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EFFECTS OF BIOTIC INTERACTIONS ON COASTAL WETLAND COMMUNITIES WITH APPLICATIONS FOR RESTORATION

by

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ABSTRACT

Coastal wetland plants serve as ecological engineers in a physiologically stressful environment and the loss of coastal wetlands can cause negative effects throughout the estuarine system. Due to increased degradation of coastal habitats worldwide, interest in restoration has increased around the world. An understanding of the biotic processes affecting species distribution and diversity is critical for future conservation, management, and restoration of coastal wetlands. The purpose of my study was to test the effects of biotic interactions on native coastal wetland plants and determine how these interactions may be incorporated into current and future restoration projects. I had three primary goals for my dissertation. First, I evaluated the effectiveness of natural regeneration of coastal wetland communities following hydrological restoration. Second, I examined effects of biotic interactions between mangroves and other wetland species by experimentally testing: 1) trapping capabilities of early successional plant species on *Rhizophora mangle* propagules, 2) effects of pre-dispersal propagule damage on native mangrove species, 3) facilitative and competitive interactions between the plants *Rhizophora mangle*, *Batis maritima*, *Sarcocornia perennis,* and the fiddler crab, *Uca pugilator* using mesocosms. Third, I evaluated the combined effects of biotic and abiotic interactions on survival and growth of *R. mangle* propagules during their first year of establishment using a manipulative field experiment. Results from my study increase our knowledge of the importance of biotic interactions in coastal wetland communities, their role in early successional stages, and have direct applications to coastal wetland restoration and management.

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CHAPTER 1. INTRODUCTION

In coastal wetlands, the colonization of substrate by plant species creates a structurally complex habitat, which supports fauna from neighboring marine, terrestrial, and estuarine habitats (Pennings and Bertness 2001). The plant species assemblage of coastal wetlands varies on a global scale with climate, exhibiting a latitudinal gradient from the temperate coastlines at higher latitudes to the tropical coastlines around the equator (Pennings and Bertness 2001). In colder climates, temperate salt marshes are dominated by a variety of halophytic grass species, including *Spartina* spp. and *Distichlis spicata* (Bertness 1991). In tropical climates, intertidal habitats are dominated by mangrove species (Odum and McIvor 1990; Tomlinson 1994). Coastal wetlands at the temperate-subtropical climate boundary have a mix of both temperate and tropical flora (Odum and McIvor 1990; Schmalzer 1995).

Coastal wetlands are one of the most diverse ecosystems in the world and provide important ecosystem services to humans and support a diverse assemblage of fauna from the neighboring terrestrial, estuarine, and marine environments (Odum & McIvor, 1990; Lugo, 1998; Imbert et al., 2000; Dybas, 2002). Ecosystem functions include shoreline protection and stabilization, protection from flooding and storm surge, interception of nutrient-rich terrestrial run-off, water filtration, nutrient cycling, carbon sequestration and habitat for shelter, breeding, and nursery grounds for endangered species, threatened species and economically important marine fishes and invertebrates (Odum & McIvor, 1990; Alongi 2009). Mangroves and halophytes (e.g. *Spartina* species) serve as ecological engineers in a physiologically stressful environment and the loss of wetland habitat can have cascading effects throughout the estuarine system (Odum and McIvor, 1990; Alongi, 2002).

Anthropogenic influences, such as development, dredging, impoundment, and pollution, have damaged or changed the natural conditions in coastal ecosystems around the world (Odum and McIvor, 1990; Lugo, 1998; Alongi 2002). In the past fifty years, approximately 35% of mangrove habitat worldwide has been destroyed or degraded (Giri et al. 2011). Salt marshes are also increasingly threatened around the world, with a loss of up to 80% of marsh habitat in some developed countries (Pennings and Bertness 2001). Recent declines in total landings of commercial fisheries may be at least partially explained by the loss and alteration of wetland habitat (Alongi, 2002; Dybas, 2002). In addition to anthropogenic changes, one of the most significant threats to coastal wetlands over the next century is increased rates of sea level rise (Gilman et al. 2008). Sea level has risen at an average rate of 3.1 mm/yr since 1993 and is predicted to increase over the next century (IPCC 2014). Erosion of shorelines and loss of intertidal habitat is expected to worsen with continued sea level rise and increased extreme weather events (IPCC 2014). Coastal wetland vegetation can help mediate sea level rise through direct and indirect biotic processes and maintain desired elevations with moderate levels of sea level rise (Morris et al. 2002; Cahoon et al. 2006), however, habitat alterations within estuaries have changed natural community structure and threatens the resistance and resilience of coastal wetlands to future climate change. Because of the extensive degradation of coastal habitats worldwide, interest in restoration has increased in the past two decades.

Coastal wetland restoration techniques vary widely and are often dependent on the reason for restoration and the goals and expected outcomes of the project. For example, habitat that has been altered during the creation of berms, spoil piles, and mosquito impoundments require different methods than areas that are being restored following clearing for logging and aquaculture. In general, two methods are used to rehabilitate the vegetation community of coastal wetlands: natural regeneration and artificial regeneration (Field 1998). Natural regeneration is defined as the act of allowing natural recruitment to occur with minimal human assistance (Field 1998). Dredging, filling and impounding often alter the elevation of the marsh substrate and change the natural hydrological regime of the system (Baustian & Turner, 2006; Rey et al. 2012). Methods to restore hydrological restoration are often needed first to restore natural abiotic conditions (Lewis 2005). Following hydrological restoration, natural regeneration can occur if sufficient propagule and seed sources are available from the neighboring environments (Lewis 2005). In comparison, artificial regeneration is defined as the act of planting seeds, propagules or seedlings in areas without adequate natural regeneration (Field 1998). Artificial regeneration is often needed in areas where "propagule limitation" occurs and natural sources of wetland seeds and propagules are not available (Lewis 2005). Artificial regeneration methods are typically more expensive than natural regeneration due to labor and material costs and can result in an unnatural structure because projects often replant with only one or two species (Field 1998). Walters (2000) found sites planted with only one or two species remained low in plant diversity after fifty years of planting, suggesting areas without sufficient natural recruitment need to be planted with a variety of species in order to recover natural diversity levels. The use of a variety of plant species during restoration activities may lead to a community structure that is more similar to reference sites (Field 1998). In addition, many mangrove restoration projects around the world do not address the cause of decline of mangroves and artificial regeneration methods have had limited success, with retention of propagules and small seedlings ranging between 1% and 20% (Gilman and Ellison 2007; Salgado Kent and Lin 1999; Lewis 2005; Samson and Rollon 2008; Kamali and Hashim 2011).

Coastal wetlands are often slow to recover and may require decades before structure and ecosystem function are similar to natural conditions (Field 1997; McKee and Faulkner 2000). Evaluating the success of rehabilitation projects is often tied to the initial goal of the project and can include determining the success rate of the planting, the cost effectiveness of the rehabilitation project, and the recovery and utilization of the restored site by flora and fauna (Field 1997). Whereas the majority of restoration projects tend to have at least a short-term monitoring plan for vegetation recovery of sites following restoration, little long-term monitoring has occurred to determine if rehabilitated areas support the large diversity of fauna supported by these coastal systems (Field 1997).

Plant distributions in tropical and subtropical coastal wetlands are influenced by tolerances to abiotic conditions and direct and indirect effects of community interactions, including competition, facilitation and consumer pressure (Odum and McIvor 1990; McKee 1995; Duke et al. 1998; Lacerda et al. 2001; Alongi 2009). Historically, the primary factors controlling vegetation structure and function in coastal wetlands were expected to be abiotic factors, such as tidal inundation and salinity, which acted as a type of bottom-up control on plant populations (Odum and McIvor 1990, Cannicci et al. 2008, Alongi 2009). Although the importance of physiologically stressful abiotic conditions of wetland habitat cannot be overlooked (Odum and McIvor 1990, McKee 1995, Elster et al. 1999, Alongi 2009), an increasing amount of research has documented the importance of biotic factors on mangrove populations through positive and negative interactions (Cannicci et al. 2008, Alongi 2009, Feller et al. 2010). Biotic interactions with flora and fauna, including competition, facilitation, and herbivory, can directly and indirectly affect plant growth, survival, and reproduction (Robertson et al. 1990, McKee 1995, Elster et al. 1999, Minchinton and Dalby-Ball 2001, Cannicci et al. 2008, Alongi 2009, Feller et al. 2010). Biotic interactions potentially have an important role in natural regeneration of coastal wetlands and research exploring biotic processes affecting wetland plants is critical for future conservation, restoration and management of ecosystems worldwide (Milbrandt and Tinsley 2006; Stevens et al. 2006; Moreno-Mateos et al. 2012; Peterson and Bell 2012). In order to improve restoration of coastal wetlands, both abiotic and biotic processes within these systems needs to be addressed.

A defining characteristic of coastal wetlands is the physiologically stressful conditions of the intertidal habitat. Frequent tidal flooding with saltwater results in saturated, anoxic soils and introduces high amounts of salts to the substrate (Odum and McIvor 1990; Pennings and Bertness 2001). Plant distribution is strongly affected by a species' tolerance to inundation and salinity (Bertness 1991; Ward et al. 2006). Salinity tolerances of mangrove and halophyte species are based on biochemical mechanisms that assist salt regulation, which can include changes in the stomata, an increase in leaf thickness as the tree ages to develop succulent leaves for water storage, changes in the ability to exclude or secrete salt, and changes in enzyme activation and protein synthesis (Odum and McIvor 1990, Tomlinson 1994).

