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Mangrove expansion into salt marshes alters associated faunal communities

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ABSTRACT

Climate change is altering the distribution of foundation species, with potential effects on organisms that inhabit these environments and changes to valuable ecosystem functions. In the Gulf of Mexico, black mangroves (*Avicennia germinans*) are expanding northward into salt marshes dominated by *Spartina alterniflora* (hereafter *Spartina*). Salt marshes are essential habitats for many organisms, including ecologically and economically important species such as blue crabs (*Callinectes sapidus*) and Penaeid shrimp (e.g., *Penaeus aztecus*), which may be affected by vegetation changes. Black mangroves occupied higher tidal elevations than *Spartina*, and *Spartina* was present only at its lowest tidal elevations in sites when mangroves were established. We compared nekton and infaunal communities within monoculture stands of *Spartina* that were bordered by mangroves to nearby areas where mangroves had not yet become established. Nekton and infaunal communities were significantly different in *Spartina* stands bordered by mangroves, even though salinity and temperature were not different. Overall abundance and biomass of nekton and infauna was significantly higher in marshes without mangroves, although crabs and fish were more abundant in mangrove areas. Black mangrove expansion as well as other ongoing vegetation shifts will continue in a warming climate. Understanding how these changes affect associated species is necessary for management, mitigation, and conservation.

1. Introduction

Foundation species are critically important for the structure and function of communities and for ecosystem processes such as carbon cycling and energy flow (Ellison et al., 2005). Landscape level shifts in the distribution and abundance of foundation species can fundamentally alter ecosystems (Armitage et al., 2015), and are presently occurring with poleward vegetation species shifts caused by climate change (Micheli et al., 2008; Osland et al., 2013; Vergés et al., 2014) in both aquatic and terrestrial ecosystems (Gonzalez et al., 2010). For example, in North Carolina, eel grass (*Zostera marina*) is being displaced by shoal grass (*Halodule wrightii*), reducing biodiversity in these areas (Micheli et al., 2008). A similar transition is underway in Texas, where shoal grass is being displaced by the tropical seagrasses *Syringodium filiforme* (manatee grass) and *Thalassia testudinum* (turtle grass), significantly changing seagrass-associated fauna (Ray et al., 2014).

Along the eastern and Gulf of Mexico coasts of the US, salt marshes are abundant and provide numerous ecosystem services including shoreline protection, carbon and nutrient cycling, and essential habitat for many species (Cuddington et al., 2011). At low tidal elevations, salt marshes are dominated by *Spartina alterniflora* (hereafter *Spartina*), an essential foundation species, that creates critical habitat for many ecologically and economically important species (e.g., blue crabs, *Callinectes sapidus* and red drum, *Sciaenops ocellatus*), and serves as a significant detrital input that forms the basis for coastal food webs (Rozas and Zimmerman, 2000; Pennings and Bertness, 2001; Simas et al., 2001; Stunz et al., 2002). Several other salt-tolerant species are present at higher tidal elevations (e.g., *Spartina patens*, *Batis maritima*, *Salicornia virginica*) and also provide habitat and shoreline protection. Primary production by marsh plants is critical for associated fauna, and detrital inputs can influence secondary production in adjacent systems (Peterson and Howarth, 1987; Pennings and Bertness, 2001).

In tropical climates, *Spartina* is outcompeted by mangrove trees that are well adapted to coastal environments (Reef et al., 2010; Simpson et al., 2013), and mangrove forests replace salt marshes

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as the primary coastal wetland. Recent studies have documented a northward migration of black mangroves (*Avicennia germinans*), attributed to a reduction in severe freezing events over the past 3 decades (Cavanaugh et al., 2014). *Spartina* also faciliates mangrove expansion by trapping seedlings in suitable growth areas (Peterson and Bell, 2012) and by creating a warmer layer that surrounds seedlings, protecting them from cold temperatures (Guo et al., 2013). Historically in the Western Gulf of Mexico, particularly in Texas, black mangroves were present, but populations periodically expanded, displacing other marsh plants, and then contracted allowing those plants to reemerge in response to variations in climate, but black mangroves did not become established in subtropical climates that experienced winter freezes (Sherrod and McMillan, 1981; Sherrod and McMillan, 1985; McMillan and Sherrod, 1986; Cavanaugh et al., 2014). However, the frequency of severe cold weather events has declined, and black mangroves have migrated northward and expanded their distribution in the Gulf of Mexico. In the Mission-Aransas Estuary near Aransas Pass, Texas, USA, only 65 acres of black mangrove forest were reported in the 1980s. From 1989 to 2005, black mangroves expanded and are estimated to cover between 15,000 and 21,500 acres (Montagna et al., 2007). Expanding mangrove populations in Texas have displaced *Spartina* and other plants (e.g., *S. virginica*, *B. maritima*) in coastal marshes (Everitt et al., 2010; Armitage et al., 2015).

