Establishing a Baseline of Estuarine Submerged Aquatic Vegetation Resources Across Salinity Zones Within Coastal Areas of the Northern Gulf of Mexico

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Abstract: Coastal ecosystems are dynamic and productive areas that are vulnerable to effects of global climate change. Despite their potentially limited spatial extent, submerged aquatic vegetation (SAV) beds function in coastal ecosystems as foundation species, and perform important ecological services. However, limited understanding of the factors controlling SAV distribution and abundance across multiple salinity zones (fresh, intermediate, brackish, and saline) in the northern Gulf of Mexico restricts the ability of models to accurately predict resource availability. We sampled 384 potential coastal SAV sites across the northern Gulf of Mexico in 2013 and 2014, and examined community and species-specific SAV distribution and biomass in relation to year, salinity, turbidity, and water depth. After two years of sampling, 14 species of SAV were documented, with three species (coontail [Ceratophyllum demersum], Eurasian watermilfoil [Myriophyllum spicatum], and widgeon grass [Ruppia maritima]) accounting for 54% of above-ground biomass collected. Salinity and water depth were dominant drivers of species assemblages but had little effect on SAV biomass. Predicted changes in salinity and water depths along the northern Gulf of Mexico coast will likely alter SAV production and species assemblages, shifting to more saline and depth-tolerant assemblages, which in turn may affect habitat and food resources for associated faunal species.

Key words: climate change, SAV, species assemblages, water depth

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 drivers of SAV biomass standing crop, production, community 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, 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 (Gutiérrez 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 zones (i.e., fresh, intermediate, brackish, saline) 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 habitat and community type (Cho and Poirrier 2005a, Carter et al. 2009). However, studies examining SAV distribution have documented high spatio-temporal variability in SAV resources 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 either 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 communities 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 resources, and community assemblage 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).

Figure 1. Map of study area from Nueces River, Texas to Mobile Bay, Alabama. A total of 384 sites, clustered in twelve subregions 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 subregion.

Sampling Design

Within the study area, we randomly selected 12 subregions using a stratified random sampling design. To achieve this, the study area was first divided into 43 subregions 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 subregions (Figure 1). We constrained our procedure to prevent the selection of adjacent subregions. This approach allowed sites to cover the range of habitats across our entire study area while ensuring the study was logistically feasible.

To create a GIS-layer for potential SAV habitat within each subregion, four spatial sublayers were developed using GIS Tools. The first two sublayers 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 sublayer 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 sublayer as potential SAV habitat. For the second sublayer, 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 sublayer 2. The third sublayer 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 sublayer 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 1011 m $^{-2}$ were deleted as they were represented as single pixels and often were not actually ponds.

We combined the final output for each of the four sublayers 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 were defined in Louisiana (Sasser et al. 2008) but were made in our project for Mississippi, Alabama, and Texas using best professional judgment. Sample sites were randomly generated, stratified by salinity zone, and replicated eight times within each salinity zone and potential SAV habitat within each subregion (i.e., 4 salinity zones x 12 subregions 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 subregions 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, Ohio), water temperature (C, YSI-85, YSI Incorporated, Ohio), and turbidity (NTU-Hach 2100Q, Hach, Colorado) were sampled from the boat before disturbing the benthic sediments. After collecting water quality data, SAV was sampled by haphazardly throwing a 0.25-x 0.25-m floating PVC quadrat three times from the boat. Within each quadrat, water depth was measured using a randomly-placed metric measuring stick perpendicular to the water’s surface 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 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 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 subregion, and subregion 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). Above-ground 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 ($F=20.67$, df = 1, 356; $P < 0.0001$) and salinity zone ($F=53.85$, df = 3, 65; $P < 0.0001$) 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 the brackish zone which was, in turn, significantly lower than the saline zone (Table 1). Temperature within and among sites differed significantly only by year, but the difference was likely not ecologically significant (0.7 C difference). Water depth differed significantly by year (F = 10.61, df = 1, 355; 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 = 3.96, df = 3, 63; P = 0.0119) with freshwater habitats being significantly deeper (0.63 m) as compared to saline, brackish, and intermediate habitats (<0.48 m).

**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). It was found at only 23% of saline sites and 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 = 23.63, df = 3, 29; P = 0.02). The saline zone had significantly lower biomass compared to the other zones in both 2013 and 2014 (Figure 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.

**Sites with SAV present.**— For sites with SAV present, there was a significant year by zone interaction (F = 3.79, df = 3, 107; P = 0.01) with 2014 freshwater sites having significantly higher biomass (mean = 157.2 g m⁻²; SE = 25.6) compared to all other single year and zone combinations (range: 38.6–83.9 g m⁻²; Figure 2). In total, 14 species of SAV were collected over the two years of sampling. Of these, 12 species of SAV were found in both 2013 and 2014 (Table 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, and lesser pondweed [Potamogeton pusillus]) were collected across all four salinity zones. Hydrilla [Hydrilla verticillata]) accounted for 73% of the above-ground biomass collected. Coontail, widgeon grass, and lesser pondweed were collected in all but saline habitat, while Eurasian watermilfoil was collected in all but fresh habitat (Table 2).