Spatial patterns of vegetation are related to changes in elevation of the substrate from the shoreline towards the upland boundary, which affects the frequency and extent of tidal inundation (Zedler et al. 2003; Alongi 2009). The frequency and depth of inundation tends to decrease with increasing distance from shore, as the elevation of substrate increases towards the landward portion of the marsh. Natural elevations are determined by geomorphological characteristics and the rate of sediment deposition and erosion, accretion and subsidence (Pennings and Bertness 2001). Sediment deposition leading to a change in elevation of as little as ten centimeters can significantly alter the composition of plant species (Lugo 1998; Zedler and Callaway 1999). Across the elevation gradient within a marsh, three separate zones with distinct abiotic differences can be identified: low, middle and high marsh (Pennings and Bertness 2001). The low marsh is immediately adjacent to shore, at the lowest elevation, and has the most frequent tidal flooding. Low marsh sediments tend to have the most saturated and anoxic soils within the marsh because of frequent flooding, but have intermediate soil salinities compared to the other two zones because regular tidal flushing prevents the accumulation of salts (Hacker and Gaines 1997; Pennings and Bertness 2001). The middle marsh is found at intermediate elevations and receives less frequent tidal flooding. Soil salinities in middle marshes are usually the highest of the three zones, particularly in sub-tropical and tropical climates, because infrequent flooding combined with high evaporation rates result in the accumulation of salt within the substrate (Pennings and Bertness 2001). The high marsh is adjacent to the landward boundary and receives irregular flooding. This zone has infrequent flooding with saltwater, increased freshwater input from rainfall and upland run-off, leading to the lowest soil salinities and higher soil oxygen levels than the low and middle marsh (Hacker and Gaines 1997; Pennings and Bertness 2001).

The distribution of plant species in marshes is influenced by abiotic factors; however, positive and negative interactions with other flora and fauna, including competition, facilitation and consumer pressure, also play important roles (Bertness 1991; Pennings and Bertness 2001; Zhang et al. 2008; Feller et al. 2010). Past research has primarily focused on negative interactions, such as competition and herbivory, and the role of positive interactions in coastal wetlands has been less studied. Direct positive interactions were defined by Hacker and Gaines (1997) as "non-trophic interactions that increase the average individual fitness of at least one species involved in the interaction without negatively affecting any other species". This can include a range of interactions, including indirect and direct mutualisms and commensalisms (Bertness and Leonard 1997). In subtropical coastal wetlands, halophytic shrubs, grasses, and herbs can be found growing with mangroves, but the role of positive community interactions on growth, recruitment and distribution of many mangrove species is largely unknown (Stevens et al. 2006). In plant communities, the effect of positive interactions may potentially increase in physiologically stressful environments because the "benefits" gained can lessen the negative effects of abiotic conditions and decrease the "cost" of the interaction with other species (Bertness and Leonard 1997; Brooker et al. 2007; Zhang et al. 2008). For example, the physiological stressors of salt marsh habitats, such as anaerobic soils, flooding, soil drainage, and limited nutrients, can be ameliorated by facilitative interactions between flora and fauna (Bertness 1991).

One type of facilitation with important applications to ecosystem restoration involves the initial colonization of plant species, which then act as “nurse plants” for other establishing species (Niering et al. 1963; Lewis 1982; Lewis 2005; Padilla and Pugnaire 2006; Lopez et al. 2007; Brooker et al. 2008). The nurse syndrome is a type of facilitation where the seedlings are the beneficiaries of adult plants, the nurse plants, and this type of interaction can be common in early successional communities, creating an aggregated distribution of seedlings associated with the nurse plant (Brooker 2006; Lopez et al. 2007). Nurse plants can help secondary species overcome recruitment limitation and increase success of establishment (Young et al. 2005). Incorporating facilitation into restoration plans is becoming more common in terrestrial ecosystem restoration (Padilla and Pugnaire 2006; Halpern et al. 2007) and inclusion of positive interactions, like nurse effects, can lead to more ecologically-based restoration methods (Padilla and Pugnaire 2006; Brooker et al. 2008). Restoration applications with nurse plants have been beneficial in terrestrial reforestation programs, such as degraded Mediterranean systems (Maestre et al. 2001, Castro et al. 2004, Gomez-Aparicio et al. 2004); however, inclusion of facilitative interactions has been less common in restoration of aquatic systems (Halpern et al. 2007). Identifying co-occurring plant and mangrove interactions and understanding the mechanisms driving these interactions is needed for inclusion in mangrove restoration and management plans. An understanding of biotic processes affecting species distribution and diversity is critical for future conservation and management of these ecologically important systems and has numerous applications to restoration of coastal wetlands worldwide (Bertness and Leonard 1997; Hacker and Bertness 1999).

Purpose of Study

The purpose of my dissertation was to examine the effects of biotic interactions on native coastal wetland plants and determine how these interactions may be incorporated into current and future restoration projects. First, I evaluated the effectiveness of natural regeneration of coastal wetland communities following mosquito impoundment restoration. Second, I examined interactions between flora and fauna by experimentally testing: 1) trapping capabilities of early successional plant species on *Rhizophora mangle* propagules, 2) effects of pre-dispersal and post-dispersal propagule consumers on native mangrove species, 3) facilitative and competitive interactions between plants *Rhizophora mangle*, *Batis maritima*, *Sarcocornia perennis,* and the fiddler crab, *Uca pugilator* using mesocosms. Third, I evaluated the combined effects of biotic and abiotic interactions on survival and growth of *R. mangle* propagules during their first year of establishment using a manipulative field experiment. The results from my dissertation provide valuable insight into the recovery rates of wetland communities following mosquito impoundment restoration, the role of positive and negative interactions within wetland systems, potential nurse plants to be used in future restoration projects in Mosquito Lagoon, and serve as a conceptual framework for other wetland restoration projects.

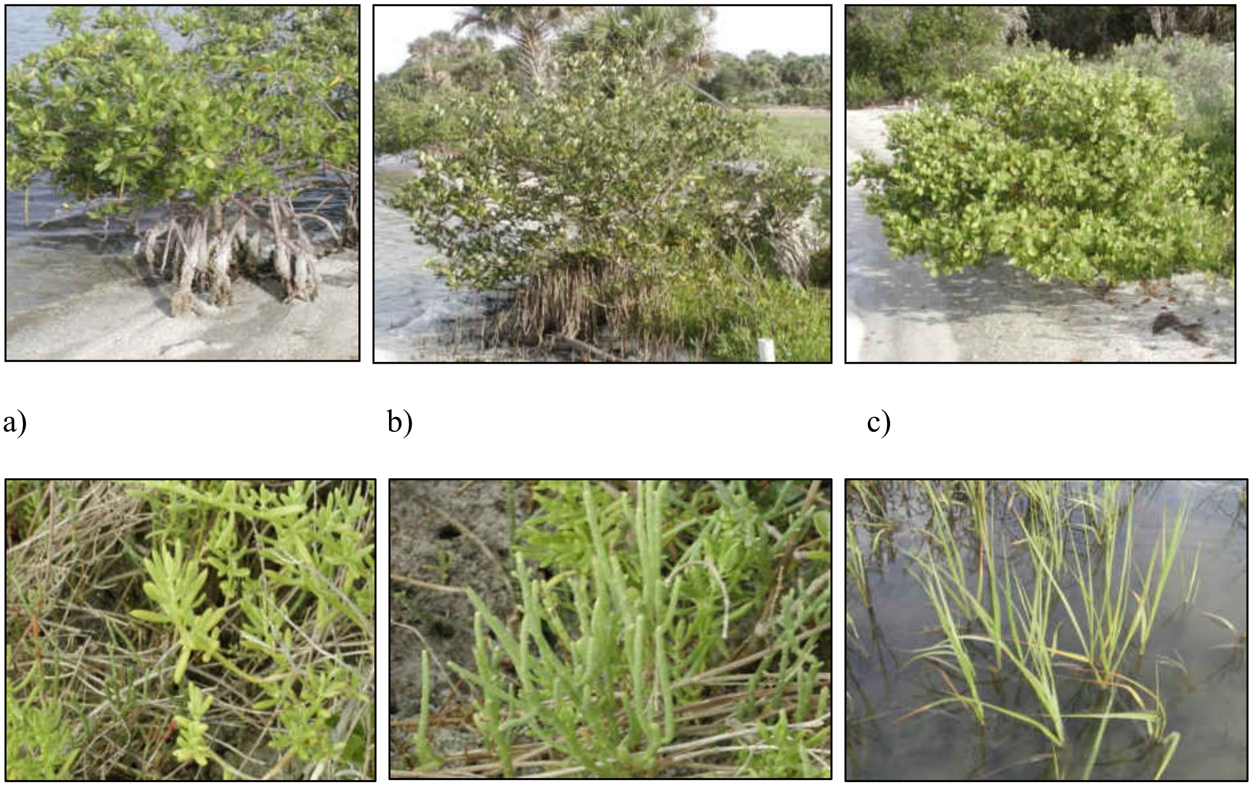
Study Site

This study was located in Mosquito Lagoon, in Canaveral National Seashore, FL (28° 53'05.81" N, 80°49'44.85" W). Canaveral National Seashore was established in 1975 and includes a mix of habitats ranging from the ocean and beach dunes to salt marsh and coastal hammocks (Green 2002). Approximately two-thirds of Canaveral National Seashore consists of the estuary, Mosquito Lagoon (Green 2002). Mosquito Lagoon is the northernmost portion of the Indian River Lagoon, a 250 km estuary located on the east coast of Florida. Currents in Mosquito Lagoon are primarily wind-driven and north and north-western winds are common during fall and winter months. Water levels in Mosquito Lagoon are microtidal and change seasonally, with high water season occurring in fall and winter (Schmalzer 1995). In Mosquito Lagoon, wetland vegetation is a mixed saltmarsh-mangrove community (Figure 1.1), with the temperate grass *Spartina alterniflora* Loiseleur (smooth cordgrass) coexisting with tropical mangrove species, *Laguncularia racemosa* (L.) C.F.Gaertrn (white mangrove), *Rhizophora mangle* L. (red mangrove), and *Avicennia germinans* (L.) L. (black mangrove) (Figure 1.2). Succulent halophytes *Batis maritima* L. (saltwort) and *Sarcocornia perennis* Mill. (perennial glasswort) dominate the understory of the wetland (Figure 1.2).