Salt marshes are among the most productive ecosystems on earth, and their detrital input is an important resource for many species in the marsh and in adjacent communities (Pennings and Bertness, 2001; Simas et al., 2001). Like marshes, mangrove forests are productive and support a diversity of fauna that are ecologically and economically important (Vaslet et al., 2012). However, there are considerable differences in the composition and allocation of biomass among marshes and mangroves. Standing biomass is greater in mangroves than marshes, while marshes tend to exhibit higher net primary productivity (Alongi, 1998; Alongi et al., 2004). Organic matter turnover is lower in mangrove forests than marshes because ~60% of the mangrove biomass is woody (Alongi, 1998; Castañeda-Moya et al., 2013). Soil conditions and biogeochemical processes also differ between these habitats (Patterson and Mendelssohn, 1991; Perry and Mendelssohna, 2009; Comeaux et al., 2012), however those differences may not be evident soon after a change in plant community composition (Henry and Twilley, 2013). Despite the noted differences in detrital production, biomass, and soil processes, few studies have assessed the impacts of mangrove encroachment into marshes on associated fauna, although two recent studies suggest that the effects on associated nekton and benthic fauna are likely to be significant (Caudill, 2005; Lunt et al., 2013).

The northward migration of mangroves in the Gulf Coast has been occurring for the past 25+ years and if populations continue to expand their range, replacement of *Spartina* as the primary coastal wetland species may occur (Montagna et al., 2007; Osland et al., 2013), but the effects on associated fauna remain obscure. Here, we measured the tidal elevation distributions of *Spartina* and black mangroves in the Western Gulf of Mexico. Then, we collected nekton and infaunal organisms at two tidal elevations in marshes dominated by black mangroves and in marshes where black mangroves were rare. These marshes were separated by <10 km and had similar abiotic conditions, allowing us to assess the effects on mangrove encroachment on associated fauna.

2. Methods

This study was performed in the Mission-Aransas National Estuarine Research Reserve (MANERR) near Rockport, Texas, USA. Mangroves are established in the southern part of the MANERR, but, not in the north. Our study marshes were intertidal, experiencing similar tidal fluctuations (~0.5 m) that are influenced by diurnal and semi-diurnal tides but primarily by prevailing southeast winds. Faunal samples were collected during periods of high monthly tides in June of 2013 (10–11 and 24–25) when the highest marsh and mangrove elevations were submerged. Water temperature was 29 °C ± 0.9 °C and 30 °C ± 1.2°, and salinity was 32 ± 2.3 ppt and 34 ± 1.8 ppt in sites with and without mangroves respectively.

2.1. Vegetation survey

We measured relative tidal elevations of *Spartina* and black mangroves. *Spartina* will not grow in subtidal areas. Therefore, we used the boundary between *Spartina* and benthic habitats (mud flats or seagrass beds in this area) as our lowest elevation point (i.e. point zero). Then, using a laser level we calculated the tidal elevations in which *Spartina* and mangroves were found relative to point zero along a transect from the lowest tidal elevation landward. In marshes where black mangroves were established and abundant, mangroves were present at higher elevations above mean lower low water while *Spartina* was present only in a narrow band ~1–4 m wide at the lowest tidal elevations (closest to mean lower low water). In contrast, *Spartina* dominated at both low and high tidal elevations in areas without abundant mangroves (Fig. 1, see Results). *Spartina* elevations are reported from sites without mangroves because *Spartina* elevations are compressed in

