Defining Aquatic Habitat Zones Across Northern Gulf of Mexico Estuarine Gradients Through Submerged Aquatic Vegetation Species Assemblage and Biomass Data

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Abstract

Submerged aquatic vegetation (SAV) creates highly productive habitats in coastal areas, providing support for many important species of fish and wildlife. Despite the importance and documented loss of SAV across fresh to marine habitats globally, we lack consistent baseline data on estuarine SAV resources, particularly in the northern Gulf of Mexico (NGOM) estuaries. To understand SAV distribution in the NGOM, SAV biomass and species identity were collected at 384 sites inter-annually (June–September; 2013–2015) from Mobile Bay, Alabama, to San Antonio Bay, Texas, USA. Coastwide, SAV distribution and biomass were consistent across years, covering an estimated 87,000 ha, and supporting approximately $16 \pm 1\%$ total cover with an average biomass of 24.5 ± 1.9 g m^{-2}. Differences in hydrology (i.e., precipitation, freshwater input, water depth) and exposure (i.e., wave and wind energy) manifested in unique SAV assemblages and biomass distributions across the region (i.e., Coastal Mississippi-Alabama, Mississippi River Coastal Wetlands, Chenier Plain, Texas Mid-Coast) and estuarine gradient (i.e., marsh zones defined as fresh, intermediate, brackish, saline). Descriptive cluster analyses identified indicator SAV species, known as medoid observations that represented combined salinity, turbidity, and depth conditions unique to different region and marsh zone combinations. While the presence of SAV is often used as an indicator of ecological health, identifying a medoid-based SAV indicator species in aquatic habitats can be used to describe estuarine conditions in more detail and develop aquatic habitat zones. Exploration and the use of this type of field data could be developed as a means to track, manage, and define aquatic habitats across regional and estuarine gradients and further develop ecosystem-based assessment and restoration activities. Identifying aquatic zones through a representative medoid associates SAV species with locations defined by both long-term salinity and salinity variability, water depth, and exposure, which is a powerful potential tool for managers and restoration decision-makers.

Keywords Estuarine gradients · Spatial and temporal patterns · Floating aquatic vegetation · Aquatic habitat · Indicator species

Introduction

Understanding how environmental factors determine species distributions remains fundamental to ecology (Hutchinson, 1957; MacArthur & Wilson, 1967; Whittaker, 1956). Relating species distribution to their environmental drivers often requires extensive field and experimental data documenting occurrence and abundance and detailed

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environmental data over long periods of time (Adams et al., 2016; Kotta et al., 2014). Recent reviews of conservation biology and ecology journals indicate a significant reduction in field data collection, which can potentially have severe impacts on our ability to effectively understand drivers for species distributions and to build predictive models to anticipate future changes (Carmel et al., 2013; Ríos-Saldaña et al., 2018). The need for these baseline data is particularly pressing in ecosystems undergoing rapid shifts in response to landscape and climate change, including estuarine systems supporting diverse assemblages of submerged aquatic vegetation (SAV) and emergent vegetation across environmental gradients (Jankowski et al., 2017; Osland et al., 2016; Watson et al., 2017).

Within estuaries, SAV provides critical habitat for many fish and wildlife species (Heck Jr. et al., 2003) and serves as an indicator of water quality (Li et al., 2007; Schneider et al., 2016). SAV exists across estuarine salinity gradients, providing beneficial habitat across a wide range of conditions. When present, SAV occupies habitats that exchange energy between the land and the ocean and are inextricably linked to changes in the abiotic environment as hydrologic parameters, including salinity, nutrients, and water clarity, are altered (Short & Neckles, 1999; Koch, 2001; Madsen et al., 2001; Jennerjahn, 2012) and can function as ecological indicators of both terrestrial and aquatic health. SAV also provides numerous physical, chemical, and ecological services including increasing accretion of sediment, minimizing erosion, and buffering wave energy (Gracia et al., 2017; Västilä & Järvelä, 2017), aiding in nutrient cycling (Juston et al., 2013; Yan et al., 2016), and providing food and habitat for important species (Brasher et al., 2012; Hitch et al., 2011; La Peyre & Gordon, 2012; Pujol et al., 2012). SAV habitats can also mitigate some of the effects of sea-level rise in the upper coastal zone (Anderson et al., 2014; Sheets et al., 2012). As land becomes submerged and shallow water areas in estuaries increase in size and extent in response to sea-level rise, aquatic habitats with SAV present may expand and will provide benefits to wildlife and the remaining wetlands (Cho & Porrier, 2005).

Although SAV is assumed to be widely distributed in NGOM estuaries, data describing the spatial extent, trends, and status across coastal estuaries are largely exclusive to marine areas and solely describe seagrass species (Handley et al., 2007) while trends across the estuarine gradient, particularly descriptions of low salinity SAV species, remain poorly documented (Merino et al., 2005; Merino et al., 2009; Hillmann et al., 2016, 2019; DeMarco et al., 2018). Having long-term data on trends is important as shifts in SAV occurrence and abundance can be rapid, related to inter-annual or seasonal variation (Cho & May, 2008; Lirman et al., 2008; Patrick & Weller, 2015), or long term, indicative of regime shifts and alternative ecological states in water bodies (Hilt et al., 2011; McCann, 2016; Rossi et al., 2016). As SAV is

responsive to changing water quality conditions, species presence and assemblages have been used as indicators of environmental conditions, relying on extensive field data to support trend analyses and model development (Berglund et al., 2002; Findlay et al., 2014; Moorman et al., 2017; Schneider et al., 2016; Topuzović et al., 2016). For example, observed SAV declines in the Chesapeake Bay region (Kemp et al., 2004; Orth and Moore 1983) resulted in significant field research efforts and drove the creation of models to predict trends in SAV biomass (Orth et al., 2017). Similar declines in SAV have been observed in other regions, but data tend to be locally specific and temporally limited resulting in geographic biases in understanding drivers (i.e., Adair et al., 1994; Estes et al., 2015; Handley et al., 2007; Poirrier et al., 2009).

The northern Gulf of Mexico (NGOM) spans ecologically distinctive climatic gradients that greatly influence the structure and function of estuarine wetlands and SAV ecosystems (Merino et al., 2005; Carter et al., 2009; Handley et al., 2007). These NGOM estuaries have unique hydrology, geology, and climate regimes, resulting in diverse ecological regions, or ecoregions, across the landscape (Omernik & Griffith, 2014; USEPA, 2013). Macroclimatic drivers such as temperature and precipitation regimes vary significantly from east to west across the NGOM landscape, often functioning as threshold conditions for many species, and as such create distinctive wetland plant community structure across the region (Gabler et al., 2017; Osland et al., 2016). Moreover, in estuaries with significant freshwater inflow (i.e., large rivers), many *within* estuarine gradients are evident. Often, these NGOM coastal habitats are classified for research and management purposes (Wilson et al., 2002) as fresh, intermediate, brackish, and saline marsh zones based on emergent wetland communities, and these broad salinity characterizations serve as a proxy for a wide range of estuarine gradients (Enwright et al., 2014; Sasser et al., 2014). While these estuarine gradients are often defined by salinity alone, other conditions, including but not limited to turbidity, inundation frequency, water column depth, physical water movement/currents/waves, and temperature, have potentially significant and variable influences on aquatic and emergent plant species. This range of environmental conditions across and within estuaries creates significant spatial and temporal estuarine gradients in NGOM aquatic habitats (Das et al., 2012; Moyle et al., 2010; Seers & Shears, 2015).

Although the same suite of conditions will determine the distribution and composition of aquatic communities across NGOM estuaries and in turn impact trophic structures and interactions (Cloern et al., 2017), submergent (i.e., SAV) and emergent (i.e., emergent plants) communities may differ in response to changing regimes. Aquatic communities in general and SAV specifically are known to respond rapidly to short-term changes in environmental conditions (Kinney

et al., 2014) meaning that methods typically used to classify emergent wetland communities (i.e., fresh, intermediate, brackish, and saline marsh zones), may not represent SAV presence, biomass, or assemblages accurately. For example, many species of SAV are cosmopolitan and highly effective dispersers, spreading both by seed and vegetatively, and can establish or decline with equal rapidity as environmental conditions change. Exposure to waves and currents, water clarity/light availability, sediment type, human activities, seasonality, and the variability of these factors have been identified as significant drivers of SAV occurrence and abundance across estuaries (Cho & Biber, 2016: Findlay et al., 2014; Koch, 2001; Martin & Valentine, 2012). The strength of these drivers manifest as unique patterns and gradients across the NGOM coastal landscape (i.e., Osland et al., 2016) and create distinct submergent and emergent communities. SAV assemblages and biomass may be descriptive of the aquatic estuarine conditions across and within ecoregions as a reflection of the dominant hydrologic patterns including their means and variability over time.

Despite extensive research on the role and importance of SAV, datasets identifying consistent environmental predictors to describe SAV distributions across spatial and temporal gradients are not widely available across the NGOM region, particularly in interior shallow water marsh areas (but see, Handley, 1995; Merino et al., 2009; Carter et al., 2009; Cho & Porrier, 2005). Field studies describing SAV distributions have been developed by wildlife managers for almost 100 years in attempts to quantify SAV habitat value (Chabreck, 1970; Joanen & Glasgow, 1965; Penfound & Hathaway, 1938), but regional variation in survey methods makes these estimates difficult to extrapolate coast-wide. More recent efforts to collect SAV occurrence data via remote sensing and aerial imagery have been met with variable success in the turbid and shallow estuaries of the NGOM (Carter et al., 2011; DeMarco et al., 2018; Vis et al., 2003; Watanabe et al., 2013). Consequently, there are no landscape-scale (e.g., comparable) estimates of SAV distribution across ecoregions and estuarine gradients, nor are there recent data on the relative abundance, extent, and variation of SAV across spatial and temporal gradients in the NGOM, although seagrass specific data are well represented (Handley et al., 2007; Handley & Lockwood, 2020).