Figure 1.1. Coastal wetlands in Mosquito Lagoon, FL support both temperate and tropical plant species.

Study Species

My focal species for this study were the three native species of mangroves. *Rhizophora mangle* (Rhizophoraceae), is characterized by prop roots which originate from the trunk or branches and penetrate the soil beneath the tree (Figure 1.2a). The prop roots stabilize the tree and contain specialized structures called lenticels, which allow oxygen to diffuse into the aerenchyma (Odum and McIvor 1990). *Rhizophora mangle* can reach heights up to 25 m and has deep green leaves which are paler green on the underside of the leaves (Tomlinson 1994). *Rhizophora mangle* produces flowers year round (Fernandes 1999) and flowers are wind-pollinated and self-compatible (Tomlinson 1994). After flowering and pollination occur, long, buoyant propagules grow up to 30 cm before leaving the parent tree (Odum and McIvor 1990). These buoyant propagules disperse by water and are viviparous (Rabinowitz 1978).



a) b) c)

d) e) f)

Figure 1.2. Common plants in coastal wetlands in Mosquito Lagoon, FL include: a) *Rhizophora mangle* (red mangrove), b) *Avicennia germinans* (black mangrove), c) *Laguncularia racemosa* (white mangrove), d) *Batis maritima* (saltwort), e) *Sarcocornia perennis* (perennial glasswort), and f) *Spartina alterniflora* (smooth cordgrass).

Avicennia germinans (Avicenniaceae) is characterized by a shallow system of laterally extending roots emerging from the substrate, known as cable roots (Tomlinson 1994; Figure

1.2b). The cable roots contain pneumatophores with lenticels on the exposed portion and can extend up to 20 cm above the substrate (Odum and McIvor 1990). *Avicennia germinans* trees reach heights of 20 m and have narrow, elliptical leaves which are deep green on the upper surfaces and white on the lower surfaces (Tomlinson 1994). The leaves of *Avicennia germinans* are encrusted with secreted salt (Odum and McIvor 1990). White flowers form in the early summer months in Florida and are the largest in this genus at ten to thirteen millimeters (Tomlinson 1994). The flowers are pollinated by short-tongued insects, particularly honeybees (Tomlinson 1994). Its propagules are small, measuring two to three centimeters. These ovoid-shaped propagules are viviparous and disperse by hydrochory (Tomlinson 1994).

Laguncularia racemosa (Combretaceae), the white mangrove, lacks prop or cable roots, but contains lenticels on the lower portion of the trunk (Odum and McIvor 1990; Figure 1.2c). *Laguncularia racemosa* can reach heights over 15 m and have flat, oval shaped leaves that are up to seven centimeters long (Odum and McIvor 1990). This species is usually dioecious; however, there is some evidence of monoecious trees and self-fertilizing flowers (Tomlinson 1994). The flowers are four to five millimeters in diameter, have a greenish-yellow color and form in the summer months in Florida (Tomlinson 1994). Flowers are pollinated by insect vectors, mostly bees (Tomlinson 1994). The small, ovoid-shaped propagules measure approximately two centimeters and are cryptoviviparous, completing germination during water dispersal (Tomlinson 1994).

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CHAPTER 2. NATURAL REGENERATION OF COASTAL WETLAND COMMUNITIES FOLLOWING MOSQUITO IMPOUNDMENT RESTORATION

Abstract

Hydrology is a critical factor in wetland diversity and function and human alterations of hydrology can negatively impact wetland structure and function. Since the 1950s, approximately 70% of coastal wetlands associated with the Indian River Lagoon were impounded by the construction of dikes around perimeter of wetlands to control interior water levels for mosquito management. Impounding wetlands caused changes in community structure and function, with terrestrial native and non-native plants invading dikes and interior wetland communities affected by limited tidal flow and manipulation of water levels. In the northern Indian River Lagoon during the late 1990s, hydrological restoration began by mechanically leveling dikes to wetland elevations. Immediately after dike leveling, all vegetation was cleared and restored habitat underwent secondary succession with natural regeneration of plants and animals through dispersal from neighboring wetlands. The purpose of our study was to document the effect of dike removal and natural regeneration on abiotic conditions and community diversity at restored sites. Phase 1 of our study began in 2007 and used a space for time substitution methodology to evaluate different stages of recovery at five impoundments ranging from one month to eight years post-restoration. Field surveys were conducted at restored sites and reference marshes through 2010 and included abiotic factors (elevation, soil moisture, soil salinity) and biotic factors (vegetation, fiddler crabs, birds, and nekton). Post-restoration monitoring of impoundments documented significant reductions in elevation, leading to increases in soil moisture and soil salinity, and natural recovery of native plant and animal communities. Recruitment of plants and fiddler crabs was observed within one month of dike removal, however, recovery of coastal wetland structure was a slow process and restored sites were still different from reference marshes after eleven years post-restoration, particularly in plant cover and bird utilization. Our study identified several important factors in habitat recovery and provided management recommendations to guide future coastal wetland restoration, including: 1) target elevations for promoting natural hydrological properties, 2) effectiveness of natural regeneration following dike leveling, 3) benefits of conserving shoreline wetland vegetation during dike removal to enhance rate of recovery, and 4) importance of abiotic conditions for preventing non-native plant recruitment.

Keywords: ecological restoration, mangroves, mosquito impoundments

Introduction

Anthropogenic habitat alteration in estuaries has increased dramatically in the past century around the world, resulting in a loss of marine habitats and associated biodiversity (Alongi 2002; Dybas 2002; Alongi 2009; Palmer 2009; Giri et al. 2011). Coastal wetland habitat has been degraded by numerous human activities, including overharvesting, pollution, eutrophication, introduction of non-native species, dredging and filling for development, agriculture, aquaculture, and impounding for mosquito control (Montague et al. 1987; Brockmeyer et al. 1997, Alongi 2002; Dybas 2002; Alongi 2009; Rey et al. 2012). Alterations to coastal wetland habitat can directly or indirectly alter the hydrology of the system and negatively affect habitat quality and ecosystem services (Montague et al. 1987; Brockmeyer et al. 1997;

Dybas 2002; Rey et al. 2012). Restoration of natural hydrological conditions can lead to the return of natural structure and functions of coastal wetlands and benefit a diverse community of native organisms and adjacent estuarine systems (Brockmeyer et al. 1997; Turner and Lewis 1997; Lewis 2005; Nilsson et al 2010; Rey et al. 2012).

A common cause of alteration to coastal wetlands is impounding, which restricts tidal flow and changes hydrological properties of the ecosystem (Brockmeyer et al. 1997; Rey et al 2012). Impoundment of wetlands has occurred worldwide for numerous purposes, including pest management, wildlife management, water storage and flood control, aquaculture, and waste treatment (Rey et al. 2012). The location of this study is the northern portion of the Indian River Lagoon system, a 250 km estuary located on the east central coast of Florida (Dybas 2002). In the 1950s, coastal wetlands in the Indian River Lagoon system were impounded for mosquito management (Dybas 2002; Rey et al. 2012). Salt marsh mosquitoes (*Aedes* spp.) lay eggs on exposed substrate of infrequently flooded marshes and eggs hatch when the surface is flooded from rain or seasonal high tides (Brockmeyer et al. 1997; Rey et al 2012). To control mosquito breeding, impoundments were created by excavating substrate from neighboring marshes and creating dikes around the exterior perimeter of the marsh (Brockmeyer et al. 1997; Rey et al 2012). Water levels in the Indian River Lagoon are microtidal (<10 cm tide cycle) and change seasonally, with high water season occurring in spring and fall months (Smith 1987; Schmalzer 1995). Therefore, construction of dikes essentially isolated the interior wetlands from tidal influences and allowed for manipulation of water levels. Interior wetlands were flooded during mosquito breeding season to prevent mosquito reproduction (Montague et al. 1987; Brockmeyer et al. 1997; Taylor et al. 1998; Rey et al 2012), using either mechanical pumps to bring in seawater from the lagoon or with freshwater from artesian wells or upland run-off into the wetland (Rey et al 2012). Construction of mosquito impoundments represented a major alteration to this estuary and isolated an estimated 70% of coastal wetland habitat throughout the Indian River Lagoon system (Dybas 2002).

