Mangrove expansion into salt marshes alters associated faunal communities

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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 Peneaus shrimp (e.g., Peneaus 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.

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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 filamentum (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...
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 facilitates 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; Arnitage 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 Bertiess, 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 Mendelssohn, 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 °C, 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.](image-url)
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 x 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 m² 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% isopropl alcohol. All organisms were identified to the lowest taxonomic level possible for use in multivariate analyses. 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 using a 500 μm sieve and transferred to jars containing 45% isopropl 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.
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 α = 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.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of squares</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass shrimp abundance (F = 4.03, P = 0.01)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mangrove Presence</td>
<td>2.47</td>
<td>1</td>
<td>8.34</td>
<td>0.006</td>
</tr>
<tr>
<td>Tidal Elevation</td>
<td>0.002</td>
<td>1</td>
<td>0.01</td>
<td>0.93</td>
</tr>
<tr>
<td>Mangrove Presence*Tidal Elevation</td>
<td>1.15</td>
<td>1</td>
<td>3.38</td>
<td>0.05</td>
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<tr>
<td>Crab abundance (F = 4.03, P = 0.032)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mangrove Presence</td>
<td>0.99</td>
<td>1</td>
<td>0.77</td>
<td>0.38</td>
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<tr>
<td>Tidal Elevation</td>
<td>2.78</td>
<td>1</td>
<td>2.15</td>
<td>0.15</td>
</tr>
<tr>
<td>Mangrove Presence*Tidal Elevation</td>
<td>1.68</td>
<td>1</td>
<td>1.30</td>
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<tr>
<td>Fish abundance (F = 4.03, P = 0.04)</td>
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<td></td>
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<tr>
<td>Mangrove Presence</td>
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<td>Tidal Elevation</td>
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<td>0.70</td>
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<tr>
<td>Mangrove Presence*Tidal Elevation</td>
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<td>0.13</td>
<td>0.72</td>
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Crab biomass (F = 1.14, P = 0.33)

<table>
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<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
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<tr>
<td>Mangrove Presence</td>
<td>0.32</td>
<td>1</td>
<td>0.85</td>
<td>0.35</td>
</tr>
<tr>
<td>Tidal Elevation</td>
<td>0.87</td>
<td>1</td>
<td>2.4</td>
<td>0.12</td>
</tr>
<tr>
<td>Mangrove Presence*Tidal Elevation</td>
<td>0.24</td>
<td>1</td>
<td>0.66</td>
<td>0.41</td>
</tr>
</tbody>
</table>

Fish biomass (F = 3.17, P = 0.04)

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of squares</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mangrove Presence</td>
<td>1.99</td>
<td>1</td>
<td>8.77</td>
<td>0.006</td>
</tr>
<tr>
<td>Tidal Elevation</td>
<td>0.003</td>
<td>1</td>
<td>0.01</td>
<td>0.90</td>
</tr>
<tr>
<td>Mangrove Presence*Tidal Elevation</td>
<td>0.15</td>
<td>1</td>
<td>0.66</td>
<td>0.42</td>
</tr>
</tbody>
</table>

3.3. Infaunal communities

Polychaetes were significantly more abundant in marsh sites without mangroves (F1, 1 = 4.43, p = 0.06), while tidal elevation did not significantly affect polychaete abundance (F1, 1 = 0.67, p = 0.43 Fig. 5), and the interaction between mangrove presence and tidal height was not significant (F1, 1 = 0.55, p = 0.47). Over 95% of the crustaceans collected were from the Tanaisidae family. Like polychaetes, crustaceans were significantly more abundant in marsh sites without mangroves (F1, 1 = 7.24, p = 0.03). Tidal elevation did not significantly affect crustacean abundance (F1, 1 = 0.14, p = 0.71 Fig. 5), and the interaction between mangrove presence and tidal height was not significant (F1, 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

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 (Peneaus 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).
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

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>
<thead>
<tr>
<th>Table 3</th>
<th>SIMPER analysis for nekton. Abundances shown were square root transformed for analysis.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Mangrove Mean abundance</td>
</tr>
<tr>
<td>Grass shrimp (Palaemonetes)</td>
<td>2.71</td>
</tr>
<tr>
<td>Mud crabs (Xanthidae/Panopeidae)</td>
<td>1.59</td>
</tr>
<tr>
<td>Brown shrimp (Penaeus aztecus)</td>
<td>0.58</td>
</tr>
<tr>
<td>Blue crabs (Callinectes sapidus)</td>
<td>0.39</td>
</tr>
</tbody>
</table>
able. We found few gulf killi

ging tides and their community composition differed consider-

Table 4

<table>
<thead>
<tr>
<th>Species</th>
<th>Mangrove Mean abundance</th>
<th>Spartina Mean abundance</th>
<th>Mangrove vs. Spartina Dissimilarity</th>
<th>% Contributed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tanaidae</td>
<td>0.14</td>
<td>2.69</td>
<td>23.4</td>
<td>27.9</td>
</tr>
<tr>
<td>Nereididae</td>
<td>1.23</td>
<td>1.28</td>
<td>14.5</td>
<td>17.3</td>
</tr>
<tr>
<td>Amphipod</td>
<td>0.34</td>
<td>1.51</td>
<td>13.2</td>
<td>15.8</td>
</tr>
<tr>
<td>Capitellidae</td>
<td>0</td>
<td>1.04</td>
<td>10.2</td>
<td>12.2</td>
</tr>
</tbody>
</table>
Vegetation shifts are occurring 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 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.

Acknowledgements

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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.

References