia maritima, Myriophyllum spicatum*), and
- (4) quantify SAV an ecosystem service by determining organic carbon stocks and overall storage in deltaic LA SAV habitats.

Study Area

The study area encompasses coastal marshes and associated shallow water habitats of the nGoM from Mobile Bay, AL to Nueces River, TX (Figure 1.1). The project boundaries were defined by Omernik Level III Ecoregions (USEPA 2013). Clustered Omernik Level IV Ecoregions broadly replicate four areas of the Gulf Coast Joint Venture Initiative Areas (Coastal Mississippi-Alabama, Mississippi River Coastal Wetlands, Chenier Plain, Texas Mid-Coast). The area encompasses approximately 1,200 km of coastal shoreline that is frequently impacted by tropical storms and hurricanes (Conner et al. 1989; Stone et al. 2005).

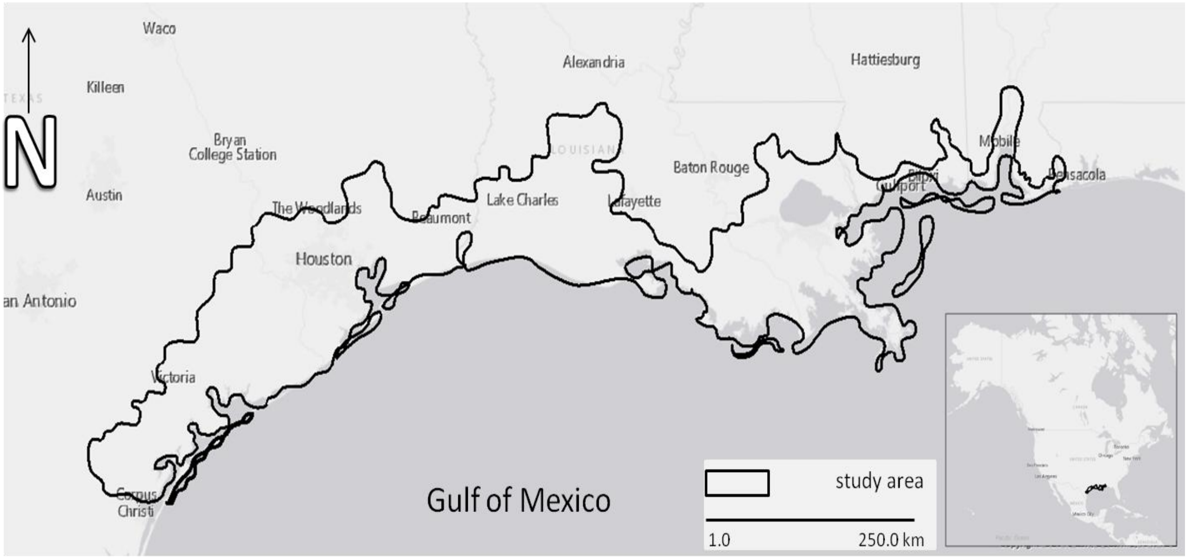

Figure 1.1. Study area along the northern Gulf of Mexico

In 2010, the Deepwater Horizon oil spill discharged 4.1 million barrels of oil into the Gulf of Mexico, resulting in extensive damage to coastal habitats, marine wildlife and local economies (Reddy et al. 2012). Along this coast, habitats are structured by salinity gradients, largely controlled by freshwater inputs limited to precipitation and restricted inflow from major river systems (i.e. Mississippi River) and Greater Intracoastal Waterway (Conner et al. 2005). Habitats consist of a mosaic of diverse estuarine and coastal plain habitat types, ranging from forested swamps, to fresh through saline marsh, extensive shallow-water habitats with mud flats, oyster reefs, submerged and floating aquatic vegetation habitats, and barrier islands.

Sampling Approach, Synopsis of Chapters and Hypotheses

Objectives 1-3 will be addressed using a three tier approach (Neckles et al., 2012). The methodology focuses on three distinct spatial and temporal scales of data sampling. Tier 1 sampling uses large study area, with numerous sampling locations, but infrequent (i.e. annual) data collection. Tier 2 sampling focuses on fewer sampling locations, but increases the frequency of data collection (i.e. quarterly, monthly). Tier 3 sampling uses greenhouse studies or intensive field studies to clarify causal relationships identified in Tier 1 and Tier 2.This approach is an important component of this research; it emphasizes awareness of and the importance of scale. Biological and ecological processes simultaneously occur and show variability at different spatial and temporal scales. An awareness of this variability at different scales reduces individual bias. Further, observations at different scales clarify mechanistic relationships among factors contributing to observed patterns (Levin 1992).

Tier 1 sampling will be used to accomplish objective (1), in Chapter 2 and Chapter 3. Chapter 2 will identify the environmental drivers of SAV assemblages and biomass distribution at the broadest scale, along a salinity gradient across coastal northern Gulf of Mexico. Chapter 3 describes the spatial and temporal variation of SAV assemblages and biomass in greater detail, incorporating geographic differences. At this scale, emerging and/or dissipating patterns are often missed. Yet, broad patterns are useful, as long as it is recognized that they are snapshots of specific conditions at a specific time. The hypotheses are:

- (1) species composition and diversity in SAV assemblages will vary across salinity zones and geographic regions
- (2) SAV biomass abundance will be inversely related to increasing salinity and will also vary across geographic regions
- (3) SAV biomass will vary interannually, throughout the duration of the study.

Tier 2 sampling will be used accomplish objective (2), in Chapter 4. In Chapter 4, I will use data (salinity, temperature, water level) collected from continuous data recorders to help illustrate and quantify the finer pattern and relationship between known environmental drivers of SAV assemblages and potentially seasonally variable biomass production. The hypotheses are:

- (1) SAV exhibits intra-annual variation, with two peaks of maximum biomass (spring, fall)
- (2) SAV assemblages can be delineated into four groups (fresh, intermediate, brackish, saline) based on salinity zonation of emergent marsh vegetation.

Tier 3 sampling will be used to accomplish objective (3) in Chapter 5. Chapter 5 will examine the relationship between commonly observed and co-occurring species from Tier 1 and Tier 2 sampling, tested against environmental factors (salinity, light) that shape SAV assemblages. Data from this study can be used as a predictive tool to estimate SAV response to some of the major effects of global climate change. The hypotheses are:

- (1) in monoculture milfoil will be more productive at lower salinity and widgeongrass will be more productive at higher salinity, and both species will be less productive in low light.
- (2) in mixture we expect widgeongrass will be more competitive at higher salinities and milfoil will be more competitive at lower salinities, and milfoil will be more competitive in low light.

Objective (4) will be addressed in Chapter 6. Chapter 6 will quantify the contribution of SAV habitat soils to regional carbon stock and storage estimates. The hypotheses are:

- (1) organic carbon stocks in SAV habitat soils will vary across salinity zones
- (2) organic carbon stocks will be highest in barrier island SAV habitat

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CHAPTER 2

ESTABLISHING A BASELINE OF ESTUARINE SUBMERGED AQUATIC VEGETATION ACROSS SALINITY ZONES WITHIN COASTAL AREAS OF THE NORTHERN GULF OF MEXICO

Coastal ecosystems are dynamic and productive habitats that are vulnerable to global climate change through changing precipitation patterns, increasing extreme weather and climatic events, and rising sea levels (Bindoff et al. 2007). Sea-level rise and changes in freshwater inflow from altered weather patterns have been identified as key drivers of change and stress associated with climate change (Karl et al. 2009, Sheets et al. 2012). Low-lying coastal areas such as the estuaries and coastal habitats of the northern Gulf of Mexico are particularly vulnerable because of locally high subsidence rates. Rising sea levels will likely alter water depths within the extensive shallow water habitats, while predicted changes in precipitation and weather patterns may impact freshwater inflow, altering salinity patterns within coastal areas (Bindoff et al. 2007). Combined, predicted changes in water depths and salinity patterns will likely affect the quantity and characteristics of coastal marsh and shallow-water communities (Harley et al. 2006).

Within these coastal areas, submerged aquatic vegetation (SAV) habitats are likely to be particularly vulnerable to predicted changes as salinity and water depth are two of the key environmental drivers of SAV biomass standing crop, production, assemblage, and distribution (Orth and Moore 1988, Orth et al. 2006, Carter et al. 2009, Merino et al. 2009). Changes in SAV habitat could have far-reaching consequences, as SAV are considered foundation species,

This chapter, previously published as Eva R. Hillmann, Establishing a baseline of estuarine submerged aquatic vegetation resources across salinity zones within coastal areas of the northern Gulf of Mexico. (2016):3, 25–32, is reprinted here by permission of the Journal of Southeastern Assocciation of Fish and Wildlife Agencies.

providing, and maintaining habitat for other organisms (Hemminga and Duarte 2000). Specifically, SAV provide important food and habitat resources for many dependent fish and wildlife species (Thayer et al. 1975, Williams and Heck 2001, Heck et al. 2003), improve water quality (Knight et al. 2003, Dierberg et al. 2005, Kosten et al. 2009) and contribute to shoreline stabilization (Gutierrez et al. 2011); therefore it is important to understand the potential effects of climate change on SAV habitats.

Despite the importance of SAV habitats, distribution and occurrence of SAV species are not widely documented along the northern coast of the Gulf of Mexico (Handley et al. 2007, Carter et al. 2009, Merino et al. 2009). Furthermore, relative abundance or extent of SAV across different coastal salinity zones (i.e., fresh, intermediate, brackish, salt) that may support different wildlife and fisheries species or communities is not widely documented. Several studies have identified water depth, water clarity and salinity as factors influencing SAV habitats (Cho and Poirrier 2005a, Carter et al. 2009). However, studies examining SAV distribution have documented high spatio-temporal variability in SAV and failed to find consistent factors that influence this variability (Merino et al. 2005), confounding any clear pattern over regional scales. Furthermore, climatic cycles have also been found to potentially affect SAV (Cho and Poirrier 2005b), making it difficult to explain SAV distribution patterns locally or on a global scale, where an overall decline of coastal SAV has been noted (Short and Wyllie-Echeverria 1996).

Coastal ecosystems are the cultural, economic, and ecological backbone of the northern Gulf of Mexico. Within this coastal region, SAV assemblages represent a significant and valuable habitat type extending inland in some areas over 200 km along a salinity gradient running from saline to fresh environments (Sasser et al. 2014). Biomass and species distribution of SAV have not been thoroughly studied and inventoried in this area (Merino et al. 2009) despite their critical importance to fisheries and waterfowl management. Thus, the objective of this project was to quantify SAV distribution, biomass and SAV assemblages across salinity zones in coastal northern Gulf of Mexico marshes.

Methods

Study area

The study was conducted in coastal marshes of the northern Gulf of Mexico from Mobile Bay, Alabama, to Nueces River, Texas. Ecoregions that included coastal marshes and plains were used to define the boundaries for this project using Omernik Level III Ecoregions (USEPA 2013; Ecoregions 34g, 34h, 73n, 73o, 75a, 75k).

Sampling design

Within the study area, we randomly selected 12 sub-regions using a stratified random sampling design. To achieve this, the study area was first divided into 43 sub-regions, which were represented by rectangles oriented North-South, and of equal East-West width. Using a random number generator, we selected a total of 12 sub-regions (Figure 2.1). We constrained our procedure to prevent the selection of adjacent sub-regions. This approach allowed sites to cover the range of habitats across our entire study area, while ensuring the study was logistically feasible.

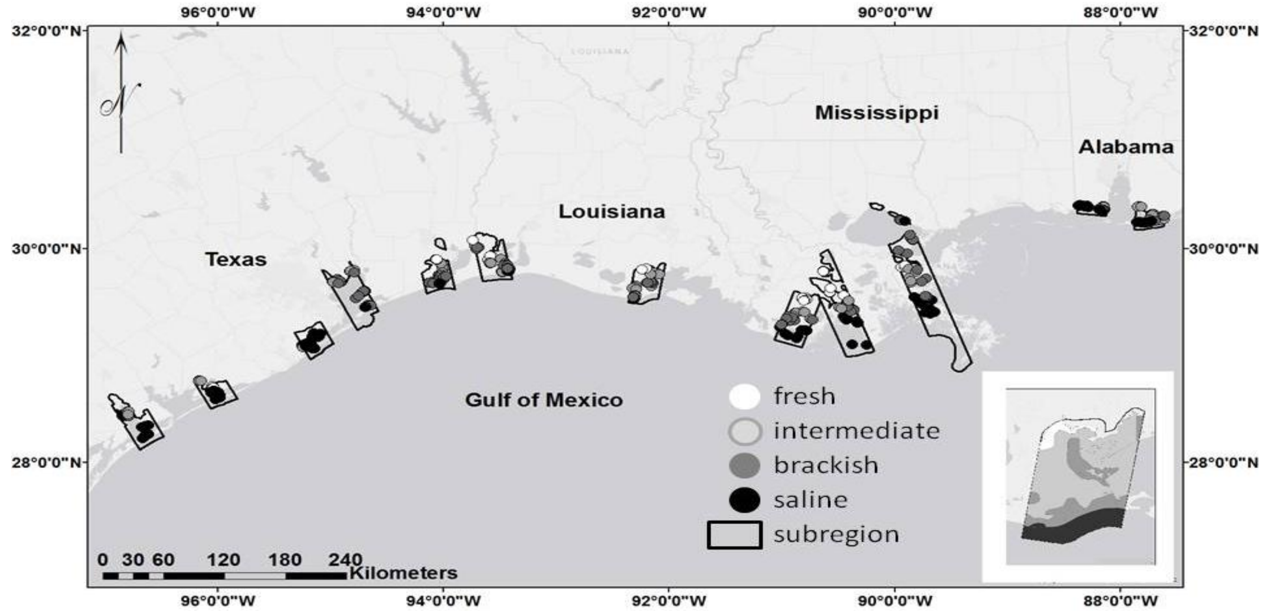

Figure 2.1. Map of study area from Nueces River, TX to Mobile Bay, AL. A total of 384 sites, clustered in twelve sub-regions were sampled in 2013 and 2014 using stratified random sampling based on salinity zones (fresh, intermediate, brackish saline). The inset on the bottom right represents an example of the salinity zone designations within one sub-region.

To create a GIS-layer for potential SAV habitat within each sub-region, four spatial sub-layers were developed using GIS Tools. The first two sub-layers relied on the use of cloud-free Landsat and satellite imagery (1984-2011). Images were stacked by path/row, with a minimum of 48 and a maximum of 124 images for any given path/row. The first sub-layer was created using an automated recognition of land-water classifications containing an SAV class. When SAV habitat was indicated in more than 10% of the available imagery, then the pixel was added to the sub-layer. For the second sub-layer, the stacked Landsat images were run through a maximum statistics tool and the output was run through an unsupervised classification on bands 4, 5, and 3. Generally, SAV is more reflective in bands 4 and 5 compared to water (B. Couvillon, USGS, personal communication). The output of the classification was coded into two classes: 1) possible SAV and 2) not SAV. When pixels were classified as possible SAV for more than 10% of the available images, it was included in sub-layer 2. The third sub-layer relied on

National Wetlands Inventory data for the region. We isolated all of the rooted vascular aquatic bed classes for the study area to create SAV Mask 3. The fourth sub-layer was generated using the maximum extent of water, aquatic bed, and unconsolidated shore from the National Land Cover Dataset (1992, 2001, and 2006) and the Coastal Change Analysis Program (1996, 2001, 2005 and 2006) datasets. Ponds less than $1011m^{-2}$ were deleted as they represent single pixels and often were not actually ponds.

We combined the final output for each of the four sub-layers to create our final SAV mask using an “or” statement. Where available, historic SAV geospatial data were used during the recoding process to help validate and refine the potential SAV mask. Salinity zone designations (fresh, intermediate, brackish, saline) were based on long-term emergent marsh vegetation patterns, which reflect long-term mean salinity range (Visser et al. 2013). These designations have been defined in Louisiana (Sasser et al. 2008), but were made using best professional judgment for Mississippi, Alabama and Texas for this project. Sample sites were randomly generated, stratified by salinity zone, and replicated eight times within each salinity zone and potential SAV habitat within each sub-region (i.e., 4 salinity zones x 12 sub-regions x 8 replicates = 384 sample sites x 3 subsamples x 2 years= 2304 samples).

Field data collection

All sampling occurred during the peak of the growing season, which was defined as mid June through early September. The order of sampling sub-regions was randomly determined each year. Each site was sampled once in 2013 and again in 2014. At each site, environmental and water quality variables, SAV presence, species composition and SAV biomass data were collected. Upon arrival at each site, water salinity (ppt, YSI-85, YSI Incorporated, OH), water temperature (C, YSI-85, YSI Incorporated, OH), and turbidity (NTU-Hach 2100Q, Hach, CO) were sampled from the boat before disturbing the benthic sediments. After collecting water quality data, SAV was sampled by throwing a 0.25 m x 0.25 m, floating PVC quadrat haphazardly three times from the boat. Within each quadrat, water depth was measured using a metric measuring stick randomly placed perpendicular and just touching the bottom (± 0.01 m).

When SAV was found, all biomass in the quadrat was harvested down to the sediment surface. Samples were kept on ice and transported to the laboratory where they were stored at 4^{o}C until processing. In the lab, samples were washed to remove sediment, debris, and epiphytic material, and biomass was separated to species level. Separated samples were dried at 60^{o}C to a constant weight, which was then recorded (± 0.001 g).

Analyses

For all tests a significance value of $p = 0.05$ was used. Differences in environmental variables (salinity, temperature, water depth, turbidity) were tested across salinity zones using a generalized linear mixed model with a normal distribution and identity link function (Proc Glimmix, SAS Institute 2010). We examined the independent and interactive effects of year (2013, 2014) and salinity zone (fresh, intermediate, brackish, saline) on the independent environmental variables (salinity, temperature, water depth, turbidity), and included random effects of sub-region, and sub-region by zone interactions, accounting for replication within each salinity zone through a nested statement. The residual effect was the repeated measure of sampling the same site each year. The SAV dataset was analyzed in its entirety for presence/absence by salinity zone using a chi-square test (SAS Institute 2010). Aboveground vegetation biomass of all sites (including zeroes) was analyzed using the same model as for environmental variables, but using a negative binomial distribution to account for the over-dispersion of data (McGarigal et al. 2013). Lastly, we also analyzed the variation of SAV biomass across sites where SAV was present using a normal distribution model and identity link function as described above (Proc Glimmix, SAS Institute 2010).

For examination of species-environment relationships, canonical correlation analysis (CCA) with backward selection was performed with CANOCO software (vers. 4.5; Wageningen UR, Netherlands; ter Braak and Smilauer 2002) to analyze the relationship between SAV biomass and environmental variables (salinity, water depth, and turbidity), combining 2013 and 2014 data of all sample sites. The two years of data were combined to increase the number of samples per species and to focus on species-environment relationships. Species-specific biomass was log 10 (x +1) transformed for the CCA to improve normality, and rare species were down weighted. A Monte Carlo simulation test was used to determine statistical significance of canonical axes with 1000 simulations on the full model.

Results

Environmental variables

Salinity differed significantly by year ($F_{1, 356} = 20.67$; $p < 0.0001$) and salinity zone ($F_{3, 65} = 53.85$; $p < 0.0001$) with 2013 having slightly higher salinity as compared to 2014. Fresh and intermediate salinity zones did not differ significantly in salinity, but were significantly lower than brackish sites, which were significantly lower than saline sites (Table 2.1). Temperature differed significantly only by year, but the difference was likely not ecologically significant (0.7^{o}C difference). Water depth differed significantly by year ($\underline{F}_{1, 355} = 10.61$; $p = 0.0012$) with 2013 having slightly greater water depths (0.51 m versus 0.47 m). Water depth also differed significantly by salinity zone ($F_{3,63} = 3.96$; $p = 0.0119$) with freshwater habitats being significantly deeper (0.63 m) as compared to saline, brackish and intermediate sites (<0.48 m).

Table 2.1. Mean (±SE) of environmental variables by salinity zone and year (2013, 2014). Ranges of reported values are indicated on the second line for each variable. Different letters indicate statistically significant differences by salinity zone for each parameter (P < 0.05).

		2013		
	Fresh	Intermediate	Brackish	Saline
Salinity (ppt)	3.92 (0.63)^A	6.81 (0.76)^A	11.1 (0.76)^B	21.82 (0.87)^C
	0.1-17.70	0.1-25.00	0-25.0	0-44.60
Temperature (C)	30.29 (0.28)^A	31.37 (0.17)^A	31.79 (0.20)^A	31.71 (0.18)^A
	26.8-37.2	21.2-36.6	27.0-36.9	26.9 -35.4
Turbidity (NTU)	52.3 (13.94)^A	51.98 (8.85)^A	58.2 (7.69)^A	53.47 (5.15)^A
	2.51-551.0	2.66-493.0	1.67-419.0	2.2 - 288.0
Water Depth (m)	0.65 (0.04)^A	0.52 (0.02)^B	0.45 (0.02)^B	0.44 (0.01)^B
	0.04-1.40	0.07 -1.0	0.06-1.69	0.05-1.3
		2014		
Salinity (ppt)	2.62 (0.51)^A	5.12 (0.63)^A	9.12 (0.64)^B	20.96 (0.87)^C
	0-16.2	0.2-27.4	0.02-24.7	0-39.0
Temperature (C)	31.74 (0.32)^A	31.78 (0.21)^A	32.03 (0.17)^A	31.64 (0.11)^A
	28.1-35.9	27.4-36.6	26.9-38.3	26.9 -35.7
Turbidity (NTU)	27.79 (4.36)^A	49.35 (5.40)^A	43.37 (2.95)^A	46.18 (2.71)^A
	4.96-198.0	1.24-254.0	5.66-157.0	5.39-184.0.0
Water Depth (m)	0.61 (0.04)^A	0.43 (0.02)^B	0.44 (0.02)^B	0.43 (0.01)^B
	0.08-1.70	0.12 -0.86	0.08-1.3	0.08-1.0

Submerged aquatic vegetation

All sampled sites. – Submerged aquatic vegetation was present at 38% of the sites sampled, which varied by salinity zone (chi-square = 19.58, p = 0.0002). SAV was found at only 23% of saline sites but was found at more than 40% of the sites in the other salinity zones. For all sites, including the zero values, there was a significant salinity zone effect for SAV biomass ($F_{3, 29} = 23.63$; $p = 0.02$). The saline zone had significantly lower biomass compared to the other zones in both 2013 and 2014 (Figure 2.2); mean biomass ranged from a low of about 10 g m^{-2} in 2014 saline sites, to a high of about 80 g m^{-2} in 2014 freshwater sites. There was no difference between years.

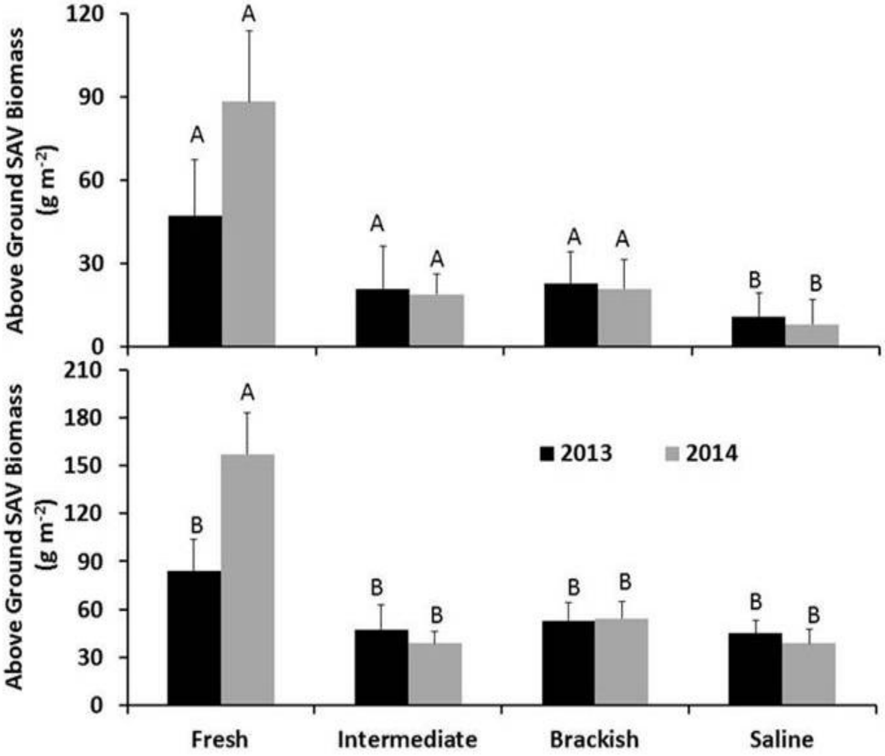

Figure 2.2. Total mean (± SE) SAV aboveground biomass across salinity zones and years for (top) all sites sampled, including sites with no SAV presence during sampling, and (bottom) only sites with SAV present. Letters above bars denote significant differences in biomass between year and salinity zone.

Sites with SAV present. -- For sites with SAV present, there was a significant year by zone interaction ($F_{3, 107} = 3.79$; p = 0.01) with 2014 freshwater sites having significantly higher biomass (mean = 157.2 m^{-2}, SE ±25.6 g m^{-2}) as compared to all other single year and zone combinations (range: 38.6-83.9 g m^{-2}; Figure 2.2). In total, 14 species of SAV were collected over the two years of sampling. Of these, twelve species of SAV were found in both 2013 and 2014 (Table 2.2) with manatee grass (*Syringodium filiforme*) unique to 2013 and star grass (*Halophila engelmannii*) unique to 2014. Eight of the 14 species comprised 97% of the SAV biomass, and all were found in both 2013 and 2014. Over the two years of sampling, four species; coontail (*Certophyllum demersum*), Eurasian watermilfoil (*Myriophyllum spicatum*), widgeon grass (*Ruppia maritima*), and hydrilla (*Hydrilla verticillata*) accounted for 73% of the above-ground biomass collected. Coontail, widgeon grass, and lesser pondweed (*Potamageton pusillus*) were collected across all four salinity zones. Hydrilla was collected only in fresh habitat; common water nymph (*Najas guadalupensis*) and wild celery (*Vallisneria americana*) were collected in all but saline habitat, while Eurasian watermilfoil was collected in all but fresh habitat (Table 2.2).

Table 2.2. Interactive effect of salinity zone and year on mean aboveground biomass (±SE) standardized to g m^{-2} by species collected. Percent (%) total indicates the amount of each species total biomass collected during the course of the study as a percent of the total aboveground biomass collected for all species. F = fresh habitat; I = intermediate habitat; B = brackish habitat; S = saline habitat.

Species	Total Cover	2013				2014			
		F	I	B	S	F	I	B	S
Widgeon grass	25.7	4.8±2.4	11.8 ±6.7	11.1±4.8	1.0±0.5	6.9±4.2	2.4±1.1	12.3±4.0	0.9±0.6
Hydrilla	18.6	18.0±8.3	-	-	-	41.9±12.9	-	<0.05	-
Coontail	16.3	12.1±6.4	0.7±0.3	1.2±0.6	<0.05	19.9±8.7	5.7±2.1	3.3±1.5	0.9±0.9
Eurasian watermilfoil	12.4	-	3.7±1.5	6.7±2.1	<0.05				
Shoal grass	9.7	-	-	-	8.0±2.4	-	-	0.1±0.1	5.7±2.0
Lesser pondweed	6.0	9.6±5.6	1.4±1.3	0.2±0.2	0.8±0.7	4.4±2.1	0.5±0.3	0.1±0.1	-
Common waternymph	4.9	0.4±0.3	<0.05	2.9±1.9	-	8.9±5.5	0.5±0.4	<0.05	-
Sago pondweed	3.8	-	3.2±2.3	<0.05	-	5.5±3.4	1.3±1.2	<0.05	-
Water star grass	0.9	1.8±1.8	-	0.5±0.5	-	0.2±0.2	<0.05	-	-
Wild celery	0.8	0.1±0.1	<0.05	0.2±0.2	-	0.7±0.6	0.6±0.6	0.2±0.2	-
Turtle grass	0.6	-	-	-	0.6±0.6	-	-	-	0.2±0.2
Star grass	0.1	-	-	-	-	-	-	-	0.2±0.2
Carolina fanwort	0.1	0.3±0.3	-	-	-	0.1±0.1	<0.05	-	-
Manatee grass	0.1	-	-	-	0.1±0.1	-	-	-	-

Species-environment relationship

The CCA indicated a significant relationship between SAV species and environmental variables (F = 23.83, p = 0.002; Figure 2.3). The horizontal axis, which explained 16.0% of the variation in species assemblage (eigenvalue = 0.35) was highly correlated with salinity (r = 0.91) and distinguished true seagrass species, shoal grass (*Halodule wrightii*), star grass, manatee grass, turtle grass (*Thalassia testudinum*) from less salt-tolerant species. The vertical axis, which accounted for 3.7% of the species-environment variation (eigenvalue = 0.08), was associated with water depth (r = 0.50). Hydrilla, Carolina fanwort (*Cabomba caroliniana*), star grass, and turtle grass were positively associated with water depth, while wild celery and common water nymph were negatively associated with water depth.

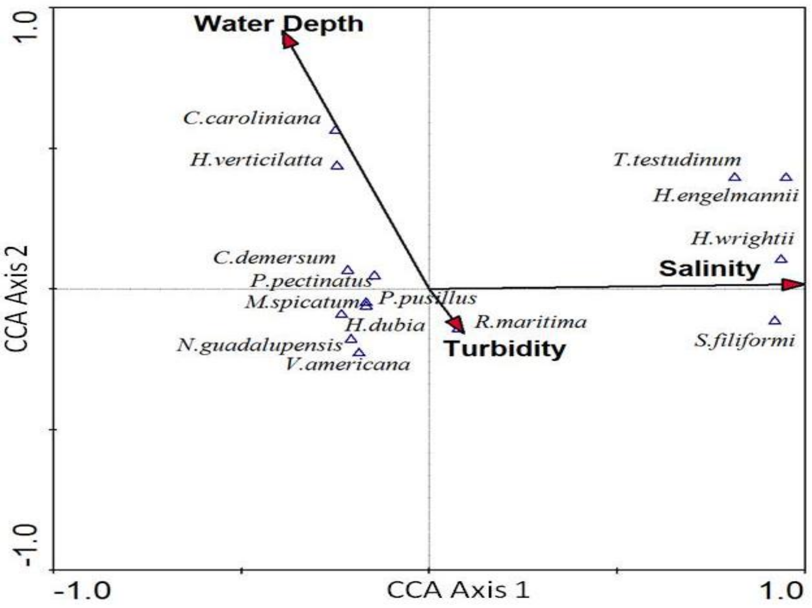

Figure 2.3. Canonical correlation analysis (CCA) of SAV species in relation to environmental variables (salinity, water depth, water turbidity).