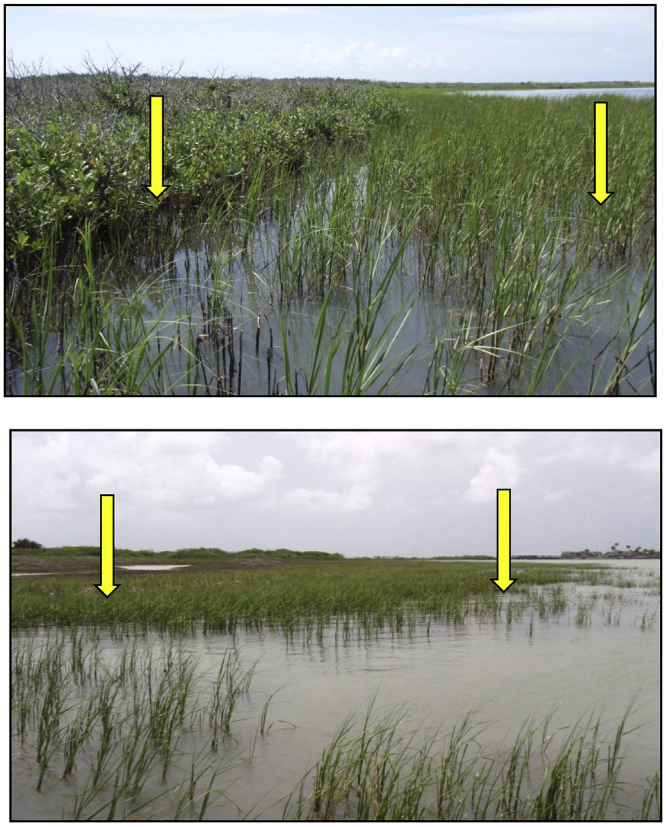

Fig. 1. Marshes with black mangroves (top) and without black mangroves (bottom). Black mangroves were present only at higher tidal elevations in a near monoculture once established. *Spartina* dominated at low and high elevations when mangroves were not present. Nekton and infaunal samples were collected from both tidal heights in both types of marshes, and the tidal elevation of *Spartina* and black mangroves was measured. In this figure, higher tidal elevations are on the left and the arrows represent paired sampling locations in each marsh type.

mangrove sites.

2.2. Faunal collections

We classified marshes into two types: those with abundant black mangroves and those where black mangroves were rare. Black mangroves were found in higher tidal elevations, and to account for both mangrove presence and tidal elevation in our sampling, our collections were made in a 2 × 2 factorial design, with mangrove presence and tidal elevation as factors. Samples at each elevation were paired and were ~ 2–3 m apart. We collected community samples at 2 tidal elevations (~0.1 m and ~0.4 m above mean lower low water) in 15 sites with and 14 sites without mangroves (58 samples total). Our intent was collect 15 paired samples in each marsh type, but our sampler malfunctioned at the last site, leaving us with 14 paired samples in marshes without mangroves. We used the lowest tidal elevation that *Spartina* was present as an estimate of mean lower low water because *Spartina* will not grow subtidal. Sampling sites were separated by more than 150 m to cover a large spatial area. In marshes with established mangroves, samples in lower elevations were collected within *Spartina* and higher elevations samples were always collected within mangrove pneumatophores. In marshes without mangroves, samples at both low and high tidal elevations were collected within *Spartina* (Fig. 1). Water depth was recorded at each sampling location, but, did not significantly influence community assemblages and is not reported. All faunal samples were collected during highest seasonal tides to ensure the highest tidal elevations were submerged.

2.2.1. Nekton communities

Nekton were collected using a suction sampler, which has been successfully used in previous coastal wetland studies (Heck et al., 1995). A 0.25 m^2 cylindrical plastic barrel (open at both ends) was placed over a selected salt marsh or black mangrove habitat and was firmly pressed into the substrate to prevent organisms from escaping. The barrel encapsulated either *Spartina* shoots or black mangrove pneumatophores, allowing us to collect organisms directly within that particular vegetation type. After the barrel was placed, water was suctioned for three minutes to ensure all organisms trapped within the barrel were collected. Preliminary sampling indicated that 3 min was sufficient time for collecting all organisms. Samples were placed into 250 μm mesh bags, labeled, and placed on ice. Upon returning from the field, samples were placed into buckets containing 10% formalin for one week, and then transferred to jars containing 45% isopropyl alcohol. All organisms were identified to the lowest taxonomic level possible for use in multivariate analyses. Total abundance of fish, shrimp, and crabs was calculated. Dry weight biomass was determined for all fish, shrimp, and crabs collected by drying samples at 90 °C for 72 h, and weighing them on an analytical balance to the nearest 0.001 g. All individual fish were weighed together for each sample, as were shrimp and crabs, to create a single measure of biomass for that group.

2.2.2. Infaunal communities

Infaunal organisms were collected using PVC cores. Two sediment cores (10 cm diameter x 10 cm depth) were taken at both low and high tidal elevations (4 total cores) in 5 sites with and 5 sites without mangroves. The number of organisms in cores taken at the same tidal elevation were combined for analysis. Benthic cores were placed into 250 μm mesh bags, gently rinsed with seawater in the field to remove excess sediment, labeled, and placed on ice. Upon returning from the field, samples were placed into buckets containing 10% formalin for a period of one week, and then washed using a 500 μm sieve and transferred to jars containing 45% isopropyl alcohol. Infaunal organisms were sorted from detritus and plant material using a dissecting microscope. Polychaetes were identified to family and all other organisms were identified to the lowest taxonomic level possible for use in multivariate analyses.