Consistent field data describing SAV across the diverse coastal and estuarine landscapes in the NGOM and beyond could significantly improve management activities and provide significant insight into ecological implications of both terrestrial and aquatic habitat change. For example, estimates of SAV cover, biomass, and species assemblages are essential to developing habitat management plans for many waterfowl species (Brasher et al., 2012; Wilson et al., 2002), and the lack of data availability and analyses has limited management actions. Similarly, estimates of

SAV are needed by coastal managers to assess the response of fish and wildlife (via habitat suitability modeling or similar methods) to coastal restoration projects (CPRA, 2017) and/or development in estuarine habitats. SAV resources are typically quantified and categorized according to (fresh, intermediate, brackish, and saline) emergent marsh zone classifications, and associated habitat quality (cover, biomass, and species assemblages) are largely assumed. While necessary given the lack of data available, this method may be insufficient to develop meaningful estimates of SAV resources and to further extrapolate those estimates into future conditions given the differential response of submergent and emergent plants to environmental drivers.

Beyond the application of SAV data in quantifying wildlife habitat quality, understanding the ecological role of SAV across the diverse NGOM coastal landscape is essential to adequately assess the impacts of human activities and changing physical and environmental conditions on ecological functions and services. Specifically, the consequences of alterations in salinity, morphology, water quality, physical activity, depth, and temperature may be significant across aquatic ecosystems. Efforts to model the impacts of restoration projects and future landscape conditions have been hindered by the lack of sufficient SAV data, particularly in interior areas. In many cases, SAV acts as an ecological engineer, and the addition or removal of SAV can in turn have autochthonous and allochthonous cascading impacts on food web dynamics, structural habitat, and water quality conditions (Cronk and Fennessy, 2001). Understanding the spatial diversity of SAV distribution across the NGOM is necessary to assess the diverse ecological benefits provided therein, and further, to understand how these benefits may be impacted as the result of landscape change.

In this study, we investigated the distribution of SAV presence, percent cover, aboveground biomass, and species assemblages across the NGOM over a 3-year period. Further, we sought to identify meaningful and distinctive spatial (region and marsh zone) and temporal patterns in SAV abundance and assemblages and determine if those patterns may have applications in SAV as an ecological indicator to provide critical information to coastal restoration and management planning in aquatic habitats.

Methods

Study Area

The study area included shallow aquatic habitats located within the estuaries and fresh to saline coastal marshes of the NGOM landscape from Mobile Bay, Alabama, to Nueces River, Texas (Fig. 1).

Fig. 1 Map of the study area in the northern Gulf of Mexico (USA) showing study sites and regional boundaries. Regional boundaries were defined using the Gulf Coast Joint Venture Habitat Initiative Areas across the NGOM (Wilson et al., 2002), which were based on Omernik Level III Ecoregions (Omernik & Griffith, 2014; US EPA, 2013) and modified to include only the coastal marshes and plains. A total of 384 study sites were sampled in the summers of 2013, 2014, and 2015
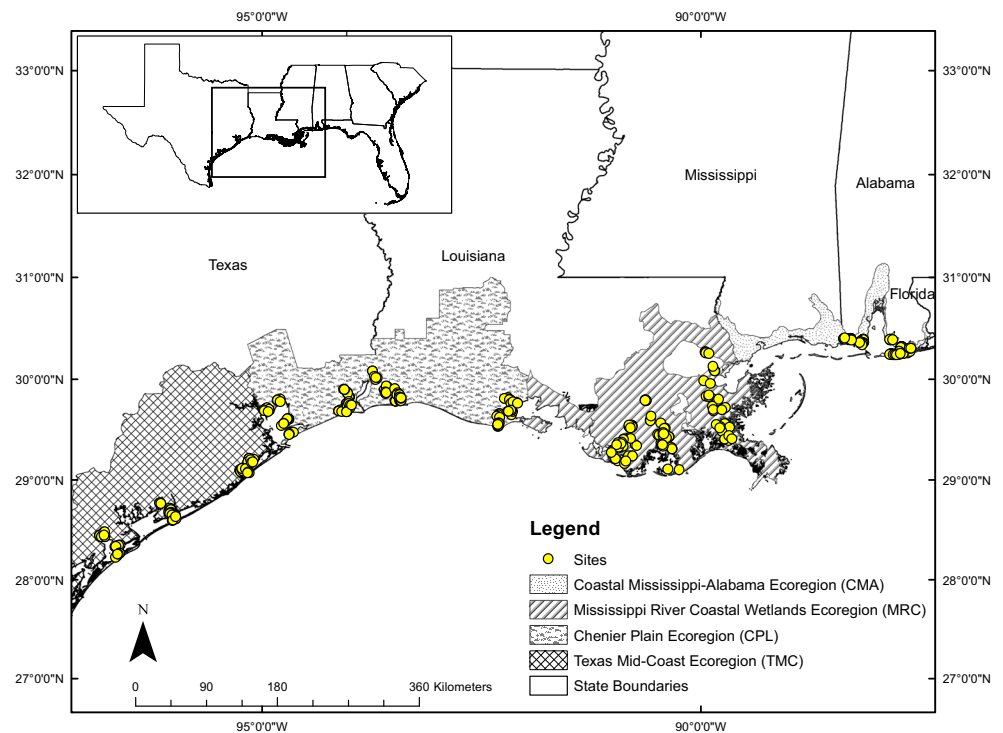
Regions

Regional boundaries were defined using the Gulf Coast Joint Venture Habitat Initiative Areas across the NGOM (Wilson et al., 2002). These coastal ecoregions were based on Omernik Level III Ecoregions (US EPA, 2013) and modified to include only the coastal marshes and plains. Omernik ecoregions are developed using a hierarchical spatial framework to create boundaries for ecologically similar areas based on the analysis of biotic and abiotic characteristics which are similar across landscapes and reflect differences in ecosystem structure and function (Omernik & Griffith, 2014). Characteristics used to identify ecoregions include geology, physiography, vegetation, climate, soils, land use, wildlife, and hydrology (US EPA, 2013).

The specific ecological regions (hereafter called regions) covered in this study are Coastal Mississippi-Alabama (CMA), Mississippi River Coastal Wetlands (MRC), Chenier Plain (CPL), and the Texas Mid-Coast (TMC) (ecoregions 34g, 34h, 73n, 73o, 75a, 75k in US EPA 2012). In order to focus on estuarine habitats, hypersaline and barrier island habitats more typically suited for exclusively seagrass species were not included in this study. These four regions are distinguished from one another by unique geomorphology and hydrology (Pendleton et al., 2010).

The CMA region includes both the Mobile and Grand Bay estuaries and is characterized by rivers lined with pine savannas and brackish and saline coastal marshes. Freshwater input from the Mobile and Tensaw Rivers along the eastern boundary in Alabama creates the large, shallow Mobile Bay, which is semi-enclosed by sandy barrier islands. The western side of the region in Mississippi is fed by the Pascagoula and Grand Bay rivers and, while bordered by a series of sandy barrier islands, is generally more turbid along the coast due to the influence of the Mississippi River (Peterson et al., 2007).

The MRC region contains the Mississippi River Delta which delivers large quantities of both freshwater and sediment to the Gulf of Mexico via the Mississippi and Atchafalaya rivers (Day et al., 2007). Although the main channels of these rivers are restricted from flowing into nearby tributaries and wetlands, the plume of freshwater carrying sediment is transported primarily by the wind into the nearby coastal marshes as well as into the regions to the east (CMA) and west (CPL) (Kolker et al., 2018). While the entire study area is microtidal, tidal movement in the MRC is extremely limited, as water levels are significantly influenced by the Mississippi River, and offshore winds are largely responsible for any inland movement of marine waters. The coastal landscape is characterized by widespread coastal ponds, brackish lakes, open bays, and marshes (Chabreck, 1970). Compared to other ecoregions, barrier islands are largely absent from the MRC, leaving the estuary and surrounding coastal marshes relatively exposed to winds and wind-driven waves.

The CPL region is distinguished by the presence of cheniers, or beach ridges, composed of shell and sand and formed by sediments transported by longshore currents from the Mississippi River outflow (Chabreck, 1970; Visser et al., 2000). The raised cheniers, known locally as "oak islands," support a variety of plant species characteristic of upland

habitats and are separated by lowlands and bottomland hardwoods, easing into coastal prairies, brackish lakes and ponds inland, and marshes coast-ward. The presence of the cheniers limits tidal exchange to a few small inlets (Visser et al., 2000), and freshwater input to marshes in the region is primarily due to precipitation. Barrier islands are absent from this region, and coastal marshes are highly exposed to waves, but interior areas protected by cheniers remain less exposed. The CPL region is heavily managed. Human-made water control structures, levees, and impoundments are commonly constructed to control the water level and salinity, significantly impacting hydrologic connectivity across much of the landscape (McGinnis et al., 2019).

The TMC region in the far west of the study area supports several estuaries (Guadalupe, Nueces, Matagorda, and Trinity-San Jacinto) that open into large saltwater bays (Galveston, Matagorda, and San Antonio). Freshwater input is limited both by rivers and precipitation for all of these bays and estuaries (Longley, 1994), due to drought and landscape changes impacting water use and delivery to the ocean (Powell et al., 2002). The coastal landscape is dominated by saline marshes and scrub-shrub maritime forests that border large, shallow bays that are protected by numerous sandy barrier islands. Notably, Galveston Bay is a highly industrial area, subject to barge traffic within the bay and adjacent canals/waterways and extensive development along the shorelines.

Marsh Zones

Marsh zones served as a proxy for estuarine gradient to describe salinity and hydrology patterns and are classified as fresh (F), intermediate (I), brackish (B), and saline (S). Marsh zones are defined by emergent marsh vegetation communities, which reflect long-term salinity and flooding patterns (Visser et al., 1998, Visser et al., 2013). To define these areas explicitly, field vegetation data (Chabreck, 1970; Visser et al., 2013) and remotely sensed vegetation classification analysis (Enwright et al., 2014) were used. Each of these zones contains distinct emergent plant communities that reflect unique salinity, inundation, and sedimentation regimes (Snedden & Steyer, 2013) and are consequently used to represent both the emergent wetlands and, currently, the adjacent aquatic habitats across the study area. Marsh zone designations used in analyses were assigned using the most currently available spatial data from Sasser et al. (2014) in Louisiana and Enwright et al. (2014) across the rest of the study area. Because spatial representations of marsh zone classifications are intended for emergent vegetation, they do not include the aquatic habitats marsh zones defined by Sasser et al. (2014) or Enwright et al. (2014) but were extended to the aquatic habitat based on the nearest marsh zone pixel and post-hoc habitat assessment.