Discussion

In the northern Gulf of Mexico, extensive marsh loss is altering the distribution of shallow-water habitats (Couvillion and Beck 2013), which may be further compounded by predicted effects of climate change on salinity and water depths (Harley et al. 2006). We found that submerged aquatic vegetation assemblage was partially driven by salinity and water depth, although overall biomass did not differ. As recent sea-level rise models predict the probable conversion of fresh coastal marsh to more saline marsh and open water habitats (Sheets et al. 2012), SAV are likely to be significantly impacted, altering the characteristics of SAV assemblages, and potential services provided. These changes could alter food and habitat resources, affecting dependent faunal species (Junk et al. 2013, Úbeda et al. 2013).

In general, SAV habitat is assumed to be valuable for invertebrate and fish species as it provides both refuge from predators and a rich source of food for estuarine nekton (Heck et al. 2003). Predicting the consequences of shifting SAV on nekton is somewhat complicated as past research has shown conflicting results. For example, a number of studies in coastal areas have found that higher densities of SAV were associated with greater numbers of invertebrates, fish (Kanouse et al. 2006, King and Sheridan 2006, Rapoza and Oviatt 2015), and waterfowl (Hansson et al. 2010). In contrast, there have been numerous suggestions that this positive association between SAV and nekton only holds true under specific conditions. For example, SAV density and morphology have been found to influence habitat use of fish (Edgar and Klumpp 2003) and predator-prey dynamics of fish and invertebrates (Chesney et al. 2000, Canion and Heck 2009). Because SAV characteristics (i.e., biomass, density, and species assemblage) may be critical factors in assessing potential habitat and food availability, understanding primary environmental drivers of SAV assemblages and potential shifts under changing conditions is essential.

While conversion of salinity zones from fresh to more saline may not necessarily alter total SAV biomass, changes in SAV assemblages will occur. Lower SAV density, production, and changed assemblages could impact carbon sequestration and overall storage, refuge availability for invertebrate and fish species, and food resource availability for other wildlife (Dionne and Folt 1991, Edgar and Klumpp 2003, Hansson et al. 2010, La Peyre and Gordon 2012). In this study, species assemblages varied by salinity zone and water depth. Only 3 of the 14 species were collected across the entire salinity gradient sampled (widgeon grass, coontail, and lesser pondweed) indicating that increasing salinity due to sea-level rise would result in altered SAV assemblages as species shifted to increasingly salt tolerant species. Based on our results, predictions of greater water depth and salinity throughout the coast will lead to a shift in SAV assemblages to more salt-tolerant species (Fulford et al. 2014).

As salinity and water depth are altered in fresh, intermediate, and brackish aquatic habitats, opportunistic species adaptable to a range of salinity conditions and able to grow in deeper waters are likely to expand into areas previously occupied by other species. For example, hydrilla is a highly opportunistic and invasive species that primarily occurs in freshwater, similar to where it was found in this study. In high-density patches, hydrilla has been shown to be associated with reduced densities of fish and invertebrates, altered fish diets, and reduced water quality (increased pH and surface water temperature) (Colon-Gaud et al. 2004, Carniatto et al. 2014). Similarly, previous studies have documented the expansion of widgeon grass into seagrass areas after salinity decreases following storm events (Fourqurean et al. 2003, Koch et al. 2007, Johnson et al. 2013). This expansion could have consequences on overall system production, as widgeon-grass-dominated beds have been found to exhibit lower peak biomass and productivity than those found in higher salinities that were dominated by turtle grass and eel grass (*Zostera marina*), a seagrass species commonly found along the Atlantic coast (Fourqueran et al. 2003). Furthermore, seagrass dependent fauna may have to adapt their home ranges or risk increased exposure to predators due to lower SAV density or changes in habitat structural morphology (Dionne and Folt 1991, Edgar and Klumpp 2003).

Climate change models predict that sea levels will continue to rise with global climate change (Pachauri and Meyer 2014). The shallow waters of the Gulf of Mexico and locally high subsidence rates make the coastal marshes along the northern Gulf particularly vulnerable to rising sea levels; increasing salinity and water depth will be two of the most acute effects (Bindoff et al. 2007, Harley et al. 2012). Several alternative changes in SAV assemblages are possible in response to predicted coastal changes. Similar to other coastal habitats, migration of SAV may occur with a shift in location of these different salinity communities following the movement of isohalines (Neckles et al. 1997, Short and Neckles 1999). If accompanied by significant sea-level rise, increased depths downstream, and barriers to migration upstream, this may result in a decline in overall SAV, or reduction in total area available for SAV habitats. If no barriers exist, SAV may continue to maintain themselves, or even expand simply with shifting locations, and into newly available areas from changes in coastal marsh availability.

Understanding current SAV availability and distribution, and factors controlling these patterns is critical for natural resource managers to effectively predict and plan for changes to SAV across the coast, and their impacts on dependent faunal species. In particular, in managing SAV as essential fish habitat for dependent faunal species, understanding key factors affecting the availability of specific SAV species and assemblages provides powerful information to managers. All SAV may not be equal in terms of fish habitat or provision of food resources (i.e., widgeon grass versus hydrilla); management can be focused to promote one species or assemblage of species over another depending on management goals (Blandon and zu Ermgassen 2014). For example, management activities to maintain freshwater inflows within coastal estuaries experiencing increased salinities might be useful if managers want to focus on maintenance of a fresher community; alternatively, control of water depths through water management in many coastal interior ponds may help to maintain shallow-water species over more deep-water adapted species. A better understanding of the current spatial distribution and environmental controls on key SAV species will help better prepare managers to focus management on desirable communities.

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CHAPTER 3

SPATIAL AND TEMPORAL VARIATION OF SUBMERGED AQUATIC VEGETATION ASSEMBLAGES AND BIOMASS ACROSS THE NORTHERN GULF OF MEXICO

Within the sub-tidal coastal zone, submerged aquatic vegetation (SAV) provides many ecosystem services, which include foraging habitat and refuge for invertebrates and fish (Blandon and zu Ermgassen 2014; La Peyre and Gordon 2012; King and Sheridan 2006; Williams and Heck 2001), food for waterfowl (Shaughnessy et al. 2012; Plattner et al. 2010; Bortolus et al. 1998; Miller et al. 1996; Url et al. 1991), improving water quality (DeBusk et al. 2011; Kosten et al. 2009; Dierberg et al. 2005, 2002; Knight et al. 2003) and shoreline stabilization (Gutiérrez et al. 2011; Hemminga and Duarte, 2000; Thayer et al. 1975). As a result, SAV availability is frequently integrated into climate change and restoration models (Visser et al., 2013). However, along rapidly changing and expansive coasts, including large deltaic regions such as the northern Gulf of Mexico (nGoM), limited data are available to describe SAV assemblages, SAV temporal variation and spatial distribution, limiting our ability to accurately predict SAV availability and ecosystem services.

Across the nGoM, SAV exists in the shallow bays, bayous, canals and ponds that dissect the landscape (Poirrier et al. 2010; Carter et al. 2009; Merino et al. 2009; Handley et al. 2007). In this region SAV exists across salinity gradients from fresh to saline water in mono-specific to multi-species beds (DeMarco et al. 2016; Hillmann et al. 2016; Merino et al. 2009). Coast-wide however, minimal data exist documenting SAV biomass and assemblage characteristics (i.e. diversity, number of species, evenness) and we lack estimates of overall habitat availability or total standing stock throughout the region. Coastal habitat maps often provide only minimal guidance on SAV availability across the nGoM.

Across the coast, a number of more local studies, both old and new, have shown that climatic cycles and storms potentially impact SAV temporal variability (Poirrier et al. 2017; Cho and Poirrier 2005), and that salinity and water depth likely influence SAV biomass abundance and assemblages (Carter et al. 2009; Cho and Poirrier, 2005b, Penland and Hathaway 1938). Penland and Hathaway (1938) reported that water was deeper in fresh marshes than in salt marshes in southeast Louisiana (later confirmed by Snedden and Steyer (2013)), and broadly described the "aquatics," including *Ceratophylum demersum* (coontail) in fresh waters, *Myriophyllum pinacoides* (Whorled watermilfoil) in brackish waters, and *Ruppia maritima* (widgeongrass/tassel pondweed) in saline waters. More recently, high spatio-temporal variability in SAV has been found. Chabreck (1971) reported that SAV coverage was inversely related to salinity, which may be attributed to salinity stress, light limitation and/or wave exposure. Despite local studies correlating SAV with some environmental factors, comparisons among studies have failed to identify consistent environmental predictors (i.e., Merino et al. 2005, Cho and Poirrier et al. 2005). Further, although enhanced water clarity in marine systems improves the accuracy of seagrass meadow aerial estimation using remote sensing techniques (Meyer and Pu 2012; Thorhaug et al. 2006; Yuan and Zhang 2008), these methods are not applicable in the river dominated, turbid waters of the nGoM. The lack of consistent patterns in factors controlling SAV, and limitations to estimating SAV spatial distribution, limit our ability to develop predictive models, or to map SAV across a broad scale. Furthermore, high regional variation in climate and environmental conditions makes it difficult to extrapolate the available data across the entire coast.

Coastal ecosystems are critically important to the functioning of coastal communities. Along low-lying coasts, SAV represents a significant and valuable habitat type vulnerable to global climate change, potentially resulting in shifting SAV assemblages. Restoration and industry also impact SAV habitats by altering environmental conditions (Peyronnin et al. 2017; Pulich and White 1991). Coastal management benefits from robust models, and uses such models to plan for changing natural resource availability. The objective of this study was to describe spatial and temporal patterns of SAV assemblages (species, diversity, biomass) across salinity zones and geographic regions along the northern Gulf of Mexico; the goal was to provide critical data to (1) develop new SAV models, and (2) refine existing habitat maps, in order to better plan for, or mitigate against, changes to SAV availability. The hypotheses are that (1), species composition and diversity in SAV assemblages will be different across salinity zones and geographic regions, (2); SAV biomass abundance will be inversely related to increasing salinity and will also vary across geographic regions, and (3), SAV biomass will vary temporally, interannually, throughout the duration of the study.

Methods

Study area

The study was conducted in coastal marshes of the nGoM from Mobile Bay, Alabama, to Nueces River, Texas (Figure 3.1). The area encompasses approximately 1,200 km of coastal shoreline that is frequently impacted by tropical storms and hurricanes (Conner et al. 1989; Stone et al. 2005). Along this coast, habitats are structured by salinity gradients, largely controlled by freshwater inputs limited to precipitation and restricted inflow from major river systems (i.e. Mississippi River) and Greater Intracoastal Waterway (Conner et al. 2005). Habitats consist of a mosaic of diverse estuarine and coastal plain habitat types, ranging from forested swamps, to fresh through saline marsh, extensive shallow-water habitats with sediment bottoms, oyster reefs, submerged and floating aquatic vegetation habitats, and barrier islands.

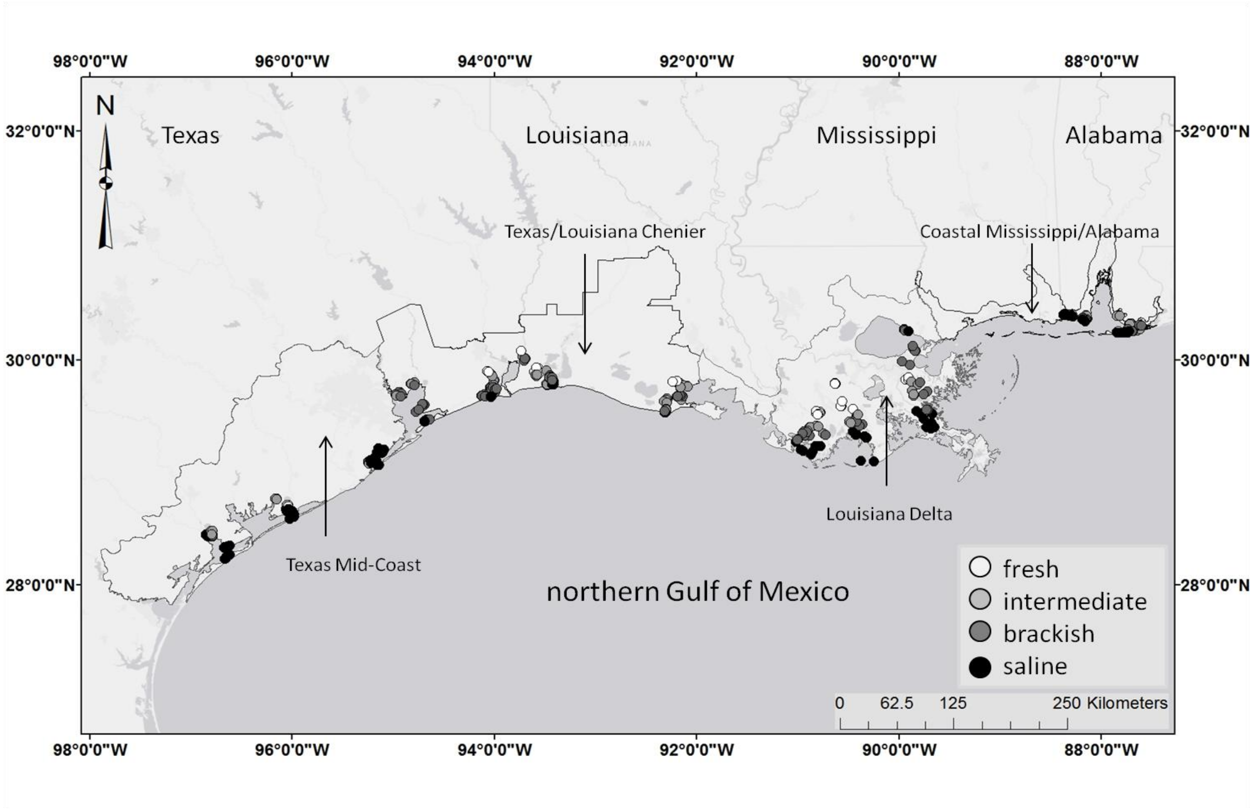


Figure 3.1. Locations of sampling sites across coastal northern Gulf of Mexico.

We used Omernik Level III Ecoregions (USEPA 2013), which include coastal marshes, ponds, bayous, bays and plains, to define the boundaries for this project. For analysis we combined clustered Level IV Ecoregions and broadly characterized geographic regions across the study area (regions: coastal Mississippi/Alabama (MS/AL), deltaic Louisiana (LAdelta), Texas/Louisiana chenier plain (TX/LAchenier), mid-coast Texas (TXmidcoast). For a complete description of this study sampling design and selection of sites please refer to Hillmann et al. (2017). Across the entire study area, sample sites were stratified by region and by salinity zone (fresh, intermediate, brackish, saline). Across the coast, we identified 12 areas for study; in each area, we selected 8 sample sites per salinity zone (12 areas x 4 zones x 8 sites x 3 years = 1152 sample sites x 3 replicates = 3456 samples).

Field data collection

All sampling occurred during the peak of the growing season, which was defined as mid June through early September. The order of sampling was randomly determined each year. Each site was sampled once in 2013 and again in 2014 and 2015. At each site, environmental and water quality data, SAV presence and species composition data, and SAV biomass were collected. Upon arrival at each site, water salinity (YSI-85, YSI Incorporated, OH), water temperature (^{o}C, YSI-85, YSI Incorporated, OH), and turbidity (NTU-Hach 2100Q, Hach, CO) were sampled from the boat before disturbing the benthic sediments. After collecting water quality data, SAV was sampled by throwing a 0.25 m x 0.25 m, floating PVC quadrat haphazardly three times from the boat. Within each quadrat, water depth was measured using a metric measuring stick randomly placed perpendicular and just touching the bottom (± 0.01 m).

When SAV was found, all aboveground biomass (AG) in replicate quadrats was harvested down to the sediment surface. Belowground biomass (BG) was collected at each site by coring 3 times to a depth of 30 cm just outside replicate quadrats using a 10 cm diameter PVC corer with plunger, because harvesting of AG biomass was found to disturb BG biomass. Samples were kept on ice and transported to the laboratory where they were stored at 4^{o}C until processing.

Laboratory processing and calculations

In the lab, AG samples were washed to remove sediment, debris, and epiphytic material, and biomass was separated to species level. Separated AG samples were dried at 60°C to a constant weight, which was then recorded (± 0.001 g).

Total and species specific AG biomass were calculated by summing species AG biomass by replicates and obtaining a mean (± SE) value by site. BG samples were rinsed on a 1.4 µm mesh screen to remove sediment and debris. Samples were separated into live and dead roots, dried at 60°C to a constant weight, and weight recorded (± 0.001 g). Mean total BG biomass values (±SE) were calculated by summing live and dead roots by replicate and averaging replicates by site. Total biomass was the sum of total AG and BG biomass.

SAV standing stock was estimated by first calculating overall mean SAV biomass (g m^{-2}, ±SE), for all sites, including zero values, which was then converted to tonnes ha^{-1}. This value was then multiplied across the extent of potential SAV habitat (100,276.2 ha) within the study area, and then extrapolated across potential SAV habitat across the nGoM (potential SAV habitat in study area equals approximately 28% of potential SAV habitat across nGoM).

Analysis

For all tests a significance value of p= 0.05 was used. Differences in environmental and water variables (salinity, temperature, water depth, turbidity) were tested across year, salinity zones, regions and their interactions using a generalized linear mixed model with a normal distribution and identity link function (Proc Glimmix, SAS Institute 2010). We examined the independent and interactive effects of year (2013, 2014, 2015) and salinity zone (fresh, intermediate, brackish, saline) and region (MS/AL, LAdelta, TX/LAchenier, TXmidcoast) on the independent environmental variables (salinity, temperature, water depth, turbidity), and included random effects of polygon, and polygon by zone interactions and polygon by region interactions, accounting for replication within each salinity zone and region through a nested statement. The residual effect was the repeated measure of sampling the same site each year. The SAV dataset was analyzed in its entirety for presence/absence by salinity zone and region (SAS Institute 2010). SAV abundance (biomass standing stock) was characterized across all sites (including zeroes) and separately across only sites with SAV presence using the same model as for environmental variables, but using a log normal distribution to account for the over-dispersion of data (McGarigal et al. 2013). SAV assemblage characteristics (diversity, richness, evenness) were analyzed at sites with SAV presence. Species diversity was calculated with Shannon-Wiener Diversity.

Results

Environmental variables

Salinity differed significantly by year ($F_{2,1124}$=36.27; $p < 0.0001$) and salinity zone ($F_{3,1123}$=195.16; $p < 0.0001$) with 2015 having lower salinity compared to 2013 and 2014. In all years fresh and intermediate salinity zones did not differ significantly in salinity, but were significantly lower than brackish sites, which were significantly lower than saline sites (Table 3.1). Temperature differed significantly only by year, but the difference was likely not ecologically significant ($\leq$0.5 ^{o}C difference). Water depth also differed significantly by year ($F_{2,1125}$=4.15; $p = 0.0160$), however differences in depth between years fell within the expected tidal range of the region (0.47 m-0.52 m). Water depth also differed significantly by salinity zone ($F_{3,1124} = 32.23$; $p < 0.0001$) with freshwater habitats being significantly deeper (mean 0.66 m, S. E. 0.01 m) as compared to saline, brackish and intermediate sites (<0.48 m).

Table 3.1. Environmental conditions (mean, ±SE) at sampling locations across coastal northern Gulf of Mexico within year and salinity zone. Different letters indicate statistically significant differences.

	Fresh	Intermediate	Brackish	Saline
		2013		
Salinity	3.92 (0.63)^{A}	6.81 (0.76)^{A}	11.1 (0.76)^{B}	21.82 (0.87)^{C}
Temperature (C)	30.29 (0.28)^{A}	31.37 (0.17)^{A}	31.79 (0.20)^{A}	31.71 (0.18)^{A}
Turbidity (NTU)	52.3 (13.94)^{A}	51.98 (8.85)^{A}	58.2 (7.69)^{A}	53.47 (5.15)^{A}
Water depth (m)	0.65 (0.04)^{A}	0.52 (0.02)^{B}	0.45 (0.02)^{B}	0.44 (0.01)^{B}
		2014		
Salinity	2.62 (0.51)^{A}	5.12 (0.63)^{A}	9.12 (0.64)^{B}	20.96 (0.87)^{C}
Temperature (C)	31.74 (0.32)^{A}	31.78 (0.21)^{A}	32.03 (0.17)^{A}	31.64 (0.11)^{A}
Turbidity (NTU)	27.79 (4.36)^{A}	49.35 (5.40)^{A}	43.37 (2.95)^{A}	46.18 (2.71)^{A}
Water depth (m)	0.61 (0.04)^{A}	0.43 (0.02)^{B}	0.44 (0.02)^{B}	0.43 (0.01)^{B}
		2015		
Salinity	4.52 (0.90)^{A,B}	3.39 (0.40)^{A}	5.79 (0.56)^{B}	11.31 (0.69)^{C}
Temperature (C)	31.81 (.34)^{A}	32.00 (0.25)^{A}	31.54 (0.20)^{A}	31.57 (0.18)^{A}
Turbidity (NTU)	34.74 (7.51)^{A}	64.14 (7.98)^{B}	58.09 (5.46)^{A}	54.28 (5.17)^{A}
Water depth (m)	0.68 (0.05)^{A}	0.51 (0.30)^{B}	0.50 (0.02)^{B}	0.48 (0.02)^{B}

Submerged aquatic vegetation

SAV biomass.- For all sites, including the zero values, there was a significant salinity zone by region interaction for SAV total biomass ($F_{9,1081}$=11.47; p< 0.0001), and a significant year by zone interaction ($F_{11,440}$=4.99; p<0.0001), with no other significant factors or interactions. For the zone by region interaction, the fresh LAdelta region had significantly higher biomass compared to all other salinity zone and region combinations (Figure 3.2A); mean total biomass ranged from a low of about 1.4 gdw m^{-2} brackish TXmidcoast sites, to a high of about 149 gdw m^{-2} in fresh LAdelta sites. For the significant year by zone interaction, the 2014 freshwater sites had significantly higher biomass (mean = 164.2 gdw m^{-2}, SE ± 26.8 gdw m^{-2}) as compared to all other single year and zone combinations (range: 42.7-107.9 gdw m^{-2}).

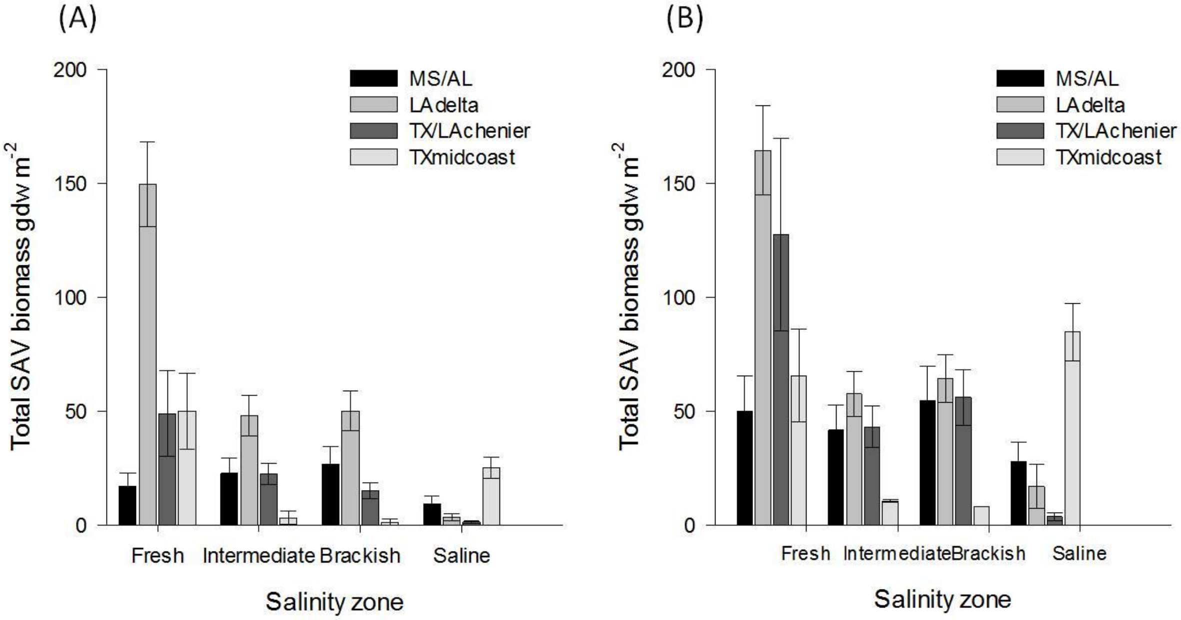


Figure 3.2. Mean total (above + belowground) submerged aquatic vegetation biomass (±SE) across salinity zones and regions. All sites including zeros (A) and sites excluding zeros (B) are shown. MS/AL = Mississippi/Alabama coastal marshes; LAdelta = Louisiana deltaic coastal plain; TX/LAchenier = Texas/Louisiana chenier plain, TXmidcoast = Texas midcoast

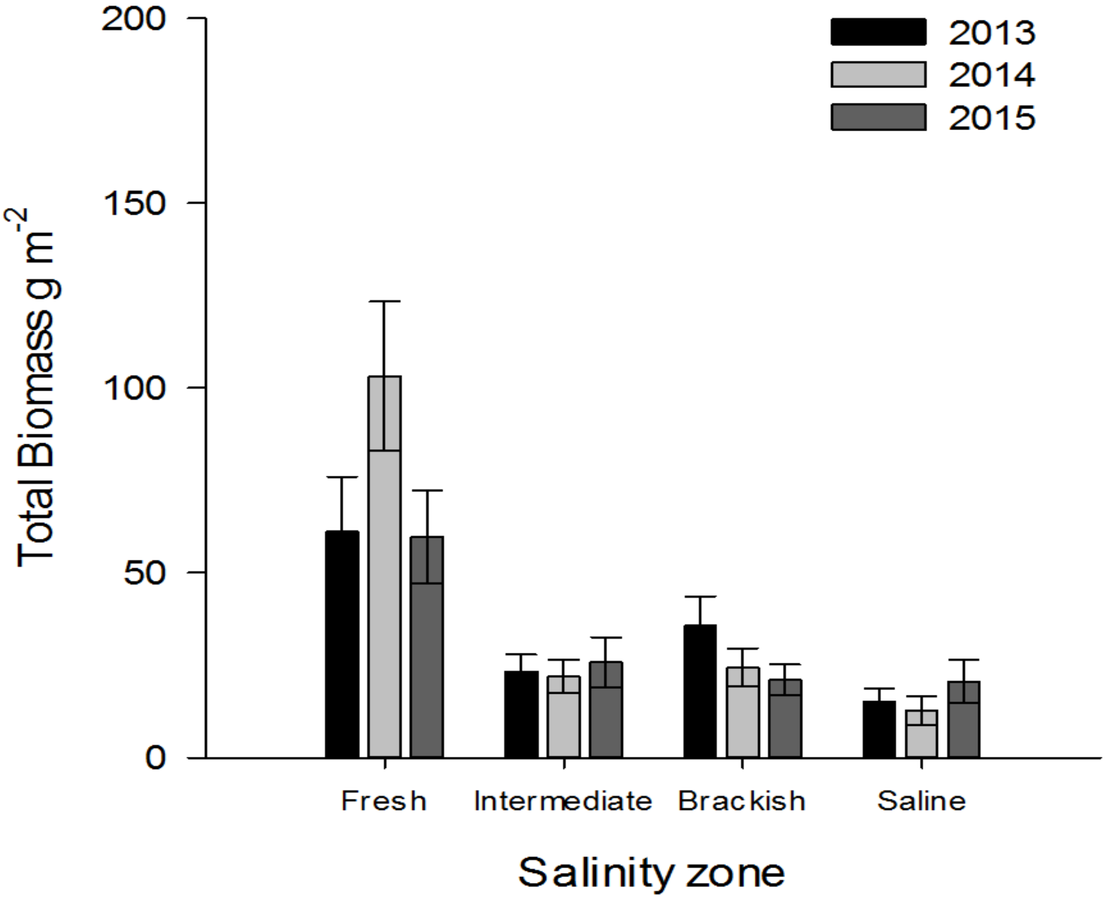
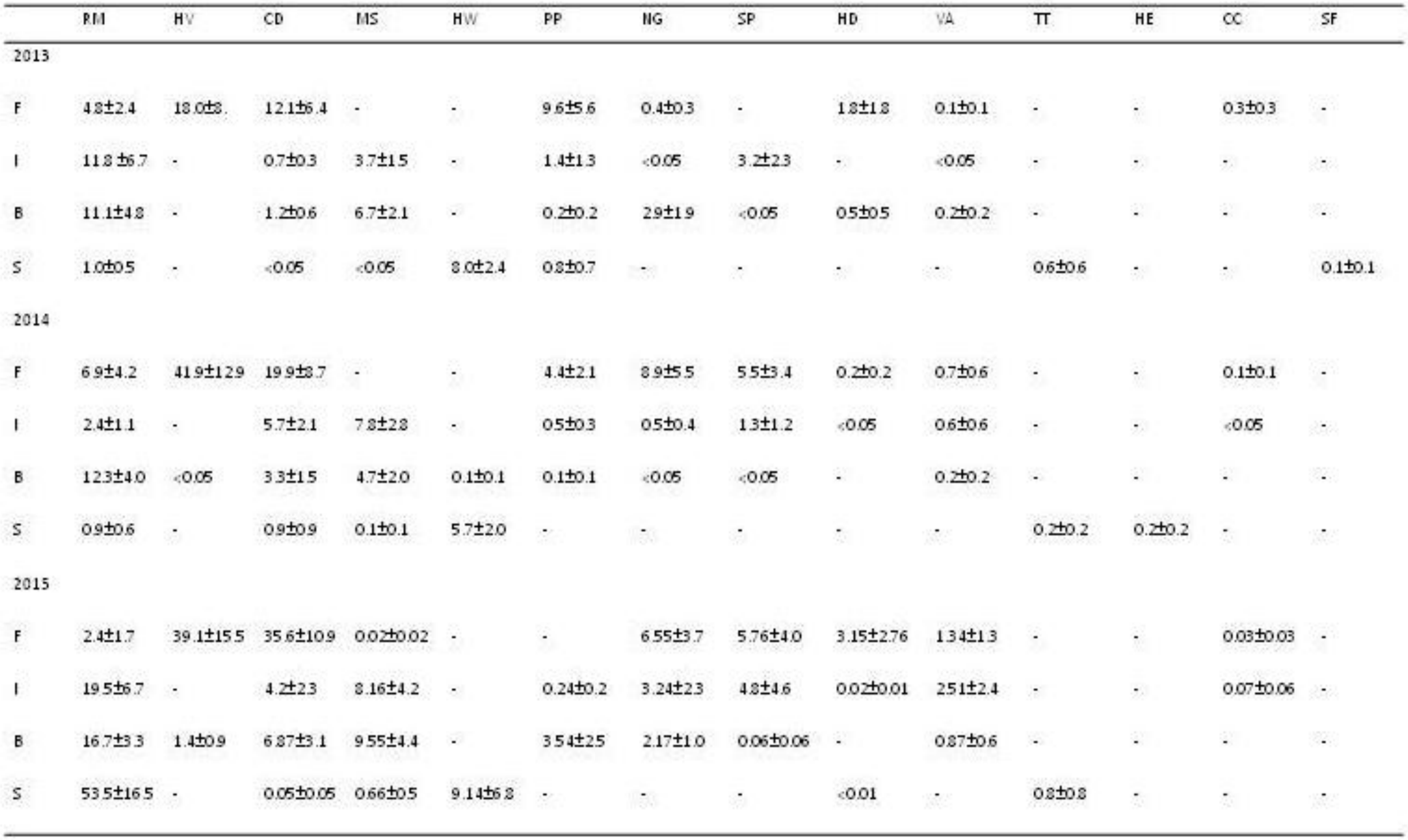


Figure 3.3. Mean total (above + belowground) submerged aquatic vegetation biomass (±SE) across salinity zones (fresh, intermediate, brackish, saline) and years (2013, 2014, 2015) for all sites including zeros.