2.3. Data analysis

Nekton and infaunal samples were examined separately using univariate analyses in JMP Pro 12 and multivariate analyses in PRIMER ™. For nekton, the total abundance of fish, crabs, and grass shrimp (*Palaemonetes* spp.), as well as the biomass of each group were compared using a two-way ANOVA with mangrove presence (present/absent) and tidal elevation (low/high) as fixed factors. For infauna, total abundance of the two most abundant groups: polychaetes and crustaceans were similarly analyzed using a two-way ANOVA with mangrove presence (present/absent) and tidal elevation (low/high) as fixed factors. Data were log transformed to meet assumptions of equal variances. For both nekton and infauna, we created metric, 2D MDS plots from mean values of communities in each sample. We also performed multivariate analyses on nekton and infaunal community assemblages within each sample using Analysis of Similarity (ANOSIM) in PRIMER ™ with mangrove presence as the factor. SIMPER analysis was also performed to determine which organisms contributed to dissimilarities between mangrove and *Spartina* habitats.

3. Results

3.1. Vegetation survey

Spartina was present at lower tidal elevations than black mangroves (median 0.35 m vs. 0.44 m), although mangroves were found over a larger range of tidal elevations (Fig. 2). In marshes sites without mangroves, *Spartina* was found in monocultures at both low and high elevations. In contrast, when black mangroves were abundant, *Spartina* was relegated to tidal elevations below ~0.2 m, and found in a narrow band bordering the dwarf mangrove forest (Fig. 1). Areas with equal mixtures of mangroves and *Spartina* at the same tidal elevations were difficult to find and were not sampled.

3.2. Nekton communities

Grass shrimp were significantly more abundant and had more biomass in marsh sites without mangroves ($p < 0.01$, Fig. 3, Tables 1 and 2), but fish were significantly more abundant and more fish biomass was found in marsh sites that had abundant mangroves

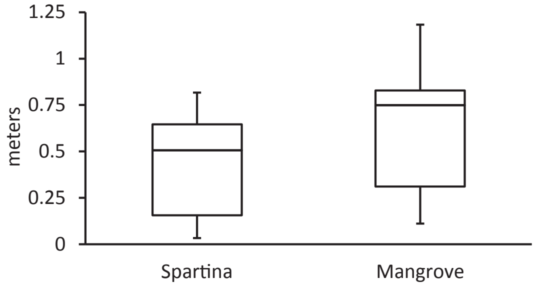

Fig. 2. Box and whiskers plot for tidal elevations of *Spartina alterniflora* and black mangroves. Boxes show median with 25% and 75% quartiles, and whiskers are range of heights that each type of vegetation was found. *Spartina* heights are reported only for sites without mangroves because mangroves displace *Spartina* at its highest tidal elevations.

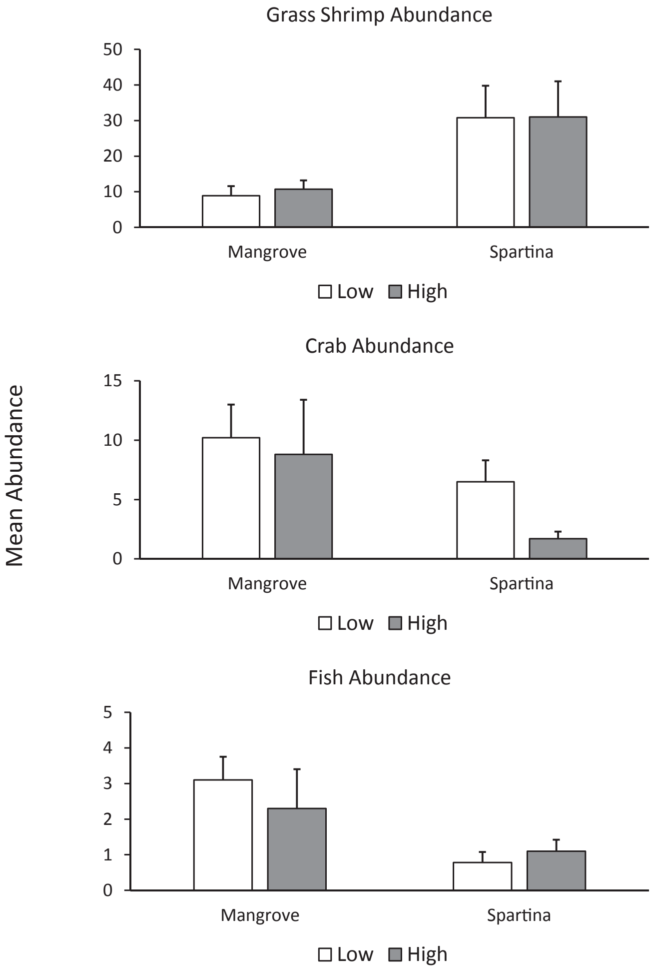

Fig. 3. Mean + SE abundances of shrimp, crabs, and fish in samples from high and low tidal elevations from marshes with and without mangroves. Shaded bars are high tidal elevations, and x axis labels are marshes with abundant mangroves vs. those with only *Spartina*. Significant differences were found for shrimp and fish at $\alpha = 0.05$. Significant differences between tidal elevations were not found.