SAV Sampling Area

To define potential SAV habitat across this area, a contiguous spatial mask of potential SAV habitat was created using four separate methods, outlined below. The final output combined each of the methods into a single potential SAV habitat mask.

The first method compiled, or stacked, cloud-free Landsat 5 (1984–2012) and Landsat 8 (2013–2015) satellite images (30-m pixel size) (U. S. Geological Survey (USGS) (2013a, 2013b)), resulting in a minimum of 48 and a maximum of 124 images for any given area. Landsat satellite data describe the type of cover present based on the level of solar radiation reflected, hereafter referred to as reflectance bands or bands. When combined with other criteria, band values provide detailed information on the presence of healthy vegetation in water and represent SAV presence at some point over the time of analyses. For this dataset, reflectance values from near infra-red (band 4 in Landsat 5 and band 5 in Landsat 8) and short-wave infra-red (band 5 in Landsat 5 and band 6 in Landsat 8) surface reflectance bands were analyzed to assess the previous occurrence of SAV across the landscape and include these areas as potential SAV habitat. Each of the bands produces spectral indices that quantify presence of water and greenness of vegetation – for these purposes, low values indicate water presence and high values indicate vegetation presence and health. Additional criteria using Landsat imagery indices were developed using the normalized difference vegetation index (NDVI), which uses near infra-red and red wavelengths of light that indicate the presence of vegetation (Rouse et al., 1973), and modified difference water index (mDWI) which uses near infra-red and green wavelengths indicative of water (Xu, 2005; Xu, 2006) were calculated on each image. These indices classified individual pixels as water or land categories using a simple threshold value applied to band 5 – for a particular pixel to be classified as potential SAV habitat, it had to first be identified as water. Once masks of water area in each image were created, user interpretation identified values in reflectance bands, NDVI and mNDWI that signaled vegetation was present in each image. Essentially, a pixel had to display a signal of both water and vegetation from one of these data sources in order to be included. When pixels identified as water also met the additional vegetation signals in more than 10% (a value determined by user interpretation and expert discussion) of the stacked images, the pixel was included as potential SAV habitat.

The second method used the same stacked collection of Landsat 5 and 8 remote sensing imagery however, in this case, a "stack maximum" was calculated for the bands and NDVI. The stack maximum calculation provided a single image that compiled the highest potential presence of SAV in water as determined by the above criteria. While method 1 provided a high number of images (minimizing error with high sample size), method 2 provided a single image that had a high likelihood of SAV that could be more heavily scrutinized via user interpretation. These pixels were then automatically separated

(using an unsupervised classification method) into classes based on similar spectral characteristics identified in the stacked maximum imagery and then were further user (supervised classification) separated into sites likely to support SAV based on image analysis.

The third method used the National Land Cover Dataset (Wickham et al., 2021) for the years 1992, 2001, and 2006 and the Coastal Change Analysis Program (NOAA, 2012) datasets for the years 1996, 2001, 2005, and 2006. All the areas identified as rooted vascular bed in any of these years were selected to create a vascular bed spatial layer.

The final method applied threshold values for water body size and depth in order to target habitats believed to support SAV based on previous assessments in interior areas (Chabreck, 1970; Chabreck, 1988), depth, and logistical feasibility. Deepwater habitats (>2 m), heavily traveled canals, dense emergent marsh, and water bodies greater than 1295 ha were excluded from the final SAV potential habitat mask. To calculate water body size, the same NCLD (2012) data was used to create a spatial layer of interior coastal marsh ponds. The land/water layer was generated in ArcGIS using the maximum extent of water, aquatic bed, and unconsolidated shore. Areas identified as less than 0.1 ha were excluded as they represented individual pixels and were potentially not actual ponds. To limit depth, a spatial layer of compiled coastal bathymetric data (CoNED, 2013) was developed and a threshold of 2 m applied. User interpretation manually excluded dense emergent marsh and heavily traveled canals from the final mask to make field sampling logistically reasonable and safe.

All pixels identified by any one of these four methods as potential SAV habitat were combined to create a single potential spatial SAV habitat layer. The final mask resulted in approximately 550,000 ha of aquatic habitat across the study potentially capable of supporting SAV, out of approximately 5 million ha of total aquatic habitat (Enwright et al., 2014) which included large (lakes, bays, etc.) and deep water bodies.

Sampling Design

A stratified random sampling design by ecological region and marsh zone was used. To ensure logistical feasibility and adequate coverage of the range of conditions across the study area, the potential SAV spatial mask was randomly divided into subregions oriented north-south and of equal east-west width across the study area. From within each ecoregion boundary, twelve subregions were selected, with the selection process preventing the selection of adjacent subregions and ensuring a minimum of two subregions within each of the ecoregions. Within each of the 12 subregions and 4 marsh zones, 8 sites were randomly selected for sampling (12 subregions × 4 marsh zones × 8 replicates = 384 total sites). Sites were located on both private and public lands across the coast. Although designed to be balanced, for logistical reasons (accessibility of sites and actual distribution of marsh zones across the selected subregions), the final distribution of sites was uneven within regions (Table 1).

Data Collection

Data were collected once each summer growing season (1 June–15 September) from all 384 sites, with 3 replicates at each site, and sampling was repeated annually in 2013, 2014, and 2015. Sites were accessed via boat (whaler, mud boat, or airboat) or by foot. Water samples for turbidity (NTU-Hach 2100Q, Hach, CO) were collected upon arrival at the site before disturbing benthic sediments. Salinity, temperature (°C), and dissolved oxygen (mg L^{-1}) were recorded (YSI Pro2030, YSI Incorporated, OH). Depth measurements (m) were recorded at each replicate and were reported as the mean depth for each site.

After collecting water quality data, a 0.25 m^2 quadrat was haphazardly thrown from the boat and anchored in place at each of the 3 replicates samples. If vegetation was present, either floating or submerged, percent cover was estimated and identified to species level. The cover of submerged and floating vegetation was assessed on a scale of 0–100%, with 100% representing the maximum cover of either combined SAV and floating aquatic vegetation (FAV) or either SAV or FAV occurring alone. All aboveground biomass, hereafter described solely as biomass, within the quadrats was harvested at the sediment surface, stored on ice, and transported to the laboratory at Louisiana State University Agricultural Center where it was stored at 4 °C until processing. In the lab, biomass samples were washed to remove sediment, debris, and

Table 1 Distribution of final sites sampled across regions and marsh zones

Marsh Zone	Texas Mid-Coast (TMC)	Chenier Plain (CPL)	Mississippi River Coastal Wetlands (MRC)	Coastal Mississippi Alabama (CMA)
Fresh (F)	7	13	20	6
Intermediate (I)	10	34	17	4
Brackish (B)	3	73	30	12
Saline (S)	76	8	29	42

epiphytic material. Samples were separated by species and dried at 60 °C to a constant weight, and the biomass of each species was recorded (± 0.001 g). Species biomass and presence values were reported as mean values of each of the 3 replicates for each site.

Analyses

All data analyses were performed in R (The R Core Team, 2016). Environmental variables (salinity, water depth (m), and turbidity (NTU)), SAV presence, and biomass (g m^{-2}) were examined by year (2013, 2014, 2015) for single and interactive effects by region (TMC, CPL, MRC CMA) and marsh zone (F, I, B, S). Mean ± SE are reported unless indicated otherwise. *P* values of <0.05 were considered statistically significant.

Environmental variables (salinity, temperature, turbidity, and water depth) were examined for single and interactive effects by year of region and marsh zone, using linear regression and ANOVA testing.

SAV occurrence was calculated as the percent of sites with SAV present, examined by marsh zone, region, and year. SAV presence was reported as presence or absence at each site (P/A). SAV percent occurrence was calculated as the percent of sites reporting SAV presence (%). Aboveground SAV biomass and percent cover were highly correlated (r^2 = 0.78, *p* < 0.0001; Electronic Supplemental Material Fig. S1); thus, further analyses are only presented on aboveground biomass. SAV presence and biomass were examined using a generalized linear model (logistic regression) and a linear regression model, respectively, evaluating the effects of year, marsh zone, and region. ANOVA and least squared means testing identified significant differences between groups (Russell, 2016).

Differences in SAV presence and environmental characteristics (salinity, turbidity, and depth) by regions and marsh zones were examined by using the partitioning around the medoid clustering algorithm, using the Gower distance formula (Kaufman & Rousseeuw, 1990). This technique clusters observations around a central, or medoid, observation that most closely represents a group of observations that are most similar. SAV species most representative of each region by marsh zone were identified as medoid species and functions as an indicator species of the estuarine conditions for each spatial combination. To develop the clusters, the Gower distance formula expresses the similarity and dissimilarity between observations, where the distance between observations is the sum of all standardized variable-specific distances (Gower, 1971). The partition around the medoid method assigned every observation of SAV presence to its medoid, the observation that most closely represented each cluster based on the variables of interest (region, marsh zone), hereafter referenced simply as the medoid and grouped according to explanatory variables

(salinity, turbidity, depth) based on the Gower distance matrix (Maechler et al., 2016). The optimal number of clusters was determined using the silhouette width validation metric, which aggregates how similar an observation is to its own cluster relative to its closest neighboring cluster. The highest silhouette value (−1 to 1) was used to determine the optimal number of clusters, and medoids and species assemblages within each cluster were identified. The clusters highlight the strength and patterns of groupings based on the categorical (region and marsh zone) and numerical (salinity, turbidity, and depth) variables assessed. Only the observations with presence were evaluated in the cluster analysis. SAV species representative of individual region by marsh zone assemblages (medoids) were identified for all spatial combinations.

Results

Environmental Variables

Salinity differed significantly in region by marsh zone combinations during each year tested (*p* < 0.0001 for all years, F values = 53.87 for 2013, 55.56 for 2014, and 25.27 for 2015; Table 2). Salinity was lowest in 2015 in TMC in intermediate, brackish, and saline marsh zones. Salinities in the MRC were lower in all years and all marsh zones compared to all other regions by marsh zone combinations. Overall, salinity values ranged as expected within marsh zones, increasing in mean salinity as the estuarine gradient transitioned from fresh to saline marsh zones. Mean salinities in fresh and intermediate marsh zones were typically similar, and lower than brackish marsh zones, which were in turn lower than saline marsh zones.

