

RESPONSES OF COASTAL WETLAND VEGETATION TO A LARGE-SCALE TIDAL RESTORATION ON
THE TEXAS UPPER COAST

A Thesis

by

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ABSTRACT

Coastal wetlands are often modified by climate- and human-driven events of various frequency, intensity, and duration. These alterations may result in substantial changes to ecosystem structure and function. For example, the closure of Rollover Pass in 2019 reduced tidal saltwater input to East Galveston Bay, thus restoring historical hydrological conditions. I studied the impacts of pass closure on the salinity and floral community composition in adjacent wetlands from 2019-2021. Some decreases to salinity occurred, but they were small in magnitude and may not lead to substantial shifts in plant communities. There were few changes in plant community composition, and those that occurred were reorganizations in the distribution and abundance of existing salt-tolerant species. The slow rate of biotic change following this large-scale restoration highlights the decadal scale needed for ecosystem restoration and is an argument for prioritizing conservation strategies in ecosystem management.

DEDICATION

*To the beautiful marshes that reminded
me why I love science in the first place.*

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CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supported by a thesis committee consisting of Drs. Anna R. Armitage [advisor], Laura J. Jurgens, and Jennifer B. Pollack of the Department of Marine Biology and Dr. Rusty A. Feagin of the Department of Ecology and Conservation Biology.

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TABLE OF CONTENTS

	Page
ABSTRACT	II
DEDICATION	III
ACKNOWLEDGEMENTS	IV
CONTRIBUTORS AND FUNDING SOURCES	VI
TABLE OF CONTENTS.....	VII
LIST OF FIGURES	VIII
INTRODUCTION	1
METHODS.....	6
RESULTS.....	9
DISCUSSION	17
CONCLUSIONS.....	26
REFERENCES	27
APPENDIX A.....	35

LIST OF FIGURES

FIGURE 1. MAP OF FIELD SITES AND THE FORMER SITE OF ROLLOVER PASS IN EAST GALVESTON BAY, TX, USA AND (INSET) LOCATION OF STUDY SITES IN RELATION TO THE GREATER GULF OF MEXICO REGION. 4

FIGURE 2. WATER COLUMN SALINITY OVER TIME AT (A) SITE 1, (B) SITE 2, (C) SITE 3, AND (D) SITE 4. MISSING POINTS REPRESENT PERIODS OF LOGGER EXPOSURE OR FAILURE. VERTICAL BARS INDICATE THE POINT AT WHICH ROLLOVER PASS WAS CLOSED IN DECEMBER 2019. IN PANEL D, DATA BEFORE 4/2020 WERE COLLECTED VIA TPWD'S LOGGER, AND THOSE AFTER 10/2020 WERE COLLECTED BY MY LOGGER..... 11

FIGURE 3. MONTHLY MEAN (\pm S.E.) AND MAXIMUM WATER COLUMN SALINITY OVER TIME AT (A) SITE 1, (B) SITE 2, (C) SITE 3, AND (D) SITE 4. S.E. IS VERY SMALL AND THUS DIFFICULT TO SEE. MONTHLY TOTAL PRECIPITATION (CM) IS SHOWN AS A BLUE 'X'. THE VERTICAL BAR ON EACH GRAPH DENOTES THE CLOSURE OF ROLLOVER PASS. 12

FIGURE 4. POREWATER SALINITY AT EACH SITE WHERE SCATTERED DOTS ARE THE INDIVIDUAL POINTS AND BARS WITH A SINGLE DOT SHOW THE MEAN AND S.E.. BAR INDICATES CLOSURE OF ROLLOVER PASS IN DECEMBER 2019. 13

FIGURE 5. NMDS PLOTS OF PLANT COMPOSITION WITHIN SITES AND ACROSS DATES AT (A) SITE 1, (B) SITE 2, (C) SITE 3, AND (D) SITE 4, * DENOTES SIGNIFICANT DIFFERENCE AMONG DATES ($P < 0.005$). 15

FIGURE 6. INTERPRETATION OF SIMPER RESULTS FOR (A) SITE 1, (B) SITE 2, (C) SITE 3, AND (D) SITE 4. EACH TABLE SHOWS THE PERCENT CONTRIBUTION TO THE DIFFERENCE BETWEEN YEARS FOR EACH SPECIES AND COLORS REPRESENT THE DIRECTION OF THE CHANGE IN PERCENT COVER (GREEN = INCREASED COVER AND RED = DECREASED COVER)..... 16

FIGURE 7. MEAN COVER (\pm S.E.) OF EACH SPECIES FOUND AT (A) SITE 1, (B) SITE 2, (C) SITE 3, AND (D) SITE 4 DURING EACH SAMPLING PERIOD. 17

INTRODUCTION

There are many types of wetlands in coastal Texas, as defined by their abiotic conditions and community composition. These wetlands can generally be divided into freshwater, brackish, or saltwater based on these dominant conditions, and each provides important ecosystem services and functions which benefit humans (Anderson 1997, Caudle 2020). Along the upper Texas coast, tidal wetlands are dominated by herbaceous vegetation, with patterns of species presence and dominance dictated by the specific abiotic and biotic conditions at the site. Many of these vegetative species make up the base of the food web for key benthic organisms and are highly adapted to the stressful areas they inhabit, often thriving in conditions inhospitable to many species, but still bound in their distribution by stressors such as salinity and inundation (Sullivan and Currin 2002, Jackson and Colmer 2005, Maricle et al. 2007). In coastal wetlands, salinity tolerance is especially important in determining the dominant vegetation type. Moving upstream, the transition from saltwater to freshwater results in brackish conditions ranging from nearly fresh to almost entirely marine, where vegetative species often exist in a delicate balance between abiotic stress tolerance and competitive ability (Pennings et al. 2005, Carus et al. 2017). In areas of lower stress (e.g., lower salinity) vegetative diversity tends to be higher due to reduced abiotic exclusion of species and thus interspecific competition is more intense (Bertness 1991, Pennings and Callaway 1992, Crain et al. 2004).

Due to existing in this balance between abiotic and biotic stress, wetland primary producer community composition can be sensitive to changes in the prevailing conditions, even though individual species are quite hardy. When conditions change, either quickly or over

longer periods, prevailing conditions can be pushed outside of species' tolerance ranges resulting in changes to the community makeup, trophic effects, and changes to the structure and function of the ecosystem (Hunter and Price 1992, Gabler et al. 2017, Moomaw et al. 2018). This can occur when species are eliminated, introduced, or simply by shifts in the dominance of individual species in any given area. Anthropogenic development, climate change, and extreme events (e.g., storms and fires) may have substantial effects on coastal wetland structure, function, and productivity via their potential impact on primary producer communities (Sklar and Browder 1998, Boorman 1999, Adam 2002). Such changes include alterations to ecosystem-defining processes such as increased erosion and sea level or either increased or decreased nutrient influx. When there are substantial changes, or those that shift conditions out of species tolerance ranges to hydrology and salinity (such as by reduced tidal influx) these shifts can drastically alter vegetation community composition, which has potential consequences for the faunal communities these ecosystems support (Day et al. 2008, Steinman et al. 2017, He and Silliman 2019). However, the time-scale of these ecosystem-type shifts can vary from months to decades based on the scale and direction of the alteration as well as the exact community makeup (He and Silliman 2019).

While hydrological changes can result from climate change and extreme events, direct human alteration is the most frequent cause of hydrological alterations resulting in changes to salinity in coastal wetlands. These alterations take many forms including jetties, seawalls, upstream dams, and shipping channels, often fundamentally altering the predominant hydrological conditions by changing volume, direction, and velocity of flow, or even completely changing the in- and out-flows, thus changing ecosystem structure and function (Ko and Day

2004). If these alterations impact limiting abiotic factors, such as salinity, they often result in stress responses which may reduce fitness, and changes to the dominant primary producer community if conditions become unbearable. This occurs due to upsetting the balance between interspecific competition and species' abiotic stress tolerance where many estuarine species exist between their competitive ability and stress tolerance, thus impacting community composition and diversity (Liancourt et al. 2005a, Maestre et al. 2009). Such changes to primary producer communities can then have cascading impacts on trophic structure and overall ecosystem structure and function.