Table 1
ANOVA results for abundances of shrimp, crabs, and fish. Significant effects ($p < 0.05$) are indicated in bold print.

Grass shrimp abundance ($F = 4.03_{3,52}$, $P = 0.01$)				
Source	**Sum of squares**	**df**	**F**	**P**
Mangrove Presence	2.47	1	8.34	**0.006**
Tidal Elevation	0.002	1	0.01	0.93
Mangrove Presence*Tidal Elevation	1.15	1	3.88	0.055
Crab abundance ($F = 4.03_{3,43}$, $P = 0.32$)				
Source	**Sum of squares**	**df**	**F**	**P**
Mangrove Presence	0.99	1	0.77	0.38
Tidal Elevation	2.78	1	2.15	0.15
Mangrove Presence*Tidal Elevation	1.68	1	1.30	0.26
Fish abundance ($F = 4.03_{3,33}$, $P = 0.04$)				
Source	**Sum of squares**	**df**	**F**	**P**
Mangrove Presence	4.79	1	9.25	**0.005**
Tidal Elevation	0.08	1	0.15	0.70
Mangrove Presence*Tidal Elevation	0.06	1	0.13	0.72

Table 2
ANOVA results for biomass of shrimp, crabs, and fish. Significant effects ($p < 0.05$) are indicated in bold print.

Grass shrimp biomass ($F = 5.23_{3,52}$, $P < 0.001$)				
Source	**Sum of squares**	**df**	**F**	**P**
Mangrove Presence	1.03	1	20.9	**<0.001**
Tidal Elevation	>0.001	1	0.02	0.89
Mangrove Presence*Tidal Elevation	>0.001	1	0.001	0.99
Crab biomass ($F = 1.17_{3,43}$, $P = 0.33$)				
Source	**Sum of squares**	**df**	**F**	**P**
Mangrove Presence	0.32	1	0.89	0.35
Tidal Elevation	0.87	1	2.4	0.12
Mangrove Presence*Tidal Elevation	0.24	1	0.66	0.41
Fish biomass ($F = 3.17_{3,33}$, $P = 0.04$)				
Source	**Sum of squares**	**df**	**F**	**P**
Mangrove Presence	1.99	1	8.77	**0.006**
Tidal Elevation	0.003	1	0.01	0.90
Mangrove Presence*Tidal Elevation	0.15	1	0.66	0.42

($p < 0.01$, Fig. 3, Tables 1 and 2). Crab abundance and biomass did not differ significantly between marshes with and without mangroves ($p = 0.38$, $p = 0.35$, Fig. 3, Tables 1 and 2). Tidal elevation was not a significant factor for any of the comparisons of grass shrimp, crab, and fish abundance or biomass for these organisms among sites (Fig. 3, Tables 1 and 2). The interaction between tidal elevation and mangrove presence was not significant for crab and fish abundance nor for biomass of any of these groups, but the interaction term was significant ($P = 0.55$) for grass shrimp abundance (Tables 1 and 2) (see Figs. 3 and 4).

A metric MDS plot revealed that the greatest differences among samples were from marshes with and without mangroves and not from low and high tidal elevations, which was consistent with univariate analysis on abundances and biomass of grass shrimp, crabs, and fish. Because tidal elevation did not have a significant effect and had a smaller effect on the community than mangrove presence, ANOSIM was performed using mangrove presence as a factor influencing community differences. ANOSIM revealed significant effects of mangrove presence on overall community assemblages ($R = 0.101$, $p = 0.001$). However, R values approaching 0, such as the 0.101 value found here, suggests high variability within the data set. Since nekton are highly mobile and capable of moving among areas, this variability is not unexpected. The greatest dissimilarity between communities was attributed to grass shrimp, brown shrimp (*Penaeus aztecus*), and blue crabs that were more abundant in areas without mangroves and mud crabs (Panopeidae, Xanthidae) that were more abundant in mangrove areas (Table 3).

3.3. *Infaunal communities*

Polychaetes were significantly more abundant in marsh sites without mangroves ($F_{1,1} = 4.43$, $p = 0.06$), while tidal elevation did not significantly affect polychaete abundance ($F_{1,1} = 0.67$, $p = 0.43$ Fig. 5), and the interaction between mangrove presence and tidal height was not significant ($F_{1,1} = 0.55$, $p = 0.47$). Over 95% of the crustaceans collected were from the Tanaididae family. Like polychaetes, crustaceans, were significantly more abundant in marsh sites without mangroves ($F_{1,1} = 7.24$, $p = 0.03$). Tidal elevation did not significantly affect crustacean abundance ($F_{1,1} = 0.14$, $p = 0.71$ Fig. 5), and the interaction between mangrove presence and tidal height was not significant ($F_{1,1} = 0.01$, $p = 0.97$). Similar to nekton findings and consistent with ANOVA results, a metric MDS plot revealed that the greatest differences among infaunal communities were from samples taken from marshes with and without mangroves and not between tidal elevations (Fig. 6). ANOSIM revealed significant effects of mangrove presence on infaunal community assemblages ($R = 0.62$, $p = 0.001$). The global R value for mangrove