**Species-Environment Relationship**

The CCA indicated a significant relationship between SAV species and environmental variables (F = 23.83, P = 0.002; Figure 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 and 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 3).

**Table 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>2013</th>
<th></th>
<th></th>
<th></th>
<th>2014</th>
<th></th>
<th></th>
<th></th>
</tr>
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<tbody>
<tr>
<td></td>
<td>% total</td>
<td>F $±$SE</td>
<td>I $±$SE</td>
<td>B $±$SE</td>
<td>S $±$SE</td>
<td>F $±$SE</td>
<td>I $±$SE</td>
<td>B $±$SE</td>
</tr>
<tr>
<td>Widgeon grass</td>
<td>25.7</td>
<td>4.8±2.4</td>
<td>11.8±6.7</td>
<td>11.1±4.8</td>
<td>1.0±0.5</td>
<td>6.9±4.2</td>
<td>2.4±1.1</td>
<td>12.3±4.0</td>
</tr>
<tr>
<td>Hydrilla</td>
<td>18.6</td>
<td>18.0±8.3</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>41.9±12.9</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Coontail</td>
<td>16.3</td>
<td>12.1±6.4</td>
<td>0.7±0.3</td>
<td>1.2±0.6</td>
<td>&lt;0.05</td>
<td>19.9±8.7</td>
<td>5.7±2.1</td>
<td>3.3±1.5</td>
</tr>
<tr>
<td>Eurasian watermilfoil</td>
<td>12.4</td>
<td>–</td>
<td>3.7±1.5</td>
<td>6.7±2.1</td>
<td>&lt;0.05</td>
<td>–</td>
<td>7.8±2.8</td>
<td>4.7±2.0</td>
</tr>
<tr>
<td>Shoal grass</td>
<td>9.7</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>8.0±2.4</td>
<td>–</td>
<td>–</td>
<td>0.1±0.1</td>
</tr>
<tr>
<td>Lesser pondweed</td>
<td>6.0</td>
<td>9.6±5.6</td>
<td>1.4±1.3</td>
<td>0.2±0.2</td>
<td>0.8±0.7</td>
<td>4.4±2.1</td>
<td>0.5±0.3</td>
<td>0.1±0.1</td>
</tr>
<tr>
<td>Common watermilfoil</td>
<td>4.9</td>
<td>0.4±0.3</td>
<td>&lt;0.05</td>
<td>2.9±1.9</td>
<td>–</td>
<td>8.9±5.5</td>
<td>0.5±0.4</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Sag pondweed</td>
<td>3.8</td>
<td>–</td>
<td>3.2±2.3</td>
<td>&lt;0.05</td>
<td>–</td>
<td>5.5±3.4</td>
<td>1.3±1.2</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Water star grass</td>
<td>0.9</td>
<td>1.8±1.8</td>
<td>–</td>
<td>0.5±0.5</td>
<td>–</td>
<td>0.2±0.2</td>
<td>&lt;0.05</td>
<td>–</td>
</tr>
<tr>
<td>Wild celery</td>
<td>0.8</td>
<td>0.1±0.1</td>
<td>&lt;0.05</td>
<td>0.2±0.2</td>
<td>–</td>
<td>0.7±0.6</td>
<td>0.6±0.6</td>
<td>0.2±0.2</td>
</tr>
<tr>
<td>Turtle grass</td>
<td>0.6</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.6±0.6</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Star grass</td>
<td>0.1</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Carolina fanwort</td>
<td>0.1</td>
<td>0.3±0.3</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.1±0.1</td>
<td>&lt;0.05</td>
<td>–</td>
</tr>
<tr>
<td>Manatee grass</td>
<td>0.1</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.1±0.1</td>
<td>–</td>
<td>–</td>
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</tr>
</tbody>
</table>

**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 community composition 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 community characteristics are likely to be significantly impacted, altering the characteristics of SAV communities 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 communities 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, which may be influenced by specific SAV community characteristics. 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 community characteristics (i.e., biomass, density, and species assemblage) may be critical factors in assessing potential habitat and food availability, understanding primary environmental drivers of community composition 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 community assemblages will occur. Lower SAV density, production, and changed community assemblages can impact the potential carbon sequestration of sites, refuge availability for invertebrate and fish species, and food resource availability for other wildlife (Dionne and Holt 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 the community 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 communities 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, hydridella 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, hydridella 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, Carniato 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 (Fourqurean 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 Holt 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 communities are possible in response to predicted coastal changes. Similar to other coastal habitats, migration of SAV communities 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 resources 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 resource availability and distribution, and factors controlling these patterns is critical for resource managers to effectively predict and plan for changes to SAV resources across the coast and their impacts on dependent faunal species. In particular, in managing SAV resources as essential fish habitat for dependent faunal species, understanding key factors affecting the availability of specific SAV communities 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 hydridella); management can be focused to promote one species or community 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 species; 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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