One example of human alteration is the construction and later removal of Rollover Pass, located in the southwestern end of the Chenier Plain on Bolivar Peninsula, TX, USA (Figure 1) (Gosselink et al. 1979, Beccasio et al. 1982). Rollover Pass was constructed in 1954 by the United States Army Corps of Engineers (USACOE) and the Texas Game and Fish Commission (now the Texas Parks and Wildlife Department (TPWD)) in an effort to improve water quality in East Galveston Bay and increase recreational fishing opportunities (Prather and Sorensen 1972, Bales and Holley 1988). Before the opening of Rollover Pass, East Galveston Bay was relatively isolated from tidal influx with the closest natural connection to the Gulf of Mexico ~34 km SW, between Galveston Island and the western tip of Bolivar Peninsula at Bolivar Roads and further restricted by the Texas city dike (constructed 1915) and Hanna reef (Figure 1) (Reid et al. 1956, Taylor 2007). This tidal isolation means that historically, the wetlands surrounding East Galveston Bay were dominated by freshwater and brackish species (Singleton 1951, Bales and Holley 1988, White 1992, White et al. 1993). In addition to the area's tidal isolation, East Galveston Bay receives most of its freshwater from riverine sources, primarily small flows from

Oyster Bayou, Onion Bayou, and East Bay Bayou and indirect effects from the Trinity and San Jacinto Rivers, the primary drainages into Galveston Bay, which similarly have their flow into East Galveston Bay restricted by Hanna reef (Gosselink et al. 1979, Wermund et al. 1988, Powell et al. 2003, Foundation 2008, Du and Park 2019). The construction of the pass resulted in substantial hydrologic changes due to the introduction of tidal flow into East Galveston Bay. After the construction of Rollover Pass, salinity levels increased and the dominant plant community shifted over the decades to include more salt-tolerant species and many of the previously common salt-intolerant species disappeared (Appendix A) (Lay and O'Neil 1942, Singleton 1951, Reid Jr 1955, Reid Jr 1956, Gosselink et al. 1979).

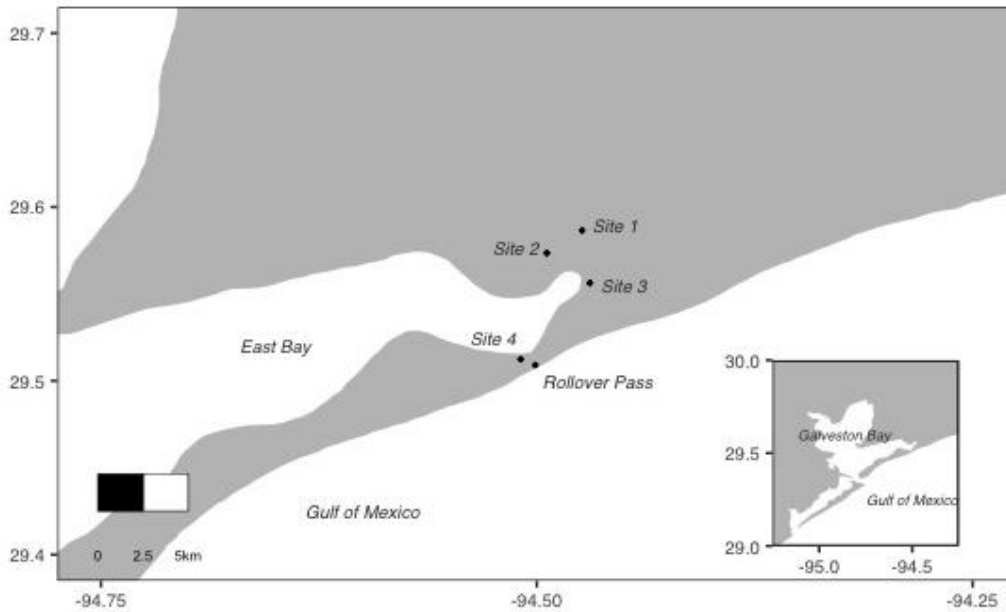


Figure 1. Map of field sites and the former site of Rollover Pass in East Galveston Bay, TX, USA and (inset) location of study sites in relation to the greater Gulf of Mexico region.

While the goals of salinizing East Galveston Bay via Rollover Pass were achieved, this project was not without consequences. In addition to altering the plant community, pass construction resulted in instability of the pass itself, deep scouring at the pass, and substantial increases in erosion on adjacent shorelines (Prather and Sorensen 1972, Morton 1975, Bales and Holley 1988, Bales and Holley 1989). The expense and time of dealing with these issues led to the decision to close Rollover Pass in 2011, but due to a series of legal battles (primarily based on public access to this popular fishing area), deconstruction did not begin until September 2019 (Sallese et al. 2012, Banks et al. 2013). Tidal flow was stopped in December 2019, and the project was ultimately completed a few months later.

The construction and closure of Rollover Pass present a unique opportunity to study near-term plant community responses to hydrological restoration at a large spatial scale. In addition, insights about the long-term ecological succession patterns can be gleaned from qualitative comparisons to historical studies in the area. There are very few published salinity datasets for the area prior to and immediately following the construction of Rollover Pass, but studies by Reid in the late 1950s reported salinities of approximately 11 psu in East Bay prior to Rollover Pass and of 22 psu after construction (Reid Jr 1956, Reid 1957). These pre-closure salinity data and historical descriptions indicated that the marshes surrounding East Galveston Bay were largely fresh to brackish before the construction of Rollover Pass, and then transitioned to a saltier regime over the decades the pass was open (Lay and O'Neil 1942, Singleton 1951, Chabreck 1972, Gosselink et al. 1979, Wermund et al. 1988). I hypothesized that:

1. Both water column and porewater salinity in East Galveston Bay would decrease following the closure of Rollover Pass.
2. The plant community in East Galveston Bay marshes would shift to include more brackish species as the salinity decreased, but this change would occur slowly over time.

METHODS

Rollover Pass (29.508287, -94.500271) was located on Bolivar Peninsula east of Galveston Island, allowing direct tidal flow into East Galveston Bay (Figure 1). To assess how the closure of the pass impacted surrounding wetland plant communities, four sites along a natural salinity gradient were selected. Sites 1, 2, and 3 were located 6-10 linear kilometers northeast of the pass along Oyster Bayou within Anahuac National Wildlife Refuge (Anahuac NWR), and Site 4 was located approximately one kilometer from the pass's eastern bay-side. Plant communities at these sites were sampled three times, once per year beginning in October 2019 at Sites 1-3 and in June 2020 at Site 4. Sites 1, 2, and 3 were sampled once prior to the December 2019 closure of Rollover Pass and twice following the closure, and Site 4 was sampled three times post closure.

At each site, a permanent 50 m transect was established perpendicular to the shoreline. At three stations along the transect (0 m, 25 m, and 50 m from the shoreline), four 0.5 m² quadrats were haphazardly placed, with two to the left of the transect and two to the right (n = 12 quadrats per site). Within each quadrat, percent cover for each plant species present was recorded via a "bird's eye view" approach, where the percent of ground covered by each

species was visually estimated, and cover in all species plus bare ground summed to 100%. The canopy was vertically simple, thus this approach wholly sampled the species present.

In the tidal channel adjacent to each site, submerged aquatic vegetation (SAV) abundance was assayed. SAV was sampled by dragging the head of a 16-tine metal rake over a one-meter area extending perpendicular from the marsh vegetation–water interface; each drag covered an area of $\sim 0.5 \text{ m}^2$ (modified from (Spears et al. 2009)). At each site, three replicate drags were conducted at least five meters apart along the shoreline. Any collected SAV was stored on ice until it could be identified to species in the lab and weighed for wet biomass.