Impoundments altered the natural landscape by destroying existing vegetation, decreasing suitable area for halophytic vegetation, and facilitating the invasion of upland vegetation previously excluded from this habitat by abiotic constraints (Montague et al. 1987; Brockmeyer et al. 1997; Taylor et al. 1998; Rey et al. 2012). On the elevated surface of the dike, tidal inundation occurred infrequently and reduced habitat for intertidal plant and animal species. In addition to the abiotic and biotic changes on the dike around the perimeter of the wetland, the loss of tidal flushing also resulted in altered salinity levels of the interior marsh (Brockmeyer et al. 1997). Impoundments flooded with saltwater could become hypersaline following evaporation of water within the interior marsh, reducing diversity of community to only those species tolerant of high salinities (Brockmeyer et al. 1997). Frequent flooding resulted in loss of all emergent vegetation in some interior marshes due to intolerable water depths while other areas with a large freshwater input were dominated by cattails (*Typha spp.*) and other freshwater species (Brockmeyer et al. 1997). Additionally, impounding limited access to essential nursery and feeding habitats for estuarine fishes and reduced diversity and abundances within impounded wetlands (Gilmore et al. 1982; Harrington and Harrington 1982).

By the 1990s, restoration of Mosquito Lagoon impoundments began by breaching dikes and opening culverts, restoring tidal movements to the interior marsh (Brockmeyer et al. 1997; Taylor et al. 1998; Poulakis et al. 2002). Installation of culverts can have an immediate, positive effect on diversity and abundance of fishes within the reconnected wetlands (Taylor et al. 1998; Poulakis et al. 2002). Complete removal of the dikes followed in the late 1990s (Rey et al. 2012). Amphibious excavators were used to remove the substrate from the elevated dike surface and fill-in the adjacent borrow ditch. In some locations, the borrow ditch was completely filled in and connected restored areas to interior wetlands, however, in some areas there was not enough material to fill-in the ditch and a narrow, shallower, remnant borrow ditch remained (R. Brockmeyer and M. Donnelly, personal observation). After substrate was leveled to natural wetland elevations, tidal flow was restored across the entire restored area, reconnecting interior marshes to the estuary (Rey et al. 2012).

After this type of hydrological restoration, the system undergoes secondary succession and provides an opportunity for research evaluating successional trajectories in these sub-tropical coastal wetlands. Natural regeneration of plant communities can begin immediately after hydrological restoration when sufficient seeds and propagules are available from neighboring areas (Brockmeyer et al. 1997; Turner and Lewis 1997; Field 1999; Lewis 2005; Rey et al. 2012). Brockmeyer et al. (1997) reported immediate recruitment of native plants to a barren mudflat previously inundated year-round after the installation of culverts restored natural tidal flow to impoundments in Indian River Lagoon, FL. In Germany, opening the dikes led to natural recruitment of native saltmarsh vegetation, with 75% of the surface vegetated after five years

(Bernhardt and Koch 2003). In addition to promoting the development of native wetland communities, restoration of hydrological properties can also prevent non-natives from recruiting to the open habitat. Intertidal habitats are often resistant to invasion by non-native plant species due to the physiologically stressful environment (Lugo, 1988). Restoration techniques that remove barriers to tidal flow can improve habitat both by promoting native plant communities and reducing potential for non-natives' invasion and establishment within the estuarine habitats.

Success of costal wetland restoration projects may be increased by focusing less on individual services or species (i.e. planting of mangroves) and instead seeking restoration solutions to improve ecosystem resilience and long-term sustainability (Moberg and Ronnback 2003), such as hydrological restoration to restore natural conditions and promote colonization of native species (Lewis 2005). In riparian and wetland habitats, restoration methods utilizing natural dispersal through hydrochory can be applied to larger areas, completed with lower project and labor costs, and maintain local genetic variation and adaptations (Nilsson et al. 2010). Our study evaluated the effects of mechanically leveling dikes to restore hydrological characteristics on native flora and fauna following restoration. Phase 1 of this study documented the diversity and abundance of vegetation, fiddler crabs, and birds using a space for time substitution methodology at five restored impoundments in different stages of recovery (one month to eight years) from 2007-2010. In October 2008, fishes and mobile invertebrates were added to the monitoring protocol and monitored through 2010. Results from phase 1 provided scientific assessment of the effectiveness of dike removal and guided a second phase of mosquito impoundment restoration at seven additional impoundments during 2009-2010. Phase 2 had three primary objectives: 1) restore natural tidal hydrology, 2) restore native plant populations, and 3) increase fiddler crab utilization of habitat. Results from this study document the effectiveness of hydrological restoration and natural regeneration, provide restoration and management applications for coastal wetlands, and provide insight into successional processes in sub-tropical systems.

Methods

Study Site

Twelve restored impoundments were monitored during this study (Phase 1: D-12S, D-12N, C-8, V-1, V-2; Phase 2: T-41, T-42, T-43, T-35, T-37B, C-20B, T-34; Figure 2.1). Three impoundments (D-12S, D-12N, C-8) were in Mosquito Lagoon and managed by Canaveral National Seashore. Five impoundments (V-1, V-2, T-41, T-42, T-43) were in Mosquito Lagoon and are co-managed by Merritt Island National Wildlife Refuge and Canaveral National Seashore. Four impoundments (T-35, T-37B, C-20B, and T-34) were in the Indian River and co-managed by NASA and Merritt Island National Wildlife Refuge. Post-restoration monitoring during phase 1 occurred at five individual impoundments and two reference marshes (Figure 2.1). Impoundments were divided into seven age classes, based on the date of dike removal (year of restoration in parentheses): V1 (1999), V2 (2000), D-12 South 1 (2003), D-12 South 2 (2004), D-12 South 3 (2006), D-12 North (February 2007), C-8 (September 2007). One impoundment, D-12S, was divided into 3 sections because it was restored over a three year time period. C-8 was monitored before and after restoration. All other impoundments were in different stages of recovery at the start of this study and ranged in time since restoration from one month to eight years. Within each of the restored impoundment age classes or reference marshes, 5 replicate sites were randomly chosen using ArcGIS (45 total sites).

Phase 1

Monitoring at each site documented elevation, soil characteristics and diversity and abundance of plants, fiddler crabs, birds, and nekton (Figure 2.2a). Relative change in elevation was estimated with a laser level (Johnson) and stadia rod (Crain). Measurements were taken at 1-m intervals along a 30 m permanent transect, running perpendicular to the shoreline, from water level in the intertidal region into the interior marsh. Elevation surveys were completed once a year, from September 2007-September 2010. Soil salinity and soil moisture were measured in the middle of restored impoundment (10 m from shoreline) and in the interior marsh (30 m from shoreline) along the elevation transect during September of each year. Soil moisture was measured by inserting an Aquaterr soil probe into the upper 12 cm of soil. Soil samples were taken with a soil probe of the upper 10 cm of substrate and returned to the lab for soil salinity analysis. Samples were air dried for one to three weeks, depending on moisture content, and soil salinity was then estimated by mixing distilled water and soil (2:1 ratio), allowing it to settle for 24 hrs and measuring the salinity of the supernatant with a handheld refractometer.

To measure vegetation, five 0.25 m^2 quadrats were marked 5 meters apart, parallel to shoreline in the following zones: zone 1- front restored marsh (intertidal region), zone 2- middle restored marsh (5 m from shoreline), zone 3- rear restored marsh (10 m from shoreline), and zone 4- interior marsh (30 m from shoreline). The same quadrats were monitored during each survey. All plants within quadrats were identified to species and counted. Mangrove species were measured and classified into one of three size categories: 1) small < 25 cm, 2) medium = 25 to 75 cm, 3) large > 75 cm. Total percent cover was estimated using a 2 x 5 grid marked on quadrat and recorded as number of points out of ten with vegetation. All sites were monitored every four months, from February 2007-October 2010. Two impoundments, D-12N and C-8, were restored in 2007 and monthly vegetation monitoring occurred at these two impoundments for the first year following restoration.

Density of fiddler crabs was estimated in one 0.25 m^2 quadrat in the zones described above for plant surveys. The location of quadrats was determined using a random number generator in Microsoft Excel along a 50 m transect and different quadrats were surveyed each monitoring period. Within each quadrat, the top 20 cm of substrate was removed with a small shovel, substrate was sifted through a 2 mm sieve with saltwater from lagoon, and all fiddler crabs were counted and identified to species. The number of fiddler crab burrows and total percent cover was recorded prior to sifting of substrate. All sites were monitored every four months, from March 2007-November 2010.

Birds were monitored in 100 m^2 quadrats (10 m parallel to shoreline x 10 m perpendicular to shoreline) at each site. Each site was observed for 20 minutes during morning hours using binoculars at a minimum distance of 100 m from quadrat. Birds present within the marked areas were identified to species and behavior (i.e. foraging, flying, loafing) was recorded. All sites were monitored every four months, from April 2007-December 2010.

Breder traps were used to capture fish and mobile invertebrates (Fulling et al. 1999). Breder traps consisted of a 30 x 15 x 15 cm box constructed of 15 mm thick plexiglass. At one end, two wings, 30 x 15 cm (5 mm thickness), were inserted into the box to create a V-shaped opening to allow for the capture of fish swimming along the shoreline. Breder traps were placed at the anterior shoreline of the restored impoundments and control marshes at 45 total sites. The traps were left in place for 4 hr during morning hours and organisms captured in traps were identified to species. Sites were monitored every four months, from October 2008-October 2010.