SAV biomass was also analyzed to examine differences among sites with SAV present. For this analysis, there was a similar significant salinity zone by region interaction on total SAV biomass ($F_{9,436}$=3.39; p=0.0005; Figure 3.2B). However, the difference occurred with the saline zone in the TXmidcoast region having the highest amount of total SAV biomass (mean 84.9 gdw m^{-2}, SE ± 12.6 gdw m^{-2}) compared to all other saline zone and region combinations. Further, the fresh zone LAdelta (mean 164.5 gdw m^{-2}, SE ± 19.4 gdw m^{-2}) and TX/LAchenier (mean 127.6 gdw m^{-2}, SE ± 42.2 gdw m^{-2}) had higher total SAV biomass than MS/AL and TXmidcoast, and did not differ from each other.

SAV assemblages.-In total 14 species of SAV were collected over the three years of sampling. Of these, twelve species of SAV were found in all years (Table 3.2) with manatee grass (*Syringodium filiforme*) unique to 2013 and star grass (*Halophila engelmannii*) unique to 2014. Eight of the 14 species comprised 98% of AG SAV biomass, and all were found in all years. Over the three years of sampling, five species; coontail (*Certophyllum demersum*), Eurasian watermilfoil (*Myriophyllum spicatum*), widgeon grass (*Ruppia maritima*), hydrilla (*Hydrilla verticillata*) and shoal grass (*Halodule wrightii*) accounted for 84% of the above-ground biomass collected. Coontail, widgeon grass, and lesser pondweed (*Potamageton pusillus*) were collected across all four salinity zones. Hydrilla was collected only in fresh habitat, common water nymph (*Najas guadalupensis*), wild celery (*Vallisneria americana*) and sago pondweed (*Stuckenia pectinata*) were collected in all but saline habitat, while Eurasian watermilfoil was collected in all but fresh habitat (Table 3.2).

Table 3.2. Interactive effect of salinity zone and year on mean aboveground biomass (±SE) standardized to g m^{-2} by species collected. F= fresh habitat; I = intermediate habitat; B = brackish habitat; S = saline habitat. RM=*Ruppia maritime*, HV= *Hydrilla verticallata*, CD=*Ceratophyllum demersum*, MS= *Myriophyllum spicatum*, HW= *Halodule wrightii*, PP= *Potamogeton pusillus*, NG= *Najas guadalupensis*, SP= *Stuckenia pectinatus*, HD= *Heteranthera dubia*, VA= *Vallisneria americana*, TT=*Thalassia testudinum*, HE= *Halodule engelmanii*, CC= *Cabomba caroliniana*, SF=*Syringodium filiforme.*



	RM	HV	CD	MS	HW	PP	NG	SP	HD	VA	TT	HE	CC	SF
2013														
F	4.8±2.4	18.0±8.	12.1±6.4	-	-	9.6±5.6	0.4±0.3	-	1.8±1.8	0.1±0.1	-	-	0.3±0.3	-
I	11.8 ±6.7	-	0.7±0.3	3.7±1.5	-	1.4±1.3	<0.05	3.2±2.3	-	<0.05	-	-	-	-
B	11.1±4.8	-	1.2±0.6	6.7±2.1	-	0.2±0.2	2.9±1.9	<0.05	0.5±0.5	0.2±0.2	-	-	-	-
S	1.0±0.5	-	<0.05	<0.05	8.0±2.4	0.8±0.7	-	-	-	-	0.6±0.6	-	-	0.1±0.1
2014														
F	6.9±4.2	41.9±12.9	19.9±8.7	-	-	4.4±2.1	8.9±5.5	5.5±3.4	0.2±0.2	0.7±0.6	-	-	0.1±0.1	-
I	2.4±1.1	-	5.7±2.1	7.8±2.8	-	0.5±0.3	0.5±0.4	1.3±1.2	<0.05	0.6±0.6	-	-	<0.05	-
B	12.3±4.0	<0.05	3.3±1.5	4.7±2.0	0.1±0.1	0.1±0.1	<0.05	<0.05	-	0.2±0.2	-	-	-	-
S	0.9±0.6	-	0.9±0.9	0.1±0.1	5.7±2.0	-	-	-	-	-	0.2±0.2	0.2±0.2	-	-
2015														
F	2.4±1.7	39.1±15.5	35.6±10.9	0.02±0.02	-	-	6.55±3.7	5.76±4.0	3.15±2.76	1.34±1.3	-	-	0.03±0.03	-
I	19.5±6.7	-	4.2±2.3	8.16±4.2	-	0.24±0.2	3.24±2.3	4.8±4.6	0.02±0.01	2.51±2.4	-	-	0.07±0.06	-
B	16.7±3.3	1.4±0.9	6.87±3.1	9.55±4.4	-	3.54±2.5	2.17±1.0	0.06±0.06	-	0.87±0.6	-	-	-	-
S	53.5±16.5	-	0.05±0.05	0.66±0.5	9.14±6.8	-	-	-	<0.01	-	0.8±0.8	-	-	-

SAV diversity increased significantly by year, with the highest diversity in 2015 ($F_{2,455}$=5.10; p=0.0065; +0.12; Figure 3.3A). There was no significant year by salinity zone, year by region, or year by zone by region interactions. However, there was a significant species diversity interaction of salinity zone and region ($F_{8,455}$=3.29; p=0.0012). First, LAdelta, TX/LAchenier and TXmidcoast fresh species diversity did not differ significantly from each other (range: 0.33-0.47), but differed and were greater than MS/AL fresh species diversity (mean=0.03, SE ± 0.03). Secondly, LAdelta and TXmidcoast intermediate salinity species diversity did not differ (range: 0.44-0.59), but were greater than MS/AL and TX/LAchenier intermediate species diversity (range: 0.02-0.12). Finally, LAdelta brackish species diversity was significantly greater (mean = 0.49, SE ± 0.06) than all other brackish region combinations (range: <0.02; Figure 3.3B). The largest diversity value, 2.0, was calculated for a brackish site in 2015 in the LAdelta region that also contained the largest number of distinct SAV species observed at an individual site (7). The lowest diversity value, 0.0, was calculated for multiple sites with mono-specific SAV beds across all years, salinity zones and regions.

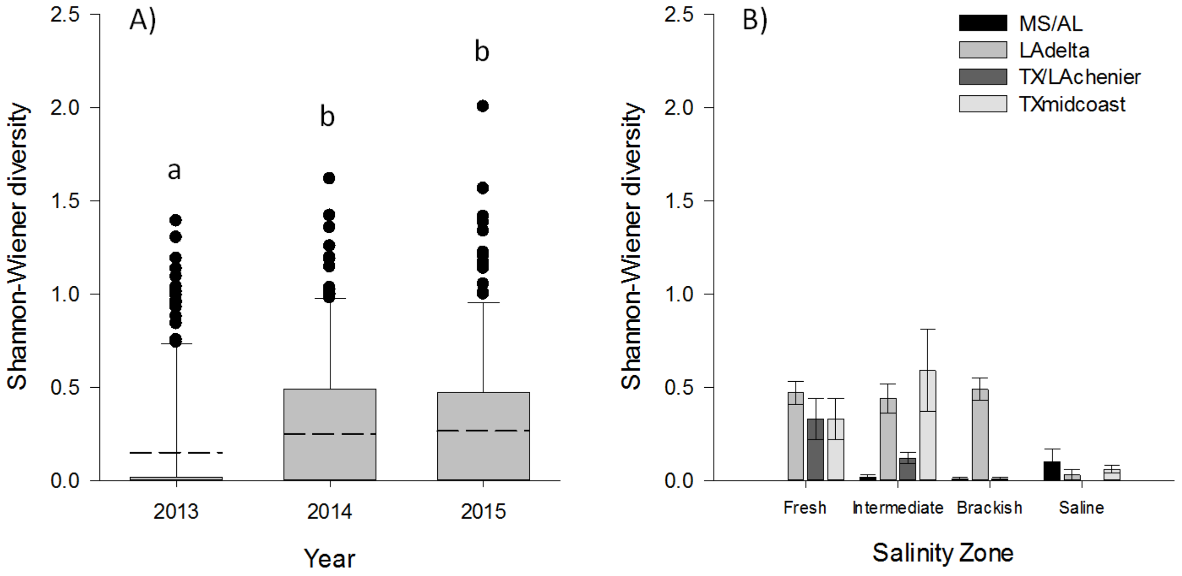


Figure 3.4. Mean Shannon-Wiener diversity (±SE) across year (5A), and salinity zones by region (5B) MS/AL = Mississippi/Alabama coastal marshes; LAdelta = Louisiana deltaic coastal plain; TX/LAchenier = Texas/Louisiana chenier plain, TXmidcoast = Texas midcoast. Different letters indicate significant differences (p=0.05).

There was a significant interaction of salinity zone and region for the mean number of species observed (Table 3.3; $F_{9,413}$=3.02,p=0.0017). All saline sites with species present, regardless of region, contained less than mean 1.2 (SE ± < 0.09) species per site. The highest mean number of species per site was 2.50 species, at intermediate TXmidcoast sites. Saline TX/LAchenier sites, brackish TXmidcoast sites, and fresh MS/AL sites were always mono-specific. The largest range in number of species observed (1-7) occurred in brackish LAdelta sites. Species evenness was positively correlated to species diversity (R^2=0.63).

Table 3.3. Submerged aquatic vegetation assemblage characteristics (diversity, number (#) of species, range, evenness) (mean, ± S.E.) across salinity zones (fresh, intermediate, brackish, saline) and regions (MS/AL= Mississippi/Alabama coastal marshes, LAdelta= Louisiana delta plain, TX/LAchenier= Texas/Louisiana chenier plain, TXmidcoast= Texas midcoast).

	Shannon-Wiener diversity (0-4)	# species	# species range	Species evenness (0-1)
Fresh				
MS/AL	0.00 (0.00)	1.00 (0.00)	1	0.00 (0.00)
LAdelta	0.46 (0.06)	2.25 (0.15)	1-5	0.07 (0.01)
TX/LAchenier	0.33 (0.11)	1.66 (0.19)	1-3	0.06 (0.02)
TXmidcoast	0.33 (0.22)	1.88 (0.27)	1-5	0.06 (0.02)
Intermediate				
MS/AL	0.02 (0.01)	1.09 (0.06)	1-2	<0.01
LAdelta	0.44 (0.08)	1.97 (0.16)	1-4	0.10 (0.02)
TX/LAchenier	0.11 (0.03)	1.30 (0.09)	1-4	0.02 (0.01)
TXmidcoast	0.59 (0.22)	2.50 (0.50)	2-3	0.14 (0.06)
Brackish				
MS/AL	0.01 (0.01)	1.05 (0.05)	1-2	<0.01
LAdelta	0.49 (0.06)	2.25 (0.15)	1-7	0.13 (0.02)
TX/LAchenier	0.01 (0.01)	1.02 (0.04)	1-2	0.02 (0.01)
TXmidcoast	0.00 (-)	1.00 (-)	1	0.00 (-)
Saline				
MS/AL	0.10 (0.07)	1.13 (0.09)	1-2	0.02 (0.02)
LAdelta	0.03 (0.03)	1.08 (0.08)	1-2	<0.01
TX/LAchenier	0.00 (0.00)	1.00 (0.00)	1	0.00 (0.00)
TXmidcoast	0.06 (0.02)	1.10 (0.04)	1-2	0.02 (0.01)

Standing stock.- Mean SAV biomass, including all sites with zero values was 0.33 tonnes ha^{-1}. The study area is estimated to contain 33,091.1 tonnes of SAV standing stock at summer maximum, extrapolated across the entire nGoM, we estimated the coast contains 118,466.3 tonnes of SAV standing stock at summer maximum.

Discussion

Across the northern Gulf of Mexico, significant shallow water habitats exist and support valuable and unique assemblages of species. This study documented extensive submerged aquatic vegetation across the entire coast and identified “SAV hotspots” supporting significant

SAV assemblages and biomass. SAV hotspots and overall biomass appeared to be stable across years, with significantly greater SAV biomass located within the fresher salinity zones, and within the Louisiana deltaic system. We estimated SAV standing stock across the coast (>118,000 tonnes) and believe it to be the first estimate of SAV biomass standing stock at this scale, specifically along the northern Gulf of Mexico coast.

SAV is considered to be valuable habitat (Heck et al. 2003), and productive SAV beds are generally assumed to indicate healthy sub-tidal ecosystems (Li et al. 2007). Observed SAV declines in the Chesapeake Bay region (Stevenson et al. 2014; Kemp et al. 2004; Orth and Moore 1983) prompted decades of research resulting in significantly better understanding of SAV ecology, human induced impacts on SAV and the development of models which capture the amount of SAV biomass over broad regions and timescales (Moore et al. 2000). Similar declines in SAV have been observed in specific regions (i.e. Mobile Bay, Lake Pontchartrain, Chandeleur Islands, Galveston Bay, etc.) along the nGoM (Estes et al. 2009; Poirrier et al. 2009; Handley et al. 2007; Adair et al. 1994). Our research resulted in a coastwide database of baseline SAV assemblage and biomass data for the nGoM that can be used to track changes to this valuable natural resource (La Peyre et al. 2017).

We identified several persistent “SAV hotspots” along the coast; areas appearing to maintain the overall stability of SAV biomass. Specifically, SAV biomass was three times higher in fresh SAV habitat compared to all other salinity zones. We observed not only more SAV presence at fresh sites, but also overall more SAV biomass. Fresh sites tended to be deeper, and these results extend the salinity/water depth relationship discussed in previous coastal surveys that focused primarily on emergent marsh vegetation (Snedden and Steyer 2013; Penfound and

Hathaway 1938) to SAV. Further, freshwater SAV species exhibit expansive growth forms (Barko et al. 1982), and are less exposed to disturbance and waves in protected ponds and bayous, likely explaining some of the observed differences in biomass between freshwater sites and other salinity zones. Commonly observed freshwater species (i.e. *Hydrilla verticillata*, *Cabomba caroliniana*, *Heteranthera dubia*) grow on strong stems towards light, profusely branching out just below the surface of the water. In contrast, saline sites were not as deep as fresh sites, and salt tolerant species like seagrasses (i.e. *Halodule wrightii*, *Thalassia testudinum*, *Halodule engelmanii* and *Syringodium filiforme*) have slender growth forms, depend on light reaching plants on water bottoms, and are more exposed to disturbance and waves, possibly contributing to less biomass overall in the saline zones compared to the fresh zones across the nGoM.

Across the coast, significant differences in SAV assemblages and biomass were also detected by region. The Louisiana deltaic region held, on average, twice as much biomass as all other regions (LAdelta mean: 54.7 gdw m^{-2}, SE ± 5.8; all other regions mean range: 19.1-23.3 gdw m^{-2}). In fact, biomass values were high across LAdelta fresh, intermediate and brackish habitats. The Louisiana deltaic region is strongly influenced by the Mississippi River, its distributaries, natural crevasses and river management. River management has resulted in extensive areas of fresh and low salinity shallow water habitat in the upper basins of the region, surpassing the areal extent of low salinity areas in other regions and providing ample habitat for freshwater SAV. The fresh zone in the LAdelta region contains persistent SAV beds which resulted in fewer sites with no SAV compared to the other regions. Emergent marshes in Louisiana are productive habitats, holding in the range of 199-900 g m^{-2} of vegetative biomass

(Delaune et al. 1979). Similarly, SAV habitats in Louisiana are extensive and contain substantial amounts of biomass.

Biomass was similar between the LAdelta and the TXmidcoast region when only sites with SAV presence were considered. Although the LAdelta region contained a large amount of SAV overall, and specifically in the fresh zone, robust seagrass beds (as in the TXmidcoast region) were absent in the LAdelta region. As seagrass beds tend to form dense, large meadows, where they exist, they contribute large amounts of biomass in contrast to fresher SAV forms which can be patchier, and may consist of less dense or robust species. The "saline" areas along Louisiana's coast are heavily influenced by the Mississippi River; salinity is highly variable (https://www.lacoast.gov/crms_viewer2/), is influenced by freshwater discharge from the Mississippi River (https://waterdata.usgs.gov/nwis/annual/), and consequently below 10 for extended periods of time during summer months. Additionally, coastal erosion and river water also limits light; conditions not favoring seagrass growth. As a result, SAV in the saline areas of Louisiana's coast is restricted to a few salt tolerant freshwater species (i.e. *Ruppia maritima*, *Myriophyllum spicatum*), limiting the extent of seagrass species compared to the MS/AL and Texas coastal regions. The similarity in biomass when comparing "SAV present" sites is due to these robust seagrass meadows in saline Texas areas (Pulich 1985) compared to the more extensive fresher SAV across the LADelta lower salinity areas.

As expected, species diversity was low in SAV habitats along the nGoM, and was similar to SAV assemblages elsewhere (Rybicki and Landwehr 2007; Hestir 2004; Kanouse et al. 2006; Pham et al. 2014). In this study 66% of SAV samples were mono-specific, and biomass was similar to reported values from other productive SAV habitats. We found no correlation between species diversity and biomass (r^2= 0.02). For instance, although high diversity areas (i.e. fresh LAdelta region (number of species range: 1-5)) held the most biomass, certain low diversity areas (i.e. saline TXmidcoast (number of species range: 1-2) also contained significant biomass. Further, as species diversity increased from 2013 to 2015, overall biomass did not increase.

Despite significant differences in spatial distribution across salinity zones, and regions, temporal variation was limited. Mean total biomass was similar across years although diversity increased slightly in 2014 and 2015. There was an increase in SAV biomass in 2014, in the fresh zone, possibly due to freshening from increased precipitation (https://www.srcc.lsu.edu/monthly_summaries) across the southeastern United States during spring months. We observed a more than two-fold increase of *Hydrilla verticillata*, a strictly freshwater species, in 2014. *Ceratophyllum demersum*, another common freshwater species, increased by nearly 50%. By 2015, fresh SAV returned to 2013 levels. No major storms passed over the study area from 2013-2015. Storm systems and hurricanes impact SAV abundance and spatial distribution, stirring up sediments, reducing light and uprooting plants (Orth et al. 2006). Other studies have discussed the impact storms have on SAV abundance across years (Poirrier 2014), but the 3-year span of this study precluded us from detecting these trends because of a lack of major storms.

We calculated what we believe is a first estimate of SAV biomass standing stock at the scale of the nGoM. The potential SAV habitat area within our study area just exceeded 100,276.2 hectares, which is approximately 28% of the potential SAV habitat area across the nGoM (irrespective of salinity zones or regions) and we estimated that this area contained an approximately 118,466.3 metric tonnes of SAV standing stock. These figures are proportionally comparable to standing stock in the Chesapeake Bay, where SAV biomass standing stock of approximately 25,000 tonnes over 30,000 hectares has been reported (Moore et al. 2000). Also important, these values highlight the substantial contribution SAV are to coastal ecosystems at regional scales along dynamic coasts (i.e. biomass, habitat, refuge, food).

In sub-tidal ecosystems along dynamic coasts, data on natural resource availability and distribution are critical for managers and scientists to predict and plan for shifting SAV. These shifts have the potential to impact an array of critical ecosystem services (Hershner and Havens 2008). New data are needed to refine existing models and develop new models for the nGoM that estimate changes in overall SAV availability, particularly biomass standing stock, which is often under-reported. Global climate change, restoration, industry and development, all factors impacting SAV availability and abundance (Kemp et al. 2004), only increases the need for fully developed models. In particular, incorporating spatial differences across salinity zones and geographic regions refines models in novel ways and provides powerful information to managers.

SAV assemblages varied by salinity zone and region; this finding enables the development of management goals targeted towards specific communities, zones or regions (Blandon and zu Ermgassen 2014). For example, management activities to maintain freshwater inflows within coastal estuaries experiencing increased salinities might be useful if managers want to focus on maintaining a fresher community of species. A better understanding of the current spatial distribution and inter-annual variation of sub-tidal SAV will help better prepare managers in light of potentially shifting submerged aquatic vegetation.

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CHAPTER 4

SALINITY AND SEASONS ARE INDICATORS OF COASTAL SUBMERGED AQUATIC VEGETATION VARIABILITY IN BARATARIA BASIN, LOUISIANA, USA

Spatial environmental variation largely controls species distributions and abundances by delineating preferred habitats that structure communities (Austin 1985; Weiher and Keddy 1995) Temporal environmental variation further shapes community structure and distribution (Wiens 2000; Hewitt et al. 2007). Describing ecological variation across multiple scales and identifying factors controlling change remains a critical need for predicting future community mosaics (Horne and Schneider 1995; Pickett and Cadenasso 1995; Santamaria 2002; Holt and Barfield 2003). Although ecological variation has been most studied in terrestrial systems (Pickett and Cadenasso 1995), there is also a growing body of research examining ecological variation in aquatic systems (Harrison 1982; Sfriso and Pier 1998; Chrysoula and Papastergiadou 2007).

Terrestrial and marine factors influence coastal areas, including the shallow water aquatic habits fringing tidal marshes. This confluence of factors alters surface water characteristics, including salinity, turbidity, light and nutrients. Surface water characteristics vary at multiple spatial scales, across landscapes (Tomasko and Dunton 1995; Thrush 1999), and along gradients (depth, salinity) (Dayton et al. 1999; Rueda and Salas 2003; Young et al. 2014), affecting survival, reproduction and growth rates. In addition, water characteristics also fluctuate between (inter-annual) and within (intra-annual) years in response to climatic cycles, disturbance and watershed management (Miller et al. 1996; Kang and King 2013), further impacting the distribution and abundance of species.

Submerged aquatic vegetation (SAV) is critical in aquatic landscapes (Gutierrez et al. 2011). SAV provide important ecological services, including food resources for waterfowl, refuge for invertebrates and fish (Hansson et al. 2010; Heck et al. 2003), nutrient cycling (Knight et al 2003), reduction of sediment re-suspension (Gutierrez et al. 2011) and organic carbon storage in bottom sediments (Chapter 5). SAV vary along environmental gradients (i.e. salinity, depth, light) at multiple spatial (Hillmann et al. 2016; Kemp et al. 2004; Dunton 1994) and temporal scales. SAV temporal variation (i.e. assemblages, diversity, biomass) results from changing surface water salinity and light conditions due to climatic patterns (precipitation, wind, storms) and human disturbances (Rooney and Kalff 2000; Correia et al. 2012), which vary inter-annually.

Intra-annual variation of SAV is less understood, although general patterns of greater species diversity and biomass have generally been observed in summer months, with declines in winter months (Sayer et al. 2010; Cho and Poirrier 2005; Dunton 1994; Lefèvre and Bellwood 2010).Reliance on remote sensing and modeling techniques that depend on assumptions and generalizations based on annual sampling (Yuan and Zhang 2008; Meyer and Pu 2012) may not accurately capture intra-annual SAV variability. Additionally, identifying the drivers of intra-annual SAV variability, especially within rapidly changing coastal areas (i.e. southeastern Louisiana), enables more accurate modeling and predictions of changing SAV with climate change and restoration.

In south Louisiana coastal habitats are structured along salinity gradients, largely controlled by freshwater inputs limited to precipitation, restricted inflow from the Mississippi River, its distributaries, wind and storms (Bianchi and Mead 2009). Within this region SAV is a foundation species, yet patterns of intra-annual variation of SAV within south Louisiana watershed basins has not been satisfactorily described. Joanen and Glasgow (1965) reported on two peaks of SAV biomass (spring and fall), which was related to observations of favorable water temperature. The idea of two SAV growing seasons was subsequently incorporated into regional SAV monitoring protocols for coastal restoration projects (Folse and West 2004). However, others regional studies have failed to detect seasonal patterns of maximum SAV abundance (Merino et al. 2005). This constitutes a critical data gap for comprehensive coastal resource management.

The main objective of this study was to document intra-annual variation in SAV assemblages and SAV biomass along a salinity gradient at 16 sites located within Barataria Basin, Louisiana. The goals were to (1), quantify SAV biomass by species, and relate changes to water quality (salinity, temperature, water depth, PAR, chl *a*) over a 12 month period, and (2), identify species assemblages, and relate changes to water quality throughout the same time period. The hypotheses are that (1) SAV exhibits intra-annual variation, with two peaks of maximum biomass (spring, fall), and (2), SAV assemblages can be delineated into four groups (fresh, intermediate, brackish, saline) based on salinity zonation of emergent marsh vegetation.

Methods

Study area

The study was carried out in Barataria Basin, Louisiana, a sub-estuary in southeast Louisiana that was once part of the Lafourche Delta complex of the Mississippi River (MR) (Figure 4.1). The basin is part of the Louisiana Coastal Plain, one of the largest areas of coastal wetlands in the United States, which has lost approximately 4877 km^2 of land since the 1930s due to management of the MR, oil and gas canals, subsidence, sea-level rise and tropical storms (Barras 2009; Deegan et al. 2012; Georgiou et al. 2017; Peyronnin et al. 2017). The basin encompasses approximately 1214 km^2, and is bordered on the north and east by the MR, on the west by Bayou Lafourche and on the south by the Gulf of Mexico. Within the basin, habitats are structured by salinity gradients, largely controlled by freshwater inputs limited to precipitation and restricted inflow from the MR and Greater Intracoastal Waterway (Conner et al 2005). Habitats consist of a mosaic of diverse estuarine habitat types, ranging from forested swamps, to fresh through saline marsh, extensive shallow-water habitats with sediment bottoms, oyster reefs, submerged and floating aquatic vegetation habitats, and barrier islands.

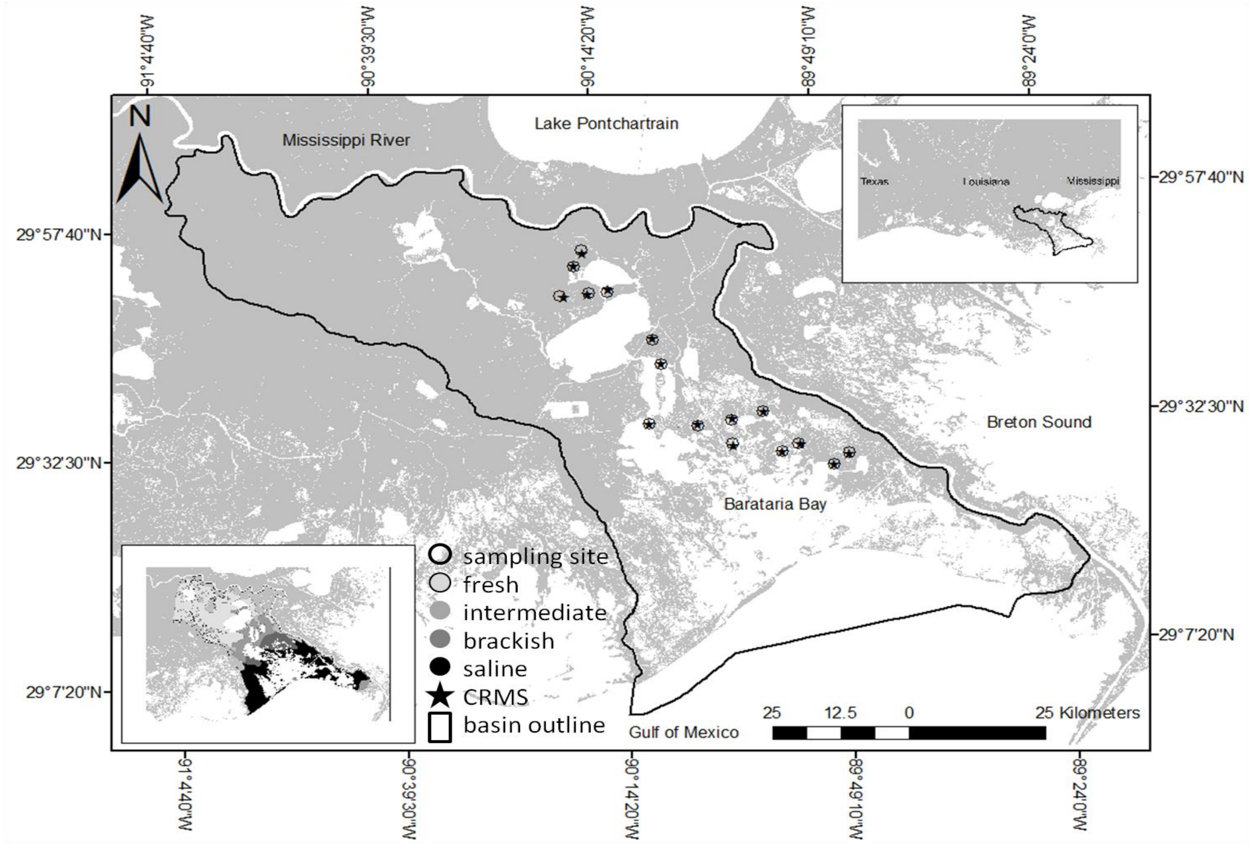

Figure 4.1. Location of study sites distributed across Barataria Basin. Inset 1 (lower-left) shows the distribution of salinity zones across the basin. Inset 2 (upper-right) shows the location of Barataria Basin along the northern Gulf of Mexico. CRMS refer to Coastwide Reference Monitoring Stations.