In addition to the plant community, changes to salinity conditions were characterized in two ways: pore water and water column. For pore water measurements, a soil core (2 cm diameter x 5 cm deep) was collected from each site adjacent to each vegetation quadrat ($n = 12$ per site) and stored on ice pending laboratory analysis. In the lab, soil cores were processed for porewater salinity by first transferring each sample to a 50 mL falcon tube then centrifuging at 2,000 rpm for 15 minutes. The supernatant was then extracted using a pipette and salinity was measured using a refractometer. For water column measurements, a Hobo conductivity logger (Model U24-002-C) was placed in the tidal creek ($\sim 0.5 \text{ m}$ deep) adjacent to each site to record conductivity ($\mu\text{S}/\text{cm}$) hourly. These conductivity ($\mu\text{S}/\text{cm}$) values were then converted to salinity (psu) using the methodology described by Hill et al. (1986). Due to periodic exposure of the logger during exceptionally low tides, all salinity values below 0.5 psu were removed from the analysis based on their discrepancies from real data. During these periods of exposure, salinity was generally less than 0.5 psu and temperatures varied substantially more (indicating measurements of air temperature) than typically measured water column temperatures. Based

on these inferences, most salinity measurements less than 0.5 psu can be assumed to be instrument error with a high degree of confidence. This cutoff threshold is presented in the data below. At Site 4, where the Hobo logger was not deployed until June 2020, additional salinity data was obtained from a sonde deployed by TPWD in October 2019 near both Rollover Pass and Site 4 which measured salinity directly (ppt) (29.51551, -94.51095). This logger was in a deeper area attached to a dock rather than placed on the shoreline and was not subject to periodic exposures and thus did not require exclusions to be made. Further, at each site gaps exist due to failure of the logger or inability to deploy one.

Each of the sites had different starting plant communities due to the natural tidal gradient and had different elevation profiles, so changes over time were analyzed separately at each site. To analyze the changes in plant community composition over time at each site, permutational multivariate analysis of variance (PERMANOVA) (using adonis from the vegan package) using semimetric and metric distance matrices were run in RStudio (Version 1.4.1103) on percent cover data. Each run was assessed for significance at $p = 0.05$. Following the PERMANOVA analyses, exploratory similarity percentages (SIMPER) analyses were used to determine which species contributed the most to differences among years. Within each site, changes in porewater salinity over time were determined to have non-normal distribution. Thus, they were then analyzed using a Kruskal-Wallis test, where date was the independent factor, followed by pairwise comparisons using Dunn tests. Open water salinity was graphed continuously (breaks for errors, logger exposure, and logger failure) over time beginning in October 2019 to assess the longer-term patterns of salinity at each site.

RESULTS

At each site, water column salinity showed a qualitative pattern of decreasing temporal variability and decreases in salinity as a whole and on average (Figure 2, Figure 3). Despite numerous logger failures, the general pattern that emerged was a decrease in variability and average salinity over time (Figure 2). This pattern was most pronounced at Sites 2 and 4, with less clarity seen at Sites 1 and 3 (Figure 2). Salinity was overall higher at sites closest to Rollover Pass and the Gulf of Mexico (Sites 3 and 4 had absolute maxima of 16 psu and 25 psu respectively) compared to more brackish conditions at upstream sites (Sites 1 and 2, 12 psu and 11 psu maxima respectively) (Figure 2). In particular, there was a dramatic decrease from 25 psu to ~15 psu at Site 4 immediately following the closure of Rollover Pass and the cessation of direct tidal influx into East Galveston Bay. Values exceeding 12 psu were not detected again during the remainder of the study period (Figure 2).

Similar patterns were observed in monthly mean and maximum salinities at each site, where salinity generally decreased after pass closure, but these patterns interacted with precipitation levels. In most cases, salinity maxima were observed prior to pass closure (Figure 3). Salinity minima were likely linked to a combination of pass closure and precipitation (Figure 3). At Site 1 the mean (6.5 psu) and maximum (11.7 psu) salinities were highest in December 2019 shortly after pass closure, but this month also correlated with a period of low precipitation (Figure 3). At Site 2, mean salinity also peaked in December 2019 at 6.2 psu with corresponding low precipitation, but the monthly maximum salinity was highest in September 2021 at 11 psu, which did not clearly correlate with reduced precipitation (Figure 3). At Site 3, mean (12 psu) and maximum (16 psu) salinity were highest in November 2020 during a period

of low precipitation. However, there were no data available prior to October 2020, so it is unknown if these values differed from pre-closure conditions (Figure 3). Site 4 experienced both its highest salinities before pass closure with the highest monthly mean in October 2019 at 14 psu and the absolute maximum salinity of 25 psu in November 2019 (Figure 3). These instances of high salinity correspond with periods of very high precipitation (Figure 3), indicating that pre-closure, this site was strongly influenced by tidal exchange. At Site 4, the lowest salinities occurred in May 2021, despite the relatively low precipitation during that time period.

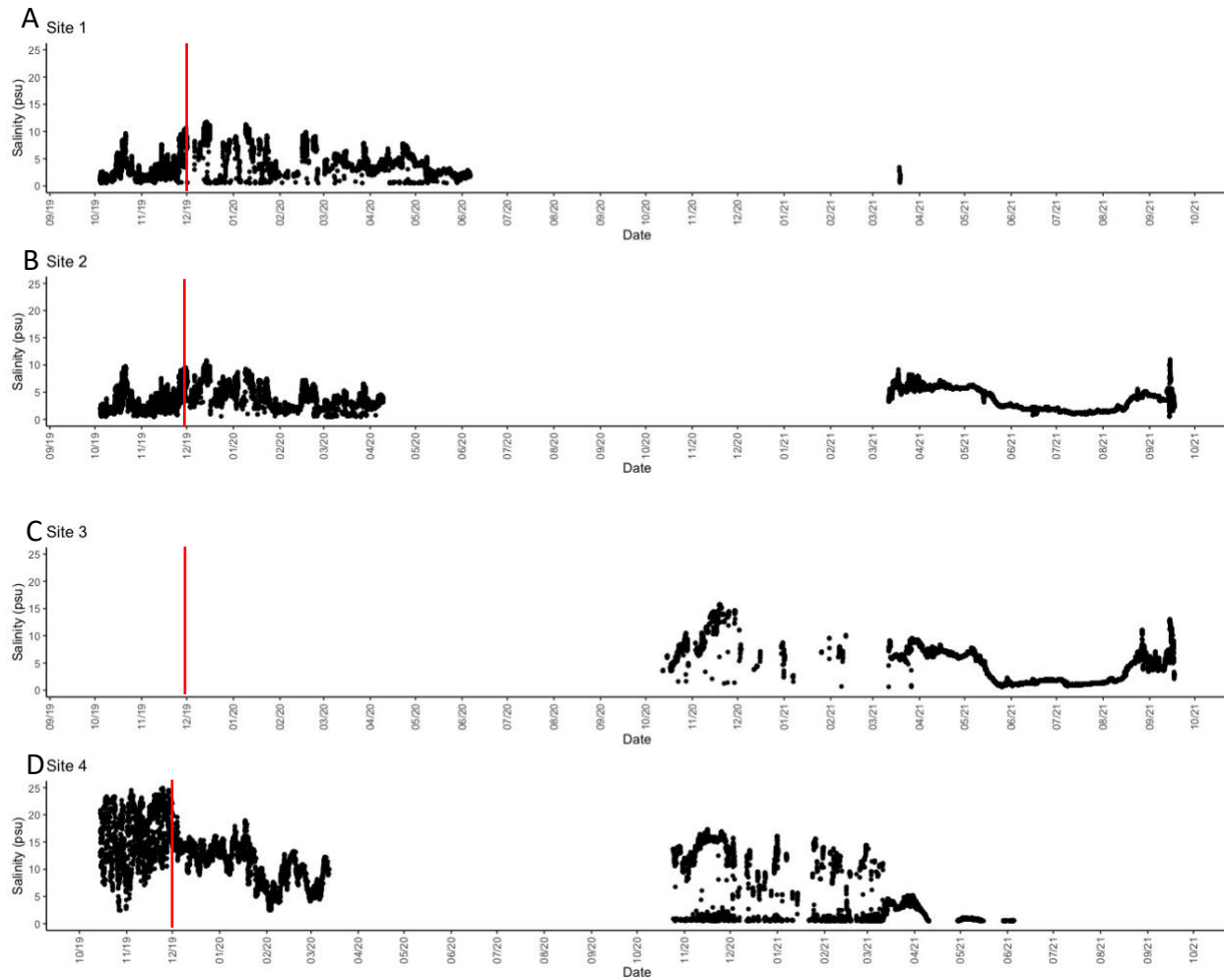


Figure 2. Water column salinity over time at (A) Site 1, (B) Site 2, (C) Site 3, and (D) Site 4. Missing points represent periods of logger exposure or failure. Vertical bars indicate the point at which Rollover Pass was closed in December 2019. In panel D, data before 4/2020 were collected via TPWD's logger, and those after 10/2020 were collected by my logger.