Statistical Analysis

Abiotic variables (maximum elevation, soil moisture, soil salinity) and plant species richness, plant percent cover, and plant density were compared using generalized linear model selection, starting with a fully saturated model and followed by removal of non-significant factors in a step-wise manner (R software; R 2.14.1; Crawley 2007). Simplified models were compared using the ANOVA function to detect significant changes in deviance when terms were removed. Initial model for soil moisture and soil salinity included the factors year of data collection, time since restoration, habitat type, and zone (10 m or 30 m from shoreline). Time since restoration was calculated from the month and year impoundment was restored to month and year of each monitoring time. At the start of our study, we estimated communities at control wetlands to be eighteen years into recovery after severe freezes in late 1980s and this was used as the starting value for time since restoration factor for control wetland sites. Reference values were control wetlands (habitat type), 2007 (year), 10 m from shoreline (zone) when applicable. For plant variables (percent cover, total plant density, and species richness) subsamples (quadrats) in each zone within each impoundment age class measured over time were averaged in order to reduce the frequency of zeroes from the dataset and prevent pseudoreplication prior to analyses. For variables in units of percent (soil moisture, percent cover), quasibinomial distribution was used for analysis as recommended by Crawley (2007) for percent values.

Non-metric multidimensional scaling was used to compare similarity of community structure of plants, fiddler crabs, birds, and nekton at impoundments in different stages of recovery with reference marshes and changes in community structure through time. Separate ordination plots were generated and compared for each of the four groups of taxa (vegetation, fiddler crabs, birds, nekton). For vegetation data, the average number of individuals of each species per year (2007-2010) was calculated for restored wetlands and interior wetlands at each impoundment age class or control wetland and used in the primary matrix. Primary matrices for fiddler crabs, birds, and nekton analyses included the total number of each species during years of monitoring for each impoundment age class or control wetland. A second matrix was included to evaluate the influence of year, time since restoration and site in all analyses. Secondary matrices for vegetation and fiddler crabs included zone (restored wetland or interior wetland), mean maximum elevation, and mean soil moisture. Analyses were performed with PC-ORD software and followed the guidelines of McCune and Grace (2002). Initial analysis used a random starting configuration, 250 runs of real data, 250 randomized runs, and Monte Carlo test of significance to identify the optimal number of dimensions for final run. Final analysis used the suggested dimensionality and the optimal configuration from the initial analysis as the starting configuration (McCune and Grace 2002). Ordination plots were visually inspected for clustering of sites based on major factors. Kendall correlations for species and abiotic variables were compared to identify influential variables on community structure.

Species with strong influences over community structure in ordination plots (tau> 40%) were analyzed individually with general linear model selection for count data to identify significant factors on abundances (R software; R 2.14.1; Crawley 2007). Prior to analyses, individual species data from subsamples within each impoundment age class measured over time were averaged in order to reduce the frequency of zeroes from the dataset and prevent pseudoreplication. For models with plant and fiddler crab species, average counts of each species per 0.25 m^2 quadrat at each impoundment age class or control wetland for each monitoring time was calculated by zone. For models with bird and nekton species, average counts of each species per survey or trap was calculated for each monitoring time. Factors included in initial saturated model were habitat type (impoundment, control wetland), time since restoration, location of sites (east vs. west in Mosquito Lagoon), zone (1-4, plant and fiddler crab species models only), month of monitoring, and year of monitoring. Non-significant factors were removed in a step-wise manner and simplified models were compared using the ANOVA function to detect significant changes in deviance when terms were removed. References for individual contrasts for categorical factors were as follows: habitat type: control wetland; location of sites: east; month of monitoring: February (plants), July (fiddler crabs), April (birds); year of monitoring: 2007. For all statistical analyses, minimum *p*-value for evaluating significance was 0.05.

Phase 2

Seven impoundments restored between 2009 and 2010 were included in phase 2 monitoring (T-41, T-42, T-43, T-35, T-37B, C-20B, T-34; Figure 2.1). At each impoundment, one location was randomly chosen using ArcGIS software. Post-restoration monitoring occurred for two years and four parameters were selected from those evaluated during phase 1 as effective for evaluation during the early stages of recovery; two parameters were abiotic characteristics, elevation and soil moisture, and two were biotic characteristics, plant cover and fiddler crab density (Table 2.1). All sites were monitored before restoration, one month post-restoration, and then every six months through two years. Monitoring design and methods were similar to those used in Phase 1 (Figure 2.2b) and differences are described below.

One elevation transect was established at each impoundment prior to substrate leveling from lowest observed water line to the interior marsh (25-m in length), perpendicular to the shoreline, using the same methods described above for phase 1. Soil moisture was measured with a soil moisture probe (Aquaterr M-300) inserted 10 cm into substrate in each quadrat in all four zones described below for vegetation. Soil salinity was measured by taking one sample in each vegetation monitoring zone from each site and analyzing in lab as described above for phase 1.

To measure vegetation, five 0.25 m^2 quadrats were randomly marked along 30-m transects, parallel to shoreline, in four zones as described for phase 1. Native plants along shoreline were conserved when dikes were leveled and zone 1 was adjacent to but did not include remaining shoreline vegetation. Locations of quadrats were generated using a random number generator in EXCEL for each site during the initial monitoring survey and the same quadrats were evaluated during all subsequent monitoring surveys. Individual quadrats were marked with small red flags and the GPS location was recorded. Plants within quadrats were identified to species and counted. Total percent cover, percent cover of native species, and percent cover of non-native species were estimated using a 5 x 2 grid marked on a 0.25 m^2 quadrat. Fiddler crabs were recorded in three randomly located 0.25 m^2 quadrats all sites in zones described above for vegetation surveys (different quadrats were used for vegetation and fiddler crabs). In each quadrat, total number of fiddler crab burrows was counted. At one of the three quadrats, 20 cm of substrate was removed and sifted through a 2 mm sieve with saltwater and all fiddler crabs were removed. Organisms were identified and counted in the field and released. Locations of quadrats were generated using a random number generator in EXCEL for each site and different quadrats were used for each monitoring survey because of the removal of substrate.

Statistical Analyses

Paired t-tests were used to compare maximum elevation of each location before and after restoration. Percent soil moisture, species richness, percent cover of native and non-native vegetation, and fiddler crab densities was compared using generalized linear modeling as described above for Phase 1.

Results

Elevation

Phase 1

Prior to substrate leveling, mean relative elevation of peaks of dikes was over one meter compared to MLLW (Figure 2.3a). After substrate leveling, mean relative elevation of restored wetlands was 25 cm or less and was similar to elevations recorded from reference marshes

(Figure 2.3b). All restored sites were inundated during high water seasons and water depths ranged between 0 cm and 34 cm.

Phase 2

Before dike removal at Phase 2 impoundments, maximum values of elevation were over 50 cm above lowest observed water level (Figure 2.4a). Maximum elevations after restoration (mean ± SE: 13.2 ± 1.1 cm) were significantly lower compared to pre-restoration (64.0 ± 6.5 cm; paired t-test: $t= 8.2$, $df= 6$, $p < 0.001$; Figure 2.4b). After dike removal, borrow ditches were filled and restored marsh elevations were similar to elevations of interior marshes (Figure 2.4a). After restoration, tidal inundation was observed across all three zones of restored impoundments during high water season, and water depths ranged between 0 cm and 26 cm.

Soil Moisture and Salinity

Phase 1

The minimal adequate model for soil moisture at all restored impoundments and reference marshes found significant variation in year of data collection ($p< 0.001$) and habitat type ($p= 0.005$; Table 2.1, Figure 2.5a). At all sites, mean soil moisture was significantly lower in 2008 compared to 2007 ($p< 0.001$). There was significant differences between habitat types of restored impoundments and reference marshes ($p= 0.007$). Overall, soil moisture at restored impoundments varied between 59% and 99% in the restored zone and between 61% and 99% in the interior marsh. At reference marshes, soil moisture ranged between 91% and 99% 10-m from the shoreline and 88% to 99% 30-m from the shoreline. There was no significant difference between zones (10 m, 30 m from shoreline) and this term was removed from the final model. On dikes at C-8 before restoration (August 2007), mean soil moisture (±SE) was 57.5 ± 1.3%. At both D-12N and C-8 during one month to two years post-restoration, mean soil moisture ranged between 75% and 99%, with a mean (± SE) of 91.0 ± 0.8%.

The only significant factor in the minimal adequate model for soil salinity was year of data collection ($p < 0.001$; Table 2.1, Figure 2.5b). Soil salinity was higher at all sites during years 2008, 2009, and 2010 compared to 2007 ($p < 0.001$ for all comparisons). Soil salinities 10 meters from the shoreline ranged between 20 ppt to 73 ppt at restored impoundments throughout this study. Highest soil salinities were observed at restored impoundments during 2009, however, there was no significant differences between habitat types or zones and these factors were removed from the final model.

Phase 2

The mean soil moisture (% ± SE) before restoration was 91.2 ± 0.9% in zone 1, 72.7 ± 0.9% in zone 2, 85.4 ± 1.1% in zone 3, and 88.7 ± 0.7% in zone 4 (Figure 2.6a). After restoration, mean soil moisture was greater than 90% in all zones after six months post-restoration through two years post-restoration (Figure 2.6a). There were significant increases in soil moisture with time since restoration ($p < 0.001$) and a significant interaction between time since restoration and zone ($p = 0.007$; Table 2.), with greatest change over time observed in zone 2 (Figure 2.6a).

Minimal adequate model for soil salinities included time since restoration ($p < 0.001$) as the only significant factor (Table 2.2; Figure 2.6b). Mean soil salinity (± SE) on dikes before restoration ranged between 15.0 ± 4.4 ppt (zone 2) and 27.0 ± 1.6 ppt (zone 4). After restoration, soil salinities increased over time and reached maximum values observed during this study 18 months post-restoration when all zones had mean soil salinities over 50 ppt. Soil salinity in all zones decreased during the period between the 18 and 24 months monitoring periods and final soil salinity at restored impoundments averaged between 40 and 50 ppt in zones 1, 2, and 3 and 32.5 ± 9.5 ppt in interior marshes.