Sampling design

Using a stratified sampling design, we selected 16 study sites stratified across a salinity gradient from fresh to saline marsh. Sites were located within 1 km of a coast-wide reference monitoring station (CRMS) (http://lacoast.gov/crms2/home.aspx) providing continuous and long-term water quality data (salinity, temperature, water level). Stratification along the salinity gradient was based on long term emergent marsh vegetation patterns which are used to identify marsh types (fresh, intermediate, brackish, saline; Visser et al. 2013). Study sites were specifically targeted based on potential for SAV presence (Hillmann et al. 2016), with four sites selected per habitat type and sampled 7 times throughout 2015 (4 habitat types x 4 replicates = 16 sample sites x 3 subsamples x 7 dates = 336 samples). Sampling occurred roughly bi-monthly, starting in February and ending in December. The order of sampling sites was randomly determined each sampling effort. At each site, environmental and water quality variables, SAV presence, species composition and SAV biomass data were collected following protocols below.

Field data collection

Upon arrival at each site, water salinity (YSI-85, YSI Incorporated, OH), photosynthetically active radiation (PAR; µmol m^{-3} s^{-1} , LI-1400, LI-COR, NE), dissolved oxygen (DO) (mg l^{-1}, YSI-85, YSI Incorporated, OH), pH (Hach Pocket Pro+, Hach, CO), turbidity (NTU-Hach 2100Q, Hach, CO), and water temperature (^{0}C, YSI-85, YSI Incorporated, OH) were sampled off-bottom, from the boat before disturbing the bottom sediments. In addition, two water samples (for chlorophyll a analysis) were collected off-bottom at each site in 205 ml amber colored Nalgene bottles and placed on ice for chlorophyll a analysis.

After collecting water quality data, SAV was sampled by throwing a 0.25 m x 0.25 m, floating PVC quadrat haphazardly three times from the boat. Within each quadrat, water depth was measured using a metric measuring stick randomly placed perpendicular and just touching the bottom (± 0.01 m). SAV presence/absence was recorded within each quadrat. When SAV was present, all aboveground (AG) biomass within the quadrat was harvested down to the sediment surface. Belowground biomass (BG) was collected at each site by coring 3 times to a depth of 30 cm just outside replicate quadrats using a 10 cm diameter PVC corer with plunger, because harvesting of AG biomass was found to disturb BG biomass. All AG and BG samples were placed in individually labeled plastic bags, kept on ice and, along with all other samples, transported to the laboratory at Louisiana State University Agricultural Center where all samples were stored at 4^{o}C until processing.

In February 2015 only, one sediment core was collected at each site and used for determination of bulk density (BD; g cm^{-3}) and organic matter (OM; %). A 5 cm diameter PVC corer with a plunger was pushed into the sediment to a depth of 20 cm. Extracted sediment cores were placed into individually labeled plastic bags and stored on ice.

Laboratory processing

AG biomass samples were washed to remove sediment, debris, and epiphytic material, and biomass was then separated to species level. Separated AG samples were dried at 60^{o}C to a constant weight, and weight recorded (± 0.001 g). Total and species specific AG biomass were calculated by summing species AG biomass by replicates and obtaining a mean (± SE) value by site. BG samples were rinsed on a 1.4 mm mesh screen to remove sediment and debris. Samples were separated into live and dead roots, dried at 60^{o}C to a constant weight, and weight recorded (± 0.001 g). Mean total BG biomass values (±SE) were calculated by summing live and dead roots by replicate and averaging replicates by site. The root to shoot ratio (RSR) was determined by dividing the dry weight of total BG biomass by the dry weight of total AG biomass.

Sediment cores (n=16) were dried at 60^{o}C to a constant weight. Dry weight was recorded (± 0.001 g) and used to calculate bulk density by dividing dry weight by the volume of sediment core. After drying and weighing, cores were homogenized using a mortar and pestle. To determine percent organic matter (OM), triplicate 4.0 g subsamples of each core were weighed out and burned at 550^{o}C for 4 hours using the loss on ignition method (Heiri et al. 2001). For chlorophyll a samples, under dim lights, a 50 mL water sample was filtered through a pre-weighed Whatman 47 mm glass fiber filter. The filter was placed in a labeled foil packet and stored at −20 ^{o}C until further processing at the Wetland Biogeochemistry Analytical Services Laboratory, at Louisiana State University, following EPA Method 445.0 for chlorophyll *a*. (Arar and Collins 1997).

Analysis

For all tests a significance value of p = 0.05 was used. Unless indicated differently, mean ± standard error is reported. Differences in environmental variables (salinity, water depth, PAR, DO, pH, turbidity, temperature, chl *a*) and soil properties (BD, OM) were tested across habitat type (habitat) and sampling months (month) using a repeated measures generalized linear mixed model with a Gaussian distribution and identity link function (Proc Glimmix, SAS Institute 2010). We examined the independent and interactive effects of month (February, April, May, July, August, October, December) and zone (fresh, intermediate, brackish, saline) on the independent environmental variables (salinity, temperature, water depth, DO, turbidity, pH, PAR, chl *a*). The residual effect was the repeated measure of sampling the same site seven times throughout the year. Total biomass and RSR were log transformed and analyzed using the same model as for environmental variables.

For examination of SAV assemblage-environment relationships, canonical correlation analysis (CCA) with backward selection was performed with CANOCO software (vers. 4.5; Wageningen UR, Netherlands; (ter Braak and Smilauer 2002)) to analyze the relationship between SAV assemblages and environmental variables (salinity, water depth, PAR, DO, pH, turbidity, chl *a* and temperature), for all sample sites separately for July 2015 and December 2015. Assemblage-specific biomass was log 10 (x +1) transformed for the CCA to improve normality, and rare species were down weighted. A Monte Carlo simulation test was used to determine statistical significance of canonical axes with 1000 simulations on the full model.

Results

Water characteristics and soils

Discrete salinity differed by habitat ($F_{3,113}$= 26.75, $p < 0.0001$) (Table 4.1), month ($F_{6,110}$=50.84, $p<0.0001$), and their interaction ($F_{18,99}$=8.24, $p<0.0001$; Table 4.1, Figure 4.2). Salinity was lowest at fresh SAV sites which did not vary significantly throughout the year (month), while other habitats had higher salinities, with distinct seasonal patterns which included higher winter salinities, and low summer salinities (Appendix 1). Water temperature ranged from 10.6^{o}C to 34.4^{o}C and differed by both habitat ($F_{3,113}$= 7.07, p= 0.0046) and month ($F_{6,110}$= 118.42, $p < 0.0001$), but not their interaction. Water temperature was significantly lower at fresh sites compared to brackish and saline sites, and followed an expected annual trend with lower temperatures in winter as compared to summer months.

Table 4.1. Mean (±SEM) of environmental and soil properties by marsh type. Ranges of reported values are indicated on the second line for each variable. Different letters indicate statistically significant differences by marsh type for each parameter ($p < 0.05$).

Salinity	0.2 ±0.1^{A}	0.6 ±0.6^{A}	4.9 ±3.1^{B}	9.4 ±4.2^{C}
ppt	0.1-0.8	0.1-1.9	0.7-12.5	3.3-16.4
Water depth	0.7 ±0.31^{A}	0.5 ±0.18^{B}	0.5 ±0.22^{B,C}	0.36 ±0.15^{C}
m	0.25-1.6	0.23-1.0	0.15-1.0	0.12-0.97
PAR	271.1 ±400.4^{A}	285.9 ±286.5^{A}	299.7 ±275.8 ^{A}	649.9 ±455.6^{B}
µmol m^{-2} s^{-1}	0.02-1316.8	9.49-1073.0	2.52-992.6	44.8-1514.7
Dissolved oxygen	4.0 ±2.5^{A}	7.1 ±3.5^{B}	7.7 ±7.7^{B}	7.1 ±2.4^{B}
mg l^{-1}	0.3-8.3	1.1-16.0	2.5-10.7	3.1-11.8
pH	6.9 ±0.7^{A}	7.5 ±1.2^{A}	7.8±0.8^{B}	7.6 ±0.6^{B}
	5.0-7.9	4.9-9.7	5.6-8.9	6.6-8.6
Turbidity	35.3 ±36.7^{A}	32.2 ±28.1^{A}	29.9 ±16.7^{A}	25.4 ±11.8^{A}
NTU	1.4-111.0	4.8-126.0	11.0-96.7	7.3-57.7
ClA	4.68±1.09^{A}	4.71±1.13^{A}	8.46±1.16^{A}	5.21±0.72^{A}
µg l^{-1}	0.15-25.4	0.26-30.1	0.43-27.2	0.17-16.16
Temperature	23.1 ±5.1^{A}	25.1 ±5.5^{A}	26.4 ±5.5^{A}	26.4 ±5.3^{A}
C	12.7-30.3	10.6-34.4	13.4-33.6	15.6-33.9
Organic matter	34.22 ±13.57^{A}	47.70 ±13.49^{A}	28.51 ±2.11^{A}	34.37 ±7.36^{A}
%	10.91-72.13	12.59-77.82	22.55-32.24	23.85-55.95
Bulk density	0.38 ±0.15^{A}	0.24 ±0.10^{A}	0.33 ±0.05^{A}	0.26 ±0.04^{A}
g cm^{-3}	0.08-0.69	0.09-0.53	0.26-0.43	0.16-0.33

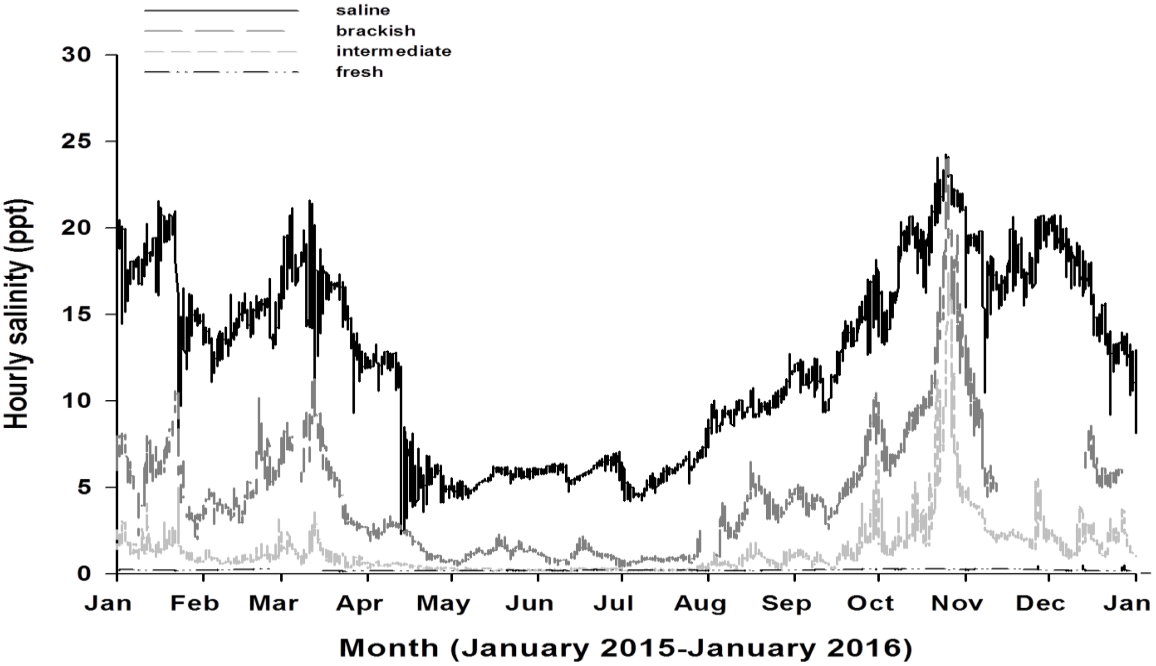

Figure 4.2. Mean daily salinity recorded at Coastwide Reference Monitoring Stations (CRMS) located within 1 km of study sites. CRMS stations were grouped by salinity zone designation (fresh, intermediate, brackish, saline) to show salinity variability by zone throughout the year.

Water depth differed significantly by habitat ($F_{3,113}$= 3.76, p = 0.0413) and month ($F_{6,110}$= 15.22, p < 0.0001; Table 4.1), but not their interaction. Water depth was greatest in the fresh habitat (mean 0.87 m, SE ± 0.08), and significantly higher than in saline habitat (mean 0.48 m, SE ±0.08), and neither differed from intermediate or brackish habitats. Water depth was lowest in February (mean 0.36 m, SE ±0.04) compared to all other months, which did not differ from one another. Similarly, PAR differed by habitat ($F_{3,113}$= 8.76, p = 0.0031) and month ($F_{6,110}$= 3.05, p = 0.0102) only. PAR was highest in saline habitat (mean 748.62 µmol m^{-3} s^{-1}, SE ±136.89) and different from PAR in the fresh, intermediate and brackish habitats, which did not differ from one another (range: 225.89 -293.64 µmol m^{-3} s^{-1}). PAR was lowest in December (mean 116.98 µmol m^{-3} s^{-1}, SE ± 48.32) and highest in February (mean 826.85 µmol m^{-3} s^{-1}, SE ± 226.41). Turbidity and chlorophyll *a* only differed significantly by month (turbidity: $F_{6,110}$= 3.27, p =

0.0065; chl *a*: $F_{6,110}$= 15.79, $p < 0.0001$). Turbidity was significantly higher in February and April compared to May, and chlorophyll *a* was highest in April and lowest in May.

Dissolved oxygen differed significantly by habitat ($F_{3, 113}$= 8.36, p = 0.0036) and month ($F_{6,110}$= 16.89, $p < 0.0001$) only. Dissolved oxygen was significantly lower (mean: 4.00 mg l^{-1}, SE ± 0.56) at fresh sites as compared to intermediate, brackish and saline sites, which did not differ from one another (range: 7.09-7.75 mg l^{-1}). DO was significantly lower in May (mean: 4.31 mg l^{-1}, SE ± 0.56) as compared to February (mean: 8.65 mg l^{-1}, SE ± 0.81). Similarly, pH differed significantly by habitat ($F_{3,113}$= 6.42 H^+, p = 0.0094) and month ($F_{6,110}$= 9.05, $p <0.0001$), but not their interaction. pH did not differ among brackish and saline sites (range: 7.60-7.75 H^+), but was significantly greater than fresh sites (mean: 6.94 H^+, SE ± 0.15). Temporally, pH was lowest in May (mean: 6.68 H^+, SE ± 0.27), and highest in October (mean: 8.21 H^+, SE ±0.14).

Sediment OM and BD were similar across all habitat types. Mean OM was 36.2 %, SE ± 4.9, and mean BD was 0.30 g cm^{-3}, SE ± 0.04.

SAV biomass

Total biomass differed significantly by month ($F_{6,110}$= 3.03, p = 0.0104) and habitat ($F_{3,113}$= 9.07, p = 0.0020), but not their interaction. May and July biomass (May mean: 63.78 g m^{-2}, SE ± 21.84; July mean: 52.04 g m^{-2}, SE ± 21.57) were significantly greater than December biomass (mean: 5.23 g m^{-2}, SE ±2.90) (Figure 4.3), and this pattern was similar across the salinity gradient. Fresh (mean: 90.14 g m^{-2}, SE ±19.8) and intermediate (mean: 60.47 g m^{-2}, SE ±13.8) sites were similar and significantly greater than brackish (mean: 5.01 g m^{-2}, SE ± 1.8) and saline (mean: 6.03 g m^{-2}, SE ± 3.2) sites, which also did not differ from one another. Number of species differed only by habitat ($F_{1,115}$= 21.34, p = 0.0004). Fresh and intermediate sites contained more species (mean: 1.65, SE ± 0.14) compared to brackish and saline sites (mean: 0.43, SE ±0.07; Figure 4.5), and further analyses grouped the fresh/intermediate and brackish/saline results. SAV root: shoot (RSR) did not differ by habitat type, month or their interaction (Figure 4.4).

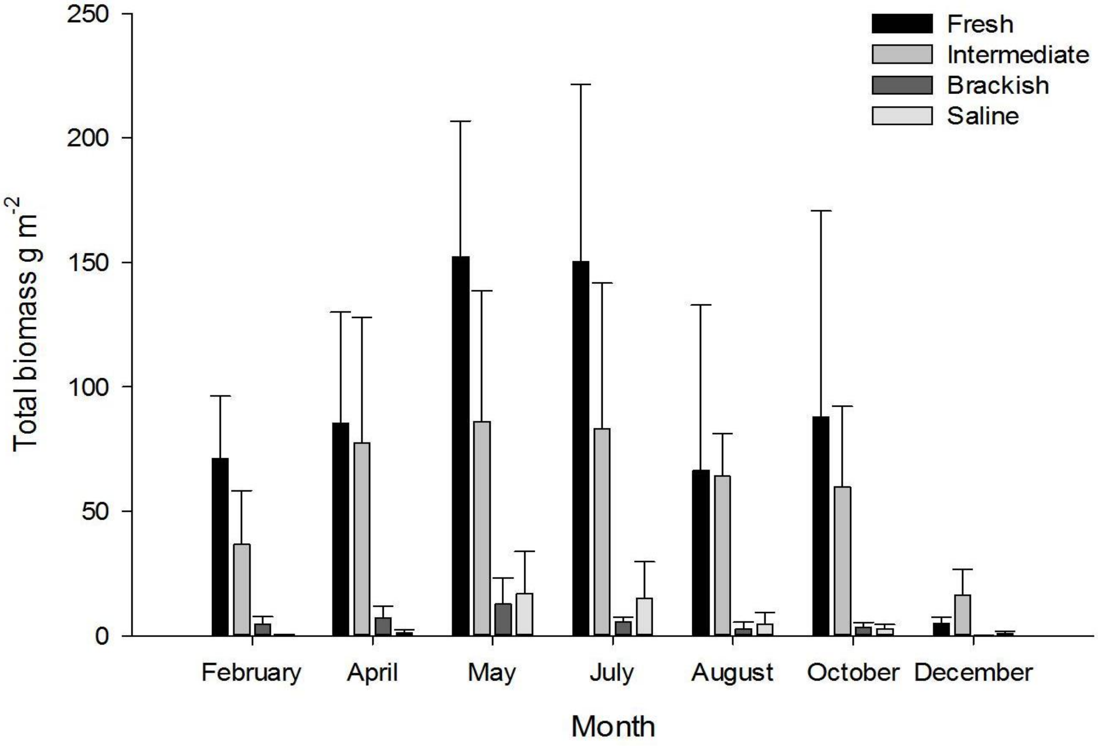

Figure 4.3. Total submerged aquatic vegetation biomass by salinity zone (fresh, intermediate, brackish, saline) throughout the year. Peak biomass occurred in May and July.

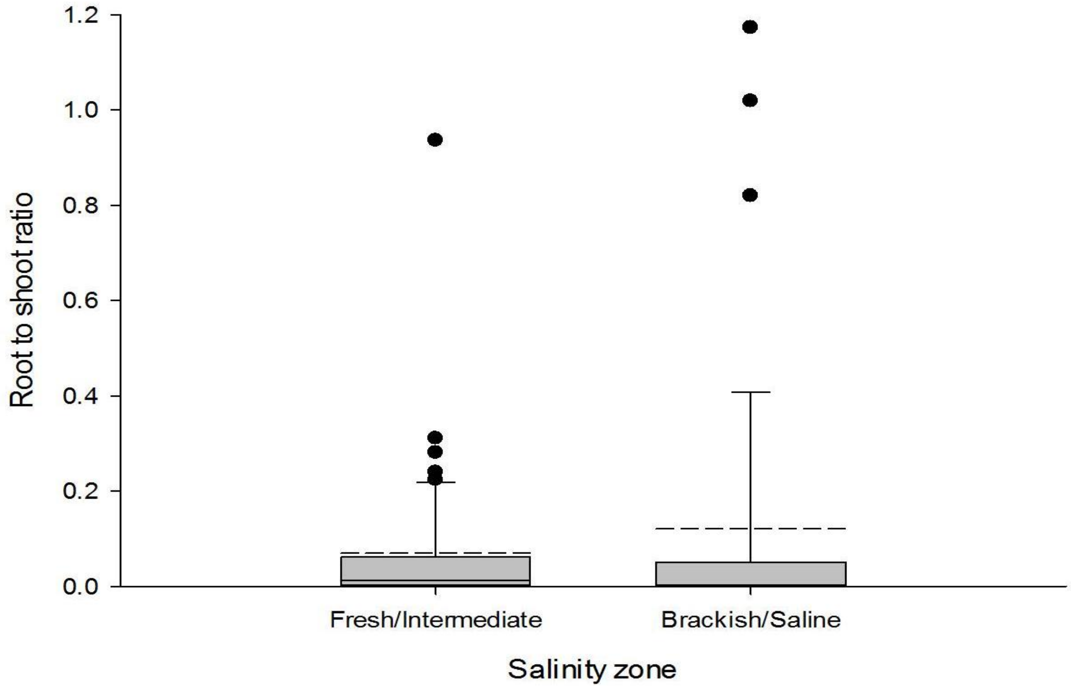

Figure 4.4. Submerged aquatic vegetation root to shoot ratio by assemblage group. There were no significant differences between the fresh/intermediate group and brackish/saline group.

SAV assemblages

Ten species of SAV were identified across all habitat types throughout the year. *Ceratophyllum demersum* (coontail), *Hydrilla verticillata* (hydrilla), *Najas guadalupensis* (najas) and *Myriophyllum spicatum* (Eurasian water milfoil) were dominant among fresh and intermediate sites while *Ruppia maritima* (wigeongrass) and Eurasian milfoil were dominant at brackish and saline sites.

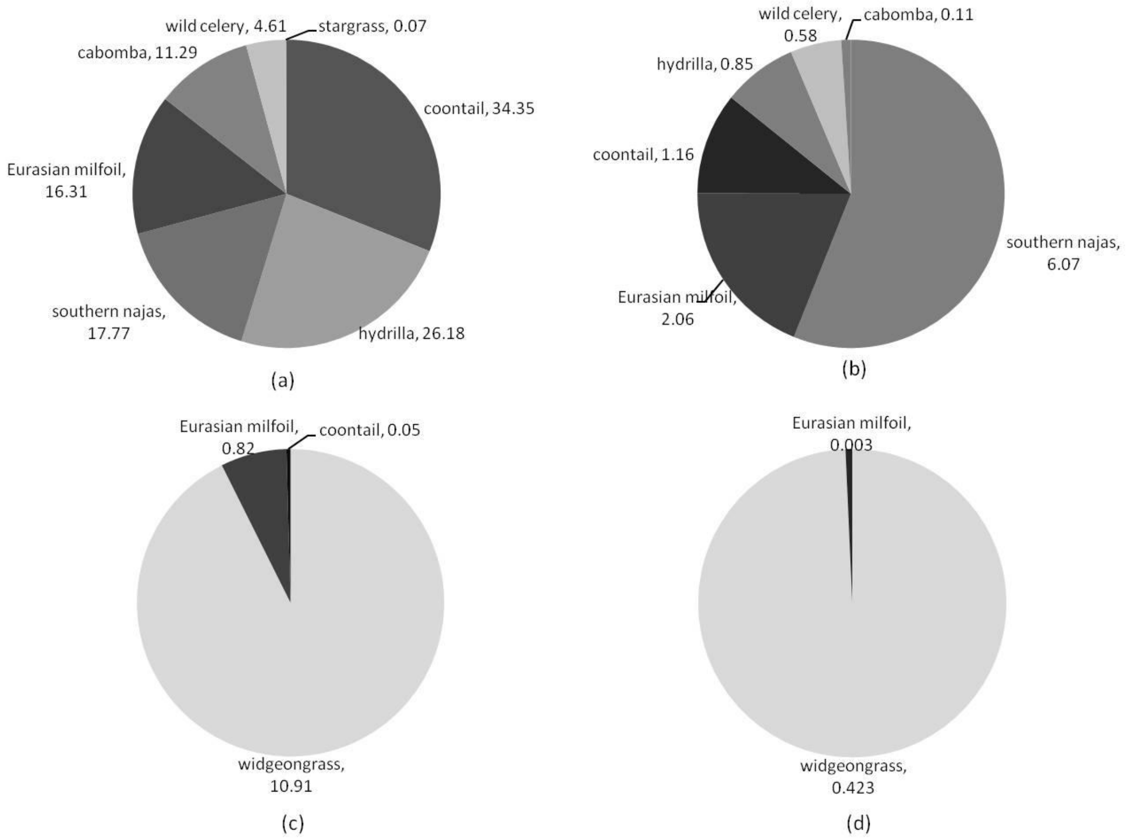

Figure 4.5. Fresh/intermediate submerged aquatic vegetation assemblage in July (a) and December (b), and brackish/saline assemblage in July (c) and December (d). For both groups number of species and overall biomass decreased in December.

Species – environment relationship

The July CCA delineates SAV species into 3 subgroups controlled mainly by salinity and water characteristics. The first two axes of the July CCA explain 79.3% of the variation between SAV species that can be explained by the environmental variables (F = 7.047, p = 0.0020; Figure 4.6). Axis one, which describes 44.6 % of the variation, largely differentiates between salt tolerant and freshwater SAV species. Specifically, widgeongrass is strongly associated with high salinity in this study and is distinct from freshwater SAV species. The second axis of the July CCA describes 34.7 % of the variation and differentiates between two groups of freshwater SAV species along an axis largely controlled by water clarity (depth, PAR, chl *a*). Specifically, the first group (hydrilla, *Cabomba caroliniana* (cabomba) and coontail), is associated with greater water depth and higher chl *a* concentration, which largely describes freshwater ponds found in the upper basin. The second group (southern najas, wild celery and Eurasian milfoil), is associated with low PAR and shallower water depth often found in the muddy, shallow aquatic conditions found throughout the middle basin.

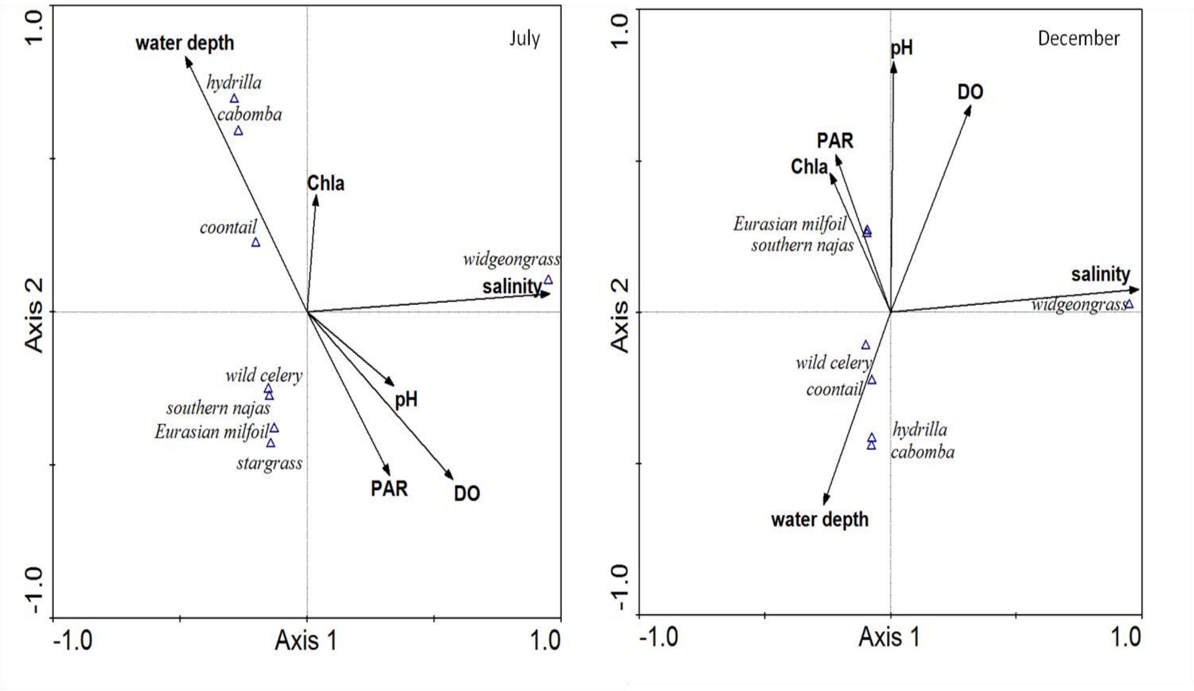

Figure 4.6. Canonical correlation analysis (CCA) of SAV species in relation to environmental variables (salinity, water depth, chl *a*, DO, PAR, pH) for July (left) and December (right).