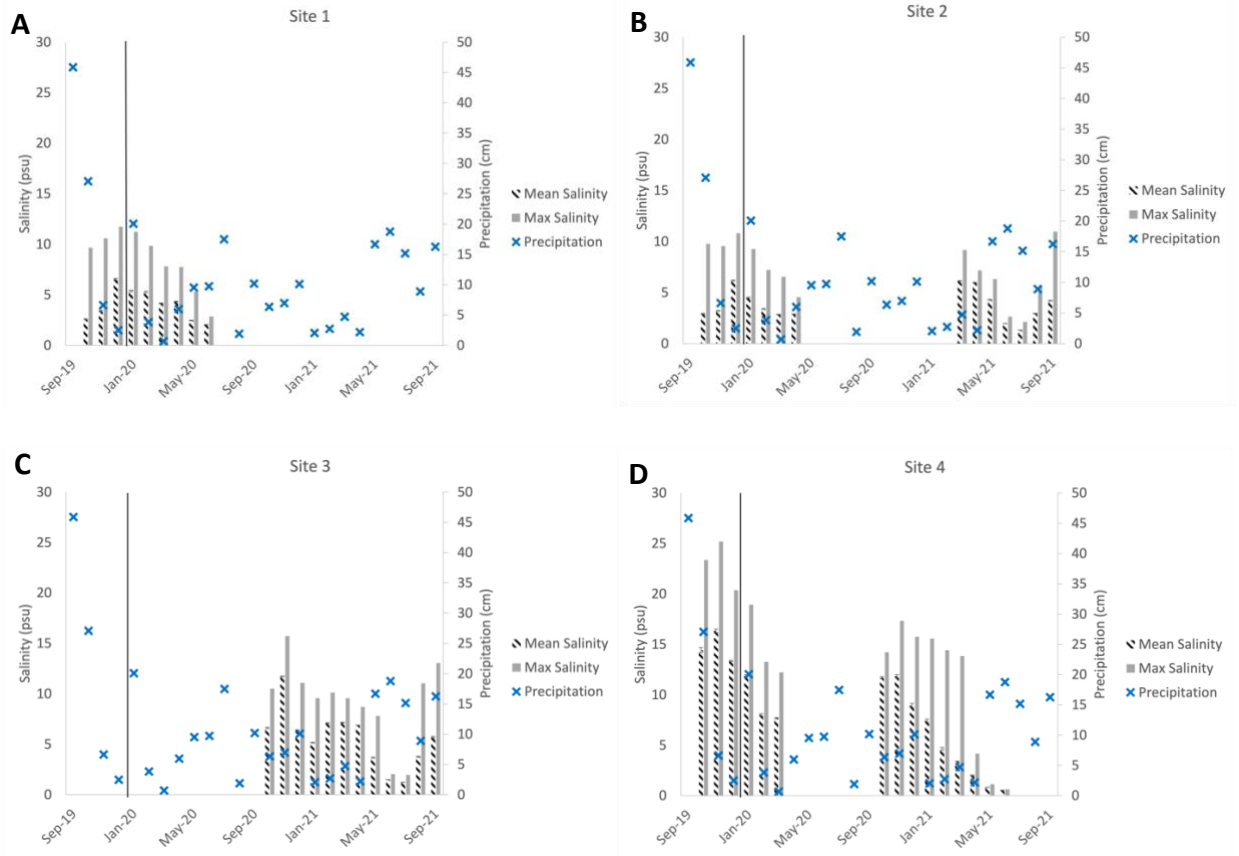


Figure 3. Monthly mean (\pm s.e.) and maximum water column salinity over time at (A) Site 1, (B) Site 2, (C) Site 3, and (D) Site 4. S.E. is very small and thus difficult to see. Monthly total precipitation (cm) is shown as a blue 'x'. The vertical bar on each graph denotes the closure of Rollover Pass.

Porewater salinity trends also showed changes in salinity after pass closure (Figure 4). The pore water salinity at all four sites differed significantly among dates (Sites 1, 2, and 4 $p < 0.001$, Site 3 $p = 0.005$) (Kruskal-Wallis). The initial analysis was then followed by Dunn pairwise comparisons among sampling dates. At Site 1, porewater salinity significantly increased from 2019 to 2020 ($p < 0.001$), while neither year differed significantly from 2021 ($p > 0.1$) (Figure 4). In contrast, at Sites 2 and 3 porewater salinity increased from 2019 to 2020 (Site 2 $p = 0.006$; Site 3 $p = 0.02$) and decreased from 2020 and 2021 (Site 2 $p < 0.001$; Site 3 $p = 0.01$); there were no significant differences between 2019 and 2021 (Site 2 $p > 0.1$; Site 3 $p > 0.1$) (Figure 4). A

different pattern was seen at Site 4, where all sampling dates differed significantly from each other (6/2020:10/2020 $p = 0.01$, 10/2020:9/2021 $p < 0.001$, 6/2020:9/2021 $p = 0.009$) (Figure 4).

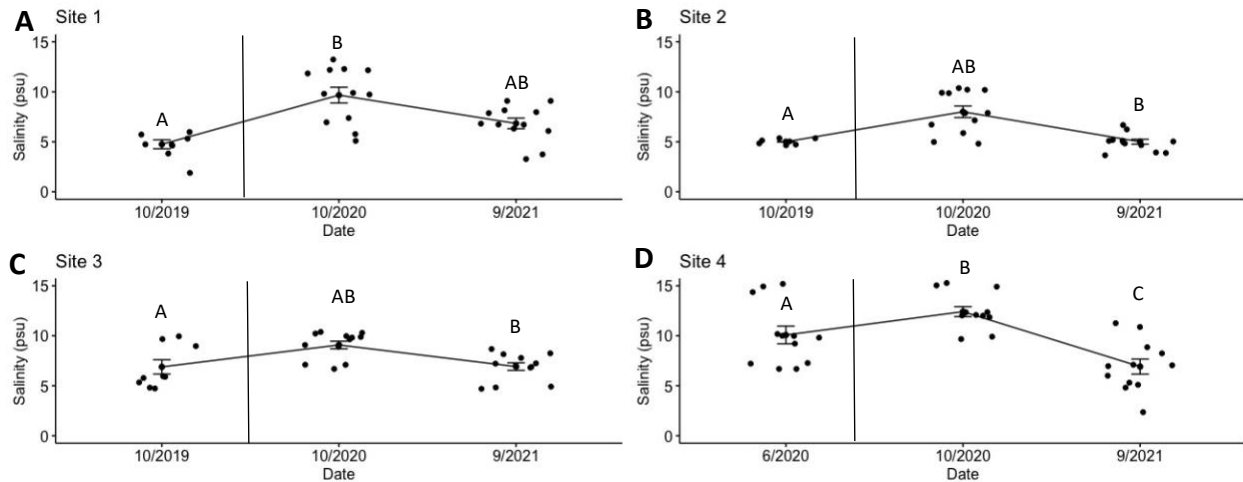


Figure 4. Porewater salinity at each site where scattered dots are the individual points and bars with a single dot show the mean and s.e.. Bar indicates closure of Rollover Pass in December 2019.

Plant community composition changed significantly over time at Sites 1, 2, and 3 ($p = 0.004$, $p = 0.001$, $p = 0.001$ respectively) but not at Site 4 ($p = 0.335$). These patterns were visualized using nonmetric multidimensional scaling (NMDS) plots, which showed substantial overlap in community composition among dates (Figure 5). At each site, the cover of the dominant species fluctuated over time, but there was no change in dominant species identity nor was there a distinct directional change towards a more diverse, less salt tolerant community (Figure 6, Figure 7). SIMPER analyses indicated that most of the changes over time were due to fluctuations in abundance of salt-tolerant species, but not due to the colonization of freshwater species (Appendix A; Figure 6).