There was a significant interaction between region and marsh zones for water depth in all years (*p* < 0.001 for all years, F value = 10.04 for 2013, 7.53 for 2014, and 9.91 for 2015) (Table 2). This interaction was largely driven by the MRC region with the greatest depths overall, specifically in the MRC fresh marsh zone, in all years, and most notably in 2015 (0.9 ± 0.1 m).

Turbidity differed in region by marsh zone combinations for 2013 and 2014 (*p* < 0.01 for both years, F value = 8.31 for 2013 and 7.59 in 2014) but not 2015 (*p* = 0.054, F value = 6.36; Table 2). Turbidity ranged from 0 to 766 NTUs, with high values in 2013 in the intermediate (164.1 ± 58.6 NTUs) and brackish (348.0 ± 68.0 NTUs) marsh zones in the TMC region that largely drove marsh by region differences. In all regions except the CMA, turbidity generally increased from fresh to saline marsh zones and was highest in the CPL and TMC regions.

Although discrete measurements of temperature were collected, they were omitted from final analyses. The temperature ranged from 21.2 to 41.0 °C across the study area.

Table 2 Environmental parameters by year, region, marsh zone as mean (± SE), and range

Year	Salinity				Depth (m)				Turbidity (NTUs)			
	Fresh	Intermediate	Brackish	Saline	Fresh	Intermediate	Brackish	Saline	Fresh	Intermediate	Brackish	Saline
Texas Mid-Coast (TMC)												
2013	1.59 (0.91)	9.52 (2.47)	19.05 (0.35)	28.0 (0.68)	0.52 (0.06)	0.51 (0.06)	0.24 (0.08)	0.37 (0.02)	61.21 (23.55)	164.08 (58.48)	348 (68)	64.5 (7.19)
	0.3–7.0	0.4–18.6	18.7–19.4	10.2–44.6	0.31–0.70	0.27–0.81	0.16–0.31	0.05–0.75	0.162	16.8–493	282–414	7.65–288
2014	1.81 (0.03)	8.47 (1.57)	17.87 (4.88)	26.47 (0.78)	0.39 (0.06)	0.44 (0.05)	0.19 (0.11)	0.41 (0.02)	13.62 (3.01)	81.8 (13.97)	65.13 (24.29)	54.24 (3.75)
	1.7–2.0	2.9–17.5	5.1–19.9	8.9–39.0	0.13–0.57	0.26–0.17	0.24–0.62	0.17–0.98	5.1–29.9	18.4–151.0	19.3–102.2	6.77–184.0
2015	2.23 (0.23)	0.91 (0.19)	1.3 (0.1)	7.92 (0.54)	0.41 (0.11)	0.42 (0.05)	0.29 (0.04)	0.41 (0.02)	54.81 (22.07)	107.6 (27.83)	243.5 (16.5)	72.26 (10.89)
	1.2–2.9	0.3–1.8	1.2–1.4	0.3–21.5	0.0–0.79	0.23–0.69	0.25–0.33	0.1–1.01	3.53–135	19.6–292	227–260	0–500
Chenier Plain (CPL)												
2013	3.48 (1.56)	6.34 (1.02)	13.95 (0.9)	21.73 (2.51)	0.6 (0.04)	0.43 (0.04)	0.39 (0.02)	0.38 (0.05)	40.41 (7.55)	79.94 (21.45)	81.64 (9.49)	64.86 (10.67)
	0.1–17.1	0.1–21.6	0–25	4.3–25.6	0.36–0.90	0.05–0.95	0.08–0.93	0.12–0.60	2.51–81.9	0–551	8.56–419	35.4–120
2014	2.07 (1.09)	2.82 (0.5)	10.67 (0.71)	14.9 (1.91)	0.57 (0.06)	0.45 (0.03)	0.40 (0.02)	0.25 (0.03)	31.61 (4.92)	53.82 (8.06)	61.27 (4.93)	70.89 (19.21)
	0.2–13.2	0.2–13.3	0.4–24.7	6.6–26.0	0.23–0.92	0.25–0.84	0.08–0.92	0.1–0.42	6.32–61.4	6.23–183.77	14.3–254	0–184
2015	0.52 (0.12)	1.91 (0.29)	5.38 (0.64)	22.37 (1.44)	0.62 (0.06)	0.41 (0.05)	0.43 (0.03)	0.26 (0.05)	38.87 (10.43)	94.64 (14.48)	92.28 (11.55)	110.21 (24.12)
	0.1–1.4	0.1–7.4	0.2–18.1	18.1–30.2	0.24–10.8	0.1–0.02	0.1–1.43	0.12–0.47	5.39–144	7.33–358	8.6–766	0–177
Mississippi River Coastal Wetlands (MRC)												
2013	0.17 (0.01)	0.77 (0.13)	3.92 (0.54)	11.44 (0.96)	0.84 (0.08)	0.51 (0.07)	0.54 (0.03)	0.54 (0.03)	16.99 (4.18)	19.15 (4.21)	17.87 (2.34)	29.13 (2.22)
	0.1–0.3	0.1–1.7	0.1–11.2	1.4–26.7	0.15–1.4	0.08–1.1	0.19–0.9	0.28–0.85	3.06–65.1	1.67–74.8	0–57.4	12.3–58.9
2014	0.16 (0.03)	0.71 (0.1)	3.38 (0.47)	10.94 (0.77)	0.79 (0.08)	0.45 (0.05)	0.56 (0.04)	0.49 (0.03)	37.81 (9.16)	25.43 (5.36)	31.31 (2.15)	31.0 (2.15)
	0.0–0.5	0.2–1.3	0.6–8.34	0.7–15.7	0.27–1.63	0.13–0.89	0.21–1.03	0.17–0.78	4.96–198	6.9–98.6	0–157	15.2–65.1
2015	0.19 (0.02)	1.84 (0.44)	4.14 (0.53)	11.57 (0.83)	0.94 (0.09)	0.54 (0.05)	0.60 (0.03)	0.66 (0.04)	13.72 (3.53)	21.41 (3.53)	22.87 (3.51)	28.84 (2.42)
	0–0.5	0.2–6.5	0.4–9.3	1.5–19.1	0.33–1.88	0.25–0.9	0.2–0.97	0.13–1.14	1.1–55.6	4.54–57.5	3.7–71.4	5.02–51.6
Coastal Mississippi Alabama Wetlands (CMA)												
2013	5.02 (2.64)	6.27 (1.92)	13.73 (2.16)	11.74 (1.12)	0.60 (0.08)	0.71 (0.06)	0.53 (0.09)	0.70 (0.05)	57.61 (48.60)	12.30 (1.74)	10.46 (1.74)	16.82 (1.55)
	0–15.2	2.9–9.6	4.3–26.5	0.2–29.8	0.3–0.76	0.61–0.87	0–0.95	0–1.69	7.36–252	9.2–15.4	2.66–24.4	2.2–44.1
2014	5.57 (2.37)	5.67 (0.95)	12.95 (2.81)	11.33 (1.42)	0.59 (0.04)	0.54 (0.08)	0.56 (0.03)	0.48 (0.02)	14.99 (6.88)	10.62 (1.46)	10.55 (1.48)	21.12 (2.82)
	0–161	4.0–8.4	0.6–31.2	1.1–33.2	0.46–0.74	0.31–0.63	0.33–0.70	0.20–0.83	1.24–48.4	6.60–13.2	1.52–21.6	5.39–85.9
2015	6.17 (2.47)	7.32 (2.76)	13.22 (2.49)	15.83 (1.43)	0.60 (0.14)	0.82 (0.10)	0.67 (0.10)	0.59 (0.04)	8.37 (1.37)	12.34 (1.94)	9.43 (1.59)	27.91 (5.06)
	0.1–19.0	0.9–13.6	3.3–32.3	0.4–34.0	0.09–1.09	0.58–1.06	0.33–1.53	0.21–1.23	3.48–13.0	7.56–16.2	0.0–19.6	0–178

Submerged Aquatic Vegetation

SAV percent occurrence across the study area was 41 ± 2% and ranged from 38 ± 2% in 2013 to a high of 45 ± 3% in 2015 (Fig. 2, Table 2). SAV percent occurrence was different in all regions by marsh zone combinations ($p < 0.0001$) during all years. Percent occurrence was highest in the MRC-F, MRC-I, MRC-B, and lowest in the MRC-S when compared to all other region by marsh zones in all years. Percent occurrence was most variable in TMC-F, ranging from 43 ± 20% in 2013 to 100 ± 0% in 2015. In general, fresh marsh zones supported higher SAV percent occurrence than the other marsh zones in the same region, with the exception of the
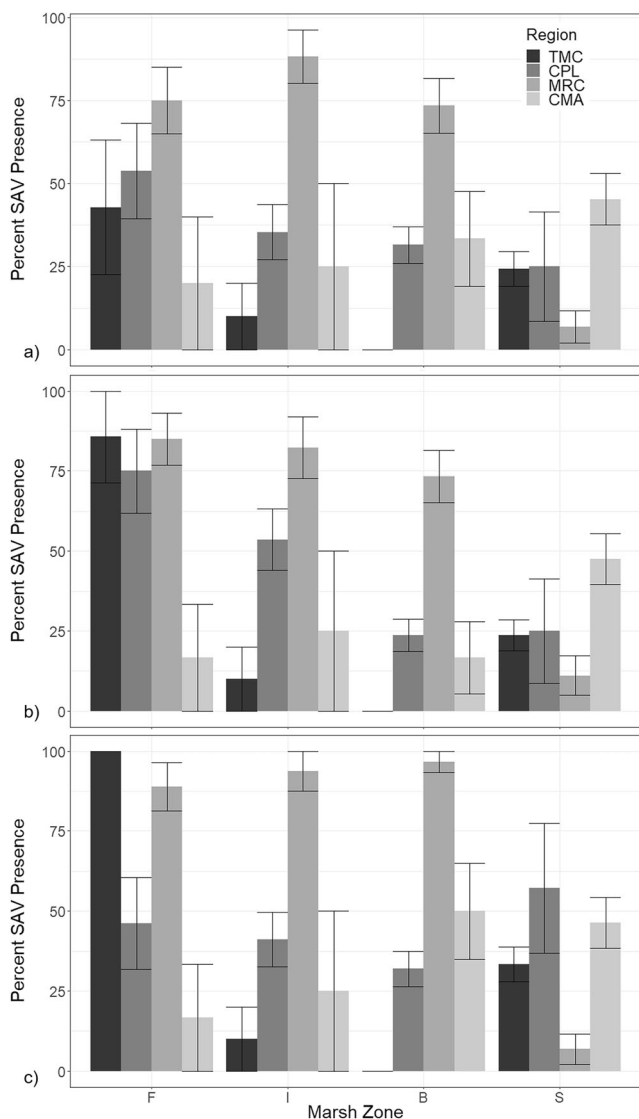
Fig. 2 Percent presence ±SE at sample sites across regions and marsh zones by year: **a** 2013, **b** 2014, and **c** 2015. *SAV*, submerged aquatic vegetation. Regions and marsh zones: *TMC*, Texas Mid-Coast; *CPL*, Chenier Plain; *MRC*, Mississippi River Coastal Wetlands; *CMA*, Coastal Mississippi-Alabama; *F*, fresh marsh zone; *I*, intermediate marsh zone; *B*, brackish marsh zone; *S*, saline marsh zone

CMA region where fresh marsh zones had the lowest percent occurrence during all years.