The December CCA provides very similar results to the July CCA, separating SAV species into 3 subgroups, although species differ slightly from the July CCA. Again, salinity and other water characteristics control species distribution along the axes. The first two axes explain 55.1% of the explainable variation among SAV species (F = 28.1, p = 0.0020; Figure 4.6). The first axis is controlled by salinity, strongly associated with widgeongrass, and explains 29.6 % of the variation. The second axis explains 25.5% of the variation among species and separates freshwater SAV species into the two groups. The axis is controlled by water clarity (depth, PAR, chl *a*) and also pH. Cabomba, hydrilla, wild celery and coontail are associated with deeper SAV sites, while southern najas and Eurasian milfoil are associated with low PAR, chl *a,* and pH.

Discussion

Unlike tidal marshes, submerged aquatic vegetation assemblages in Barataria Basin, Louisiana, USA, separated into two distinct groups: fresh/intermediate and brackish/saline. Salinity affected SAV assemblages (number of species, biomass) and was the primary environmental driver distinguishing the two groups from each other. Water clarity indicators (water depth, PAR, chl *a*) were secondary drivers of organization, specifically in the fresh/intermediate group in winter. Significant intra-annual variation in terms of biomass, and species composition occurred between summer and winter months, and indicated one prolonged peak of maximum SAV biomass from May through July, which was generally observed across the salinity gradient. Water characteristics are highly variable in estuarine environments, resulting in rapidly changing SAV assemblages throughout the year. Concurrent change in SAV biomass availability may directly impact dependent fish and waterfowl species. These data will enable better SAV management with improved SAV mapping and modeling.

Coastal habitats in southeast Louisiana have historically been characterized based on emergent marsh vegetation and their salinity tolerances and adaptation to flooding (fresh, intermediate, brackish, saline; Visser et al 2013). For SAV, we identified two distinct SAV assemblages in Barataria Basin (fresh/intermediate (F/I) and brackish/saline (B/S)), suggesting that marsh type classification does not accurately describe submersed habitats. Another study characterizing SAV along the northern Gulf of Mexico identified 3 broad groups of SAV in river deltas extending from Mobile Bay, Alabama to the Pearl River area of Mississippi (Cho and Biber 2016). Groupings in that study were based on salinity and disturbance tolerance, with the third group including *Halodule wrightii*, a marine seagrass not observed in this study. Lack of marine seagrasses in this study may explain why only two SAV groups were identified in Barataria Basin compared to other watershed basins along the northern Gulf.

The southern end of Barataria Basin is influenced by the Mississippi River; river water discharges into the open Gulf of Mexico, and is pushed back towards lower Barataria by currents and wind (Inoue et al. 2008). Fresh and turbid water from the Mississippi River contributes to variable, but generally low mean (<15) salinity in the mid to lower basin (CPRA 2017), and also decreases water clarity which likely contributes to the absence of marine seagrasses in the lower basin (Handley et al. 2007). The B/S assemblage dominated the lower basin, and included Eurasian watermilfoil and widgeongrass. Eurasian watermilfoil and widgeongrass were observed together throughout the study, likely due to both species' salinity tolerance compared to less salt tolerant species of the upper basin, and their association with the F/I group.

Salinity was the principle environmental driver differentiating SAV assemblages, including number of species and SAV biomass. The F/I group contained more species compared to the B/S group, similar to past regional surveys and observations in other estuaries (Orth and Moore 1988; Dunton and Dunton 1990; Merino et al. 2009; Lopez-Calderon et al. 2010). For instance, the B/S group was dominated by just two species; in contrast, ten species were observed in the F/I group throughout the year. Higher salinity areas are often dominated by mono-specific beds or just a few species. For instance, two species, widgeongrass and *Zostera* *marina* (eelgrass) are found in the saline Chesapeake Bay, (Patrick and Weller 2015), three species (*Halodule wrightii* (shoalgrass), *Thalassia testudinum* (turtlegrass), *Syringodium filiforme* (manateegrass)) dominate saline lagoons in Texas, and one species, widgeongrass, grows in some saline Mexican lagoons (Dunton 1996; Flores-Verdugo et al. 1988). According to previous SAV surveys along the northern Gulf, in Louisiana SAV diversity and biomass is often greater in fresh/intermediate compared to brackish/saline areas (Hillmann et al. 2016). Barataria SAV biomass follows a similar trend; the F/I assemblage contained more biomass, while B/S biomass was lower. Increasing salinities within generally fresher estuarine areas could shift the SAV assemblages from F/I to B/S.

Shifts in assemblages have implications beyond species composition. For example, marine seagrasses often contain more biomass belowground than aboveground (Pulich 1985), with slender growth forms able to weather wave disturbance, and together these factors may contribute to greater seagrass bed stability overall. SAV further up-estuary is morphologically more complex, fragile, and exhibit “flashy” growth patterns (Trebitz et al. 1993). Subsequently, freshwater SAV may be more susceptible to exposure and storms (DeMarco et al. in review), and possibly less effective at shoreline protection than their marine counterparts. For instance, one of the most common species in the freshwater SAV habitats, coontail, contributed significantly to total SAV biomass, despite no real root system (Mishra et al. 2006). Coontail was also observed within some B/S assemblages during low salinity summer months. The pervasiveness of coontail throughout the basin may even partially explain low Barataria SAV RSR (0.08 ±0.02) compared to SAV and seagrass RSR elsewhere, which typically ranges between 1 and 5 (Dunton 1996).

The second most important factors separating SAV groups in Barataria Basin were other water characteristics related to water depth and light (PAR, chl *a*). These findings are similar to past studies that also found that water depth and light are important factors structuring SAV assemblages (Kemp et al 2004; Cho and Poirrier 2005b), but comparisons can be difficult because water depth and water clarity are both used as proxies for light, while some have taken direct measurements. Interestingly, within the F/I assemblage, species divided into two subgroups, with some species more sensitive to light and water depth than others. For instance, our analyses consistently co-related cabomba and hydrilla, freshwater species identified with increasing water depth, indicating similar abilities to compensate for low light with structural adaptations (i.e. long stems), similar to widgeongrass in a recent greenhouse experiment, in which low light yielded sparser, yet longer plant stems (Chapter 5). Additionally, Eurasian watermilfoil and southern najas in Barataria also often co-occurred at sites with more light, similar to widgeongrass around the nearshore areas of Lake Pontchartrain, in the Pontchartrain Basin (Cho and Poirrier 2005a). However, salinity and light are highly variable throughout the year possibly affecting SAV presence, overall distribution and abundance. Strong intra-annual variation in SAV biomass and species composition may result from highly variable environmental conditions within the basin. Specifically, salinity and light in coastal estuaries are controlled by a combination of factors, including freshwater inputs and marine forcing. Currently, freshwater input into Barataria Basin varies throughout the year, largely depending on river management and precipitation patterns (Conner and Day 1987). Moreover, freshwater inflow in springtime, as well as higher precipitation in summer months likely affect SAV distribution and biomass, and may increase the spatial extent of F/I assemblage further down into the basin. However, reduced river flow in winter months coupled with strong southerly winds can increase salinities, and likely restricts some freshwater SAV to the upper basin. Variability of important forcing factors throughout the year may also partially explain observed “flashy” growth patterns of estuarine SAV. For instance, in this study several less common SAV species (stargrass, horned pondweed) observed during lower salinity summer months were absent during higher salinity winter months.

SAV biomass also exhibited similar seasonal trends. We observed strong intra-annual variation in biomass; biomass was highest in early to mid summer and lowest in early winter. This pattern extended across the salinity gradient (fresh max: 149.06 gdw m^{-2} (May), fresh min: 4.71 gdw m^{-2} (Dec); intermediate max: 83.03 gdw m^{-2} (May), intermediate min: 15.42 gdw m^{-2} (Dec); brackish max: 8.84 gdw m^{-2} (May), brackish min: 0.0006 gdw m^{-2} (Dec); saline max: 16.71 gdw m^{-2} (May), saline min: 0.84 gdw m^{-2} (Dec)).These results are similar to observations in other sub-tropical regions (Lirman et al. 2008), including other basins in coastal Louisiana (Cho and Poirrier 2005c), however similar, our results showed only one prolonged peak of maximum SAV biomass extending at least from May through July,

Our findings are based on SAV assemblages in Barataria Basin, LA, and more study is needed to determine whether these patterns occur in less productive regions along the northern Gulf of Mexico. However, in this study SAV biomass was more than 10-fold greater in summer months compared to winter months, indicating potentially more habitat, refuge and food resource availability in summers for other community members (i.e. waterfowl, priority fish species).. SAV habitats continue to be impacted by climate change and river management (Merino et al. 2005; Kanouse et al. 2006), likely increasing variability of SAV.

Current climate projections along the northern Gulf predict increasing temperature and variable precipitation over the next 100 years (Keim et al. 2011), conditions likely to impact the intra-annual variability of SAV distribution and biomass. Temperature is expected to rise by 1.5 ^{o}C, and precipitation is predicted to increase in summer months. This research indicates that wetter summers point towards an increase (distribution, biomass) of F/I SAV. However, higher temperatures could simultaneously increase evapotranspiration, thereby potentially limiting runoff (Keim et al. 2011). Less runoff results in less freshwater input into upper Barataria Basin, possibly constricting the fresher areas and allowing the saltier areas to expand. Throughout the year biomass in the brackish/saline waters of southeast Louisiana is generally low (Roy 2006; Carter et al. 2009). However, an increase in the extent of B/S SAV habitat area simultaneously increases the amount of B/S SAV biomass, resulting in more food, habitat and refuge for species dependent on this habitat specifically. The impacts of proposed river management and marine forcing are similarly complex.

Proposed river management (i.e. diversion operation) and marine forcing (i.e. sea-level rise) also affect habitat conditions in waters throughout the basin. Barataria Basin has lost at least 17% of its land area over the past 100 years (Britsch et al. 1993; Couvillion et al. 2010). River diversions are considered an important tool for coastal restoration, moving freshwater, sediment and nutrients into estuaries in order to control salinity and build land (Das et al. 2012). Hydrodynamic modeling shows river diversions strongly affecting conditions in the mid to lower basin by reducing salinity, likely increasing fresh/intermediate SAV habitat. However, marine forcing along coastal Barataria is strong due to the area’s proximity to the Gulf and even at maximum capacity, proposed river diversions are not expected to significantly alter salinity regimes directly along the coast of Barataria Basin. On the other hand, hydrodynamic modeling outputs also show SLR impacting salinity in the upper and lower Breton Basin under baseline conditions of no diversion (Wang et al. 2017), potentially increasing brackish/saline SAV habitat.

Predictions of changing SAV are difficult because change occurs at multiple scales (spatial, temporal) in the context of uncertain coastal restoration scenarios and climatic processes. It appears fresh/intermediate SAV habitat may increase in distribution and overall biomass abundance at least during some months of the year (summers) as a result of increased precipitation and proposed river management. Winter months are harder to predict. Despite marine forcing and SLR, expansion of brackish/saline habitats will likely only occur during extreme drought, or if river diversion operations cease altogether, because even small diversions maintain lower salinities.

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CHAPTER 5

EFFECTS OF SALINITY AND LIGHT ON GROWTH AND COMPETITION BETWEEN TWO CO-OCCURRING SPECIES OF SUBMERGED AQUATIC VEGETATION: *MYRIOPHYLLUM SPICATUM L.* AND *RUPPIA MARITIMA L.*

Environmental gradients act as species filters, restricting community membership and defining habitat types by creating selective environments that affect species distributions and abundances (Austin 1985; Weiher and Keddy 1995). Along these gradients, competition among species shapes communities (Keddy et al. 1998). In contrast to organisms with mobility that can move when environmental conditions become stressful, plants undergo physiological changes in response to environmental stress and competition (Feder 2002), or die. While significant research has examined factors controlling plants across terrestrial landscapes (Brooker et al. 2008), fewer studies have examined factors controlling aquatic plant assemblages distributed across submersed landscapes, particularly in estuarine environments (but see Koch 2001; French and Moore 2003; Kemp et al. 2004; Poirrier et al. 2009)

Abundant and diverse submerged aquatic vegetation (SAV) exists across estuarine salinity gradients (Cerco and Moore 2001; Hillmann et al. 2016; Shields and Moore 2016). Within these coastal estuaries, SAV presence largely depends on favorable light conditions in water, specifically, enough light needs to reach SAV leaves for photosynthesis and subsequent growth (Kemp et al. 2004; Dennison et al. 1993; Koch 2001). While light availability critically controls SAV presence, which species persist is likely determined by both biotic and abiotic factors, including competition, salinity, substrate type, wave energy, and nutrients (Haller et al. 1974; McCreary 1991; Adair et al. 1994; Kemp et al. 2004). These factors have been shown to affect individual species differently, impacting growth rates, root to shoot ratio, growth morphology, and stem densities, overall impacting SAV assemblages and their distribution (McCreary 1991; Doyle and Smart 2001; Zhu et al. 2008; Gustafsson and Bostrom 2011; Shields and Moore 2016). Within coastal estuaries, salinity controls SAV directly through individual species tolerances to salinity, and indirectly, through impacts on competition outcomes (Borgnis and Boyer 2015; Shields and Moore 2016). Understanding the dominant factors controlling SAV assemblages, including abundance and individual species' distribution, provides critical information to inform models predicting changes in habitat availability.

In southeast Louisiana, coastal estuaries are structured along salinity gradients, largely controlled by freshwater inputs limited to precipitation, restricted inflow from the Mississippi River, its distributaries, wind and storms (Bianchi and Mead 2009). These estuaries consist of a mosaic of diverse estuarine habitat types, ranging from forested swamps, to fresh through saline marsh, extensive shallow-water habitats with sediment bottoms, oyster reefs, submerged and floating aquatic vegetation habitats, and barrier islands. Of these habitats, submerged aquatic vegetation within the shallow-water areas provides critical habitat across the extensive shallow waters of these regions, extending from fresh to true saline conditions (La Peyre and Gordon 2012). Some studies suggest that salinity structures SAV assemblages, while water temperature and light attenuation affect SAV distribution and abundance (Cho and Poirrier 2005), although this has only been shown in fresh to intermediate habitats. Diverse SAV assemblages exist in the upper estuaries in fresh to intermediate salinity marsh areas (Poirrier et al. 2010), with fewer species down estuary (Hillmann et al. 2016). Across the salinity gradient, changes in riverine inflow and precipitation would likely affect salinity and light availability which could influence not only SAV presence, but also SAV assemblages. While brackish assemblages contain select members from both freshwater and saline SAV assemblages, only a few of these species exist across the salinity gradient, and may potentially adapt to changing environmental conditions (Patrick et al. 2014; Hillmann et al. 2016).

Across the estuarine salinity gradient, *Myriophyllum spicatum* (Eurasian watermilfoil) and *Ruppia maritima L*. (widgeongrass) are ubiquitous species that dominate the less diverse SAV assemblages found in brackish to saline waters (Carter et al. 2009; Merino et al. 2009; Hillmann et al. 2016). However, as yet, not much is known about what specifically controls each of these species distribution and relative abundance. Further, does their co-occurrence increase overall SAV abundance (complementarity) or depress it?

Eurasian watermilfoil, henceforth milfoil, is a non-native species of SAV introduced into the United States through the Chesapeake Bay area in the 1880s (Nichols and Shaw 1986; Les and Mehrhoff 1999). Described as a salt tolerant freshwater species, milfoil is a perennial with whorled leaves and long stems. The species has relatively low light requirements (1-2% surface light) compared to other submersed plants (Wetzel and Grace 1978), and thrives in salinities from 0 to 10 (Haller et al. 1974). Milfoil spreads quickly through fragmentation of plant parts, and is considered a nuisance due to its aggressive growth, forming dense beds which choke waterways (Martin and Valentine, 2012). However, milfoil also increases fish abundances and forage for waterfowl, providing important ecosystem services (Madsen et al. 1995; Wicker and Endres 1995; Duffy and Baltz 1998). A recent year long survey across Barataria Basin, Louisiana, showed that in brackish habitat milfoil biomass was greater than all other SAV species combined (3.28 ±1.41 g m^2), and was even 4 times greater than widgeongrass (0.82 ±0.39 g m^2), the second most abundant SAV species observed in brackish waters (Hillmann et al. 2016).

Widgeongrass grows as annual and perennial plants, with slender, branched leaves and shallow root systems (Kantrud 1991). Common in aquatic environments, widgeongrass has broad salinity tolerances (0->100; Kantrud 1991), and spreads through seed dispersal and adventitious roots (Kantrud 1991). Despite its environmental tolerances, widgeongrass occurrence is thought to be limited by water clarity, wave exposure (Dunton 1990) and salinity variability (Strazisar et al. 2015). Widgeongrass has been described as a disturbance tolerant species (Cho and Poirrier 2005; Johnson et al. 2003), but some research found widgeongrass limited by even more tolerant species (Strazisar et al. 2015). Salinity and light may be the two dominant abiotic factors restricting widgeongrass growth (Verhoeven 1979; Bonis et al. 1993; Adair et al. 1994), with competition from other species as a critical limiting factor (Verhoeven 1979; Pulich and White 1991). Widgeongrass is highly valued for the refuge it provides for fish and invertebrates, and as food for waterfowl (Bortolus et al. 1998; Kanouse et al. 2006). Recent surveys indicate widgeongrass growing across the salinity gradient in southeastern Louisiana, and widgeongrass was found to be one of only a few species in brackish SAV habitat (Hillmann et al. 2016), and the only species observed in estuarine saline SAV habitat (Hillmann et al. 2016).

In southeast Louisiana milfoil and widgeongrass grow in both monospecific and mixed beds, often with one another. However, whether their co-occurrence actually increases or inhibits overall SAV production is unknown. Further, salinity and light are predicted to change due to on-going and proposed river management operations, and climate change (i.e., Das et al. 2012; Wang et al. 2016), and it’s unclear how changing environmental conditions will affect these species, or their competitive interactions within SAV habitats. In particular, in this region proposed river diversions divert fresh riverwater and sediment into upper estuaries, likely resulting in lowered salinity and increased turbidity across the estuarine gradient (Allison and Meselhe 2010; Wang et al. 2016), potentially impacting SAV habitats. While some studies predict that freshwater aquatic habitats may expand, displacing brackish habitats and their species (Das et al. 2012), it is unclear exactly how brackish SAV species and assemblages will be impacted. For instance, what affect will changing environmental conditions have on SAV abundance? Understanding how overall production is impacted along abiotic gradients will enable better prediction of shifting SAV habitats and result in more focused management decisions.

As the two dominant aquatic plant species in southeast Louisiana estuarine waters, understanding how milfoil and widgeongrass respond to d salinity and light, as single species, and in competition with one another is critical to determining and predicting their distribution, SAV habitat availability, and productivity. This study examines growth and competition between milfoil and widgeongrass in varying conditions of salinity and light. Specifically, this research examines: a) what effect will different salinity and light regimes have on milfoil and widgeongrass growing separately in monoculture, and b) how will the different treatments affect species interactions when plants are grown in mixture? The hypotheses are (1), in monoculture milfoil will be more productive at lower salinity and widgeongrass will be more productive at higher salinity, and both species will be less productive in low light. In mixture we expect (2) widgeongrass will be more competitive at higher salinities and milfoil will be more competitive at lower salinities, and milfoil will be more competitive in low light. This research can provide critical information necessary to understand how SAV habitat may shift over time across this landscape.

Methods

This experiment was conducted in an indoor greenhouse located at Louisiana State University Agricultural Center (LSU) during the summer/fall of 2016. A factorial experiment of salinity (0, 5, 10, 15, 20), light intensity (50% ambient light, 20% ambient light), and species (milfoil, widgeongrass) in monoculture, and in mixture (at salinity of 0, 10, 20 and both light treatments), was used for a total of 26 treatment combinations. Each treatment combination was replicated three times for a total of 78 experimental units (pots; 10.0 cm diameter), which were placed into plastic, translucent tanks (0.7m × 0.35m × 0.4m) in a completely randomized design.

Milfoil plants were collected from Fuci Bayou, LA, USA (29.504806, -89.668214; 1.0 salinity) and widgeongrass plants were collected from the northern shore of Lake Pontchartrain, LA, USA, (30.261215, -89.956350; 3.0 salinity) on August 7 and 8, 2016. Sediment was also collected at both locations for use in the experiment. Plants and sediment were brought back to the LSU greenhouses in covered bins. Equal amounts of sediment from both sites were combined, homogenized and each pot was filled with approximately 450 ml of sediment. Plants of similar stem lengths (milfoil: 8.20 cm ±0.49; widgeongrass: 11.81 cm ±0.21; mean ± SE) and stem density (milfoil: 1.0 ± 0.0; widgeongrass: 8.95 ± 0.95; mean ±SE) were selected for the experiments. A subset of 10 plants from each species was sampled for initial dry weight values (milfoil: 0.13 gdw; SE ± 0.03; widgeongrass: 0.07 gdw; SE ± 0.01). One plant was planted in each monoculture pot and one plant of each species was planted in each mixture pot.

After planting, the pots were randomly placed into tanks which were filled with freshwater adjusted to a salinity of 10 using Instant Ocean Sea Salt (Instant Ocean, St. Blacksburg, VA. 24060). Pots were acclimated for 7 days prior to commencing the experiments. Starting on August 14, 2016, salinity was adjusted at a rate of 3 every 3 days until the target salinities were reached for each treatment. Treatments were randomly assigned to tanks prior to adjustments. Water levels were maintained at 3 cm below the top of the tank, approximately 15 cm above the top of the pot. Experiments were initiated on August 26, 2016 and run for 8 weeks. A neutral density (50% light reduction) shade cloth was placed over the top of the low light treatment tanks to mimic natural high turbidity/reduced light field conditions. The low light treatment tanks maintained ~20% ambient light throughout the experiment, and high light treatment tanks maintained ~50% ambient light conditions. Light intensity (photosynthetically active radiation, PAR; $\mu mol\ m^{-2}\ s^{-1}$) was monitored weekly throughout the experiment using a light intensity meter (LI-1400 LI-COR, NE). On the first day of the experiment, all stem lengths (cm), and stem densities (#) were measured for each pot and recorded. Throughout the experiment, salinity, temperature (^{o}C), and dissolved oxygen ($mg\ L^{-1}$) were monitored every 3 days using a handheld YSI 6000 (Yellow Springs Instrument, Inc.). Salinity was adjusted as needed to maintain treatment target values.

At the end of the experiment, all plant material was harvested and brought to the lab for measurements of stem length, stem density, and aboveground (AG) and belowground (BG) biomass. Biomass was determined by drying the plants at $60^{o}C$ until a constant weight was obtained (g DW). Total growth rate (TGR) was based on dry weights of total biomass (AG + BG). The average initial dry weight values calculated for each species were subtracted from final dry weight values and divided by the number of days in the experiment (gdw day^{-1}). Root to shoot (RSR) was determined by dividing the BG biomass (gdw d^{-1}) by the AG biomass (gdw d^{-1}). Stem length growth rate (SLGR) was determined by subtracting initial stem lengths from final stem lengths and dividing by the number of days in the experiment (cm day^{-1}). Stem density was determined at the end of the experiment by visually counting the number of vertical stems ascending from roots.

Competition among species was analyzed by calculating relative yielding (RY); relative yield totals (RYT) were used to determine species complementarity (an overall increase in productivity of bicultures compared to monocultures) (Hooper 1998; Shields and Moore 2016). In this study RY was based on TGR, and was determined by first calculating the expected mean of TGR for each species in monoculture across all treatments and treatment combinations. Next, the TGR of each species in mixture was calculated and this value was divided by the expected mean in monoculture, resulting in a ratio of yielding in monoculture versus biculture. Overyielding occurs when a species RY> 1 and underyielding occurs when RY< 1. Therefore, interspecific competition is considered strong when one species significantly over yields while the other under yields in mixture (Shields and Moore 2016), but can also occur if both species underyield. RYTs were used to determine what effect competition had on overall SAV production, specifically, whether overall production increased and whether that was driven by both species (complementarity) or a single species (species identity). RYTs were calculated by averaging the RYs of each species in each treatment. When RYT > 1, species are considered complementary as long as each species has an individual RYT > 1, likewise if RYT in monoculture was greater and different than RYT in mixture, species identity was considered to drive productivity (Gustafsson and Bostrom 2011; Shields and Moore 2016).

For all tests a significance value of $p < 0.05$ was used. Data were tested for assumptions of normality (Shapiro–Wilk test statistic) and homogeneity of variance. Analyses of variance (ANOVA) was run for both species separately in monoculture for TGR, RSR, stem density, and SLGR, with salinity and light as fixed factors, and container as a random effect. Tukey's HSD tests were run when significant differences were found. Two-sample t-tests were run on TGR means of species in mixture and monoculture for all combinations of factors tested to determine whether species RY and RYTs differed from 1. All data analyses were performed in SAS 9.4 (SAS Institute 2010). Mean and standard error are reported unless indicated otherwise.

Results

Environmental variables

Mean salinities remained consistent across all treatments with all salinity targets remaining ± 1 from the target salinity. Mean measured ambient light inside the greenhouse throughout the experiment was 731.66, SE ± 132.04 µmol m^{-2} s^{-1}. Mean high light in the experimental tanks was 353.58, SE ±124.21 µmol m^{-2} s^{-1} and mean low light was 149.99, SE ± 47.41 µmol m^{-2} s^{-1} (Table 1). High light was consistently ~50% of ambient light and low light was consistently ~20% ambient light. Temperature remained constant across all tanks and days of the experiment ($31.7 \pm 0.10^{o}C$).

Table 5.1. Recorded environmental conditions. All mean values reported with ± SE Ambient light=atmospheric light measured inside greenhouse; high light= light just below surface water in tanks/no shade cloth; low light=light just below surface water in tanks/with shade cloth.

	Water Characteristics				
	0	5	10	15	20
salinity	0.91 ±0.21	5.21 ±0.06	10.14 ±0.08	15.09 ±0.09	19.86 ±0.23
DO mgl^{-3}	7.57 ±0.26	6.51 ±0.19	6.14 ±0.17	5.48 ±0.12	5.20 ±0.12
temperature	31.6 ±0.23	31.57 ±0.22	31.85 ±0.23	31.73 ±0.23	31.74 ±0.23
	Light				
	ambient	high	low		
PAR µmol m^{-2} s^{-1}	731 ±132	353 ±124	149 ±47		

Monocultures

Salinity and light significantly affected milfoil growth (Figure 5.1, Figure 5.2). Salinity impacted TGR ($F_{4,20}$= 22.57, p < 0.0001), stem density ($F_{4,20}$= 5.01, p = 0.0058), and SLGR ($F_{4,20}$= 15.55, p < 0.0001), with higher TGR at 0 higher compared to all other salinities, which did not differ. Milfoil stem density and SLGR were also higher at 0 compared to 15 and 20. Light impacted milfoil TGR and RSR. TGR was higher in high light compared to low light (high: 0.012 gdw d^{-1} ± 0.004 SE; low: 0.007 gdw d^{-1} ± 0.004 SE) ($F_{1,20}$=4.44, p=0.0480)., RSR also increased in high light (high: 0.79 ± 0.21 SE; low: 0.35 ± 0.06 SE) ($F_{1,19}$= 7.33, p = 0.0139). The interaction of salinity and light did not have a significant effect on any factor tested for milfoil growth.

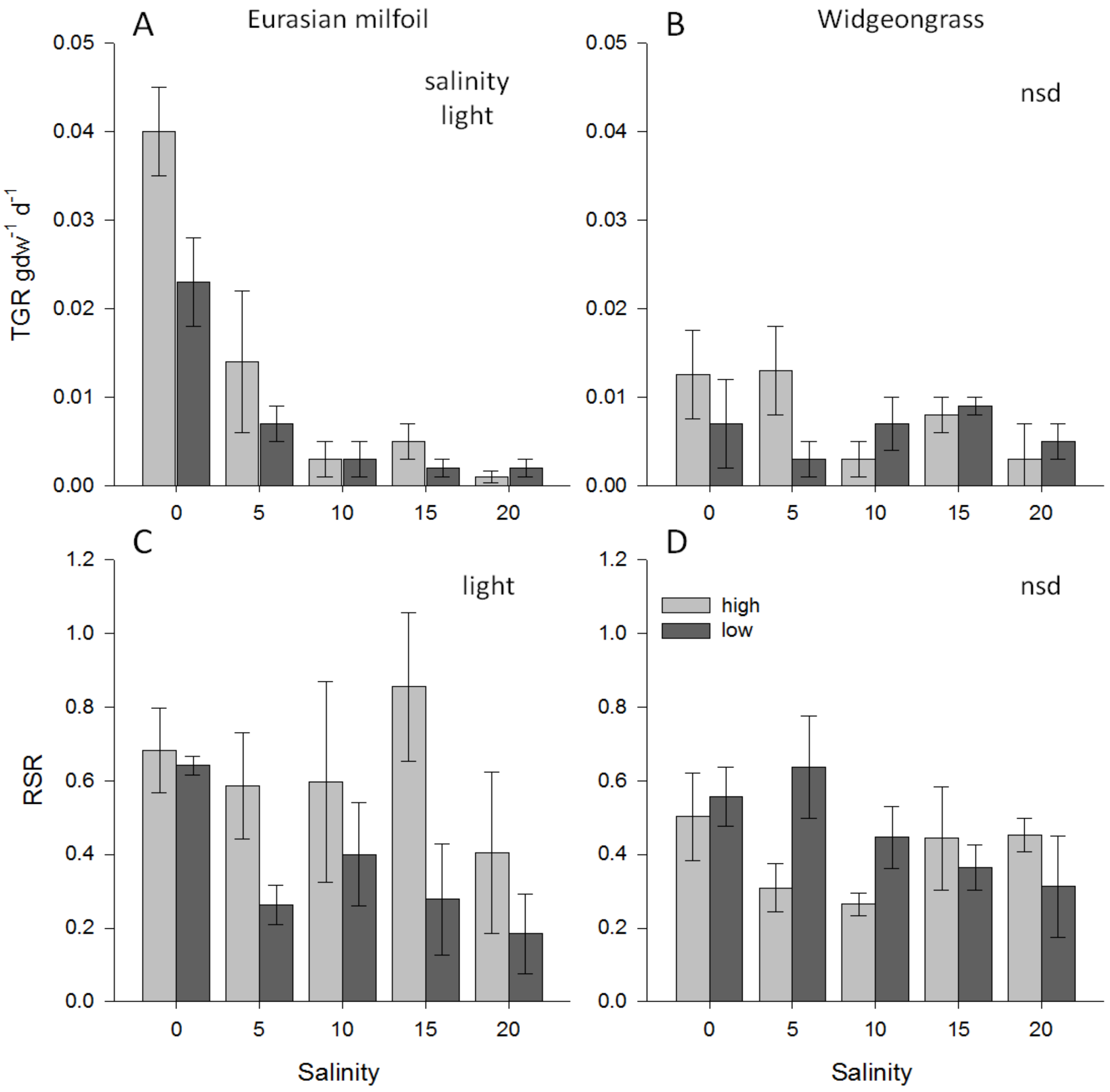

Figure 5.1. Total growth rate (TGR) and root to shoot ratio (RSR) of Eurasian milfoil (left; Figure 5.1a and 1c) and widgeongrass (right; Figure 5.1b and 1d) in monoculture across all salinity and light treatments. Values are mean ± 1 SE, n = 3. Factors with significant differences are indicated in the upper-right of each graph. Not significant=nsd.