At Site 1, the species driving differences among years were all salt-tolerant (Figure 6) (Duncan 1974). At Site 1, *Distichlis spicata* and *Schoenoplectus robustus* decreased in cover after 2019 but there was little change in *Spartina patens* which was the dominant species (cover > 50%) in all three years (Figure 7). Fluctuations in halophytic species cover also occurred at Sites 2 and 3. *Spartina alterniflora* cover increased at Site 2 and decreased at Site 3, *Schoenoplectus robustus* increased at both sites (Figure 6, Figure 7). At Site 4, where there was no significant change in plant community composition among years, the community remained dominated by halophytic species such as *S. alterniflora* and *D. spicata* (Figure 6, Figure 7). Species richness varied between sites, with higher richness further upstream (Site 1: 13; Site 2: 9; Sites 3 and 4: 4; Figure 7).

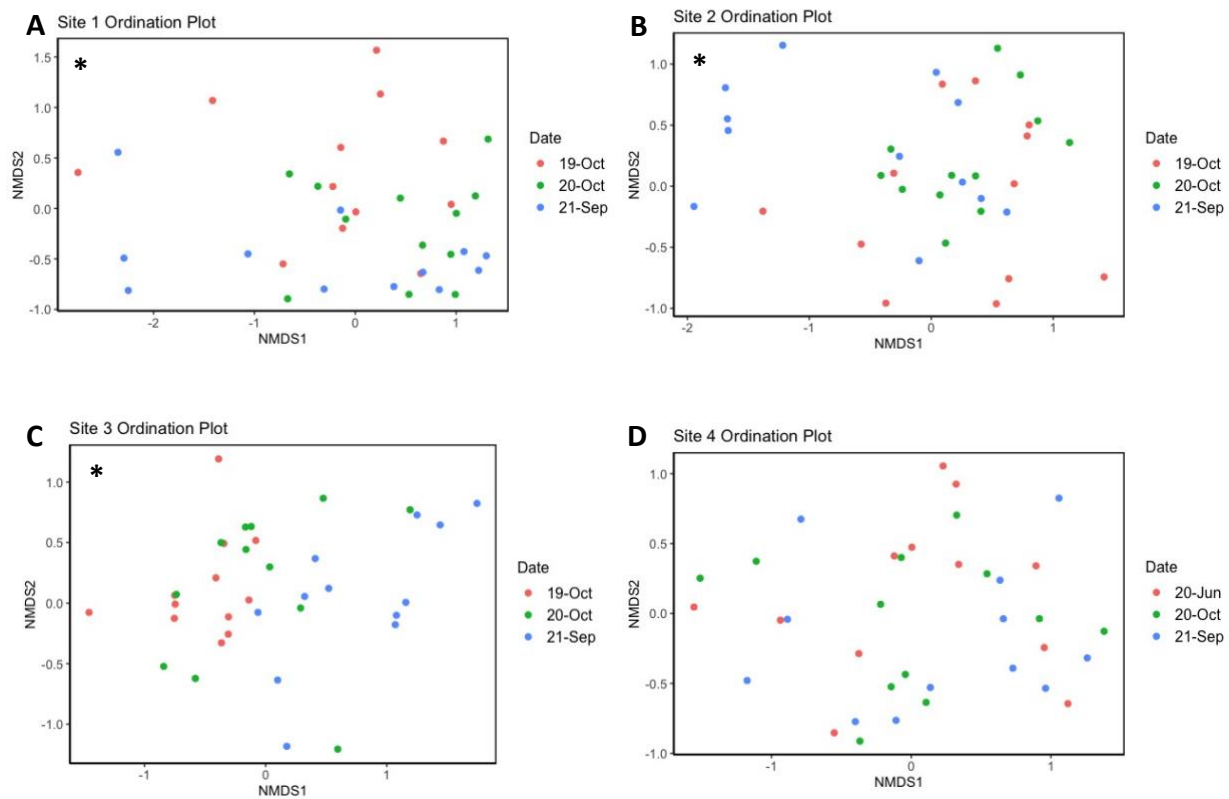


Figure 5. NMDS plots of plant composition within sites and across dates at (A) Site 1, (B) Site 2, (C) Site 3, and (D) Site 4, * denotes significant difference among dates ($p < 0.005$).

Site 1			
Species	10/2019 – 10/2020	10/2020 – 9/2021	10/2019 – 9/2021
<i>Cuscuta sp.</i>	12%		
<i>Distichlis spicata</i>	17%		18%
<i>Iva frutescens</i>	16%	24%	23%
<i>Schoenoplectus pungens</i>	14%	17%	
<i>Schoenoplectus robustus</i>		13%	13%
<i>Spartina patens</i>	18%	17%	22%

Site 2			
Species	10/2019 – 10/2020	10/2020 – 9/2021	10/2019 – 9/2021
<i>Schoenoplectus americanus</i>	13%		
<i>Schoenoplectus robustus</i>	25%	21%	26%
<i>Spartina alterniflora</i>	19%	28%	22%
<i>Spartina patens</i>	19%	21%	18%
<i>Symphiotrichum tenuifolius</i>		14%	12%

Site 3			
Species	10/2019 – 10/2020	10/2020 – 9/2021	10/2019 – 9/2021
<i>Schoenoplectus robustus</i>	33%	36%	41%
<i>Spartina alterniflora</i>	30%	32%	34%
<i>Symphiotrichum tenuifolius</i>	31%	32%	

Site 4			
Species	6/2020 – 10/2020	10/2020 – 9/2021	6/2020 – 9/2021
<i>Batis maritima</i>	23%		
<i>Distichlis spicata</i>	36%	43%	41%
<i>Spartina alterniflora</i>	29%	29%	30%

Figure 6. Interpretation of SIMPER results for (A) Site 1, (B) Site 2, (C) Site 3, and (D) Site 4. Each table shows the percent contribution to the difference between years for each species and colors represent the direction of the change in percent cover (green = increased cover and red = decreased cover).

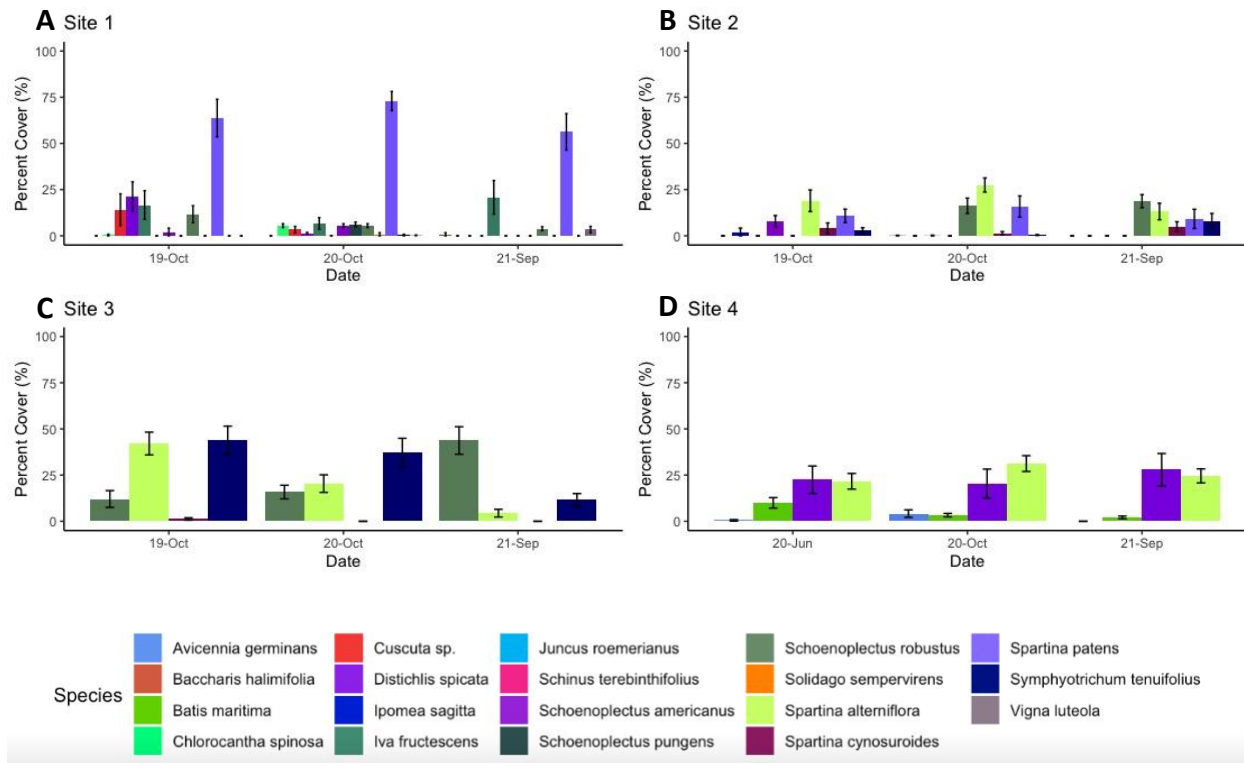


Figure 7. Mean cover (\pm s.e.) of each species found at (A) Site 1, (B) Site 2, (C) Site 3, and (D) Site 4 during each sampling period.