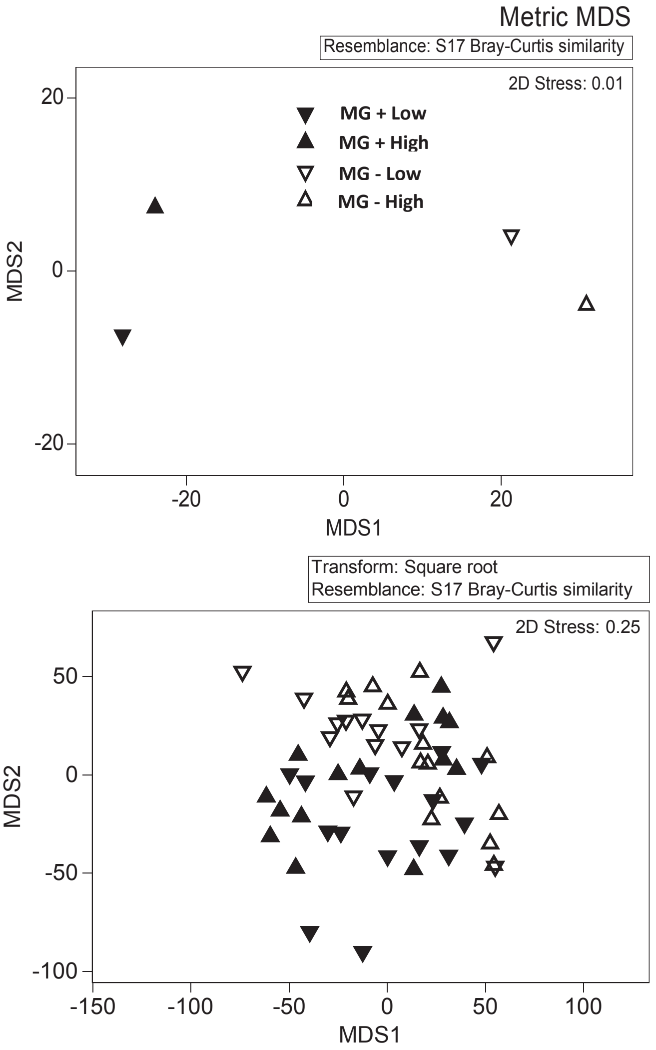

Fig. 4. Metric MDS plot showing (A) mean and (B) all distances between nekton samples from marshes with and without mangroves at low and high tidal elevations. Black triangles indicate mangroves were present (MG+), and white triangles indicate they were absent (MG-). Triangles point up for high elevation and down for low elevation.

effects on infaunal communities was much higher than found for nekton communities, probably because infaunal communities are far less mobile than nekton. The greatest dissimilarity between communities was attributed to Tanaidae, Nereididae, Amphipods, and Capitellidae (Table 4).

4. Discussion

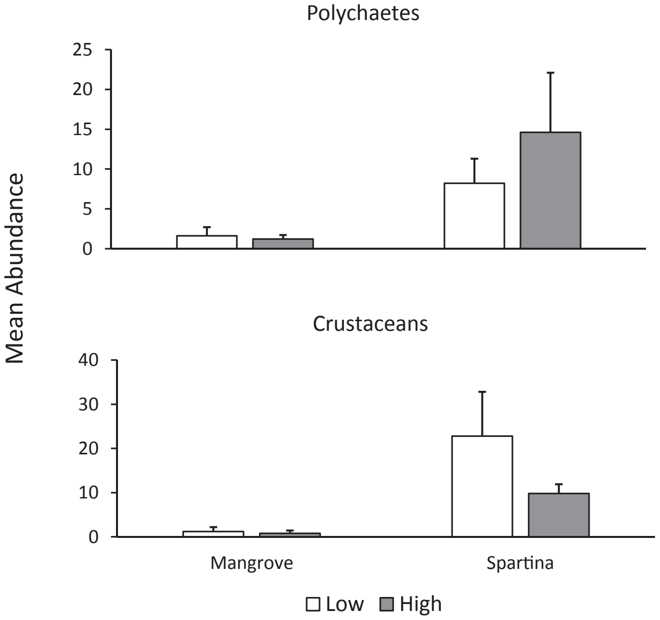

Fig. 5. Mean + SE abundances of polychaetes and crustaceans from infaunal samples collected in high and low tidal elevations from marshes with and without mangroves. Shaded bars are high tidal elevations, and x axis labels are marshes with abundant mangroves vs. those with only *Spartina*. Significantly more polychaetes and crustaceans were found in marshes without mangroves at $\alpha = 0.05$. Significant differences between tidal elevations were not found.