A total of 15 species were collected over the 3 years of sampling (Fig. 3, Table 3). *Ruppia maritima* (widgeon grass) and *Ceratophyllum demersum* (coontail) were the most widespread species and collected across all marsh zones. The species observed included several invasive species observed including *Hydrilla verticillata* and *Myriophyllum spicatum*, primarily in the MRC and CPL regions, respectively, with one observation of *Potamogeton crispus*. *Hydrilla verticillata* occurred only in the fresh marsh zone and *Halodule wrightii* (shoal grass) only in the saline marsh zone, while *M. spicatum* occurred in all marsh zones except fresh. Floating aquatic vegetation (FAV) was present primarily in fresh and intermediate marsh zones, was completely absent in saline marsh zones of all regions, and was sparse in brackish marsh zones. FAV species included *Eichhornia crassipes*, *Alternanthera philoxeroides*, *Nelumbo lutea*, *Utricularia* sp., *Lemna minor*, and *Salvinia* sp. Species composition was similar across years (all species except *Halophila engelmannii* and *Syringodium filiforme* were present all 3 years).

Coast-wide, mean SAV biomass (all species combined) was 24.5 ± 1.9 g m^{-2} (16 ± 1% cover) and ranged from 21.0 ± 3.0 g m^{-2}(16 ± 2% cover) in 2013, 27.2 3.6 ± g m^{-2} (14 ± 1% cover) in 2014, and 25.2 ± 3.2 g m^{-2} (16 ± 1% cover). Across marsh zones, SAV biomass averaged 75.9 ± 9.9 g m^{-2}, 22.9 ± 3.5 g m^{-2}, 18.1 ± 2.8 g m^{-2}, and 14.4 ± 1.9 g m^{-2} in fresh, intermediate, brackish, and saline marshes, respectively. Differences in aboveground biomass were observed between marsh zones in 2013 ($p < 0.0001$, F value = 2.39), with an interaction between region and marsh zone in 2014 ($p < 0.0001$, F value = 16.68) and 2015 ($p = 0.0013$, F value = 10.24; Fig. 3). Marsh zone differences were driven by high biomass in fresh and intermediate zones, with especially high biomass in the MRC-F, during all years. Regional differences can be explained by especially high biomass in all marsh zones of the MRC region, excluding the saline marsh zone, where there was almost no biomass (or occurrence). Over 3 years of sampling and 15 total species observed, five species, *C. demersum*, *M. spicatum*, *R. maritima*, *H. verticillata*, and *H. wrightii*, accounted for ~84% of the biomass.

Extrapolating SAV occurrence, percent cover, and biomass across the coast, these results indicate that an estimated 225,500 (± 11,000) ha of SAV habitat occurs (550,000 ha * 41 (± 2) % occurrence). Incorporating percent cover to estimate actual SAV indicates that actual SAV coverage averaged 86,000 (± 4180) ha (225,000 ha * 38% cover). This area ranged from a low of 79, 420 (± 4180) ha in 2013 to a high of 94, 050 (± 6270) ha in 2015. Using total percent cover across all sites (presence and absence) yields a similar estimate (~87,000 ha SAV; 550, 000 *16%).

Table 3 Submerged aquatic vegetation presence, cover, and biomass (± SE) across all years, marsh zones, and regions. Regions and marsh zones: TMC = Texas Mid-Coast, CPL = Chenier Plain, MRC = Mississippi River Coastal Wetlands, CMA = Coastal Mississippi-Alabama, F = Fresh marsh zone, I = Intermediate marsh zone, B = Brackish marsh zone, S = Saline marsh zone