Vegetation

Phase 1

Before restoration, the C-8 impoundment had 17 total plant species on the dike and 6 total species in interior wetlands (Table 2.3). Before restoration, C-8 had a plant community with a mix of upland, facultative, and obligate wetland species, including mangroves along the shorelines and interior marshes and upland plants colonizing the dike peaks. Mangroves were only found in zones 1 and 3 along the front and back portion of the dike and mean density of mangroves was less 0.5 trees per m^2. The elevated substrate of the dike was invaded by the non-native *Schinus terebinthifolius* prior to restoration and accounted for 23.4% of plant abundance. Within the interior wetland of mosquito impoundments, plant communities were limited to species in obligate, facultative wetland, and facultative categories, before and after restoration.

After restoration, 14 total plant species were identified in the restored area and 16 species were found in interior area of restored mosquito impoundments (Table 2.3). The plant community at restored impoundments was comprised of only obligate and facultative wetland species, as observed in reference marshes. Species richness varied with time since restoration ($p < 0.001$) and there was a significant interaction between zones and habitat type ($p < 0.001$; Table 2.4). Species richness increased with time since restoration, ranging from 1 species per site after one month post-restoration to 9 species per site after eleven years post-restoration. At restored impoundments in zones 1-3, species richness was lower compared to reference marshes and zone 4 ($p < 0.001$; Table 2.4).

Dominant plant species (combined relative abundance > 50%) at all impoundments and control wetlands were *Avicennia germinans* (black mangrove), *Batis maritima* (saltwort), *Sarcocornia perennis* (perennial glasswort), *Sesuvium portulacastum* (sea purslane), and *Distichlis spicata* (saltgrass). These five species were initial colonizers of restored areas following dike removal; recruitment occurred through seed recruitment and vegetative propagation within one month post-restoration. Two additional mangrove species were observed at reference marshes and restored impoundments, *Rhizophora mangle* (red mangrove) and *Laguncularia racemosa* (white mangrove). *Laguncularia racemosa* was present at all restored impoundment sites; two impoundments in later stages of recovery (V-1, V-2) had mature trees at start of study. Impoundments in early stages of recovery (D-12N, C-8) had recruitment of *L. racemosa* seedlings primarily in zone 2 one-year post-restoration. *Rhizophora mangle* was observed at two impoundments (D-12N, C-8) after one year of recovery from local propagule sources in interior marshes and shoreline vegetation left intact during dike leveling. Recruitment of *R. mangle* and *L. racemosa* at restored sites only occurred in quadrats where other plant species (primarily *B. maritima* and *S. perennis*) had colonized and percent cover was over 20%. Abundance and distribution of non-native species was limited at restored impoundments and a total of thirteen *Schinus terebinthifolius* trees were identified at only one impoundment (D-12S).

The ordination plot from non-metric multidimensional scaling showed separation of vegetation communities on dikes before restoration compared to restored mosquito impoundments and reference marshes (Figure 2.8). During initial analysis, a two dimensional solution was identified as the best configuration of sites (final stress= 16.9; final instability= 0.0001). At the start of the study in 2007, sites were spread across both axis 1 and 2, with control wetlands and interior wetlands clustered in center of plot (Figure 2.8). Over time, plant communities became more similar to control wetlands, resulting in closer groupings of all sites in the center of the plot (Figure 2.8). Axis 1 was strongly correlated with abundances of two species, *B. maritima* (tau= 0.62) and *S. perennis* (tau= 0.60). Axis 2 was correlated with abundances of *D. spicata* (tau= 0.49) and *A. germinans* (tau= 0.48). Model selection was used to identify significant factors on abundance of these correlated species. Minimal adequate models for all four species included the factors month and year of data collection and zone (Table 2.5). There was significant variation over time in abundances of all four species, with *A. germinans* and *B. maritima* increasing in abundance from 2007 to 2010 and abundances of *S. perennis* and *D. spicata* decreasing during study period. All four species had higher abundances in zone 4 (interior wetland) compared to zones 1-3, with the exception of *A. germinans* in zone 3. At restored mosquito impoundments, zone 2 had the lowest abundances of plants for all four species. Models for *A. germinans*, *B. maritima*, and *S. perennis* also included habitat type and abundances were significantly higher at control wetlands compared to restored impoundment sites (Table 2.5). However, differences between restored impoundments and control wetlands were not significant for *D. spicata* and removed from final model (Table 2.5). Location in

Mosquito Lagoon was also significant for *A. germinans* and *D. spicata*. *Avicennia germinans* was found in higher abundances at restored impoundments and control wetlands on the west side of Mosquito Lagoon compared to those on the eastern side. In comparison, *D. spicata* was more abundant at sites on the east side of the estuary compared to the west side.

Time since restoration was a significant factor for minimal adequate models of both total plant density and percent cover ($p < 0.001$ for both models; Table 2.4). There was also a significant interaction between habitat type and zone, with restored zones at mosquito impoundments having significantly lower plant cover (zones 1-3) and density (zones 1, 2) compared to control wetlands (Table 2.4). All zones in control wetlands and interior wetlands had 90% or greater percent cover throughout the study. Impoundments in older stages of recovery during this study (V-1, V-2, D-12S) averaged less than 60% percent cover up to 11 years post-restoration in restored zones (Figure 2.9). Plant recruitment and vegetative spreading was observed immediately after hydrological restoration at D-12N and C-8 impoundments (Figure 2.10). Percent cover increased at a faster rate in zones 1 and zone 3 at both D-12N and C-8 compared to zone 2 during the first two years of recovery (Figure 2.10). Fastest increase in percent cover was observed at D-12N in zone 1, with an estimated percent cover of 89.0% after 3.5 yrs post-restoration (Figure 2.10a).

Phase 2

Percent cover targets for native plants for Phase 2 impoundments were set at 5% after six months, 10% after one year, 15% after 18 months, and 25% after two years (Table 2.1). For non-native plants, targets were set at less than 10% cover for all time periods (Table 2.1). Before restoration, a total of 24 plant species were found at mosquito impoundments, 21 native species and three non-native species (Brazilian pepper (*Schinus terebinthifolius*), hairy indigo (*Indigofera hirsuta*), and torpedograss (*Panicum repens*)) (Table 2.4). The dike of mosquito impoundments had more overall plant species (21 species) than the interior marsh (10 species); however, species richness on dikes was higher because of greater numbers of non-halophytic and terrestrial species compared to the interior marsh (Table 2.3). The mean percent cover of native species before restoration was greater than 90% in zones 1 (front of dike), 2 (peak of dike) and 4 (interior marsh) (Figure 2.11a). Mean percent cover of non-native species was highest in zones 2 and 3, but was less than 10% in all zones (Figure 2.11b).

Two-years post-restoration, 30 species were documented at mosquito impoundments, 29 native species and one non-native species (*S. terebinthifolius*). There were significant increases in species richness on the restored marsh compared to the dike (paired t-test : t= -3.6, df= 6, p = 0.011) before restoration and in interior marshes post-restoration (paired t-test : t= -7.1, df= 6, p < 0.001). In restored zones, there were less facultative and upland species compared to the dike before restoration and an increase in obligate wetland species. Seedlings from all three native mangrove species recruited to the restored marsh within one year post-restoration (Table 2.3). Interior marshes of restored mosquito impoundments increased numbers of obligate wetland plants, however, there were also increases in number of facultative and upland plant species following restoration. This increase was caused by expansion and recruitment of *S. terebinthifolius*, as well as the native weedy species, *Ambrosia artemisiifolia* (common ragweed), and native coastal shrubs, *Cakile lanceolata* (coastal searocket) and *Baccharis halimifolia* (groundsel) (Table 2.3).

The minimal adequate model for percent cover of natives included time since restoration ($p < 0.001$) and zone ($p < 0.001$) as significant factors (Table 2.6). Percent cover of natives increased significantly over time in all three zones, but restored zones had significantly less cover compared to the interior marsh (means ranged between 85% and 100% during two years, $p < 0.001$). After dikes were leveled, initial recruitment of plants was observed within one month at all sites. By six-months post-restoration, mean percent cover of native plants (% ± SE) had increased to 31.5 ± 4.7% in zone 1, 9.4 ± 2.2% in zone 2, and 25.0 ± 3.5% in zone 3 (figure 2.11a). After one-year post-restoration, the fastest rate of recovery was observed in zones 1 and zone 2 where mean percent cover was greater than 40% (Figure 2.11a). After two years post-restoration, mean percent cover (± SE) had increased to 74.0 ±2.6%, 58.9 ± 5.0%, and 82.0 ± 2.6% in zones 1, 2, and 3 respectively (Figure 2.11a).

Minimal adequate model for non-native plant percent cover included time since restoration ($p < 0.001$) and zone ($p < 0.001$) as significant factors (Table 2.6). Non-native plants were not observed in the restored marsh zones one month after dike removal or during any subsequent monitoring (Figure 2.11b). *Schinus terebinthifolius* remained in zone 4 (interior marsh) at four sites after dikes were removed and increased in mean percent cover by ~11% during the first six months post-restoration (Figure 2.11b). From six months to two years post-restoration, percent cover of this non-native species decreased and final mean percent cover of *S. terebinthifolius* was 5.1 ± 2.3% (Figure 2.11b).