In contrast to emergent vegetation, SAV was extremely rare during the study period. The only instance of SAV at any site was in October 2021 at Site 1, where a small amount (wet weight 185 g/m²) of *Ruppia maritima* was found in the channel adjacent to the site. No other seagrasses were found during the study at any other site.

DISCUSSION

The closure of Rollover Pass was a substantial modification to the tidal hydrology of East Galveston Bay, but any impacts on the emergent and submerged plant communities will likely be slow to develop. Results to date indicate slow changes to salinity and even slower changes

to floral community composition, which thus far was primarily driven by shifts within the existing community rather than the appearance of new species. This may be explained in part by the relatively small decreases in salinity. Since low salinity is generally considered to correlated with low abiotic stress, decreased salinity will not necessarily exclude salt-adapted floral species. Rather, the slower process of interspecific competition will be an important driver of change to species composition (Dunson and Travis 1991, Crain et al. 2004, Adler et al. 2018). However, coastal wetland species are often resilient to biotic and abiotic stressors, suggesting that substantial community composition changes may require a disturbance event that causes stress or even removes existing species, opening space for new species to potentially take hold (Sousa 1980, Petraitis et al. 1989, McIntyre et al. 1995). Without such an event like a storm surge or fire, a complete shift of the community will likely occur over decades as more competitive species remain dominant in the area.

Due to their location along a natural salinity gradient based on distance from tidal and freshwater inputs, each site had different species richness, community composition, and elevation profiles. Thus, the sites were not statistically compared, but there is some insight that can be obtained from qualitative comparisons along the salinity gradient. Consistent with ecological theories, species richness was highest at sites with the least abiotic salinity stress and lower at sites with greater salinity stress (Scrosati et al. 2011, Zwerschke et al. 2013) (Kunza and Pennings 2008). Further, upstream sites had species that are more characteristic of brackish than marine conditions, such as *Schoenoplectus pungens* (Partridge and Wilson 1988). However, the upstream preference of *S. pungens* could be due to additional abiotic and biotic factors, which were not characterized in this study (Dodd and Webb 1975, Wilson et al. 1996).

Limiting abiotic factors such as sediment grain size, soil moisture, wave energy, and inundation depth and duration are linked to the elevational profile of a marsh (Yang et al. 2008, Oosterlee et al. 2018). Thus, species composition at sites may also have been influenced by their distinct elevational profiles. The upstream sites (Sites 1 and 2) had a distinct berm at the water's edge, meaning they had little low elevation habitat at the edge of the site where the study transects began. In contrast, the downstream sites (Sites 3 and 4) had a smooth transition from the water through low elevations and then to higher elevations. These differences contribute to the diversity of the plant community found within sites due to the variable tolerance of species to abiotic stressors such as flooding, anoxia, sediment texture, and wave energy (Davy et al. 2011).

Each site exhibited unique dynamics over time, owing to their specific characteristics. Farthest upstream at Site 1, salinity decreased slightly over the study period and experienced fewer extremes with a maximum of 12 psu (December 2019) and an overall mean of 4 psu (± 0.5), but the highest and lowest salinities lined up with periods of low and high rainfall, respectively (Figure 3). Porewater salinity showed a different pattern, with the highest values in the middle (2020) of the study period. These temporal variations in water column and pore water salinity suggest that weather conditions (e.g., rainfall or prevailing wind direction) likely had stronger influences on upstream salinity than did the Pass closure. A similar pattern emerged at Site 2, where there was no clear pattern of salinity change and some indication of decreased temporal variation after Rollover Pass closed (Figure 2, Figure 3). The highest salinity here was 11 psu, and the mean salinity throughout the study period was 4 psu (± 0.3) (Figure 3). Here mean high salinity and the lowest mean and maximum salinities line up with rainfall

patterns, but the absolute maximum does not as clearly correlate with rainfall conditions indicating another factor (such as pass closure) driving this salinity (Figure 3). In the future, additional sensors will be deployed to more accurately track logger immersion. Nevertheless, despite some missing data points, the general indication from the available water column and porewater data indicate that changes in upstream salinity were relatively modest following pass closure.

Moving to the downstream sites, salinity data from Site 3 were collected about one year after pass closure. These data indicated that salinity was in the brackish (< 16 psu) range, and maximum and minimum salinities correlated with periods of low and high precipitation. However, the dominance of halophytic species such as *Spartina alterniflora* at the site indicated a history of strong saltwater tidal influence prior to pass closure. Finally at Site 4, the site closest to the former site of Rollover Pass, salinity immediately decreased after the pass's closure. There was also less variability over time at this site, reflecting the cessation of daily tidal input. The highest mean and maximum salinities at this site lined up with both pass closure and low rainfall, indicating a dual cause, but the minimum salinities appear to be less driven by rainfall (Figure 3). At Site 4 the lowest mean and maximum monthly salinities occurred in May of 2021, during a period of low rainfall. This disconnect between precipitation and salinity suggests that this site was more sensitive to the closure of Rollover Pass. This inference is supported by the gradual decrease in porewater salinity over time, suggesting that pass closure is leading to a gradual but ongoing decrease in saltwater input.

Overall, the available water column and porewater data indicate that salinity is gradually but incrementally decreasing since pass closure, though precipitation events continue to have

strong but temporary effects on salinity. If salinity continues to decrease towards fully brackish or even fresh conditions, there may be substantial ecological consequences. Since decreases in salinity are not acutely stressful for marine species, halophytes will not be negatively impacted by this change itself (Partridge and Wilson 1988, Wilson et al. 1996). Instead, any changes to community composition will be largely driven by interspecific competition that eventually pushes out less competitive species, which includes many of the highly salt-tolerant species seen in this study (Carus et al. 2017, Adler et al. 2018). Although some changes occurred in the plant community over the study period, these changes were shifts in already present marine and brackish species, not the appearance or expansion of less salt-tolerant, more competitive species (Jackson et al. 2001, HilleRisLambers et al. 2013). Further, these existing shifts were not directional, as in many cases the most common species fluctuated in abundance from year to year. The persistence of halophytes in this system was likely because salinity remained high enough to exclude many brackish but highly competitive plant species.

At Site 1, throughout the study period, *S. patens* was the densest species at this upstream site. *S. patens* has substantial intraspecific variation in individual salt tolerance, but is generally quite tolerant of brackish conditions (Hester et al. 1996, 2001). Based on the wide range of salinities tolerated by *S. patens*, it is not unexpected that it persisted at the upstream site. If in the future the area becomes consistently fresh, *S. patens* will face increased intraspecific competition and may be pushed out of its current dominant condition by more competitive, freshwater species (Greiner La Peyre et al. 2001).

In addition to emergent vegetation, *R. maritima* was found at Site 1 during the final sampling year (2021), and additional patches were observed near the sampling area. The

prevalence of submerged vegetation may not have been well captured by the rake-toss sampling method, but visual examination of the area suggests this species is still rare. Since *R. maritima* can occupy a wide range of salinities, its rarity may be due to a variety of other limiting factors including lack of light, pollution, and dredging which have largely reduced cover of seagrasses throughout the Galveston Bay system since the 1950s (Kantrud 1991, Sheridan et al. 1998, Handley et al. 2007). Still, the presence of this species at all is a hopeful sign for seagrass recovery in East Galveston Bay since while Singleton (1951) reported it in the area, later Sheridan (1988) reported a complete lack of SAV in East Galveston Bay.