| Year	Presence (% occurrence)					Cover (%)					Biomass (gm^{-2})				
	Fresh	Intermediate	Brackish	Saline	Total	Fresh	Intermediate	Brackish	Saline	Total	Fresh	Intermediate	Brackish	Saline	Total
Texas Mid-Coast (TMC)															
2013	42.9 (20.0)	10.0 (10.0)	0	24.3 (5.2)	24.0 (4.5)	17.1 (13.6)	0.3 (0.3)	0	17.3 (4.2)	15.0 (3.5)	14.8 (14.2)	0.4 (0.4)	0	15.6 (4.4)	13.5 (3.6)
2014	85.7 (14.3)	10.0 (10.0)	0	2307 (4.9)	2.0 (4.5)	42.7 (15.2)	4.2 (4.2)	0	10.9 (3.0)	12.1 (2.8)	73.2 (38.3)	1.0 (1.0)	0	11.1 (3.5)	14.2 (4.2)
2015	100 (0.0)	10.0 (10.0)	0	33.3 (5.5)	35.1 (4.9)	49.5 (14.1)	4.7 (4.7)	0	16.7 (3.4)	17.5 (6.1)	41.2 (17.5)	1.1 (1.1)	0	32.8 (9.9)	29.4 (8.0)
All Years	76.2 (9.5)	10.0 (5.6)	0	27.2 (5.9)	28.3 (2.7)	36.4 (17.6)	3.1 (4.2)	0	14.9 (4.0)	14.8 (3.5)	43.3 (15.0)	0.8 (0.8)	0	19.9 (7.6)	19.1 (3.3)
Chenier Plain (CPL)															
2013	53.8 (14.4)	35.3 (8.3)	31.5 (5.5)	25.0 (16.4)	34.4 (4.2)	16.3 (8.2)	9.8 (3.3)	10.0 (2.7)	2.0 (1.5)	10.1 (2.0)	31.7 (26.4)	10.4 (4.3)	22.4 (10.2)	1.3 (1.3)	18.8 (6.5)
2014	75.0 (13.1)	53.6 (9.6)	23.6 (5.0)	25.0 (20.2)	35.8 (4.4)	24.2 (10.6)	18.5 (5.3)	7.0 (2.1)	0.1 (0.1)	11.0 (4.2)	71.2 (43.6)	31.3 (9.3)	10.1 (3.6)	<0.001	20.5 (5.5)
2015	46.1 (14.4)	41.1 (8.6)	31.9 (5.5)	57.1 (20.2)	37.3 (4.3)	24.4 (10.2)	10.6 (3.8)	8.4 (2.0)	4.7 (4.5)	10.3 (3.7)	50.0 (24.7)	11.0 (6.0)	8.2 (2.4)	0.5 (0.5)	12.5 (3.4)
All Years	57.9 (8.1)	42.7 (5.1)	29.0 (3.1)	34.8 (10.1)	35.8 (2.5)	21.1 (5.4)	12.6 (4.7)	8.4 (1.3)	2.4 (1.4)	10.4 (1.2)	50.4 (18.2)	16.7 (7.6)	13.6 (7.4)	0.6 (0.5)	17.3 (3.1)
Mississippi River Coastal Wetlands (MRC)															
2013	75.0 (9.9)	88.2 (8.1)	73.3 (8.2)	6.9 (4.8)	56.3 (6.9)	52.5 (9.1)	36.0 (6.0)	26.9 (5.9)	0.8 (0.7)	25.2 (3.4)	82.5 (25.2)	27.0 (8.7)	37.5 (10.0)	0.4 (0.4)	33.8 (6.9)
2014	85.0 (8.2)	82.4 (9.5)	73.3 (8.2)	11.1 (6.2)	59.6 (5.1)	57.0 (8.2)	25.6 (6.8)	16.0 (3.9)	1.2 (1.1)	22.2 (3.2)	178.3 (31.5)	47.7 (13.6)	20.8 (7.1)	4.9 (4.9)	54.6 (10.1)
2015	88.9 (7.6)	93.8 (6.3)	96.7 (6.3)	6.9 (4.8)	66.7 (4.9)	52.8 (8.6)	24.7 (5.3)	26.9 (4.6)	1.0 (0.8)	23.5 (3.0)	120.7 (25.1)	60.8 (18.6)	39.0 (10.5)	0.7 (0.6)	46.6 (7.9)
All Years	82.8 (3.8)	88.0 (4.6)	81.1 (4.1)	8.2 (3.0)	60.8 (2.9)	52.9 (5.0)	28.8 (3.5)	23.2 (2.8)	1.0 (1.0)	23.6 (1.9)	127.4 (16.5)	44.8 (8.2)	32.5 (5.4)	1.9 (1.6)	44.9 (4.9)
Coastal Mississippi Alabama Wetlands (CMA)															
2013	20.0 (20.0)	25.0 (25.0)	33.3 (14.2)	45.2 (7.8)	39.7 (6.2)	7.0 (7.0)	8.8 (8.8)	17.1 (9.4)	16.1 (4.1)	15.2 (3.3)	4.7 (4.7)	22.6 (22.6)	10.2 (5.8)	19.2 (5.2)	15.6 (3.9)
2014	16.7 (16.7)	25.0 (25.0)	16.7 (11.2)	47.5 (8.0)	37.1 (6.2)	0.1 (0.1)	19.2 (19.2)	1.2 (0.9)	14.7 (4.1)	10.9 (3.0)	0.1 (0.1)	75.4 (75.4)	0.1 (0.1)	21.2 (7.8)	18.9 (3.0)
2015	16.7 (16.7)	25.0 (25.0)	50.0 (15.1)	46.3 (7.9)	42.9 (6.3)	1.7 (1.7)	14.2 (14.2)	22.8 (11.8)	15.5 (3.7)	16.4 (3.5)	1.0 (1.0)	10.8 (10.8)	29.7 (15.7)	8.7 (2.6)	12.2 (3.6)
All Years	17.6 (8.0)	25.0 (13.1)	33.3 (8.0)	46.3 (4.5)	40.0 (3.6)	2.7 (5.2)	14.0 (7.7)	15.5 (5.2)	15.4 (2.3)	14.2 (1.9)	1.8 (1.4)	36.3 (25.4)	13.3 (5.8)	16.5 (3.2)	15.8 (5.7)
All regions															
2013	57.8 (7.4)	44.6 (6.2)	41.9 (4.6)	26.8 (3.6)	38.3 (2.5)	29.8 (5.6)	15.1 (2.8)	14.9 (2.5)	12.9 (2.3)	16.0 (3.9)	48.6 (14.3)	13.9 (3.6)	24.6 (6.9)	12.9 (2.6)	21.1 (6.0)
2014	73.3 (6.7)	52.5 (4.4)	35.0 (3.7)	27.8 (3.7)	39.5 (2.5)	38.5 (5.9)	18.2 (3.5)	8.5 (1.7)	9.6 (1.9)	14.1 (2.7)	109.6 (21.1)	33.9 (7.7)	11.6 (2.9)	12.2 (2.9)	27.2 (7.0)
2015	68.2 (12.3)	48.5 (6.3)	50.0 (4.7)	32.9 (3.8)	44.9 (2.6)	36.6 (5.8)	13.5 (2.7)	15.0 (2.2)	12.8 (2.0)	16.4 (2.7)	71.0 (14.3)	21.9 (6.2)	18.2 (3.7)	18.7 (5.0)	25.2 (6.2)
All Years	66.4 (4.1)	48.4 (2.1)	42.3 (2.6)	29.2 (2.1)	(40.9 (1.5))	35.2 (3.3)	15.5 (1.7)	12.8 (1.3)	11.8 (1.2)	15.5 (0.8)	75.9 (9.9)	22.9 (3.5)	18.1 (2.8)	14.4 (2.1)	24.1 (1.9)
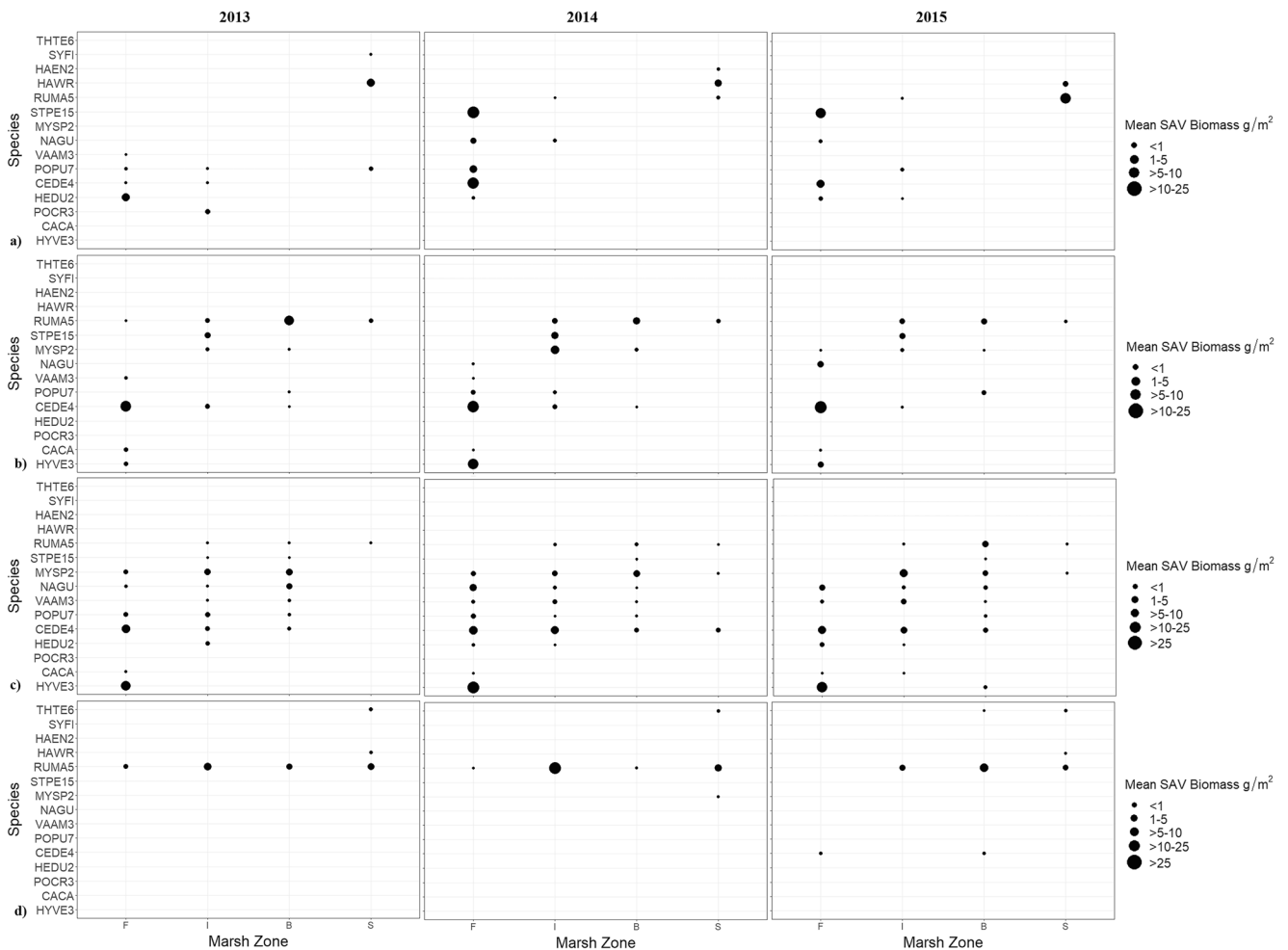
Fig. 3 Mean submerged aquatic vegetation aboveground biomass by year, region, species (y) and marsh zone (x). Regions and marsh zones: **a** *TMC*, Texas Mid-Coast; **b** *CPL*, Chenier Plain; **c** *MRC*, Mississippi River Coastal Wetlands; **d** *CMA*, Coastal Mississippi-Alabama; *F*, fresh marsh zone; *I*, intermediate marsh zone; *B*, brackish marsh zone; *S*, saline marsh zone. Species codes: HYVE3, *Hydrilla verticillata*; CACA, *Cabomba caroliniana*; POCR3, *Potamogeton crispus*;

HEDU4, *Heteranthera dubia*; CEDE4, *Ceratophyllum demersum*; POPU7, *Potamogeton pusillus*; VAAM3, *Vallisneria americana*; NAGU, *Najas guadalupensis*; MYSP2, *Myriophyllum spicatum*; STPE15, *Stuckenia pectinata*; RUMA5, *Ruppia maritima*; HAWR, *Halodule wrightii*; HAEN2, *Halophila engelmannii*; SYFI, *Syringodium filiforme*; THTE6, *Thalassia testudinum*

The final cluster analysis did not differentiate clusters by year; species composition was similar across the entire study period. The distance between clusters shows that while species assemblages differed strongly across marsh zones, regional differences further separated SAV communities (Fig. 4; Table 4). Tight clusters in the CPL region indicate more similarity in these environmental characteristics while the larger "line-like" clusters in the MRC region spread indicate more variability. Medoids showed similarity in species assemblages, and therefore environmental conditions, between saline and brackish marsh zones across all regions except in the MRC region, and stronger differences between the fresh and intermediate marsh zones across all regions. The TMC brackish marsh zone and the CMA fresh and saline marsh zones were not assigned a medoid due to a small sample size and lack of presence in the TMC and a high degree of similarity in the CMA region. The most similar species were

M. spicatum and *C. demersum*, both located in the brackish marsh zone of the MRC region. The fresh, intermediate, and brackish marsh zones of the MRC and the CPL regions were strongly dissimilar, represented by the large distance between clusters. The most dissimilar species were *H. verticillata* in the fresh marsh zone of the MRC region and *R. maritima* in the brackish marsh region of the CP region. The medoid species for brackish and saline marsh in the TMC, CPL, and CMA regions was *R. maritima* and *M. spicatum* in the MRC (Table 4). For the fresh marsh zones, *C. demersum* represented the CPL, *H. verticillata* in the MRC, and *Heteranthera dubia* in the TMC region. The intermediate marsh zone medoid species was *Potamogeton pusillus* in the TMC, *M. spicatum* in the CPL, and *Vallisneria americana* in the MRC.

Detailed results of statistical analyses and individual species biomass can be located in Electronic Supplemental

Fig. 4 Cluster analysis of species assemblages using partitioning around medoids. XY axis represents the Gower distance or dissimilarity between clusters. Regions and marsh zones: *TMC*, Texas Mid-Coast; *CPL*, Chenier Plain; *MRC*, Mississippi River Coastal Wetlands; *CMA*, Coastal Mississippi-Alabama; *F*, fresh marsh zone; *I*, intermediate marsh zone; *B*, brackish marsh zone; *S*, saline marsh zone
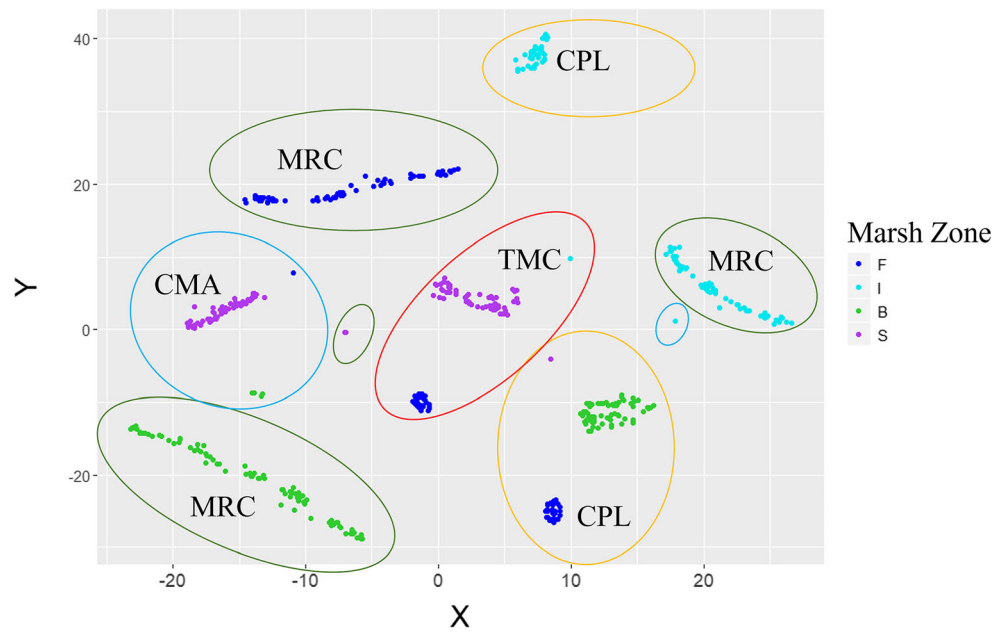
Material Table S1 and S2. Raw data for this study are publicly available in ScienceBase.gov online database (La Peyre et al., 2017).