Climate change and invasion of exotic species, which in some cases are facilitated by a warming climate, are altering foundation species in coastal wetlands (Gonzalez et al., 2010; Barbier et al., 2011; Comeaux et al., 2012), often with profound impacts on ecosystem processes and associated fauna (Micheli et al., 2008; Armitage et al., 2015). Invasion by the common reed (*Phragmites australis*) decreased faunal abundance and diversity in US Atlantic salt marshes (Osgood et al., 2003; Kimball et al., 2010) as did changes in seagrass species in North Carolina (Micheli et al., 2008) and Texas (Ray et al., 2014). Expansion of mangroves into salt marshes has occurred in North and South America and Australia, decreasing marsh habitat (Saintilan et al., 2014). In the Gulf of Mexico, black mangroves are displacing *Spartina* and other marsh plants (Armitage et al., 2015), altering wetland elevations and ecosystem processes such as nutrient cycling (Comeaux et al., 2012).

Our findings indicate that changes from *Spartina* dominated to mangrove dominated coastal wetlands will have significant impacts on associated fauna in the Gulf of Mexico. Infaunal communities, blue crabs, and both grass and brown shrimp were less abundant in marshes with abundant mangroves, even when collected from low tidal elevations where *Spartina* was present. In contrast, mud crabs and fish were more abundant in marshes dominated by mangroves. Similarly, Lunt et al. (2013) found infauna to be lower in mangrove areas. In Louisiana, mangrove effects on nekton differed from those reported here (Caudill, 2005), with fish

Table 3
SIMPER analysis for nekton. Abundances shown were square root transformed for analysis.

Species	Mangrove	*Spartina*	Mangrove vs. *Spartina*	
	Mean abundance	Mean abundance	Dissimilarity	% Contributed
Grass shrimp (*Palaemonetes*)	2.71	4.74	19.3	29.8
Mud crabs (Xanthidae/Panopeidae)	1.59	1.05	9.9	15.3
Brown shrimp (*Penaeus aztecus*)	0.58	0.91	5.9	9.1
Blue crabs (*Callinectes sapidus*)	0.39	0.48	3.6	5.6

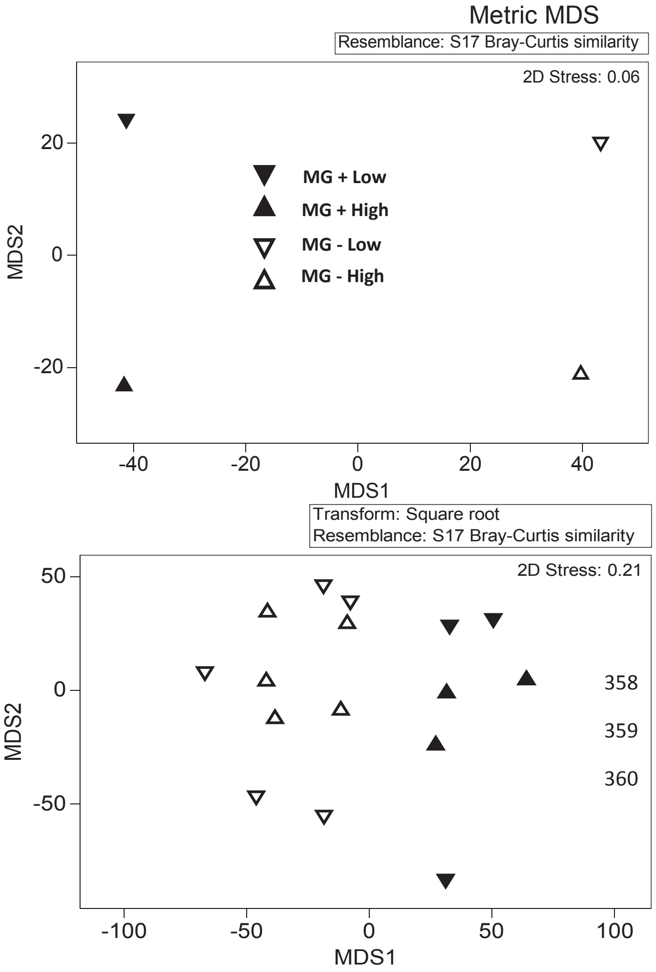

Fig. 6. Metric MDS plot showing (A) mean and (B) all distances between infaunal samples from marshes with and without mangroves at low and high tidal elevations. Black triangles indicate mangroves were present (MG+), and white triangles indicate they were absent (MG-). Triangles point up for high elevation and down for low elevation.

