

Mangrove expansion into salt marshes alters associated faunal communities



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ARTICLE INFO

Article history:

Received 6 April 2016

Received in revised form

26 January 2017

Accepted 3 February 2017

Available online 4 February 2017

Keywords:

Spartina alterniflora

Avicennia germinans

Vegetation shift

Climate change

Shrimp

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.

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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 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 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; 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 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 south-east 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 $29 \text{ }^\circ\text{C} \pm 0.9 \text{ }^\circ\text{C}$ and $30 \text{ }^\circ\text{C} \pm 1.2^\circ$, 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

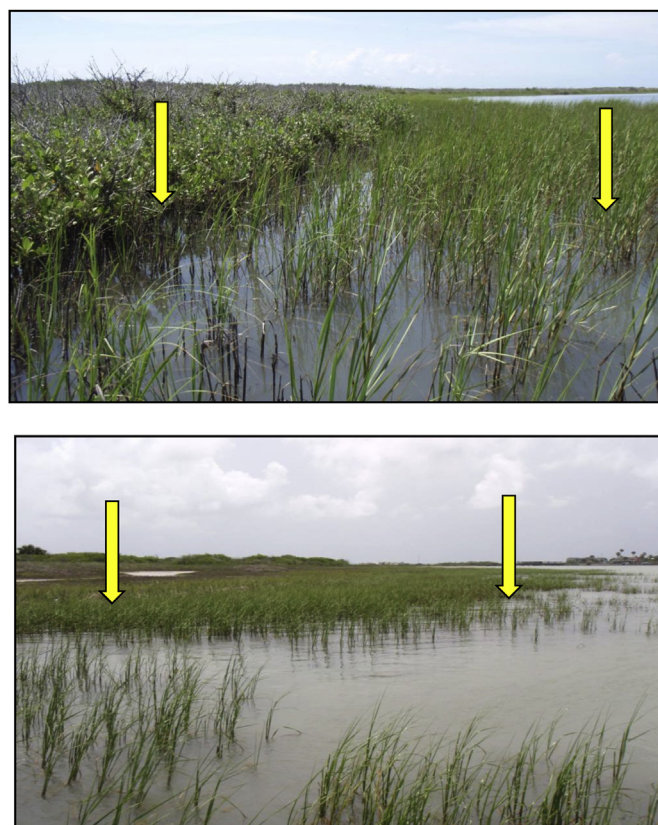


Fig. 1. Marshes with black mangroves (top) and without black mangroves (bottom). Black mangroves were present only at higher tidal elevations in a near monoculture once established. *Spartina* dominated at low and high elevations when mangroves were not present. Nekton and infaunal samples were collected 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.

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