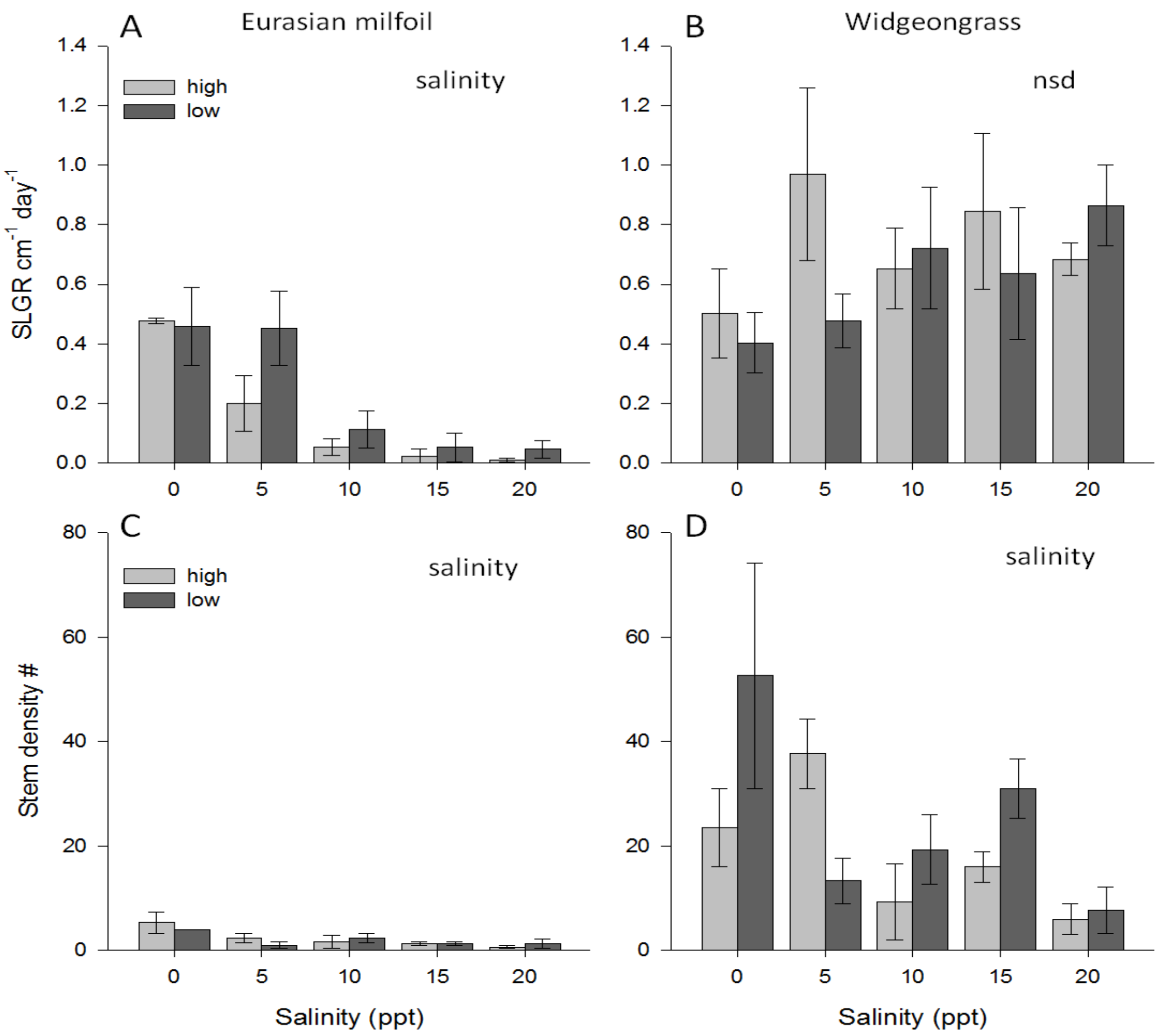

Figure 5.2. Stem length growth rate (SLGR) and stem density increase of Eurasian milfoil (left; Figure 2a and 2c) and widgeongrass (right; Figure 2b and 2d) in monoculture across all salinity and light treatments. Values are mean ± 1 SE, n = 3. Factors with significant differences are indicated in the upper-right of each graph. Not significant=nsd.

Salinity had a significant impact only on widgeongrass stem density ($F_{4,19}$= 3.34, p = 0.0163), with greater stem density at 0 compared to 20 (Figure 5.2d). Neither light, nor the interaction of salinity and light had a significant effect on widgeongrass growth.

Competition

Interspecific competition was strong, although neither species significantly overyielded in mixture with the other species under any combination of salinity and light (Figure 5.3). Milfoil in mixture underyielded at 20 in high light, while widgeongrass underyielded in mixture at 0 and 10 salinity in high light. In low light milfoil underyielded at 0 and 10, widgeongrass underyielded at 10, and neither species overyielded. Although neither species overyielded in mixture, milfoil and widgeongrass both underyielded at 10 in low light. Competition did not increase overall biomass production; complementarity did not occur.

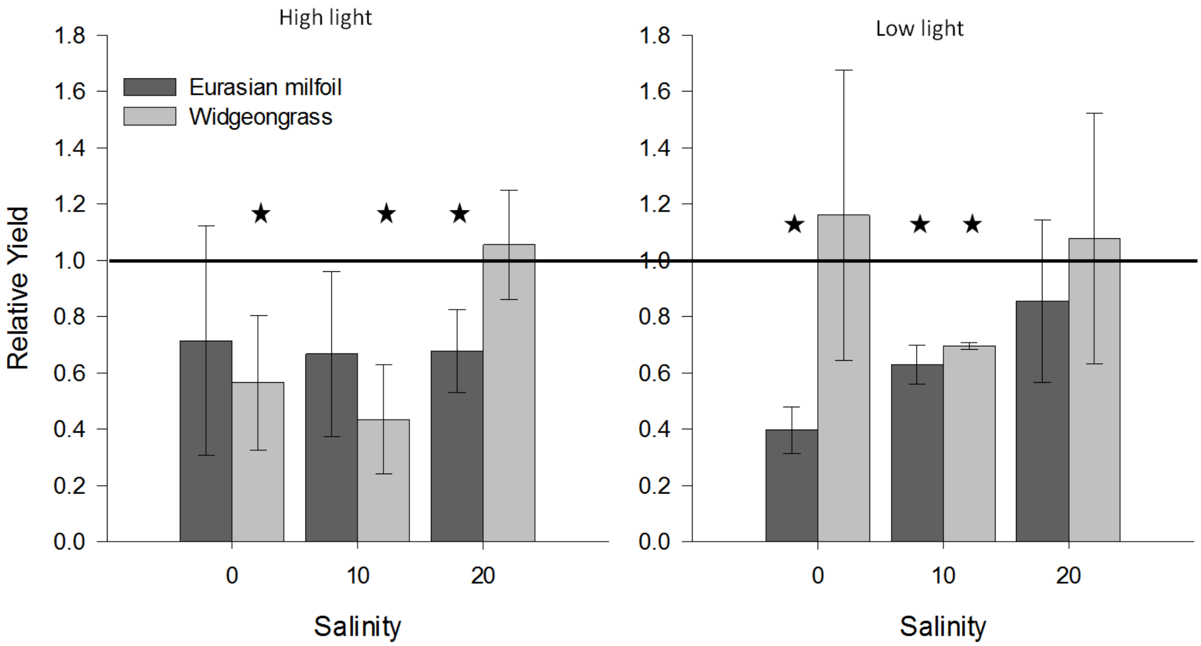

Figure 5.3.Relative yield calculated based on total growth rate (TGR) for Eurasian milfoil and widgeongrass in all salinity and light treatments. High light treatment (353.6 ±124.2 µmol m^{-2} s^{-1}) on left panel, low light treatment (149.9 ±47.4 µmol m^{-2} s^{-}1) on right panel. Dark grey is Eurasian milfoil, light grey is widgeongrass. Values are mean ± 1 SE, n = 3. A line is drawn across a relative yield of 1 which represents species performing equally well in mixture compared with monoculture. Stars indicate significant over- or underyielding.

Discussion

Both species displayed a wide tolerance to salinity and light conditions which likely explains their ubiquitous presence across the estuarine salinity gradient. Similar to past studies, both salinity and light were found to affect SAV growth (Moore and Wetzel 2000; Zhu et al. 2008; Shields et al. 2011). Differences in milfoil and widgeongrass response to both salinity and light however suggest potential different impacts on individual species abundance and dominance across the estuarine gradient with changing conditions. Specifically, while widgeongrass growth rate was not affected by salinity, milfoil growth was significantly reduced with increasing salinity. Similarly, widgeongrass was not affected by light availability, while milfoil displayed differences in TGR and biomass allocation with higher TGR in high light and lower RSR in low light. For both species competition decreased yield in some, but not all salinity by light combinations compared to their monocultures. However, under no scenario did overall production increase in mixtures over monocultures, suggesting both species are affected by strong abiotic gradients which likely control these species growth across the estuarine landscape in competition.

Salinity was a strong indicator of growth in milfoil monocultures. In fact, similar to other biological indicators tested, milfoil TGR was 7-fold greater at 0 than at 20, which suggests that long term salinity increases will likely negatively impact milfoil abundance and restrict milfoil distribution. Light affected milfoil TGR and RSR, which decreased in low light (RSR: high 0.61 ±0.08; low 0.35 ±0.06), suggesting changes in biomass allocation and overall morphology could potentially impact erosion/wave abatement (shoots), and habitat provision (roots) provided by milfoil beds (Ward et al. 1984; Valinoti et al. 2011). This growth difference was detected at 20% ambient light (~150 umol m^{-3} s^{-1}); past studies have shown milfoil growing in 1-2% ambient light (Grace and Wetzel 1978) (~< 10 umol m^{-3} s^{-1}), which matches observations from Louisiana where milfoil grew in 2.52-992.6 umol m^{-3} s^{-1} (Hillmann, Chapter 4). Understanding milfoil biomass allocation along light gradients provides more insight into how this species adapts to changing conditions. These results are consistent with other studies that show high milfoil abundance in low light (Zhu et al. 2008), suggesting an advantage over other species in turbid waters, such as within disturbed and changing coasts, and deltaic environments.

In contrast, widgeongrass growth was minimally affected by either salinity or light. Our findings agree with past studies that show widgeongrass growing best between 4-22 salinity (Kantrud 1991). Although 6-fold fewer widgeongrass stems were observed at 20 than 0, no other indicators were significantly affected. Pulses of freshwater have previously been shown to decrease widgeongrass growth rates (La Peyre and Rowe 2003), but sustained freshwater conditions as in this study do not appear to have negative effects on growth. Widgeongrass SLGR appeared to increase at higher salinities as overall stem density decreased, resulting in sparse plants with long stems. Studies examining widgeongrass and light have yielded inconsistent results, with widgeongrass at times performing better with high light, but also tolerating frequent periods of increased turbidity (see Kantrud 1991). Light had no affect on widgeongrass in monoculture in this study, which may be due to the range of light treatments used. We mimicked the observed average high (353.58 ±124.21 µmol m^{-2} s^{-1}) and low light (149.99 ± 47.41 µmol m^{-2} s^{-1}) conditions recorded during previous field surveys in regional brackish habitats, which did not capture the extremes (range: 2.52-992.6 µmol m^{-2} s^{-1}; Hillmann, Chapter 4). In contrast, other studies found differences in growth rates when the lower and higher limits of light availability were tested (i.e., Kemp et al. 2004). It may be that the “extremes” of light availability affect SAV growth patterns, not more subtle differences within an expected range, which was the focus of this study.

Salinity and light impacted both species in mixture compared to their monocultures. Competition altered the growth of both species at various combinations of salinity and light conditions tested. Under no conditions were mixtures more productive than monocultures. Often, one species underyielded in mixture while the other species performed equally well in mixture as in monoculture. In only one instance (10, low light) did both species underyield, likely indicating direct competition for resources. Instead, density-dependent impacts related to the initial experimental design may be why no species significantly overyielded (Roush et al. 1989). Specifically, this study examined competition at densities of 20 plants m^{-2} (milfoil) and 180 plants m^{-2} (widgeongrass), which is typical within these habitats. Lack of overyielding may be due to the density used, or the initial number of stems per plant (milfoil: 1.0 ± 0.0; widgeongrass: 8.94 ± 0.95; mean ± SE). At the species and assemblage level, some research has shown a negative correlation between SAV stem density and growth and biomass allocation of co-occurring species (Wolfer and Straile 2004). While these findings were generated in a study using higher initial stem densities than this study (15 and 40 per pot versus 1 and 8), the suggestion is that initial low starting densities may result in a failure to reach density thresholds necessary to expose negative density dependent relationships between plant species. In our study the initial starting density for both species were within the reported range observed across the salinity gradient for these species. However, widgeongrass especially can reach stem densities that far exceed the initial conditions of this study (see Kandtrud 1991), and therefore it was difficult to identify a critical density threshold. Future studies may want to consider using multiple starting densities.

Even so, on a larger scale (i.e. habitat level, landscape level) overall positive impacts are attributed to density dependent interactions (van der Heide et al. 2011). For instance, denser SAV beds retain more sediment and can improve light conditions, which promotes growth in positive feedback loops. However, this study was not designed to capture density dependent effects at that level, and we can only infer that milfoil and widgeongrass result in similar feedback loops.

We also may have failed to capture the competitive strategies that give individual species their competitive edge. For example, past studies suggest that milfoil thrives through its ability to easily spread, and establish across the landscape (Smith et al. 1991; Zhu and Georgian 2014). Its competitive ability appears linked to dispersal method, biomass allocation and timing of recruitment into communities (Smith et al. 1991). Fragmentation of plant parts and dispersal along water currents enables milfoil establishment in aquatic habitats hospitable to SAV where milfoil can outcompete slower growing seed dispersed species. Within established beds of native SAV milfoil production is often depressed, failing to outcompete existing species (Madsen et al. 1995; Doyle and Smart 2001), similar to the results in this study. Dispersal method and timing of recruitment were not examined in this study. We planted one specimen from each species of comparable size together in pots, essentially negating the advantages of milfoil dispersal through fragmentation and timing of establishment. Under the conditions tested, milfoil growth was significantly impacted by the presence of widgeongrass, particularly at 20 in high light, and 0 and 10 in low light. However, under the other conditions milfoil growth was not depressed, and milfoil may continue to thrive as salinity and light are decreased from increasing river diversions and precipitation. These continued changes likely provide new areas for SAV establishment well within the salinity and light tolerances of milfoil.

Despite its ubiquitous nature widgeongrass is not considered a strong competitor, but rather an opportunistic, highly tolerant species (Verhoeven 1979; Pulich 1985; Strasizar et al.

2015). Other species better adapted to specific salinity regimes (i.e. freshwater SAV, seagrass) often outcompete widgeongrass under stable conditions (Montague and Ley 1993; Frankovich et al. 2012). However, widgeongrass likely thrives across estuaries due to its broad tolerance to both salinity and light (Moore et al. 2014). In fact, widgeongrass has been found to replace seagrass species such as *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme* and *Zostera marina* in areas with frequent disturbances (Johnson et al. 2003; Cho et al. 2009). Widgeongrass expansion has been hypothesized to be a result of its ability to tolerate broad salinity and light gradients, colonizing rapidly through sexual and asexual reproduction (Johnson et al. 2003; Cho and Poirrier 2005; Cho et al. 2009; Strazisar et al. 2013). Increased variation in salinity and light from river management, increased storms, and/or increased precipitation may ultimately favor widgeongrass as these abiotic factors impact species within estuarine areas, and support similar widgeongrass growth.

Environmental conditions are changing in estuarine aquatic habitats as a result of climate change, human disturbance and restoration activities. In southeast Louisiana, the separate and combined effects from sea level rise, coastal land loss and river diversions impact salinity and light gradients (Das et al. 2012; Wang et al. 2014), and likely result in shifting SAV habitats, which are dominated by milfoil and widgeongrass. This greenhouse study highlights how abiotic factors may control individual species growth, and impact SAV assemblages through differential species responses, but also impact habitat characteristics through changes in species biomass allocation. Competition never increased overall production, in fact overall production decreased at 10, in low light. Depressed SAV affects density dependent faunal species (i.e. waterfowl, fish, invertebrates), by disturbing habitats, reducing refuge areas and food resources (Thayer et al. 1975; Hemminga and Duarte 2000; Williams and Heck 2001; Heck et al. 2008). However, under most of the conditions tested species in mixture did not have a negative impact on overall production, suggesting that monospecific and multispecies SAV beds provide similar ecosystem services within the broader community. Understanding the critical environmental drivers of SAV provides for better estimations of changing SAV and predictions of density dependent species impacts.

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CHAPTER 6

ESTUARINE SUBMERGED AQUATIC VEGETATION BEDS PROVIDE SUBSTANTIAL CARBON STORAGE IN DELTAIC ENVIRONMENTS

Terrestrial and coastal ecosystems store significant amounts of organic carbon (C_{org}) within plant biomass and organic-rich soils, yet only a few ecosystems have C_{org} sequestration, stock and storage estimates (Keith et al. 2009; Mcleod et al. 2011). Sequestration occurs when atmospheric carbon dioxide (CO_2) is taken up by vegetation through photosynthesis and subsequently stored in plant biomass, and soils, which provides potential short-term (plant biomass), and long-term (soils) storage of C_{org}. The ability of natural ecosystems to sequester and store organic carbon is a potential means of climate change mitigation (Pendleton et al. 2012). As a result, significant interest exists in not only understanding sequestration rates of C_{org}, but in quantifying C_{org} stocks and storage across a range of ecosystems to better understand the consequences of habitat shifts, loss, and restoration (Alongi et al. 2016; Pendleton et al. 2012).

Originally conceived for terrestrial forested systems (Schulze et al. 2000), C_{org} storage as a means to offset climate change has more recently been explored in coastal ecosystems (Chmura et al. 2003). Referred to as blue carbon, coastal ecosystems (seagrass, salt marsh, mangrove) sequester C_{org} at estimated rates of > 110 Tg C_{org} yr^{-1} (Mcleod et al. 2011; Kennedy et al. 2010; Keith et al. 2009; Duarte et al. 2005). In contrast to terrestrial ecosystems and oceans, which respectively store carbon primarily in live biomass and aerobic soils or dissolved within the water column (Grimsditch et al. 2013), coastal ecosystems store carbon primarily in organic-rich anaerobic soils (Chmura et al. 2003; Kennedy et al. 2010; Mcleod et al. 2011). Undisturbed, these coastal soils may retain C_{org} on much longer time scales than terrestrial forests, acting as hotspots of carbon sequestration and storage (Laffoley and Grimsditch, 2009).

Current estimates of blue carbon stocks span a wide range (140 – 471 Mg C ha^{-1}) (CEC 2016), which likely reflects the diversity of environmental conditions across which these carbon stocks are generated. Salinity, temperature, inorganic nutrients, as well as plant structural characteristics may affect organic matter production and accumulation through differences in productivity, particle trapping and sediment stabilization (Potoutoglou et al. 2017; Armitage and Fourqurean 2016; Stockmann et al., 2013; Tilman et al. 2006; Craft and Campbell 2002; Jacoby and Jackson 2000; Enriquez et al. 1993; Valiela et al. 1976). Furthermore, environmental setting may have significant impacts on regional sediment accumulation, as water depths, subsidence rates, storm events and adjacent habitats may all influence accretion rates, as well as export and re-deposition of organic matter (Smith and Osterman, 2014; Lavery et al. 2013; Bernal and Mitsch 2012; van Katwijk et al. 2011; Mckee and Cherry, 2009;Turner et al. 2006;). For example, total carbon stocks in depressional wetlands (Ohio, U.S.A) were more than double the total carbon stocks found in nearby riverine communities (Bernal and Mitsch, 2012). Similarly, C_{org} stock estimates across a range of seagrass meadows were found to vary by as much as 18x, and these differences are postulated to result from species differences and environmental setting, such as depositional environment, water depth and grain size differences (Lavery et al. 2013). Expanding our inventory of carbon stock estimates would help to better capture and understand controls on blue carbon.

Blue carbon stock and storage estimates remain largely limited to seagrass, salt marsh and mangrove ecosystems, despite other coastal habitats sharing similar characteristics, including a potentially equivalent capacity to sequester and store C_{org}. High net primary production coupled with low decomposition rates, along with high allochthonous and autochthonous organic matter deposition contribute to greater C_{org} accumulation and storage in coastal ecosystems; these conditions extend up-estuary into brackish to fresh coastal vegetated systems (i.e., freshwater wetlands, submerged aquatic vegetation (SAV)) (Mitsch and Gosselink, 2000). In coastal marshes, studies examining short and long-term sequestration rates across fresh to saline marshes found similar carbon accumulation rates across marsh types (Baustian et al.2016; Nyman et al. 2006; Hatton et al. 1983; Smith et al. 1983). Similar to coastal marshes, SAV habitats extend from coastal fresh, intermediate, brackish and saline settings to seagrass meadows. These habitats, which exist across extensive deltaic estuaries, may also contain substantial C_{org} stocks.

SAV exists extensively within the turbid, shallow water areas of coastal Louisiana (Hillmann et al. 2016), providing valuable habitat for fish and wildlife (Heck et al. 2003) along with other important ecosystem services (i.e., water quality (Knight et al. 2003); shoreline stabilization (Gutierrez et al. 2011)). Along with a few seagrass species (Darnell et al. 2017), many non-seagrass SAV species are found across the estuarine gradient of the Mississippi River Delta Plain (MRDP) (Hillmann et al. 2016). These SAV habitats support a diversity of species with varying structural and morphological characteristics, exist within anoxic soils, and, if extended out to the barrier islands, present a range of soil characteristics and environmental settings. However, non-seagrass SAV habitats are currently not included in estimates of blue carbon.

The objectives of this study were therefore to assess C_{org} stocks in SAV habitats along a salinity gradient, and estimate C_{org} storage in the top meter of SAV soils within the southeast Louisiana MRDP. Specifically, we addressed the following questions: 1) how does soil C_{org} content differ among SAV habitats across the estuarine salinity gradient, 2) how do salinity and soil characteristics influence C_{org} stocks, and 3) what is the estimated C_{org} storage value of SAV habitats across the MRDP? The hypotheses are: 1) SAV habitat soil C_{org} will vary across the salinity gradient, and 2) barrier island SAV habitat soils will contain more C_{org} compared to all other SAV habitats.

Methods

Study area

The Louisiana coastal plain is a dynamic environment, characterized by chenier plains to the west and by deltaic watershed basins of the Mississippi River to the east. The coastal plain has lost approximately 4,877 km^2 of land since the 1930s due to management of the Mississippi River, oil and gas canals, subsidence, sea-level rise and tropical storms (Georgiou et al. 2017; Peyronnin et al. 2017; Deegan et al. 2012; Barras 2009).

Within this area, the deltaic watersheds of the MRDP consist of 1.2 million hectares which are bounded by Vermilion Bay to the west and the Chandeleur Islands to the southeast (Couvillion et al. 2010; Penland and Suter 1988). Habitats within the MRDP are structured by salinity (Visser et al. 2013) and sediment gradients, which are largely controlled by large-river inputs (Mississippi River to the east, Atchafalaya River to the west) (Bianchi and Meade 2009). The interior deltaic region consists of a mosaic of diverse estuarine habitat types, ranging from forested swamps, to fresh through saline marshes, extensive shallow-water habitats with sediment bottoms, oyster reefs, submerged and floating aquatic vegetation habitats, and barrier islands. The Chandeleur Islands is one such barrier island complex, formed by the reworked sediments of the abandoned St. Bernard Delta. The barrier islands are in a transgressive phase and their footprint is primarily influenced by hurricanes and tropical storms (Fitzgerald et al. 2016; Bianchi and Meade 2009).

Field data collection

Within the MRDP (Figure 6.1) we sampled twenty-five sites with SAV presence, stratified by salinity zones (fresh, intermediate, brackish, saline; henceforth habitat types) (Visser et al. 2013) and located within previously identified potential SAV habitat areas (Hillmann et al. 2016). Twenty sites were co-located with Coastwide Reference Monitoring System (CRMS) stations (http://lacoast.gov/crms2/home.aspx) providing records of daily water quality conditions (salinity, temperature, water level) (CPRA 2017). We further divided the saline habitat into saline SAV and barrier island SAV sites. Barrier island SAV sites were all located near the Chandeleur Islands. Study sites were haphazardly selected from a set of previous field survey locations indicating SAV presence (Hillmann et al. 2017; La Peyre et al. 2017; Handley and Demay 2007). Due to logistical constraints, we ultimately included 5 sites each in fresh, intermediate and barrier island SAV habitat, 6 sites in brackish SAV habitat and 4 sites in saline SAV habitat. All sites were sampled once during 2015 or 2016.

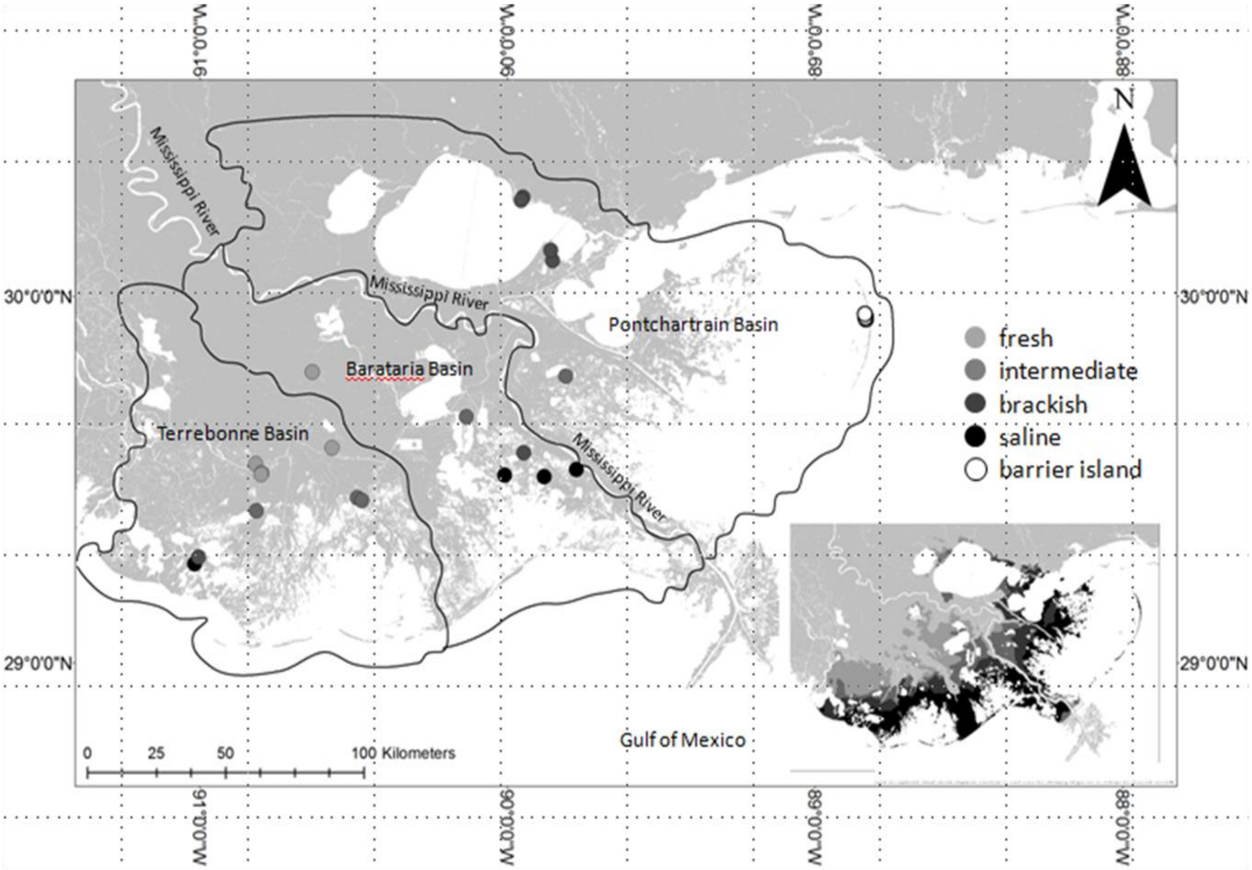

Figure 6.1. Map of study area within the Mississippi River Delta Plain. A total of 25 sites, distributed across submerged aquatic vegetation habitats (5 fresh, 5 intermediate, 6 brackish, 4 saline, 5 barrier island) across three Mississippi River basins (Terrebonne, Barataria, Pontchartrain) were sampled once in 2015 to 2016. The inset on the bottom right represents an example of the salinity stratification across the study area (Visser et al. 2013).