At Site 2, changes in the plant community among dates were largely rearrangements within the existing community and not shifts towards a freshwater community. From 2019 to 2021 there were steady declines in *S. alterniflora* and *S. patens* cover, offset by modest increases in *S. robustus* and *Symphyotrichum tenuifolius* (Figure 6). All of these species, and particularly *S. alterniflora*, are ubiquitous salt marsh species with high tolerance for salinity and other stressors common to saline environments. These species differ in competitive ability; for example, *S. alterniflora* is sensitive to competitive stress in less saline conditions (Hester et al. 2001, Crain et al. 2004, Vasquez et al. 2006), whereas *S. robustus* is less tolerant of high salinities than *S. alterniflora* but is a better competitor and less negatively impacted by neighbor species (Crain et al. 2004). If salinity continues to decline over time, the coexistence of these two species may change as *S. alterniflora* struggles to compete in a less saline environment.

The makeup of the plant community at Site 3 was also significantly different between years, but similarly to the other sites, this was due to the reorganization of existing species.

These differences were driven by declines in *S. alterniflora* and increases in *S. robustus*, which are likely related to the same forces described for Site 2 (Figure 6). Here the densest species in 2019 and 2020 was *S. tenuifolius* (a very close second in 2019 was *S. alterniflora*) and *S. robustus* in 2021. Like *S. robustus*, *S. tenuifolius* thrives in brackish conditions so its decline may be due to intraspecific competition or other factors not captured in this study such as sediment texture or seed bank availability (Wilson et al. 1996, Nichols and Nichols 2008, Davy et al. 2011).

Finally, at Site 4 there was no significant difference in the makeup of the plant community among sampling years. The only noticeable change in the plant community was unrelated to the pass closure: a severe freeze in February 2021 resulted in near total mortality of *Avicennia germinans* and led to substantial decreases in its coverage at this site (Doss-Gollin et al. 2021, Thompson 2021). It remains to be seen whether *A. germinans* will recover or if it will remain rare at this site, potentially opening space for other species. Throughout the study, the dominant species were *D. spicata* and *S. alterniflora*, which are both highly salt-tolerant.

As we consider what these changes, or their subtlety, mean ecologically, it is necessary to further examine the natural history of East Galveston Bay and that of Rollover Pass. By examining the general condition of East Galveston Bay during the periods before, during, and after Rollover Pass, several important observations and implications become clear. Notably, the vegetation community responses to both pass opening and closure were slow, occurring over decades. Before the construction of Rollover Pass and the consequential increase in saltwater and tidal flow, East Bay marshes were described as estuarine and/or brackish (Lay and O'Neil 1942, Reid et al. 1956). Lay and O'Neil (1942) noted the presence of freshwater marsh species

Juncus militaris) in a marsh on Oyster Bayou (within the current Anahuac NWR), along with several and halophytic species, including *S. alterniflora*, *S. robustus*, and *Juncus roemerianus* with *Spartina spartinae* at the upland transition and *Phragmites australis* at the water's edge (scientific names were determined based on common names used in Lay and O'Neil (1942). Immediately following the construction of Rollover Pass, the ecology and hydrology of East Galveston Bay was substantially altered (Reid Jr 1956). Bay salinity increased two-fold to 22 psu at Rollover Pass and decreased incrementally with distance from the pass within East Galveston Bay (minimum of 13 psu) due to the introduction of salty Gulf of Mexico waters, potentially excluding some brackish species or otherwise reducing their fitness (Reid Jr 1956, Reid 1957). Over the following decades, the overall ecosystem structure in East Galveston Bay shifted towards a more marine system due to the introduced tidal flux and the corresponding impacts to the biotic community along the salinity gradient.

In the early 1990s (nearly 40 years after the construction of Rollover Pass) wetland habitats in East Bay, nearest to Rollover Pass (Sites 3 and 4) were still predominately brackish with an increased presences of typical salt marsh species (White 1992). As can be seen today, there was a salinity gradient leading away from the pass, ranging from marine near the pass to brackish upstream. In addition, there was a greater diversity of species found upstream as compared to the downstream sites during the same period (Appendix A) (White 1992). During the same time, upstream sites (Sites 1 and 2) within Anahuac NWR were primarily brackish and fresh marshes (White 1992). These patterns indicate that the plant community in East Galveston Bay was always somewhat brackish, with variation along a salinity gradient that has persisted over the decades. Overall, there are few salt-intolerant species in any site and there

is greater diversity upstream, suggesting resiliency of this system to change (Appendix A, Figure 7).

The plant community in the wetlands of East Galveston Bay changed slowly over decades after the construction of Rollover Pass to include more marine species, so it is reasonable to hypothesize that changes after pass closure will occur on a similarly long timescale. Wetlands are frequently quite resilient ecosystems due to their existence in high-stress conditions and to a variety of response variables, including anoxia, flooding, and in the case of coastal wetlands salinity (Stagg et al. 2016, S.E.Grenfell et al. 2019, Zhang et al. 2019). Further, any changes likely will not be homogenous across the landscape due to the variety of existing communities and their inherent differences (elevation, position along freshwater inflows, etc.). Based on previous evidence, it is likely that sites will experience different patterns of change along the existing salinity gradient that has persisted through the iterations of tidal influx into East Galveston Bay (Lay and O'Neil 1942, Reid Jr 1955, White 1992). The timescale and endpoint of biotic responses to an abiotic alteration vary substantially depending on the specifics of the change and the makeup of the community, and the path of change may not be as simple as 'A' causes 'B' (Burkett et al. 2005, Nitschke and Innes 2008, McLauchlan et al. 2013). Variations in ecosystem structure mean that some changes have no substantial effect and others are as consequential as alternative stable states, due to the complexity of ecological interactions and responses of the specific species (Beisner et al. 2003, Côté and Darling 2010, Ponce-Campos et al. 2013).

Since wetlands are stressful environments, the organisms that live in them can be quite resilient if the change does not completely breach the species' tolerance. In the case of salinity

changes, the direction of the change may drive the speed and intensity of the change. After the construction of Rollover Pass, and the resulting increase in salinity, some species may have been immediately pushed beyond their preferred or tolerable salinity ranges which would have substantially decreased their fitness and competitive ability. However, in this study, after the salinity slightly decreased following the closure of the pass, none of the plants present were negatively impacted by these less stressful conditions. Over time, existing species may begin to experience more competition from species that are no longer experiencing reduced fitness. While some salt-intolerant species may expand, competition with established salt-tolerant species will likely delay substantial changes to the plant community makeup even though high-stress tolerance is a trade-off with high competitive ability (Liancourt et al. 2005a, Liancourt et al. 2005b, Qi et al. 2018). Further, sites upstream (Sites 1 and 2) may show changes to the plant community sooner than downstream sites (Sites 3 and 4) due to the existing greater diversity and potentially being closer to seed stores of a greater diversity of species. Regardless of the exact path, magnitude, and type of changes to salinity regimes and plant communities following the closure of Rollover Pass, it will likely take decades for ecologically meaningful alterations to occur.

CONCLUSIONS

Unless conditions become inhospitable, wetland floral communities generally take time to respond to changes in abiotic conditions (Cronk 2016). This is especially true when alterations result in reduced abiotic stress, even if there is cooccurring biotic stress (Yackulic 2017). This study and the history of the area show that altered salinity and tidal regimes have

an impact on the floral community, but these changes occur very slowly and may take decades to result in ecologically meaningful differences. Furthermore, changes to abiotic characteristics of coastal ecosystems also occur over long time scales in response to ongoing anthropogenic alterations and global climate change. This study has shown that while a large hydrological restoration occurred, an equally large change to the wetland plant community did not manifest. Therefore, assessing the success of this restoration project through an ecological lens is complicated by the time scale of plant responses. This has important implications for the success of other large-scale restoration projects as well as being a strong argument for conservation over restoration. Management practitioners must gather empirical data showing that restoring historic tidal exchange conditions will not result in an immediate return to those historical plant assemblages, or that such an end-goal is even possible or reasonable (Bradshaw 1996, Kopf et al. 2015, Buisson et al. 2019). Without this type of empirical evidence that shows the difficulty of changing an ecosystem back to a more pristine state, restoration will remain an imperfect solution to the unwise changes of the past and of any yet to come. However, data such as this may inform new best practices and regulatory policy that reduce or prevent similar alterations in the future.