Discussion

SAV occurrence and biomass were remarkably consistent across the NGOM coastal landscape in all estuarine areas and marsh zones over the study period. Estimates of SAV over the entire study area and time period (i.e., including absence data) show that SAV occurred at 41 (± 2) % of the sites, suggesting an estimated 225, 000 (11,000) ha of SAV habitat exists across the region (2013: 79240 ha, 2015: 94, 050 ha). Where SAV exists, sites on average supported 38 (± 1) % percent cover and 59 g m^{-2} of SAV, or approximately 86,000 (± 5500) ha of SAV, and over 5 M kg of SAV biomass, with a greater proportion occurring in fresh and intermediate

Table 4 Medoid species associated categorical and environmental data for cluster analysis

	Salinity	Depth (m)	Turbidity (NTUs)	Species
Texas Mid-Coast (TMC)				
Fresh	1.80	0.55	15.40	*Heteranthera dubia*
Intermediate	0.30	0.29	48.50	*Potamogeton pusillus*
Brackish	N/A	N/A	N/A	*N/A*
Saline	0.80	0.38	34.80	*Halodule wrightii*
Chenier Plain (CPL)				
Fresh	1.40	0.57	24.90	*Ceratophyllum demersum*
Intermediate	2.10	0.42	33.60	*Myriophyllum spicatum*
Brackish	14.40	0.33	61.40	*Ruppia maritima*
Saline	4.30	0.31	79.50	*Ruppia maritima*
Mississippi River Coastal Wetlands (MRC)				
Fresh	0.20	0.87	5.97	*Hydrilla verticillata*
Intermediate	0.20	0.46	13.70	*Vallisneria americana*
Brackish	7.10	0.60	16.70	*Myriophyllum spicatum*
Saline	1.50	0.51	43.00	*Myriophyllum spicatum*
Coastal Mississippi-Alabama (CMA)				
Fresh	N/A	N/A	N/A	*N/A*
Intermediate	N/A	N/A	N/A	*N/A*
Brackish	1.40	0.60	15.40	*Ruppia maritima*
Saline	7.70	0.50	14.20	*Ruppia maritima*

regions. According to this study, fresh to brackish SAV species rarely considered in coastal management and restoration decision-making (CPRA, 2017; Wilson et al., 2002) provide an extensive area of habitat (food and cover) and occupy a meaningful role in the estuarine ecosystems in the NGOM region. Including these habitats and SAV species in assessment, ecosystem management, and restoration could benefit coastal and estuarine managers as these habitats have been shown to dramatically impact wildlife populations and ecosystem services (Brasher et al., 2012; Castellanos & Rozas, 2001; Hansson et al., 2010; Hitch et al., 2011; Kanouse et al., 2006; La Peyre & Gordon, 2012). Specifically, incorporation of these occurrence and distribution estimates of this foundational species are necessary to consider in predictions of the possible future coastal landscape as water bodies with SAV present provide different ecological benefits (i.e., sediment stabilization, nutrient cycling, impacts to water movement) than those without, as well as provide more accurate estimates of fish and wildlife populations (food and habitat provisioning).

Meaningful differences in environmental conditions and habitat value of SAV, and therefore aquatic habitats, were not fully captured by marsh zone classifications, both between and within regions, as indicated by cluster analysis. While long-term salinity and flooding do play a fundamental role in structuring aquatic vegetation assemblages (Burgos-León et al., 2013; Lirman et al., 2008; Rodríguez-Gallego et al., 2015) and may impact SAV coverage (Chabreck, 1970), factors affecting SAV distribution across estuarine gradients appear to be divergent from those that shape emergent plant communities. Data here indicate that SAV biomass and species assemblages represent unique aquatic habitats which differ from more commonly discussed emergent marsh zones that are defined based on long-term salinity and hydrology. It is evident that strong regional differences manifest in the drivers for SAV presence, biomass, and assemblages. Our data describe a diverse aquatic landscape with distinctive and consequential assemblages and biomass of SAV that are not represented when grouped together in emergent marsh classifications. This spatial heterogeneity is significant in its ability to support a similarly diverse array of fish and wildlife species and ecological services (Gracia et al., 2017; Juston et al., 2013; Nyman & DeLaune, 1999; Yan et al., 2016).

There appear to be strong regional and marsh zone differences in aquatic habitat quality and, consequently, associated ecological benefits. Although fresh marsh zones consistently supported high SAV biomass, species assemblages and conditions suggest that these "hotspots" for biomass may not necessarily represent increased habitat value (Fig. 3). While all fresh marsh zones were generally characterized by deeper waters and lower salinity compared to other zones, these conditions were especially pronounced in the MRC. SAV percent presence was increased in fresh marsh zones compared to

saline, partly related to the ability of SAV to tolerate deeper water in the absence of salinity stress and/or turbidity (Barko et al., 1986; Bornette & Puijalon, 2011).

Further, when assessing aquatic habitats, biomass and species assemblages could be considered separately, as high biomass or cover does not necessarily indicate high-quality habitat coast-wide. Fresh marsh zones were often dominated by invasive SAV and FAV species which tend to form dense monocultures and create conditions generally not considered to be desirable species for wildlife, including *H. verticillata*, *E. crassipes*, and *Salvinia* sp. In the absence of salinity stress, the rapid growth of these species often limits light availability and prevents the growth and establishment of those generally more beneficial for wildlife, such as *V. americana*, *N. guadalupensis*, and various species of *Potamogeton* (Barko et al., 1986; Kautsky, 1988; Langeland, 1996). *Hydrilla verticillata* is uniquely suited to these conditions, as it is able to establish in deepwater and low-light conditions via vegetative cloning and rapid growth rates at low salinities (Cronk & Fennessy, 2001; Haller et al., 1974), enabling it to outcompete other SAV species for resources, particularly in the MRC-F region. Additionally, waterfowl foraging preference and success decrease with increasing water depth (Behney, 2020; Lantz et al., 2010; Osborn et al., 2017). For example, dabbling ducks decrease feeding by 10% for each 10.7 cm increase in water depth (Hagy & Kaminski, 2015), further limiting the habitat value in fresh marsh zones for wildlife.

Although the presence of invasive SAV may not directly cause the decline of higher trophic-level predators such as waterfowl (Goecker et al., 2006), reduced foraging efficiency for macroinvertebrates has been documented in extremely dense stands of *H. verticillata* and *M. spicatum* SAV beds versus beds dominated by native species (Chaplin & Valentine, 2009; Valinoti et al., 2011). Native SAV species considered valuable to waterfowl, including *Stuckenia pectinata*, *V. americana*, and *R. maritima*, often found in intermediate and brackish marsh zones, can exist in habitats with higher mean salinities or salinity pulses (i.e., high tide or storm events pushing salt water inland), lower water clarity, and greater exposure to physical disturbances than many of the invasive SAV and FAV species limited to freshwater (Borgnis & Boyer, 2016; Rodríguez-Gallego et al., 2015; Shields et al., 2012; Shields & Moore, 2016). Additionally, SAV food biomass (roots, shoots, tubers, and seeds) for waterfowl in the same study area was highest in intermediate and brackish marsh zones (DeMarco, 2018; DeMarco et al., 2016), further suggesting high-quality habitat value in these areas.

These differences in species assemblages and abundance across regions highlight meaningful differences in environmental conditions and habitat value that were not captured by the marsh zone classifications. Although marsh zones are

useful in examining broad patterns across the coastal landscape impacting emergent communities, submerged aquatic conditions within marsh zones supporting SAV could be extremely dissimilar as was indicated by the distance between clusters (Fig. 4). For example, SAV assemblages differed between MRC and TMC, potentially providing different ecological benefits and habitat resources; MRC-F was both deeper and fresher than the TMC-F, supporting different species assemblages (*H. verticillata* dominant in MRC-F and *S. pectinata* dominant in TMC-F) and biomass. Comparing the same regions, we see almost a complete absence of SAV in the MRC-S (7–11% occurrence) versus high frequency of SAV occurrence, specifically *H. wrightii* and *R. maritima*, in the TMC-S zones (45–48%). Despite being classified as the same marsh zone across the NGOM landscape, the submerged aquatic habitats are difficult to compare with respect to water quality conditions and habitat resources. The impact of these differences manifests across trophic levels as these marsh zones are not equal across regions in their ability to support assemblages of SAV species considered desirable for waterfowl and wildlife. As such, efforts to describe aquatic conditions in estuaries and understand ecological patterns are likely limited by applying emergent marsh zone classifications to describe submerged habitats.