Upon arrival at each site, water salinity (YSI-85, YSI Incorporated, OH), water temperature (^{o}C, YSI-85, YSI Incorporated, OH), and turbidity (NTU-Hach 2100Q, Hach, CO) were sampled from the boat. After collecting water column data, a 0.25 m x 0.25 m floating PVC quadrat was thrown haphazardly three times from the boat. Within each replicate, water depth was measured using a metric measuring stick (± 0.01 m) and percent total SAV cover and cover by species was then estimated using a modified Braun-Blanquet technique (Wikum and Stanholtzer 1978).

All aboveground (AG) biomass within each replicate was harvested at the sediment surface, placed in labeled plastic bags and placed on ice in a cooler. Belowground (BG) biomass was collected using a soil corer (10 cm diameter x 30 cm depth). The BG core samples were rinsed in the field using a 1.0 mm mesh bottom bucket to remove most of the sediment and reduce bulk before being placed in labeled plastic bags and placed on ice. All samples were kept on ice and transported to the laboratory at Louisiana State University Agricultural Center (LSU) where they were stored at 4^{o}C until further processing.

Within SAV beds adjacent to each replicate AG quadrat, soil cores were collected in duplicate using PVC corers (5 cm diameter). The corer was pushed in the soil to collect a 1 m core, or until refusal. The depths to which cores penetrated and the lengths of cores extracted were recorded in the field. Any attached AG SAV tissue was removed and extracted soil cores were then partitioned into 10 cm slices in the field, placed in individually labeled plastic bags, and transported on ice to LSU for processing.

Laboratory processing and calculations

In the lab, AG samples were washed with tap water to remove sediment, debris, and epiphytes, and AG biomass was separated to species level. Separated samples were dried at 60^{o}C to a constant weight, which was then recorded (± 0.001 g). BG biomass was washed over a 1.4 mm sieve to further remove sediment and debris and dried at 60^{o}C to a constant weight, which was then recorded (± 0.001). AG and BG sample dry weights (per site) were summed by replicate, averaged (per site) and mean total SAV biomass was converted to carbon equivalents assuming a carbon content of SAV biomass of 34% (live biomass carbon content (CC_{SAV}) = (AG + BG tissue biomass) * 0.34; Mg C ha^{-1}) (Duarte 1990). This value is similar to CC_{SAV} of SAV biomass from a previous regional study (34.52%; Hillmann unpublished data). AG and BG biomass at barrier island SAV sites, where biomass samples were not collected, were estimated based on species-specific correlations between cover values and biomass from previous field surveys (Hillmann et al. 2017).

Sediment slices (n=330) were dried at 60^{o}C to a constant weight, recorded (± 0.001 g), and used to calculate dry bulk density (BD; gdw cm^{-3}) by dividing dry weight by volume of the slice, corrected for compaction. Specifically, slices from individual cores were corrected for minor compaction and expansion by applying a correction factor evenly across all 10 cm sediment slices in a core (Howard et al.2014). Soil compaction was < 1 % overall, but ranged between 10 % compaction and 10 % expansion for individual cores. After drying and weighing, sediment slices were homogenized using a mortar and pestle. To determine percent organic matter (%, OM), 4.0 g subsamples of each slice were weighed out and burned at 550^{o}C for 4 hours to calculate OM using the loss on ignition method (Heiri et al. 2001). To determine soil percent total carbon (%, TC) and percent nitrogen (%, TN), a second set of subsamples (0.011 - 0.012 g) were weighed out, placed in tin packages and analyzed using an elemental analyzer (Wetland Biogeochemistry Analytical Services Laboratory, Louisiana State University, Baton Rouge, LA). To determine soil percent organic carbon (%, C_{org}), a third set of subsamples were weighed out (0.030-0.040 g), placed in silver packages and analyzed using HCl fumigation (Wetland Biogeochemistry Analytical Services Laboratory, Louisiana State University, Baton Rouge, LA) (Zimmerman et al. 1997). The percent inorganic carbon (IC) was determined by subtracting C_{org} from TC.

To determine overall C_{org} stocks, the organic carbon content (CC) of each sediment slice was calculated from measured C_{org} and BD using the following equation (Campbell et al. 2015):

$CC_{sedX} = Z_{sliceX} * BD_{sliceX} * (C_{org\ sliceX}/100)$;

where X references the sediment slice (depth by site) and Z refers to thickness of slice (cm). To determine the C_{org} stock in the top 10 cm, 50 cm and 100 cm of soil, CC_{SED} values were summed for each core to the appropriate depth. For the 50 cm core sections and full 100 cm cores, regression analysis was used to extrapolate values down core when cores were not of sufficient length (i.e., < 50 cm or < 100 cm) to provide measured values (Appendix 2). When down core trends were not clear, we assumed a CC_{SED} of 0 (23 of 50 cores), which likely resulted in an overall conservative estimate for CC_{SED} stocks.

Analysis

Differences in discrete water column characteristics (salinity, temperature, water depth, turbidity), soil characteristics (BD, OM, $C_{org,}$ TN) and carbon content (CC_{SAV}, CC_{SED}) were tested across SAV habitats using a generalized linear mixed model with a lognormal distribution and identity link function (Proc Glimmix) (SAS 2013). When significant differences were detected, these analyses were followed by post-hoc comparisons using the Tukey's procedure (SAS 2013). Bulk density, OM, C_{org}, CC_{SAV}, and CC_{SED} (10, 50, 100 cm) were averaged across site replicates by SAV habitat, and this mean was used for all statistical tests as we were interested in between site and not within site variability. Prior to comparing SAV habitats, all soil properties (BD, OM, C_{org} and N) were examined using Spearman's correlation and regression analysis was used to examine the relationship between CC_{SED} and SAV cover and CC_{SED} and CC_{SAV} (SAS 2013). Mean and standard error are reported unless otherwise indicated. For all tests a significance value of $p = 0.05$ was used.

We examined differences in water (salinity), soil (BD, C_{org}) and vegetation factors (CC_{sav}) and SAV habitat types with a correlation matrix on $\log_{10}$ transformed data using canonical correlation analysis (CCA) (ter Braak and Smilauer 2002).

Results

Water column characteristics

Discrete salinity differed significantly by SAV habitat types ($F_{4, 20} = 10.73$, $p<0.0001$), with higher values at the barrier island SAV sites (15.6 ± 0.1), lower values at the freshwater SAV sites (0.1 ± 0.04) and no difference in mean salinity between intermediate, brackish and saline SAV sites (Table 6.1). Turbidity of surface waters ranged from a low of 1.10 NTU to a high of 89.9 NTU, and there was a significant difference in turbidity between SAV habitats ($F_{4, 20} = 5.30$, $p=0.0045$) with lower turbidity at fresh and barrier island SAV sites compared to saline sites, and brackish and intermediate sites being similar to all other sites. Water depth across all locations ranged from 10 cm to 125 cm, with no significant differences in mean water depth between SAV habitat types. Temperature did not differ between habitats.

Table 6.1. Submerged aquatic vegetation (SAV) and mean values (± SE) of environmental conditions across habitats. Fresh, intermediate, brackish and saline sites co-located with Coastwide Reference Monitoring System (CRMS) stations (http://lacoast.gov/crms2/home.aspx) (CPRA 2017). Mean salinity and 10-year range provided by CRMS hourly salinity data. SAV species names follow USDA naming conventions for vegetation (http://plants.usda.gov) (USDA 2006). CEDE4=*Cerataphyllum demersum*, HEDU2=*Heteranthera dubia*, HYVU3=*Hydrilla ventricillatta*, MYSP2=*Myriophyllum spicatum*, RUMA5=*Ruppia maritima*, STPE5=*Stuckenia pectinata*, THTE6=*Thalassia testudinum*, VAAM3=*Valisnaria americana*. Species presence within SAV habitats is noted with an "X".

SAV habitat	Core depth	Water depth	Turbidity	Salinity	Salinity	Salinity	CEDE4	HEDU2	HYVE3	MYSP2	NAGU	RUMA5	STPE15	THTE6	VAAM3	Total Cover %
	cm	cm	NTU	ppt	10-year range	10-year mean					Presence/Absence					range
Fresh	82.7 ±3.92	83.1 ±19.94	7.83 ±4.53	0.2 ±0.04	0.0-10.9	0.2 ±0.05	X		X		X					10-100
Intermediate	59.3 ±8.39	43.3 ±11.3	31.22 ±15.20	3.7 ±1.48	0.1-29.22	4.1 ±3.0	X	X		X	X	X			X	15-75
Brackish	59.9 ±10.31	61.8 ±4.7	19.26 ±7.80	4.4 ±0.88	0.1-28.18	5.3 ±0.7	X			X	X	X	X		X	5-95
Saline	66.3 ±3.60	45.0 ±10.5	35.65 ±9.28	4.8 ±1.57	0.1-31.5	8.2 ±0.8				X		X	X			25-45
Barrier Island	41.8 ±2.64	80.6 ±4.5	5.52±1.39	15.64±0.07	NA	NA						X		X		35-100

Vegetation

SAV cover ranged from a low of 5% to a high of 100% across sites, with no difference in SAV cover by SAV habitat type. In total, nine species of SAV, which includes one seagrass species, were identified across all 25 sampling sites, but species presence differed by habitat type (Table 6.1). *Ceratophyllum demersum* and *Hydrilla verticillata* were dominant in freshwater habitats, and were found at 4 out of 5 freshwater sites. Six SAV species were identified in both intermediate and brackish SAV habitat, but species composition differed. *C. demersum*, *Myriophyllum spicatum, Najas guadalupensis and Ruppia maritima* were frequently found at intermediate sites, while the dominant species at brackish sites were limited to *M. spicatum* and *R. maritima*. *R. maritima* also dominated the saline habitat sites and the barrier island sites. *Thalassia testudinum*, a true seagrass, was observed at 3 out of 5 barrier island sites. The most frequently encountered species was *R. maritima*, which was found at 12 of 25 sites.

Soils

Soil core depths ranged from a minimum of 31 cm to a maximum of 100 cm (Table 6.1). Spearman's correlation indicated that C_{org}, OM and TN were positively correlated ($r > 0.93$). Further analysis occurred using only C_{org} and BD. BD ranged from 0.07 to 1.76 gdw cm^{-3}, and differed across SAV habitats ($F_{4, 20} = 14.11$, $p < 0.0001$). Specifically, barrier island SAV soils had significantly higher BD (1.46 cm^{-3} ± 0.05) compared to all other SAV sites (Figure 6.2A). BD was variable with depth (down core), with no clear trends among SAV habitats (Figure 6.2B).

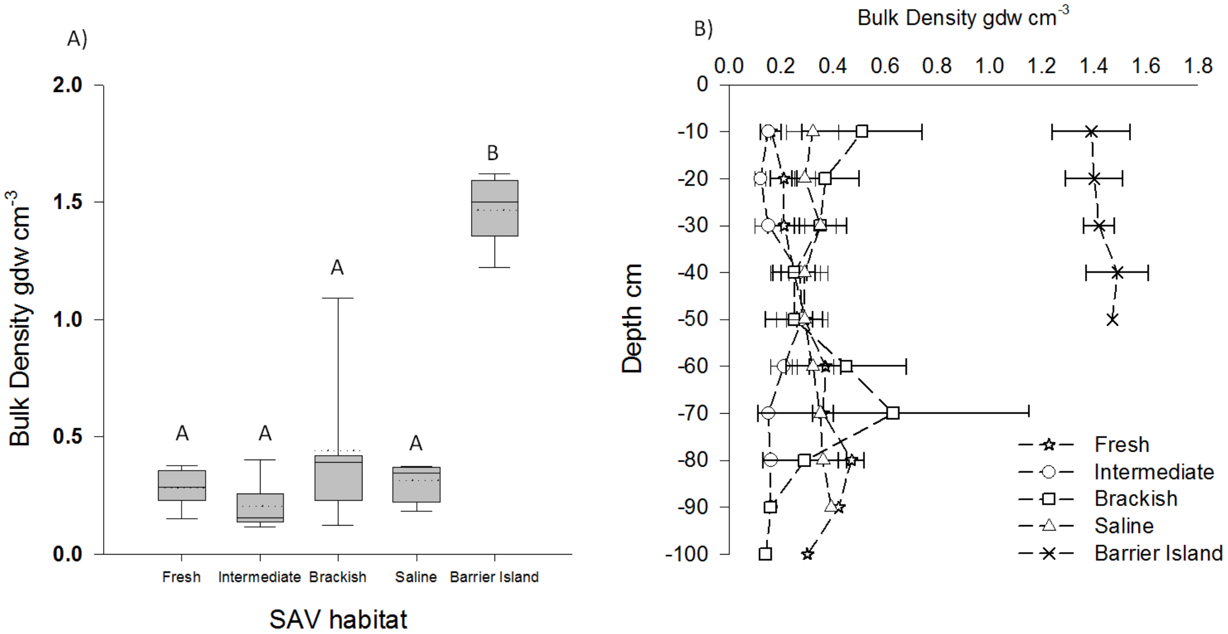

Figure 6.2. Bulk density (gdw cm^{-1}; mean ± 1 SE) across submerged aquatic vegetation (SAV) habitats within the Mississippi River Delta Plain (A). SAV habitat is defined by marsh zones determined by long-term salinity (Visser et al. 2013) as fresh, intermediate, brackish and saline interior deltaic habitat, and saline barrier island habitat. Different letters indicate statistical differences. The dotted lines indicate mean values, with solid lines representing median values. Down core profiles of soil bulk density (mean ± 1 SE) (B).

Soil C_{org} differed across SAV habitats ($F_{4, 20}$ = 28.80, p<0.0001) (Figure 6.3A), and ranged from a minimum below detection (< 0.02 %) to a maximum of 41.4 %. Intermediate SAV habitat had the highest mean C_{org} (24.3 ± 3.0%) which was statistically similar to fresh and brackish SAV habitat $C_{org.}$ and greater than saline and barrier island habitat. Fresh and brackish SAV habitat however did not differ from saline SAV habitat. In contrast, barrier island SAV habitat C_{org} was substantially lower (0.5 ± 0.1 %) compared to all other SAV habitats. C_{org} was variable with depth across all SAV habitats with no clear trends (Figure 6.3B).

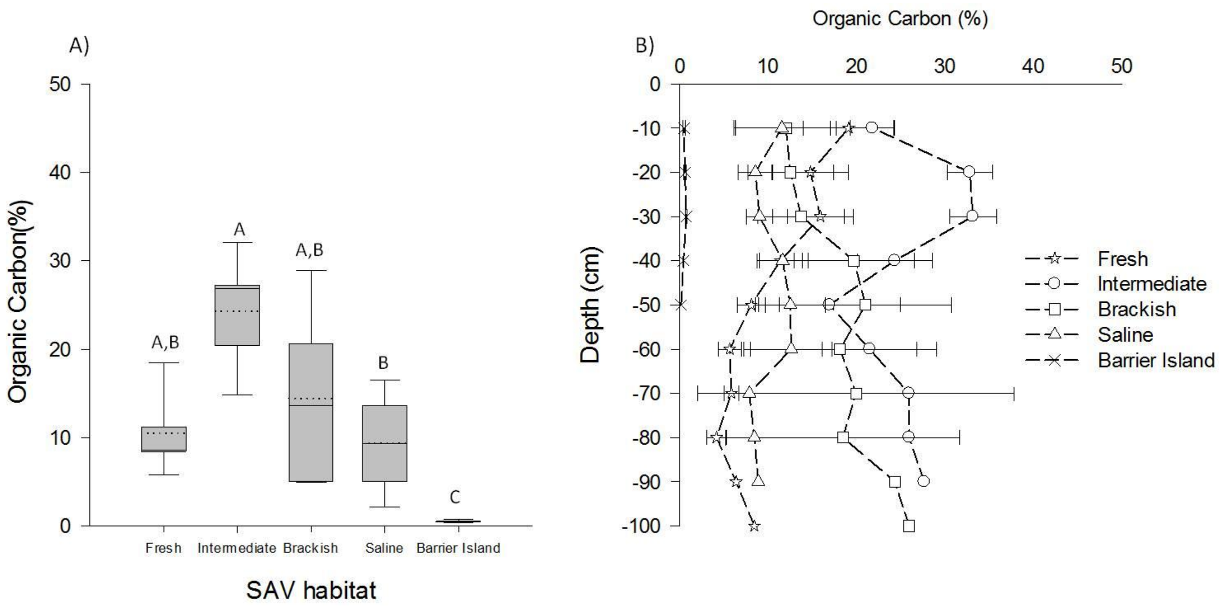

Figure 6.3. Organic carbon (means ± 1 SE) across (A) submerged aquatic vegetation (SAV) habitats. Different letters indicate statistical differences. The dotted lines indicate mean values, with solid lines representing median values. Down core profiles of organic carbon (mean ± 1 SE) (B). SAV habitat is defined by marsh zones determined by long-term salinity (Visser et al. 2013) as fresh, intermediate, brackish and saline interior deltaic habitat, and saline barrier island habitat.

Organic carbon content

<u>Vegetation.-</u> CC_{SAV} ranged from 0.004 to 3.41 Mg C ha^{-1} and was significantly different across SAV habitat classifications ($F_{4, 20}$ = 5.02, p=0.0058). Barrier island CC_{SAV} was significantly greater than brackish CC_{SAV}, but neither barrier island nor brackish CC_{SAV} differed statistically from fresh, intermediate or saline CC_{SAV}.

<u>Soils.-</u> CC_{SED} differed significantly by SAV habitat ($F_{4,20}$ = 13.76, p<0.0001), with barrier island SAV soils storing significantly less carbon compared to all other SAV habitats, which did not differ from one another (Figure 4). This pattern held true regardless of core length (i.e., 10, 50, 100 cm) used for storage calculations, although absolute storage values calculated varied based on core lengths used (Figure 6.4). There was no significant relationship between the percent cover of living plant biomass (or CC_{SAV}) and CC_{SED} (Figure 6.5).

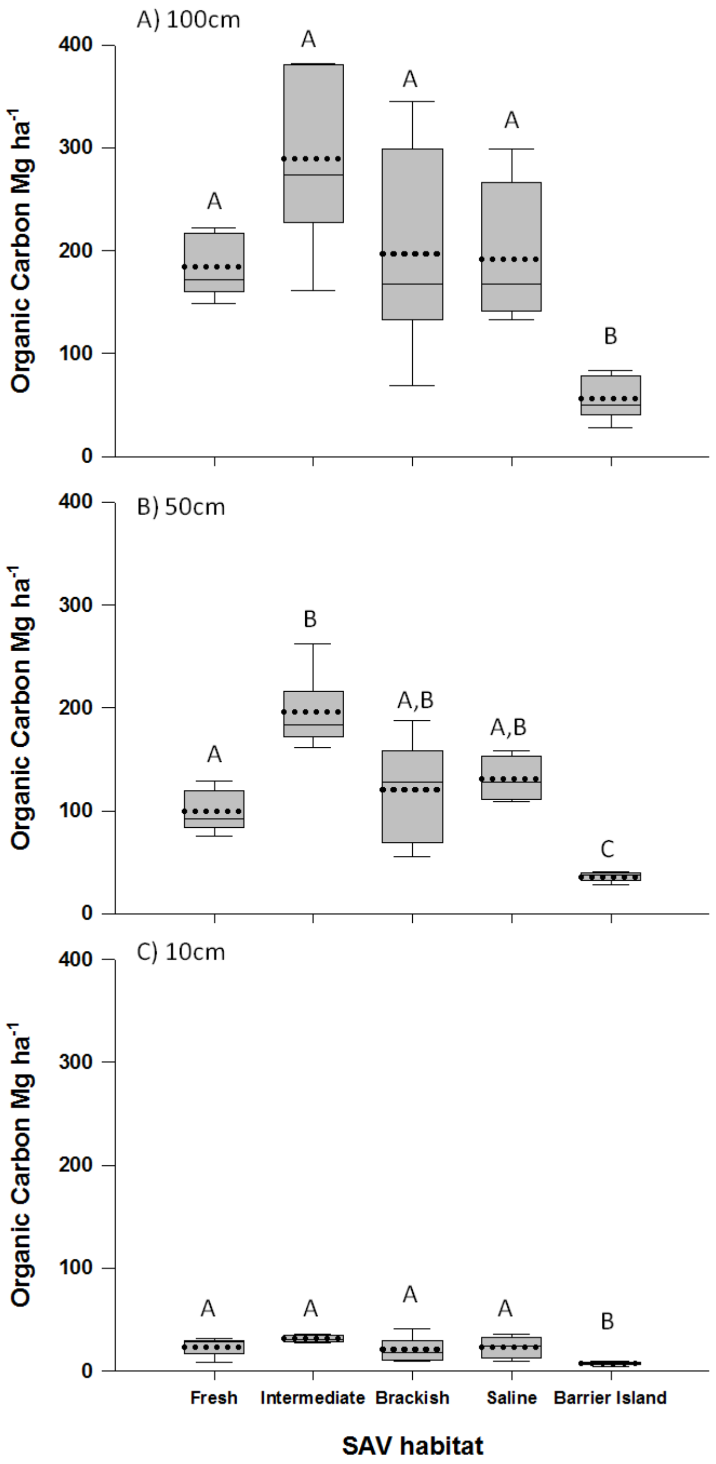

Figure 6.4. Box plots of organic carbon stock (Mg C ha^{-1}) in top 100 cm (A) of soil, top 50 cm (B) of soil and top 10 cm (C) of soil. Different letters indicate differences in means across habitats. Dotted lines indicate mean values. Black lines indicate median values

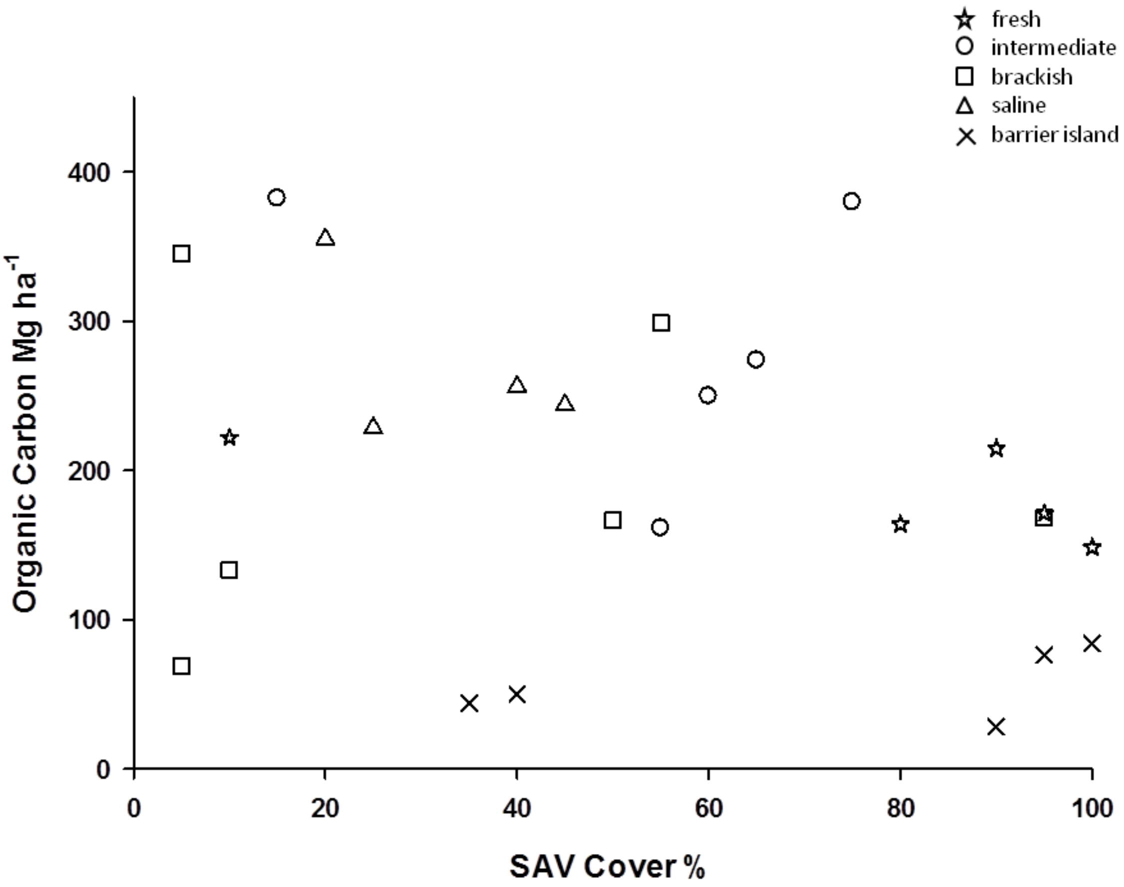

Figure 6.5. Relationship between submerged aquatic vegetation (SAV) cover and soil organic carbon stock across sites in SAV habitat areas. Fresh = ☆, Intermediate = O, Brackish = □, Saline = Δ, Barrier Island = X.

Explanatory variables

The first two axes of the CCA explain 81.1 % of the environmental variation in CC_{SED} among SAV habitat types. Axis one, which explains 53.0 % of the variation, largely differentiates between high salinity and mineral sites from lower salinity and highly organic sites ($F_{4, 20}$ =6.030, p=0.002; Figure 6.6). Specifically, salinity and BD were correlated and positively associated with CC_{SED} of barrier island SAV sites, while intermediate and most brackish and saline sites were highly associated with C_{org}. Axis two, which explains 28.7 % of the variation, differentiates between fresh and intermediate sites. Fresh SAV habitat sites were not strongly associated with C_{org}, or any other environmental factor tested in this study.

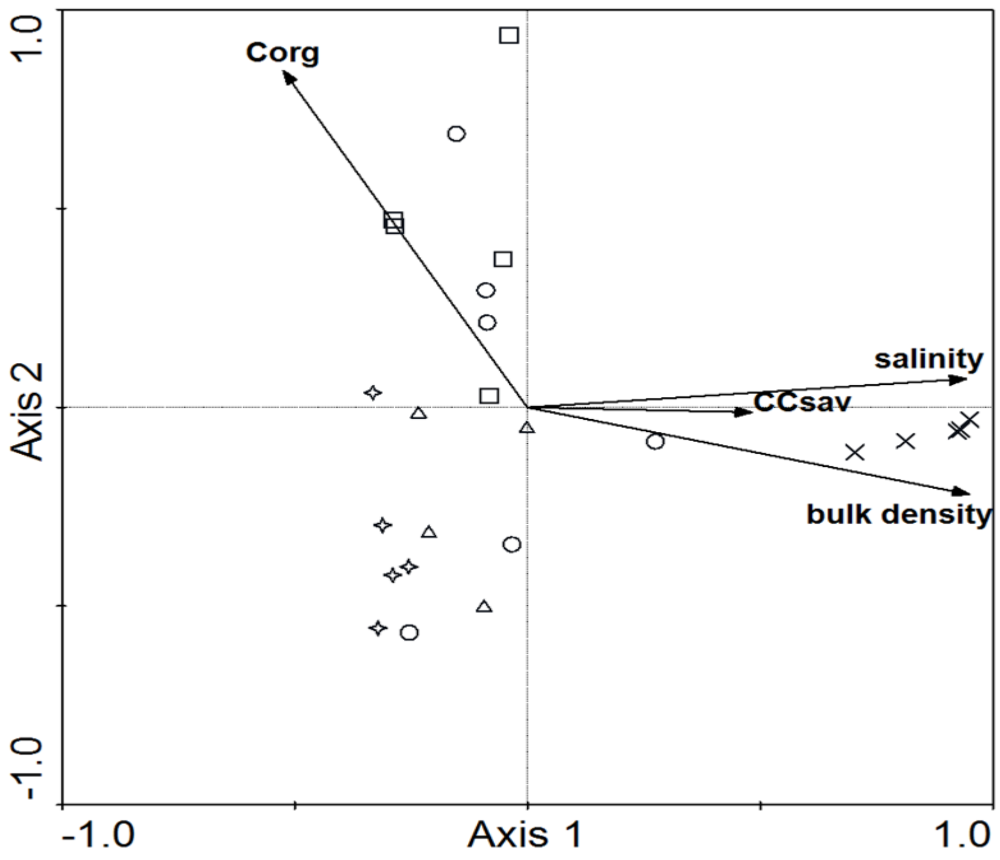

Figure 6.6. Canonical correlation analysis (CCA) biplot of soil properties, biomass carbon and water column characteristics (factors) against submerged aquatic vegetation (SAV) habitat types (vectors). The soil properties included bulk density and percent organic carbon (C_{org}). The water column characteristic was discreet salinity and biomass carbon was total carbon of SAV vegetation (CC_{SAV}). Fresh habitat =✧, intermediate habitat = O, brackish habitat = □, saline habitat = Δ, barrier island habitat = X.

Discussion

Submerged aquatic vegetation habitat across the Mississippi River Delta Plain stored substantial amounts of organic carbon within their soils. Across the salinity gradient, within interior deltaic SAV habitats, organic carbon stock in the top meter of soils averaged over 200 Mg C ha^{-1}. In contrast, barrier island saline SAV habitat, located near the Chandeleur Islands, contained less organic carbon stock (56.6 ± 10.4 Mg C ha^{-1}), although all estimates were within the global range reported for seagrass (48-1,467 Mg C ha-^{1}) (Fourqurean 2012; Duarte and Chiscano 1999). The study area is largely influenced by freshwater from the Mississippi River and marine water from the Gulf of Mexico. Differences in salinity, SAV species composition and water depth did not appear to drive the differences between interior deltaic and barrier island sites in this study. Instead, soil properties and environmental setting (i.e., interior marsh versus barrier island) may be more predictive of observed organic carbon stocks (Gullström et al. 2017). Extrapolating coastal ecosystem blue carbon estimates requires better understanding of factors that control organic carbon stocks across coastal habitats. Incorporating non-seagrass SAV habitats in regional and global carbon stock estimates of estuarine environments would provide more accurate carbon stock estimates, better supporting coastal mitigation and restoration planning.