Fiddler Crabs

Phase 1

Fiddler crabs were found at all restored sites and reference marshes and four species were identified at phase 1 impoundments (Table 2.7). Two species were commonly found year-round at all sites, *Uca pugilator* and *Uca pugnax*. *Uca pugilator* was the only species found at C-8 impoundment before restoration, but was limited to zones 1 and 3 and not observed at the highest elevations. Within one month of leveling at D-12N and C-8 impoundments, *U. pugilator* was found in all zones of the restored marsh area. Two additional species were only observed at one impoundment (D-12N) after restoration during this study, *U. rapax* and *U. thayeri*.

The ordination plot from non-metric multidimensional scaling showed minimal separation of fiddler crab communities between restored mosquito impoundments and control wetlands and between zones (Figure 2.8b). Minimal change over time was also observed in distribution of points, with a slight shift along axis 1 from 2007 to 2010 (Figure 2.8b). During initial analysis, a two dimensional solution was identified as the best configuration of sites (final stress= 10.7; final instability= 0.0002). Axis 1 was correlated with the dominant fiddler crab, *Uca pugilator*, which explained 94% of variation along axis 1. This species was observed at all impoundments and control wetlands and was more abundant than other fiddler crab species. *Uca pugnax* was correlated with axis 2 and explained 69% of the variation along the second axis. *Uca pugnax* had the second highest abundance of fiddler crab species, found in the intertidal region at control wetlands and D-12N, V-1, and V-2. Model selection comparing abundances of *U. pugilator* and *U. pugnax* found month and year of collection and zone to be significant factors (Table 2.9). Fiddler crab densities varied seasonally and annually with water levels and were highest during July (mean (± SE) = 12.4 ± 2.1 crabs per m^2) and lowest during March and November (mean ~7 crabs per m^2 for both months), corresponding to extended inundation during high water periods in spring and fall in Mosquito Lagoon. *Uca pugilator* was most common in zone 1 and interior marshes of both restored impoundments and control sites. In comparison, *U. pugnax* was more common in zone 2 and interior wetlands. Habitat type was significant for *U. pugilator*, with higher abundances occurring at control wetlands compared to restored impoundments ($p < 0.001$; Table 2.9). Location in Mosquito Lagoon was significant for *U. pugnax* and this species was more abundant at restored impoundments and control wetlands on the east side of the estuary ($p < 0.001$; Table 2.9).

Phase 2

Fiddler crabs were not found on dike peaks (zone 2) at any sites before restoration (Figure 2.12). Fiddler crabs were using zones 1 and 3 on dikes before restoration and had a mean density (± SE) of 4.0 ± 1.8 and 5.1 ± 2.6 fiddler crabs m^{-2}, respectively. One species, *U. pugilator*, was found at mosquito impoundments before restoration on dikes and in interior wetlands (Table 2.7). Fiddler crab densities were highest in interior marshes of mosquito impoundments before restoration (mean ± SE = 6.9 ± 3.1 fiddler crabs m^{-2}; Figure 2.12). Within one month of leveling, fiddler crab burrows were observed in restored marshes and fiddler crabs were found in low densities (less than 2 fiddler crabs m^{-2}) in all three restored zones (Figure 2.12). After restoration, three species were identified using the restored area (in order of abundance): *U. pugilator, U. pugnax,* and *U. rapax* (Table 2.6). Minimal adequate model included time since restoration ($p < 0.001$) and zone ($p = 0.003$) as significant factors (Table 2.7). Mean density of fiddler crabs in interior wetlands ranged between 2.3 and 9.1 crabs per m^2

during two years of monitoring. Mean densities of fiddler crabs were lowest in zone 2 compared to interior wetlands for all monitoring dates ($p < 0.001$), however, there were no significant differences between zones 1 and 3 compared to the interior marsh (Table 2.7).

Birds

Phase 1

A total of 25 species of birds used phase 1 impoundments after restoration and control wetlands between 2007 and 2010; this included both resident and migratory species (Table 2.9). The total number of species observed at each restored impoundment site ranged from 10 species (C-8) to 17 species (D-12S2), with a mean number of species per site (± SE) of 13.1 ± 0.8 species. At all sites, numbers of birds observed during each monitoring date were low, ranging between 0 to 8 individuals per survey. Mean number of birds observed during each survey ranged between 0 and 4.6 birds per site and there were no significant differences in total numbers of birds per site between habitat type, site, month, or year of collection (Figure 2.13). The majority of bird species at both control wetlands and restored impoundments were wading birds and shorebirds (Table 2.9). Restored sites were utilized by a variety of foraging wading birds, including *Eudocimus albus* (white ibis), *Egretta caerulea* (little blue heron) and *Egretta rufescens* (reddish egrets). Water birds, including *Pelecanus occidentalis* (brown pelican) and migratory *Pelecanus erythrorhynchos* (white pelican), were observed resting in restored areas. Aerial birds, such *Agelaius phoeniceus* (redwing black bird) and *Pandion haliaetus* (osprey), were observed at both restored impoundments and control wetlands. However, aerial birds and raptors utilized the two habitat types differently. Both types of bird species were more commonly observed perching on mature trees in control wetlands (>70% of observed behaviors were perching); in restored sites, these species were only briefly observed as they flew through the site (>90% of observed behavior was flying through study area). A breeding pair of Wilson's Plovers (*Charadrius wilsonia*) was documented nesting during June 2009 at the D-12N impoundment (~2.5 yrs post-restoration). Two adults were observed with 3 hatchlings and discarded egg shells were found on the restored marsh.

The ordination plot from non-metric multidimensional scaling showed variation in bird communities from year to year, however, no separation was apparent between restored mosquito impoundments and control wetlands (Figure 2.8c). During initial analysis, a two dimensional solution was identified as the best configuration of sites (final stress= 23.5; final instability< 0.0001). Axis 1 was correlated with abundances of *E. albus* and *P. haliaetus,* which explained 58% and 33% of variation, respectively. Both species were observed at all restored impoundments and control wetlands and were more abundant compared to other bird species. *Egretta caerulea*, also observed at all study sites, had the highest correlation with axis 2 and explained 41% of the variation along the second axis. An aerial bird, *A. phoeniceus*, explained the second highest amount of variation (tau= 0.34). Model selection on abundances of *E. albus* and *E. caerulea* found significant variation between month and year of data collection for both species (Table 2.10). Abundances of *E. albus* also varied with habitat type (p= 0.03), with higher abundances observed at restored impoundments compared to control wetlands (Table 2.10). *Egretta caerulea* did not vary between habitat types and this factor was removed from the final model, however, location in Mosquito Lagoon was marginally significant (p= 0.051) and higher abundances were observed on the east side of the estuary (Table 2.10). Model selection for abundances of *P. haliaetus* found significant variation between habitat types ($p < 0.001$) and osprey were more abundant in control wetlands compared to restored impoundment sites (Table 2.10). Abundances of *A. phoeniceus* were significantly different between months of collection and higher abundances were observed during April and August compared to December ($p = 0.001$; Table 2.10). Habitat type was also significant for *A. phoeniceus* ($p < 0.001$) and higher abundances of this species were found in control wetlands compared to restored impoundment sites (Table 2.10).

Nekton

Phase 1

Total fish species caught in Breder traps was 10 species at restored sites and control wetlands (Table 2.11). Total number of macroinvertebrates was 3 species (Table 2.11). The only species collected at all sites was *Palaemontetes pugio* (grass shrimp); this species was also the most abundant during our study (35% of total organisms collected). The number of species ranged from 2 species (D-12S3) to 7 species (control wetlands, D-12S1, C-8, D-12N) observed from 2008 to 2010, with a mean number of species per site (± SE) of 5.4 ± 0.71 species. At all sites, numbers of organisms caught in Breder traps during each collection date were low, ranging between 0 to 5 individuals. Mean number of individual organisms ranged between 0 and 1.8 organisms per trap for all sites and there were no significant differences in total numbers of nekton per site between habitat type, site, month, or year of collection (Figure 2.13). The ordination plot from non-metric multidimensional scaling showed variation in nekton communities from year to year, with separation between sites decreasing from 2008 to 2010. During initial analysis, a one dimensional solution was identified as the best configuration of sites (final stress= 31.48; final instability < 0.0001). *Palaemontetes pugio* had the highest correlation with axis 1, explaining 64% of variation. Model selection on abundances of *P. pugio* did not identify any significant variation between our factors of interest for this widespread and abundant species.

Discussion

Hydrology is a critical factor in wetland diversity, community structure and ecosystem functions (Alongi 2009) and restoring hydrology in human-altered wetlands is the first step in restoration of the ecosystem (Lewis 2005). Our study documented successful restoration of natural hydrological conditions to coastal wetlands through dike removal and natural regeneration of native communities at restored mosquito impoundments in the Indian River Lagoon. Before restoration, mosquito impoundments in the Indian River Lagoon system had altered hydrology due to the presence of dikes along the outer perimeter of the wetland, which negatively impacted wetlands beyond the intended management goals of mosquito control (Montague et al. 1987; Brockmeyer et al. 1997; Taylor et al. 1998). After dike removal at mosquito impoundments, tidal flow across the leveled area was restored, creating the salty, saturated conditions characteristic of a coastal wetland system and reconnecting the interior wetland to the greater estuarine system. Hydrological restoration led to natural abiotic conditions of wetland habitat, leading to the development of native wetland communities and acted as an abiotic barrier to invasion by non-native plant species. Our study identified several important factors in habitat recovery and provided management recommendations to guide future coastal wetland restoration, including: 1) target elevations for promoting natural hydrological properties, 2) effectiveness of natural regeneration following dike removal, 3) benefits of conserving shoreline wetland vegetation during dike removal to enhance rate of recovery, and 4) importance of abiotic conditions for preventing non-native plant recruitment.