The absence of SAV in a unique region by marsh zone combinations has wide-ranging ecological implications, particularly as researchers are increasingly being asked to provide guidance for improving habitat suitability for SAV by managers. Some potential habitats are clearly unsuitable for SAV while some areas promote extensive growth that could potentially be undesirable either due to extremely high biomass or species assemblages. These extreme situations (complete absence versus excessive growth) function as indicators in their areas – habitat suitability for wildlife declines and inferences can be made about environmental and water quality conditions. Across the NGOM, riverine inflow and the extent of protective physical features (i.e., barrier islands) may drive differences in SAV occurrence, biomass/cover, and assemblages. Most notably, each respective marsh zone within MRC differed significantly from marsh zones in other regions due to the high Mississippi River inflow and the lack of major barrier islands. All the marsh zones in the MRC region generally experience highly variable salinity, with extended low salinity periods and increased water depths (CRMS, 2020). High sediment loads are associated with high river events during spring and summer inflow periods (USGS, 2020), resulting in pulsed freshwater events carrying sediment to MRC marshes and aquatic habitats, particularly in the brackish and saline zones outside the reach of river levees. High turbidity conditions affecting water clarity may act in concert with high exposure conditions (DeMarco et al., 2018) in these zones to hinder or prevent the growth of SAV species able to tolerate these salinity regimes (Booth et al., 2000; White &

Visser, 2016). Seagrass species in particular are sensitive to water clarity and would be significantly limited in turbid saline marsh zones (Dunton, 1994; Fonseca & Bell, 1998; Hemminga & Duarte, 2000). As a result, SAV in the saline marsh zones of the MRC region is restricted to the sparse occurrence and low biomass of more salt-tolerant species (i.e., *R. maritima*, *M. spicatum*) and the absence of true seagrass species. In contrast, TMC supported the highest seagrass occurrence and biomass, likely reflecting the low riverine inflow (Montagna & Kalke, 1991; Powell et al., 2002), higher salinities, and extensive barrier islands across the region. Additional factors responsible for absence may include human activities (boat/barge/shipping traffic, development, sediment alterations) and pollution.

Identifying areas of significant SAV absence and developing a medoid-based SAV indicator species for future aquatic habitat classifications could provide a more informative approach, based on the range and variability of key environmental factors which drive SAV presence, rather than long-term means of salinity and water level, which drive emergent vegetation. Describing aquatic habitats in estuaries using a medoid species tracks more closely with the classification method often used for emergent marsh zones (i.e., Visser et al., 1998; Snedden & Steyer, 2013) wherein species' physiological tolerances describe estuarine conditions. Using this method, medoid species identified can serve as a proxy for aquatic conditions, as they represent the observation that most closely describes the variables investigated (salinity, depth, turbidity) in each region by marsh zone combination. For example, *V. americana* was identified as the medoid species for the MRC-I, while *H. verticillata* was the medoid for the MRC-F. Emergent marsh classifications in these habitats are characterized by the long-term emergent marsh zone salinity and hydrology means, but the MRC is an area known to have highly variable salinity and moving waters from the Mississippi River discharge (Holm Jr. & Sasser, 2001; Kolker et al., 2018). Past studies have found that *V. americana* is often found in areas with high salinity variability and moving, rather than stagnant, waters (Jarvis & Moore, 2008), while *H. verticillata* is more abundant in highly stable, fresh salinities in deeper waters (Barko & Smart, 1981; Kautsky, 1988). The divergent evolutionary trade-offs manifest as physiological tolerance to stress and competitive ability in these two species (Barko et al., 1986; Bornette & Puijalon, 2011; Grime, 1977; *V. americana* = stress tolerant versus *H. verticillata* = superior competitor). Specifically, differences in estuarine conditions manifest as salinity stress for aquatic plants and play important roles in structuring communities. In Louisiana's Mississippi River Delta region (i.e., MRC), planning and restoration focused on emergent habitats tends to group fresh and intermediate marsh zones together (CPRA, 2017). Our results suggest that differences in salinity variability and depth between the fresh and intermediate

habitats create significantly different ecological communities in aquatic habitats, and these SAV communities may require unique management approaches.

The interpretation of different medoid species to describe aquatic habitats should be applied against a background of environmental context and unique species physiology. For example, *R. maritima* was identified as the medoid species across both the CPL and CMA brackish and saline areas. Studies show that this commonly occurring brackish species (Merino et al., 2009) is tolerant of disturbance, can handle periodically high turbidities, and may function as a pioneer species in aquatic communities (Cho et al., 2009; Kantrud, 1991; La Peyre & Rowe, 2003). Consequently, its presence and abundance can indicate a level, frequency, or time from disturbance. It is entirely possible that this species is representative in multiple marsh zones for different reasons: in the saline marsh zones due to disturbance (storms/hurricanes/exposure; Cho & Biber, 2016) causing periodically high turbidities and in the brackish marsh zones due to salinity-based community structuring (Burgos-León et al., 2013).

Although coast-wide SAV biomass was consistent across the 3 years of the study, there is some evidence for temporal shifts in species biomass and assemblages. Such shifts may be more important than previously recognized now that long-term data on stream discharge and sea-level rise change in the Gulf of Mexico manifest and as long-term data become more available (CRMS, 2020; Sadeghi et al., 2019). More recently, from 2013 to 2015 in the TMC-S, there was a significant shift from *H. wrightii*- to *R. maritima*-dominated assemblages (Fig. 4). This area experienced high rainfall events during the spring and late summer of 2015, which decreased salinities in these habitats from 20 to 0.2 in some instances (TXWB, 2020). While this time period may not be long enough to identify a long-term regime shift from a seagrass (*H. wrightii*) habitat to one dominated by species better adapted to disturbance (*R. maritima*), these data support previous studies identifying short-term significant changes in SAV assemblages within a localized area (Cho & May, 2008) and highlight why SAV may be valuable as indicator species. Further, using cluster analyses and identification of medoid SAV species over different time periods may be an especially useful proxy for recognizing changing environmental conditions especially when conditions appear to have changed significantly at the end of our data collection.

Changes in region by zones by year support findings that SAV is more sensitive to temporal changes in macroclimatic drivers such as precipitation and temperature than emergent vegetation species. Osland et al. (2016) describe several "zones of instability" across the NGOM where coastal wetlands are especially sensitive to macroclimatic drivers that alter rainfall and temperature patterns over time. A large portion of the south and central Texas coast was identified as a rainfall-driven zone of instability where small changes in freshwater availability

(precipitation) could affect salinity regimes and result in comparatively large changes in the assemblage of wetland plants (i.e., transition from salt marsh grasses to unvegetated salt flats). Importantly, a study evaluating the effects of drought in brackish marsh zones of Texas found that SAV response was significantly greater than that of emergent plant communities, even though the severity of the drought, measured as increased salinity, was spatially uniform across the study site (Kinney et al., 2014). Small-scale, within region analyses may provide additional clarity describing spatial and temporal patterns of occurrence and abundance across estuaries.

These data taken in concert suggest SAV biomass/cover and species assemblage data provide a better indication of changing aquatic and terrestrial conditions over time, and a corresponding understanding of the strength of these drivers on SAV will better define aquatic zones used to make critical management and restoration decisions. Aquatic habitat zones that build on marsh zone classifications but identify medoid SAV species have the potential to help in the development of more precise applications of indicator species in habitat assessments when interpreted in the context of local conditions and species biology. Further, as SAV is generally more immediately responsive to changes in local conditions as compared to emergent marsh vegetation species, the use of medoid SAV species may provide valuable information on regime shifts and indicate changes in aquatic habitats within estuaries not necessarily captured in emergent marsh studies (Kinney et al., 2014).

Conclusion

Across the NGOM, shallow aquatic habitats support valuable and unique assemblages of SAV species; yet, until this study, we lacked region-wide data to define these resources. This research documented extensive SAV across the entire region and identified "SAV hotspots" supporting significant SAV biomass. SAV hotspots and overall biomass appeared to be stable across years, with significantly greater SAV biomass located within the fresh marsh zones and within the Louisiana deltaic system as compared to the other areas sampled. While the highest biomass occurred in fresh zones, species assemblages considered most valuable to fish and wildlife species occurred more frequently in intermediate, brackish, and saline marsh zones.

Regionally distinctive environmental conditions acted in combination with estuarine gradients to create unique distributions of SAV. Environmental drivers that differ locally across the NGOM coast include riverine and tidal processes, subsidence, sea-level rise, rainfall, and anthropogenic management activities (Cho & Biber, 2016; Ejankowski & Lenard, 2015; Quiros et al., 2017; Sharpe & Baldwin, 2012). The differences in range and variability of these drivers created spatially distinctive aquatic zones that, while designated

into the same marsh zone class across regions, are dissimilar in terms of their ability to support coastal SAV across regions. Because of these differences, classifying SAV assemblages by emergent marsh zone may be misleading. Specifically, because SAV responds more rapidly to environmental changes, SAV aquatic zones could be identified through a medoid species-type approach, where dominant SAV species are associated with locations defined by both long-term salinity and hydrology (i.e., marsh zones) but also salinity variability, water depth, and exposure variables (i.e., regional variables).

Anticipated changes to macroclimatic drivers will further amplify spatial and temporal changes in aquatic ecological communities (Gabler et al., 2017; Grilo et al., 2011; Osland et al., 2016). Because SAV is generally more responsive to changes in environmental conditions, the use of SAV as an indicator could be highly beneficial to restoration and management planning in estuaries. Efforts to describe and classify aquatic habitats in general and SAV assemblages in particular would be better represented by a finer classification method. The use of categorical features including marsh zone and region to distinguish environmental conditions that drive species composition and distribution may be more useful across large spatial scales than continuous variables (Cho & Biber, 2016), but the development of zones and classifiers specific to aquatic habitats and SAV into coastal planning is needed to fully capture the effects of coastal restoration activities, assess habitat value, and develop holistic coastal management plans for NGOM estuaries.

Using this new SAV data to develop and categorize distinctive aquatic zones and describe SAV niche dynamics across the NGOM could be beneficial to evaluating the impacts of changing aquatic conditions (i.e., landscape changes from development or restoration projects including river diversions) on habitats and species, in describing ecological health and primary productivity, and in understanding community and ecosystem dynamics across coastal and estuarine landscapes needed to guide restoration and management decisions. Distinguishing the factors that influence submergent versus emergent plant communities may provide a more robust understanding and assessment of aquatic ecosystems in the NGOM and across the globe. These transitional habitats are at the forefront of climate change and are highly vulnerable to a wide variety of human activities. Understanding the manner in which submergent and emergent communities function holistically may assist in developing a more balanced ecosystem approach to restoration and management activities.

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