Coastal ecosystems store large amounts of carbon, but estimates of blue carbon have largely been limited to salt marsh, mangrove and seagrass habitats (Howard et al. 2017). In this study, non-seagrass SAV habitat was found to contribute substantially to blue carbon, with interior deltaic SAV habitat storing 231.63 ± 19.53 Mg C ha^{-1}, well above the global median for seagrass (139.7 Mg C ha^{-1}) (Campbell et al 2015; Fourqurean 2012). In contrast, lower storage was estimated for the barrier islands, the one location in this study where seagrass species are found (56.6 ± 10.4 Mg C ha^{-1}). Although lower than the global seagrass median, this storage is similar to that reported in seagrass meadows along the Arabian coast (49.1 ± 7.0 Mg C ha^{-1}) (Campbell et al. 2015), the U.S. north Pacific coast (64.4 Mg C ha^{-1}) (Fourqurean 2012; Kairis and Rybczyk 2010), the U.S. north Atlantic coast (48.7 Mg C ha^{-1}) (Fourqurean 2012; Orth et al.

2006), and is complementary to the broader northern Gulf of Mexico (25.7 ± 6.7 Mg ha^{-1} (top 20 cm)) (Thoroug et a. 2017). In many of these studies, these lower estimates related to high mineral soils and species composition of the specific sites examined (i.e., less robust species) (Campbell et al. 2015).

A combination of factors, including the balance between biomass production and microbial decomposition, high inputs of C_{org} (autochthonous and allochthonous), and anoxic soils, control soil characteristics and contribute to carbon storage in coastal ecosystems (Alongi et al. 2016; Duarte et al. 2013; Mcleod et al. 2011; Kennedy et al. 2010). Additionally, in estuarine environments, salinity often controls species composition, and affects plant productivity and decomposition (Staag et al. 2017; Mcleod et al. 2011; Mitsch and Gosseling 2000). In coastal marshes, studies suggest slower production and decomposition rates at fresher sites compared to more saline sites (Williams and Rosenheim 2015; Craft2007), or no effect (Craft 2007; Neubauer et al. 2005). However, recent surveys of SAV across the salinity gradient along the northern Gulf of Mexico found significantly greater standing stock of SAV in fresh compared to more saline sites (Hillmann et al. 2016; Hillmann et al. 2017), suggesting higher rates of production, which may contribute to autochthonous organic matter available for burial. This may also partially explain the difference between C_{org} in the interior deltaic sites versus the more saline barrier island sites. Similar to our findings across the interior SAV deltaic sites, past studies in coastal Louisiana marsh have failed to detect a salinity gradient effect (Baustian et al. 2017; Nyman et al. 2006; Hatton et al. 1983; Smith et al. 1983). Better understanding of production and decomposition rates in these habitats may help clarify factors that influence burial rates and lead to a better understanding and estimations of organic carbon stocks.

Allochthonous organic matter and particle trapping efficiency within interior deltaic SAV habitats may have a greater impact on soil characteristics than production and decomposition of in situ SAV biomass. Seagrass canopies attenuate wave energy, impact water currents and directly filter suspended sediments from the water column (Duarte et al. 2013; Hendriks et al. 2008; Fonseca and Cahalan 1992; Gambi et al. 1990), and the effect of seagrass canopies on water is amplified in shallow water where more of the water column is occupied by seagrass biomass (Granata et al. 2001). Further, wave attenuation subsequently prevents re-suspension of sediments (Duarte et al. 2013), impacting soil properties and leading to carbon preservation. Similar processes affect soil properties further up the estuary (Ward et al. 1984). In particular, interior deltaic SAV habitats are located within a mosaic of extensive productive marsh, and materials exported from these marshes are likely a major contributing source of organic carbon. Furthermore, these interior sites are in more protected, closed waters, as compared to the barrier island SAV habitats in this study, where C_{org} may be more easily exported to marine waters.

Differences in soil properties between the interior deltaic and barrier island sites may further elucidate differences in retention of organic carbon. Specifically, barrier island BD (1.47 ± 0.07 gdw cm^{-3}) was 5 times higher than interior deltaic BD (0.31 ± 0.02 gdw cm^{-3}). The barrier island BD values are similar to some of the seagrass sites reporting lower C_{org} and OM (Duarte et al. 2013;Krause-Jensen et al. 2012). While past studies have demonstrated increasing BD with salinity (Baustian et al. 2017; Hansen and Nestlerode 2014; Craft 2007), our study of sub-tidal SAV beds did not find differences across the interior deltaic salinity gradient, although the salinity gradient in this region was low (from 0-15), and thus impacts on production and decomposition may have been minimal.

Across SAV habitats within the MRDP, soil C_{org} followed similar trends to BD; weak differences across the salinity gradient within the interior deltaic habitats, but significant differences between interior deltaic (15.3 ± 0.7 %) and barrier island SAV habitat (0.5 ± 0.1 %). These soil property differences likely reflect to some degree the availability and source of organic matter, with barrier island SAV located adjacent to a more mineral environment, and lacking the substantial adjacent marsh production compared to the interior deltaic SAV. Adjacent to SAV beds, eroding marshes throughout the MRDP interior may be a major contributing source of organic carbon, especially considering that the C_{org} content in interior deltaic SAV soils was approximately 4 times the amount in barrier island SAV soils, despite 3 times more C_{org} stocks derived from barrier island CC_{SAV} than interior deltaic CC_{SAV}. Regardless, C_{org} bound in SAV biomass throughout the MRDP (0.02 Tg or 20 Gg of C_{org}, 1-2%) was minimal compared to soils, with carbon allocation between soil and live biomass similar to patterns observed globally in seagrasses; with live seagrass biomass accounting for only 1-5 % of the total seagrass carbon pool (Fourqurean 2012).

Among seagrasses, the largest organic carbon stocks have been found in seagrass meadows dominated by long lived, robust species along the Mediterranean, western Australian and Indo-Pacific coasts (Fourqurean 2012). For example, *Posidonea oceanica* optimizes carbon storage because of its robust growth and extensive roots (Mcleod et al. 2011). Similar findings in freshwater wetland communities support the concept that community type influences organic carbon stocks (Bernal and Mitsch 2012). The efficiency of organic carbon storage in both the interior deltaic and barrier island SAV systems in this study further support the contention that habitats dominated by small bodied species may also function to store carbon within coastal systems (Campbell et al. 2015). While this region supports year-round production of SAV (Hillmann et al. 2017), and although not explicitly examined here, the balance of C_{org} likely comes from vegetative slowing of wave energies and subsequent trapping of sediments and detritus from adjacent marsh communities due to SAV structure while in situ biomass may directly contribute less to overall carbon storage than allochthonous organic matter production from adjacent habitats, further, environmental setting may determine CC_{SED} preservation.

Environmental setting influences organic carbon stocks, and may be critical in determining long-term storage. For example, *Zostera marina* thrives in Danish estuarine bays with extensive meadows retaining autochthonous C_{org} as the environmental setting limits carbon export into marine waters (Röhr et al 2016). Similarly, within freshwater wetlands, isolated wetlands were found to store more than twice the amount of C_{org} as compared to riverine wetlands (Lavery et al. 2013). Within interior deltaic habitats in the MRDP, SAV grow in protected waters that trap and retain both SAV detritus and allochthonous organic matter from the highly productive adjacent marshes. In contrast, the barrier island SAV does not contain extensive marshes and continually shifts due to direct storm impacts, as well as the islands' transgressive movement towards the mainland (Fitzgerald et al. 2017; Penland and Suter 1988).

Higher C_{org} stock within the interior deltaic sites may reflect potentially longer residence times, higher sedimentation rates, and less frequent erosional events than the barrier island setting, which further determines whether a habitat may function as long-term storage of carbon (Rohr et al. 2016; Mitsch and Gosselink 2000; Hedges and Keil 1995). While carbon stored in MDRP marshes may be lost through marsh erosion (DeLaune and White 2012), some of this carbon may actually be retained and preserved in soils of the extensive shallow-water, and fringing submerged aquatic vegetation beds. Within the MRDP, despite substantial erosion of coastal marshes, long term carbon storage may be occurring due to retention below the fair-weather wave base (Allison et al. 2007; Corbett et al. 2006; Wright and Nittrouer 1995), and the impact on regional carbon budgets will be clarified as more complete records of sedimentation and carbon stocks are captured (Ward et al. 2017). The actual fate of marsh detritus and sediments from eroding marshes in this region, including the impacts of large storm events, could critically affect carbon stocks, long-term carbon storage (Delaune and White 2012), and regional carbon budgets.

Submerged aquatic vegetation habitat throughout the MRDP is estimated at 159,609 hectares (La Peyre et al. 2017), with approximately 25% of the habitat area, or 39,902 ha, supporting SAV at any one time suggesting a potential of 9.2 x 10^6 Mg of C_{org} or 9.2 Tg of C_{org} in the top meter of SAV habitat soils. This represents a conservative estimate, as interior deltaic SAV beds within this setting tend to be temporally and spatially heterogeneous, and C_{org} was not related directly to SAV cover during this study. SAV are sensitive to changes in the environment that affect light penetration and water quality (Dennison et al. 1993), including direct exposure to storms (Harrison 1982), and therefore exhibit 'boom or bust' growth patterns (Li et al. 2007; Trebitz et al.1993). These cycles of precipitous increase in SAV density, followed by declines occur in time and space resulting in the entire 160,000 ha SAV habitat area within the MRDP potentially storing C_{org} at the quantities captured at sites in this study. While our site selections were restricted to areas likely to support SAV, during this study, sites ranged from less than 5% to 100% cover of SAV. Ultimately, the percent cover was not related to measured C stock. Subsequently, the regional SAV soil organic carbon pool (storage) may be as high as 3.2×10^7 Mg of C_{org} or 32 Tg of C_{org}. This represents a substantial and as yet unaccounted for pool of stored blue carbon, particularly when these numbers are extrapolated across the Gulf Coast, and globally into other extensive deltaic SAV habitats.

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CHAPTER 7
CONCLUSIONS

Within the sub-tidal zone submerged aquatic vegetation (SAV) provides many critical ecosystem services and grows along salinity gradients from fresh to saline waters. Despite its importance, valuable information is lacking about SAV assemblages, biomass, standing stock and diversity, across spatial and temporal gradients, along expansive coasts such as the northern Gulf of Mexico. I surveyed potential SAV habitat along the nGoM from June to September in a 3-year study (2013-2015), across salinity zones (fresh, intermediate, brackish, saline) and geographic regions (coastal Mississippi/Alabama, Louisiana delta, Texas/Louisiana chenier plain, Texas mid-coast). Inter-annual variation was low; there was no difference in total SAV biomass across years. However, I identified 2 “SAV hotspots” within the study area; (1) more SAV biomass in the fresh salinity zone compared to all other zones, and (2) more SAV biomass standing stock in the Louisiana delta region compared to all other regions. I calculated what I believe is a first estimate of SAV biomass standing stock at the scale of the nGoM and estimated that the nGoM holds more than 118,466 tonnes of SAV standing stock at summer maximum. These are new data that provide a better understanding of the current spatial distribution and inter-annual variation of SAV which provides baseline data for managers in light of potentially shifting SAV assemblages.

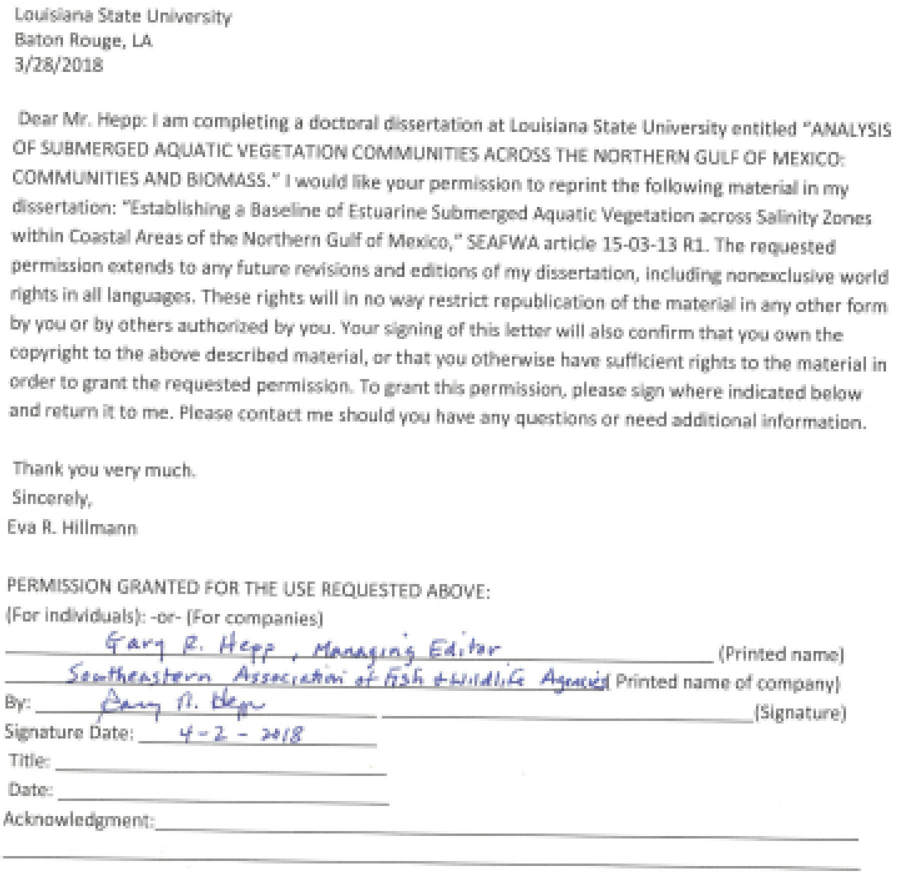
Previous studies have indicated that salinity, water depth, and water clarity are key predictors of SAV assemblages, but we lack data and understanding of what controls SAV presence and biomass throughout the year. I documented SAV assemblages, biomass and local water characteristics (salinity, water depth, photosynthetically active radiation, dissolved oxygen, water pH) bi-monthly, at sixteen sites, stratified by salinity zones in Barataria Basin, Louisiana over a 12 month period. *Ceratophylum demersum* and *Myriophylum spicatum* were the most abundant SAV species observed, however, only *Ruppia maritima* was found across the salinity gradient. Throughout the year, fresh and intermediate salinity sites contained more SAV species and biomass than brackish and saline sites. One prolonged peak of maximum SAV biomass was detected (May through July), while lowest total SAV biomass occurred in December. Temperature and turbidity were similar across all sites however salinity, water depth, and light varied temporally at individual sites, and spatially among sites, with brackish and saline sites being exposed to the greatest range of mean bimonthly values throughout the year. Predictive models based on annual sampling likely capture only a small fraction of the variability and diversity in SAV assemblages and biomass across salinity gradients along the northern Gulf of Mexico. Further, these data indicate that salinity in Barataria Basin, LA groups SAV into two assemblages (fresh/intermediate (F/I); brackish/saline (B/S)). Understanding variation is key to successful management, and more precise models enable natural resource managers to more precisely predict effects of climate change and restoration on SAV and their associated fish and wildlife.

In southeast Louisiana highly variable and saline estuarine water restricts SAV membership in assemblages to just a few species. In this region the two dominant and most common SAV species observed are *Myriophyllum spicatum* (Eurasian watermilfoil) and *Ruppia maritima L.* (widgeongrass). Growing across the estuarine gradient, these species exist across a wide range of salinity and light conditions, and their growth and presence may be impacted by both these abiotic conditions as well as competition. I planted Eurasian milfoil and widgeongrass in a greenhouse designed to test growth and competition under a range of salinity (0, 5, 10, 15, 20) and light (high: 50% ambient light; low: 20% ambient light). In monoculture, Eurasian milfoil was sensitive to salinity, decreasing in total growth rate (TGR) (salinity 0: 0.03 ± 0.003 g day^{-1}; salinity 20: 0.003 ± 0.0009 g day^{-1}), stem density (#) (0: 4.66 ±0.95; 20: 1.0 ±0.44) and stem length growth rate (SLGR) (0: 0.47 ± 0.059 cm day^{-1}; 20: 0.029 ± 0.016 cm day^{-1}) with higher salinity. In contrast, only widgeongrass stem density was sensitive to salinity (0: 41.0 ±14.05 #; 20: 6.83 ±2.38 cm day^{-1}). Light impacted Eurasian milfoil root to shoot ratio (RSR); high light resulted in higher RSR (high: 0.62 ± 0.08, low: 0.35 ±0.06) in milfoil, but did not affect widgeongrass growth. There were no significant interactions of salinity and light for either species in monoculture. I observed strong interspcific competition. Both species significantly underyielded in mixture at various combinations of salinity and light, but neither species ever overyielded., and overall production in mixture was never greater than in monocultures These results suggest that strong abiotic gradients (salinity and light) may control these species growth across the estuarine landscape. As both coastal restoration and climate change may impact salinity gradients and water clarity within coastal estuaries, these results provide critical inputs to enable natural resource managers to better plan for changes in SAV distribution.

Tidal marshes, mangroves, and seagrass capture and retain organic carbon (C_{org}) playing significant roles in the global carbon cycle. Across estuaries SAV provides similar ecosystem services as those habitats, however, their capacity for C_{org} storage has not been quantified. I estimated C_{org} stocks in SAV habitat in the Mississippi River Delta Plain (MRDP), from coastal freshwater to saline marsh (interior deltaic), out to the Chandeleur Islands (barrier island).

Interior deltaic SAV bed C_{org} stocks did not differ across the salinity gradient, but were greater than at barrier island sites (interior deltaic: 231.6 ± 19.5 Mg C_{org} ha^{-1}; barrier island: 56.6 ± 10.4 Mg C_{org} ha^{-1}). Similarly, soil C_{org} estimates for interior deltaic SAV sites (15.3 ± 0.7 %) was greater than barrier island SAV estimates (0.5 ± 0.1 %). Differences in soil properties and environmental setting likely contributed to these differences. Interior deltaic SAV soils (organic matter (OM), %: 33.9 ± 1.3; bulk density (BD), gdw cm^{-3}: 0.31 ± 0.02), were possibly impacted by in situ SAV production, and externally, by adjacent marshes. In contrast, barrier island SAV soils were more mineral (OM, %: 1.4 ± 0.1; BD, gdw cm^{-3}: 1.6 ± 0.07), and exist adjacent to shifting barrier islands. Estimates of interior deltaic SAV habitat across the MRDP (159, 609 ha) suggest that C_{org} storage is potentially greater than $3.2 * 10^7$ Mg. This represents an unaccounted for pool of blue carbon, particularly when these values are extrapolated across the Gulf Coast, and globally into other deltaic SAV habitats.

APPENDIX 1. COPYRIGHT INFORMATION



Louisiana State University
Baton Rouge, LA
3/28/2018

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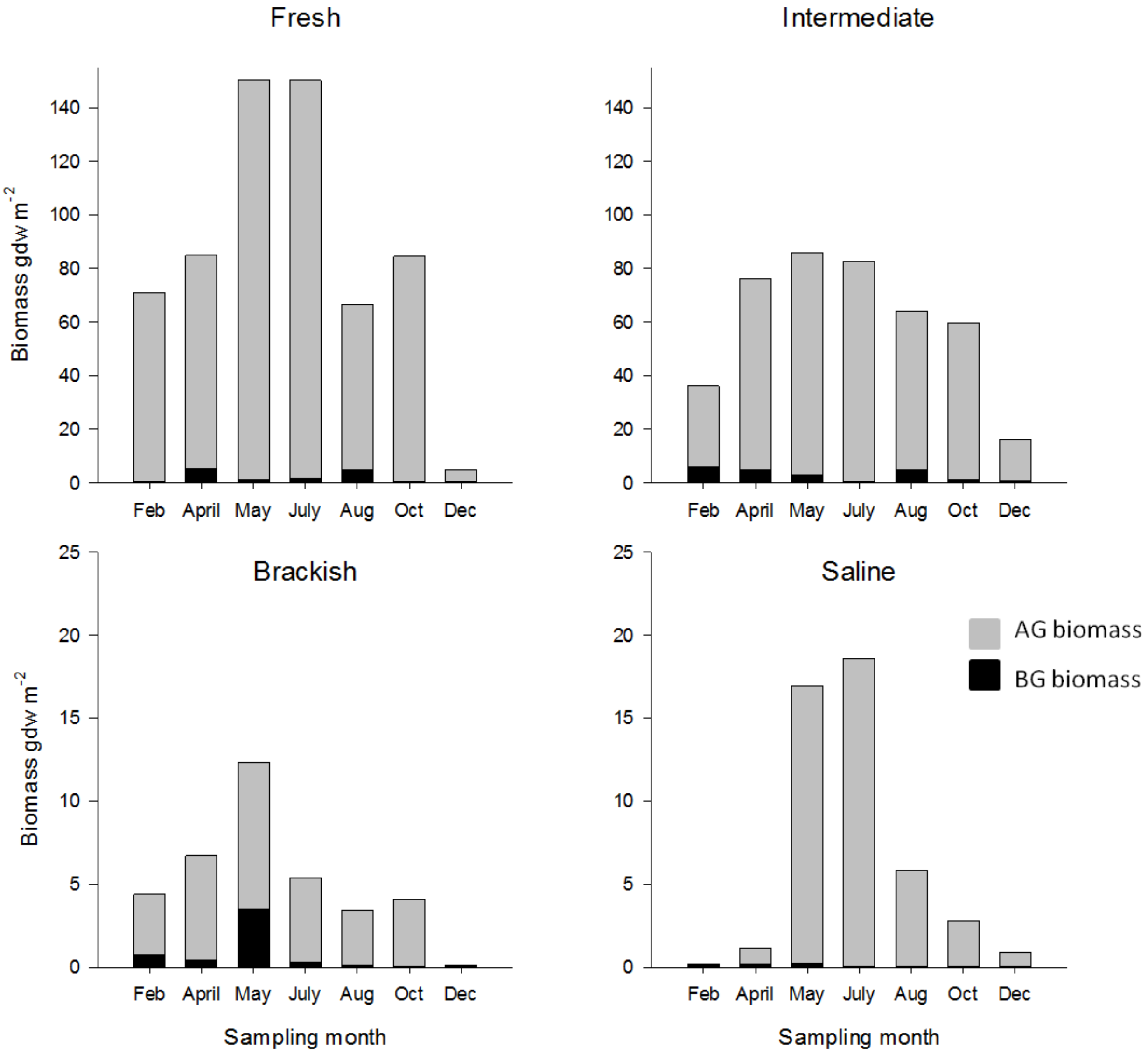
APPENDIX 2. MEAN (±SEM) OF ENVIRONMENTAL VARIABLES BY MARSH TYPE.

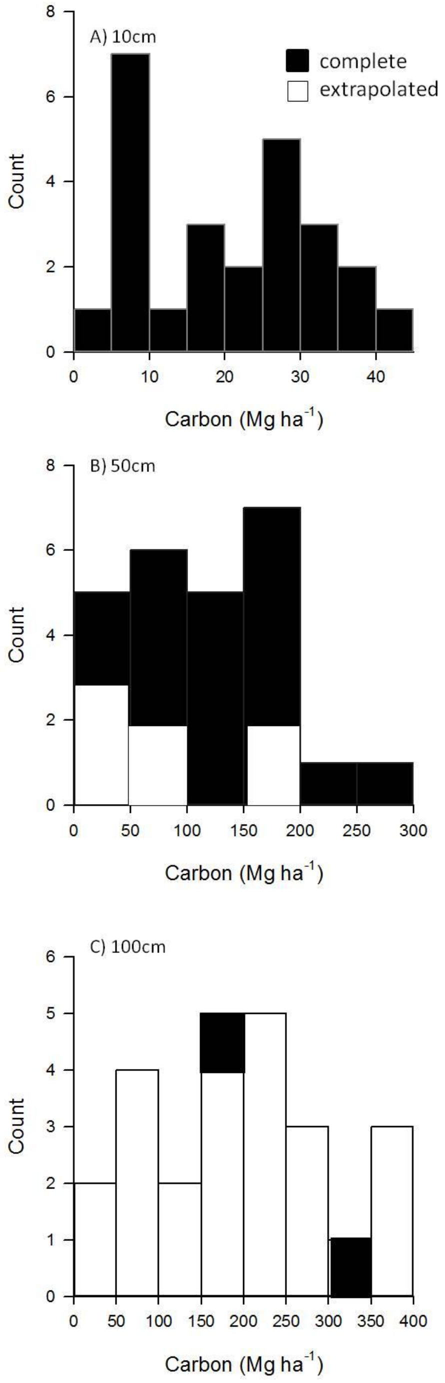
				Fresh			
	February	April	May	July	August	October	
depth	0.43±.09	0.77±.13	1.05±0.15	0.95±.30	0.87±.15	0.99±0.15	
PAR	804± 276	202±109	102±19.6	216±194	2.9±1.4	-	
turbidity	36.2±18.1	39.7±23.8	18.5±15.7	25.5±17.9	42.6±20.7	44.9±33.6	
temp	13.9 ±0.5	22.7±2.4	27.3±0.9	28.5±0.9	27.3±1.4	23.9±0.4	
DO	5.42±1.1	5.32±1.1	2.70±1.2	3.75±1.3	2.50±1.4	2.70±1.4	
pH	5.83±0.5	7.12±0.2	6.77±0.3	7.36±0.1	7.47±0.2	7.44±0.2	
				Intermediate			
salinity	0.7±0.17	0.4±0.06	0.3±0.08	0.2±0.06	0.3±0.03	1.3±0.39	
depth	0.42±0.08	0.72±0.10	0.70±0.08	0.61±0.08	0.57±0.02	0.69±0.03	
PAR	568±256	218±51.8	187±62.5	281±143	360±161	227±122	
turbidity	56.9±24.4	46.8±13.6	11.5±3.5	28.6±9.4	35.2±18.2	15.5±5.4	
temp	14.7±1.7	25.3±0.3	27.8±0.5	30.9±1.3	29.8±0.4	26.1±0.85	
DO	11.73±2.0	8.67±1.2	3.43±1.4	4.96±1.4	6.18±0.9	5.85±1.4	
pH	7.89±0.7	8.18±0.3	5.68±0.6	7.94±1.1	7.54±0.5	7.99±0.3	
				Brackish			
salinity	5.5 ±1.2	4.8 ±1.1	2.7±0.4	2.0±0.4	4.6±0.6	7.6±1.4	
depth	0.30±0.1	0.73±0.1	0.74±0.1	0.40±0.1	0.47±0.2	0.37±0.1	
PAR	418± 335	237±174	234±157	325±310	222±193	417±281	
turbidity	39.5±7.6	38.9±4.6	22.2±2.3	39.8±14.3	27.3±3.6	23.6±5.8	
temp	15.9	26.9±0.16	30.6±0.81	31.4±0.6	29.9±0.5	25.8±1.9	
DO	8.73±1.12	8.33±0.19	5.44±0.76	7.36±0.22	6.57±0.9	9.74±0.3	
pH	7.75±0.7	7.58±0.1	6.69±0.6	8.26±0.1	7.80±0.2	8.59±0.1	
				Saline			
salinity	13.8±1.3	9.6±1.3	5.7±0.4	4.5±0.58	6.7±0.84	13.3±0.93	
depth	0.28±0.04	0.56±0.11	0.42±0.04	0.50±0.07	0.51±0.03	0.32±0.04	
PAR	1414±746	609±211	663±227	325±159	534±158	1139±160	-
turbidity	25.8±4.8	28.9±4.57	22.9±2.30	34.4±4.4	23.1±4.9	33.0±8.5	
temp	20.9±0.9	27.5±0.6	30.6±1.1	31.8±0.6	29.8±0.7	25.4±0.9	
DO	8.75±0.6	6.80±0.3	5.40±0.8	6.58±0.7	4.05±0.6	8.20±0.6	
pH	7.82±0.1	7.07±0.1	7.58±0.1	7.82±0.1	6.90±0.7	8.54±0.1	

Units: depth (m), photsynthetically active radiation (PAR, µmol m^{-2} s^{-1}, turbidity (NTU), temp (temperature, ^{0}C), DO (dissolved oxygen, mgl^{-3}), pH ($^{+}$H).

APPENDIX 3. ABOVEGROUND (AG) AND BELOWGROUND (BG) BIOMASS OF SUBMERGED AQUATIC VEGETATION, BARATARIA BASIN, LA.



APPENDIX 4. FREQUENCY COUNT OF COMPLETE CORES VERSUS CORES WITH EXTRAPOLATED DATA



VITA

Eva Rebecca Hillmann was born in Bremen, Germany, in 1969. She is the daughter of Erda and Hans Hillmann. She moved to the United States with her family in 1978 and graduated from Stratford Senior High School, in Houston, Texas in 1988. After a few years, Eva attended Tulane University-University College and graduated in 1997 with a major in political science and a minor in environmental studies. In 2008, Eva entered the graduate program in biological sciences at Southeastern Louisiana University (SELU). At SELU she studied the nutrient impacts on belowground biomass of wetland plants under different hydrological regimes in an expansive greenhouse experiment, while also doing extensive field work in the Maurepas swamp. Eva graduated with a Master of Science degree in 2011. After graduation Eva was hired as a contract coastal scientist with the Lake Pontchartrain Basin Foundation (LPBF). At LPBF Eva developed a wetland tree planting and monitoring program, which to date has planted over 50,000 trees throughout the Pontchartrain basin. In 2013 Eva accepted a PhD assistantship in Dr. Megan La Pyres' lab in the School of Renewable Natural Resources, and entered the doctoral program at LSU. Since that time she has performed aquatic ecology research in shallow water habitats across the northern Gulf of Mexico, with a special focus on submerged aquatic vegetation. Eva plans to graduate in May 2018, and will continue in her position at LPBF. She is married to Daniel S. M^{c}Cabe, PLS and has three grown children, Levon, Ecko and de’Ette.