more abundant in marsh sites and shrimp more abundant in mangrove areas. Caudill's differing findings may be related to methodology as they used lift nets to capture organisms on outgoing tides and their community composition differed considerably. We found few gulf killifish *Fundulus grandis* and no white shrimp *Litopenaeus setiferus*, but, both were abundant in Caudill's (2005) study. Further, grass shrimp were abundant in our study but and rarely collected by Caudill (2005), perhaps due to variation in sampling gear. Regardless of whether differences in these studies result from different sampling methods or different communities in the northern vs. southern Gulf of Mexico, both studies suggest mangroves affect faunal composition. Our findings indicate mangrove presence influenced associated marsh fauna in adjacent areas that were dominated by other plant species (i.e. *Spartina*). We do not yet know how mangroves are influencing wetland species but hypothesize that mangroves alter food webs through changes in the outcomes of predatory interactions (Hammerschlag et al., 2010) and/or by affecting abiotic conditions and resource availability to make habitats less suitable for some species (Alongi et al., 2004; Castañeda-Moya et al., 2013; Comeaux et al., 2012).

Black mangrove edge habitats are used by predators as hunting corridors (Hammerschlag et al., 2010), and mangrove encroachment into *Spartina* marshes may alter food webs by changing the foraging environment for predators and prey. In sites with mangroves, fish and crabs were more abundant while infaunal organisms and grass shrimp, common prey items for fish and crabs, (Kneib and Wagner, 1994), were less abundant. Mangroves accumulate sediment, raising the tidal elevation and reducing emergence time for the areas where they are found (Comeaux et al., 2012). Thus, common wetland aquatic species would spend less time in the highest tidal elevations and more time in the fringing *Spartina* marshes. By altering the landscape, mangroves may place predators and prey in close proximity and concentrate them by reducing suitable habitat area, thereby altering encounter rates, predation levels, and food web structure.

Additionally, resource availability via detrital inputs is vastly different from woody mangroves and *Spartina*, and likely influence food webs through bottom-up forces (Alongi, 1998; Alongi et al., 2004; Castañeda-Moya et al., 2013). Geochemical processes, sediment accretion, and carbon sequestration and turnover differ significantly among black mangrove and *Spartina* habitats (Alongi et al., 2004; Castañeda-Moya et al., 2013; Comeaux et al., 2012), and the distribution of organisms, particularly infaunal species, are often influences by changes in these factors (Baguley et al., 2006). Mangroves may simultaneously influence both top-down and bottom-up factors, thereby influencing the diversity and abundance of associated fauna. Clearly more research is needed to elucidate the mechanisms by which mangroves affect associated fauna.

Tidal elevation and inundation often have significant effects on coastal communities, influencing nekton abundance in coastal wetlands (Rozas and Minello, 1998; Rozas and Zimmerman, 2000). Brown shrimp and grass shrimp can be more abundant at lower tidal elevations (Minello et al., 1994), but in our study, tidal elevation did not significantly affect community assemblages or abundances of individual organisms. Consistent with our findings, communities in Chesapeake Bay were not significantly different in salt marshes between low and high tidal elevations (Posey et al., 2003). We sampled at the lowest tidal elevations possible that would allow us to collect organisms in both *Spartina* and mangrove areas, and perhaps the differences in tidal elevations were not large enough to observe differences seen in other studies (Rozas and Zimmerman, 2000). Regardless, the presence of mangroves influenced community composition at the lowest elevations that were dominated by *Spartina*, independent of tidal height sampled, which provides strong evidence that mangroves are influencing wetland fauna.

Table 4
SIMPER analysis for infauna. Abundances shown were square root transformed for analysis.

Species	Mangrove	Spartina	Mangrove vs. Spartina	
	Mean abundance	Mean abundance	Dissimilarity	% Contributed
Tanaidae	0.14	2.69	23.4	27.9
Nereididae	1.23	1.28	14.5	17.3
Amphipod	0.34	1.51	13.2	15.8
Capitellidae	0	1.04	10.2	12.2

Vegetation shifts are occurring across the globe in response to anthropogenic effects including climate change (Gonzalez et al., 2010), which can alter fauna that utilize these habitats (Micheli et al., 2008; Ray et al., 2014). Both nekton and infaunal communities were significantly different in locations where mangroves became established, suggesting that mangrove expansion into marsh areas previously dominated by *Spartina* will have significant effects on estuarine food webs and biodiversity. Our results provide a baseline for future studies examining effects of mangrove encroachment on fauna that inhabit coastal wetlands. The mechanisms by which mangroves are affecting fauna and the broader ecosystem consequences of faunal changes requires further investigation, but understanding how these changes affect alter species diversity and abundance are necessary for management, mitigation, and conservation of coastal wetlands and associated species.

Author contributions

DLS, JAS, and CT conceived the idea and designed the experiment. DLS and CT acquired funding. DLS, JAS, and MD collected the samples and generated the data. DLS, JAS, MD, and CT analyzed the data, and then wrote and edited the manuscript.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2017.02.005.

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