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APPENDIX A

Species reported in marshes surrounding field sites in other studies and species found at field sites during this study in the 2010s and 2020s. Bolded species indicate those that only occur in one of the periods in the site group and asterisks indicate less salt-tolerant species.

Species Found in East Galveston Bay (1942) ¹	
<i>Juncus militaris</i> *	<i>Spartina alterniflora</i>
<i>Juncus roemerianus</i>	<i>Spartina spartinae</i>
<i>Schoenoplectus robustus</i>	<i>Phragmites australis</i>
Species Found in Far Southwestern Chenier Plain (Including Anahuac NWR) (1951) ²	
<i>Cladium jamaicense</i>	<i>Potamogeton foliosus</i> *
<i>Echinochloa walteri</i>	<i>Ruppia maritima</i>
<i>Echinodorus cordifolius</i> *	<i>Rynchospora corniculata</i> *
<i>Eleocharis quadrangulate</i> *	<i>Salicornia sp.</i>
<i>Leersia oryzoides</i> *	<i>Schoenoplectus americanus</i>
<i>Polygonum hydropiperoides</i> *	<i>Schoenoplectus californicus</i> *
<i>Pontederia cordata</i> *	<i>Schoenoplectus robustus</i>

Species Found Nearest to Sites 1 and 2 (classified as fresh marsh) (1979) ³	Species Found Nearest to Site 3 (classified as brackish marsh) (1979) ³	Species Found Nearest to Site 4 (classified as salt marsh) (1979) ³
<p><i>Alternanthera philoxeroides</i></p> <p><i>Sagittaria lancifolia</i>*</p> <p><i>Spartina patens</i></p> <p><i>Panicum hemitomon</i>*</p>	<p><i>Phragmites australis</i></p> <p><i>Sagittaria lancifolia</i>*</p> <p><i>Spartina patens</i></p>	<p><i>Distichlis spicata</i></p> <p><i>Juncus roemerianus</i></p> <p><i>Spartina alterniflora</i></p> <p><i>Spartina patens</i></p>
Species Found Nearest to Sites 1 and 2 (1992) ⁴		Species Found Nearest to Sites 3 and 4 (1992) ⁴
<p><i>Borrichia frutescens</i></p> <p><i>Echinichloa crus-galli</i>*</p> <p><i>Iva frutescens</i></p> <p><i>Juncus effusus</i>*</p> <p><i>Panicum virgatum</i>*</p> <p><i>Paspalum vaginatum</i></p> <p><i>Schoenoplectus americanus</i></p> <p><i>Schoenoplectus maritimus</i></p> <p><i>Setaria geniculata</i></p> <p><i>Spartina patens</i></p> <p><i>Spartina spartinae</i></p> <p><i>Sporobolus virginicus</i></p> <p><i>Typha sp.</i>*</p>	<p><i>Aster sp.</i>*</p> <p><i>Batis sp.</i></p> <p><i>Borrichia sp.</i></p> <p><i>Distichlis spicata</i></p> <p><i>Juncus roemerianus</i></p> <p><i>Limonium sp.</i></p> <p><i>Monanthochloe sp.</i></p> <p><i>Salicornia spp.</i></p> <p><i>Schoenoplectus maritimus</i></p> <p><i>Spartina alterniflora</i></p> <p><i>Spartina patens</i></p> <p><i>Spartina spartinae</i></p> <p><i>Suaeda sp.</i></p>	

Species Found Nearest to Sites (2011) ⁵	
<p><i>Ambrosia psilostachya</i></p> <p><i>Baptista bracteata</i></p> <p><i>Borrichia frutescens</i></p> <p><i>Distichlis spicata</i></p> <p><i>Eleocharis montevidensis</i></p> <p><i>Ipomea sagitta</i></p> <p><i>Iva annua</i></p> <p><i>Juncus brachycarpus</i>*</p> <p><i>Juncus interior</i>*</p> <p><i>Juncus roemerianus</i></p> <p><i>Lycium carolinianum</i></p> <p><i>Mimosa strigillosa</i>*</p>	<p><i>Paspalum vaginatum</i></p> <p><i>Phragmites australis</i></p> <p><i>Rubus spp.</i></p> <p><i>Schoenoplectus americanus</i></p> <p><i>Schoenoplectus californicus</i>*</p> <p><i>Schoenoplectus robustus</i></p> <p><i>Schoenoplectus pungens</i>*</p> <p><i>Spartina patens</i></p> <p><i>Spartina spartinae</i></p> <p><i>Suaeda linearis</i></p> <p><i>Typha angustifolia</i>*</p>
Species Found in Sites 1 and 2 (2010s and 2020s)	Species Found in Sites 3 and 4 (2010s and 2020s)
<p><i>Baccharis halimifolia</i></p> <p><i>Chlorocantha spinosa</i></p> <p><i>Cuscuta sp.</i></p> <p><i>Distichlis spicata</i></p> <p><i>Ipomea sagitta</i></p> <p><i>Iva frutescens</i></p> <p><i>Juncus roemerianus</i></p> <p><i>Ruppia maritima</i></p> <p><i>Schinus terebinthifolius</i></p> <p><i>Schoenoplectus americanus</i></p>	<p><i>Avicennia germinans</i></p> <p><i>Batis maritima</i></p> <p><i>Distichlis spicata</i></p> <p><i>Spartina alterniflora</i></p> <p><i>Spartina cynosuroides</i></p> <p><i>Spartina patens</i></p> <p><i>Schoenoplectus robustus</i></p> <p><i>Symphyotrichum tenuifolius</i></p>

<p><i>Schoenoplectus pungens*</i></p> <p><i>Schoenoplectus robustus</i></p> <p><i>Solidago sempervirens</i></p> <p><i>Spartina alterniflora</i></p> <p><i>Spartina cynosuroides</i></p> <p><i>Spartina patens</i></p> <p><i>Sporobolus virginicus</i></p> <p><i>Symphotrichum tenuifolius</i></p> <p><i>Vigna luteola</i></p>	
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Notes:

Where appropriate, scientific names have been updated to reflect modern taxonomic nomenclature (e.g. *Scirpus robustus* is reported here as *Schoenoplectus robustus*).

¹Lay and O'Neill (1942)

- Did not rigorously study or describe the entire floral community, so this species list is likely incomplete
- Site was located along Oyster Bayou (Anahuac NWR).
- Species names determined based on common names given in the text and due to variation in use temporally and spatially there could be errors. This is especially true for *Juncus militaris*, which was determined based on the given common name “bayonet rush” but this species is not known to occur in Texas based on the USDA Plants Database (<https://plants.usda.gov/home>).

- Tharp (1926) was not specific to East Galveston Bay, but describes additional salt-intolerant species as occurring in Texas coastal marshes east of the Brazos River to the Louisiana state line.
 - *Rynchospora corniculata*, *Typha* sp., *Scirpus lacustris*, *Arundo donax*, and *Zizaniopsis* sp.

²Singleton (1951)

- Study was conducted in Chambers, Jefferson and Orange counties and specifically selected species to study that are food sources for waterfowl, thus this species list may be incomplete.
- Characterized wetlands as freshwater, intermediate, and brackish.
- It was not stated exactly how far inland survey sites ranged but said that most were subject to tides or their influence, thus they were primarily coastal.

³Gosselink, Cordes, and Parsons (1979)

- Study area was in East Galveston Bay.
- Described a decreasing salinity gradient from west to east across the bay.
- Described the marshes closest to my Site 4 as salt marsh, those closest to Sites 2 and 3 as brackish/intermediate marsh, and Site 1 as fresh marsh.

⁴White (1992)

- Species found closest to this study's sites, while White collected data throughout the Galveston Bay system.

⁵Johnson (2011)

- Species found closest to this study's sites, while Johnson collected data throughout Anahuac NWR and the adjacent Canada Ranch.