Target elevations for hydrological restoration

The primary goal of this restoration project was to remove dikes to restore natural elevations and hydrological characteristics. Results from the pre-restoration monitoring of mosquito impoundments found the high elevation of dikes altered the abiotic properties of the habitat and dike peaks had lower soil moisture and soil salinity compared to control wetlands. These changes in abiotic conditions changed the diversity and distribution of plant and animal communities. Higher elevations of dikes changed the abiotic properties of the system and facilitated the invasion of native and exotic flora not found in natural wetlands. The elevated dike peak was too dry to support wetland fauna, such as fiddler crabs, and was unavailable to the numerous nektonic species reliant on coastal wetland habitat for breeding, feeding, and protection. Obtaining correct elevations when dikes were removed was a key factor in the recovery at these restored sites, as substrate left at elevations too high would not support obligate wetland species and substrate left too low would become mudflat or seagrass habitats. The elevation of substrate controls the frequency and extent of tidal inundation and changes of only a few centimeters can have severe consequences on community structure (Lugo 1998). Wetlands within the Indian River Lagoon system are particularly vulnerable to even small changes in elevation because this estuary is a shallow, microtidal system (Walters et al. 2001). Reducing substrate elevation was successful in restoring tidal flow across the wetland and promoted the development of native wetland plant communities. This is important because coastal wetland vegetation can help mediate sea level rise through direct and indirect biotic processes and maintain desired elevations with moderate levels of sea level rise (Morris et al. 2002; Cahoon et al. 2006). A wetland's resistance to change is high when substrate elevation increases through natural processes at rates greater than local sea level rise (Gilman et al. 2008).

We used soil moisture as one parameter to evaluate the effectiveness of dike removal to restore natural hydrological conditions. After one-year post-restoration, soil moisture was significantly higher in all restored marsh zones and in the interior marshes. Soil moisture in coastal wetlands is primarily affected by a combination of tidal inundation and groundwater levels (Alongi 2009). The Indian River Lagoon system has seasonal changes in tides and spring and fall seasons typically have higher water levels compared to summer and winter water levels (Walters et al. 2001). However, elevations of dikes prior to restoration were high enough to limit flooding to extreme storm events and decrease the influence of groundwater, creating a drier habitat on dike peaks compared to shorelines. After restoration, substrate elevations were low enough to allow tidal inundation across the restored area and into the interior wetland during high water seasons. Although restored mosquito impoundments were not flooded at high tide during every monitoring period, soil moisture remained over 90% during data collection.

Effectiveness of natural regeneration following dike removal

Natural regeneration following hydrological restoration is an effective method of plant community recovery in areas where substantial seeds and propagules are available (Field 1999; Lewis 2005). The Indian River Lagoon system spans the temperate-subtropical climate boundary and natural coastal wetlands contain both temperate and tropical flora. Sub-tropical wetlands in Florida are often in a state of transition between saltmarsh and mangrove dominated plant communities, based on the time since the last freeze or other major disturbance causing mortality in mangrove species (Stevens et al. 2006). Our study area was within protected federal lands where natural wetlands were able to act as a seed source and recruitment of native wetland vegetation occurred at all restored impoundments. Here, we documented successful natural regeneration of wetland plant communities following dike removal and return of tidal flow. Hydrological restoration at mosquito impoundments restricted the diversity of flora to mangroves and halophytic flora, leading to the development of plant communities similar to unimpounded coastal wetlands. Prior to 2007, all vegetation was removed from dikes during the leveling process and natural recovery was dependent on dispersal of seeds and propagules from neighboring areas. Recruitment of mangroves and other halophytic vegetation occurred at all sites, however, increases in percent cover were relatively slow and sites over ten years post-restoration were still significantly lower than control wetlands. Full restoration of wetland systems can take decades (Field 1998; McKee and Faulkner 2000; Proffitt and Devlin 2005) and the results of this project represent the initial recovery in the restoration of these coastal wetland sites. For example, the oldest restored marsh in this study was approximately eight years post-restoration at the start of monitoring. It had species richness and abundance similar to the neighboring control marshes, however, still had lower plant cover compared to control wetlands. The similarity in structure and composition of flora at the restored sites compared to control wetlands is similar to results from southwest Florida marshes (McKee and Faulkner 2000; Proffitt and Devlin 2005). Although the recovery of vegetation structure and habitat function is important, it does not equal full recovery of ecological functions (McKee and Faulkner 2000; Proffitt and Devlin 2005) and may still differ from control sites in mangrove tree size and plant densities after eighteen years (Proffitt and Devlin 2005).

At the restored impoundments, interior marshes exhibited similar composition and structure to control marshes. Although past studies have shown impoundment can negatively affect the interior marsh by restricting tidal flow (Brockmeyer et al. 1997), breaching dikes and opening culverts within this system during the 1990s facilitated the recovery of vegetation in the interior portion of the impounded wetland. The presence of mangroves and halophytic shrubs within the interior wetland may have assisted with the recovery of the anterior portion of the wetland directly impacted by leveling by serving as a nearby seed and propagule source after hydrological restoration. Because natural regeneration relies on recruitment from nearby areas (Field 1999; Lewis 2005), the presence of reproductively mature mangroves and other halophytic vegetation in the interior wetland provided a readily available source of propagules, vegetative fragments, and seeds for colonization of newly restored habitat.

Successional trajectories of plant communities following a disturbance can be affected by early colonizers and colonization of vegetation following restoration during early stages of succession can have a positive effect on later recruitment, growth and survival of plants (Connell and Slatyer 1977). Connell and Slatyer (1977) proposed three models of succession for natural systems, including facilitation, tolerance, and inhibition, based on the life-history characteristics of colonizing species. In our study, evidence of facilitative interactions was observed in the early stages of recovery at mosquito impoundments and included increases in species richness over time and frequent observations of mangrove recruitment into quadrats with existing vegetation. Based on these observations, facilitative interactions may be important for recruitment and establishment of mangrove species, particularly *R. mangle* and *L. racemosa*. These two mangrove species were only observed in quadrats containing other halophytic species. The most common species observed at restored mosquito impoundments were two herbaceous halophytes *B. maritima* and *Sarcocornia perennis*. These commonly co-occurring species are found in coastal wetlands throughout Florida and the Caribbean (Rey 1994; Schmalzer 1995; McKee 1995; Lacerda et al. 2001; Lewis 2005; Rey et al. 2012). Both species are perennial, low-growing (height <1 m), succulent plants that create thick mats of vegetation (Tiner 1993, Taylor 1998) and were observed at restored mosquito impoundments within one month of dike removal. Additionally, *S. portulacastrum* (low-growing, succulent halophyte) and *D. spicata* (salt-tolerant grass species) were observed during initial recovery stages; both species can rapidly increase in cover through vegetative propagation (Tiner 1993).

Early colonizers can facilitate recruitment of other species through multiple mechanisms, including amelioration of environmental conditions, propagule trapping, and structural support. Milbrandt and Tinsley (2006) found *B. maritima* significantly increased survival of *A. germinans* seedlings and attributed this positive effect on mangrove survival to greater surface elevation caused by the dense root system of *B. maritima*. Amelioration of abiotic conditions by early colonizers may also have a positive effect on further plant recruitment. A study by McKee et al. (2007) in Belize documented positive effects of *S. portulacastrum* and *D. spicata* on *R. mangle*. Both of these species increased establishment of *R. mangle* by propagule trapping, reduction of soil temperature and salinity, and improved soil aeration (McKee et al. 2007). Coastal wetland substrate without plant cover in hot climates can develop high soil salinities caused by evaporation, which can have a negative effect on mangrove recruitment (Alongi 2009). In this study, two initial colonizers, *B. maritima* and *S. perennis*, were halophytes with a high tolerance for salinity (Davy et al. 2006; Debez et al. 2010) and these two species have been observed colonizing bare patches at restored impoundment sites where salinity was greater than 70 ppt during the dry season. In our study, the only mangrove species to recruit immediately following substrate leveling and into quadrats without existing vegetation was *A. germinans*. This mangrove species has higher salinity tolerances (up to 100 ppt) compared to *L. racemosa* and *R. mangle* (Tomlinson 1994). After colonization, vegetated areas at restored mosquito impoundments had lower soil salinities on average (10-20 ppt less) compared to unvegetated areas and this decrease in soil salinity may have facilitated the recruitment of other wetland species with lower salinity tolerances.

Natural regeneration following hydrological restoration is dependent on successful recruitment, retention, and establishment of seeds and propagules from surrounding areas. Recruitment of water-dispersed propagules and seeds can be facilitated through trapping by emergent vegetation in riparian and estuarine habitats (Stevens et al. 2006; McKee et al. 2007; Nilsson et al. 2010; Peterson and Bell 2012; Donnelly and Walters 2014). Mangrove propagules disperse by hydrochory (water dispersal) and stranding and retention in suitable habitat are critical steps for successful establishment after dispersal (Rabinowitz 1978). Stevens et al. (2006) found high numbers of propagules dropped by mature mangroves (primarily *A. germinans*) were trapped within 5-15 m of parent trees by vegetation in a subtropical wetland in Florida. The grass species *Spartina alterniflora* facilitated propagule retention in Florida wetlands and was particularly beneficial in areas where high wave energy was problematic for mangrove recruitment (Lewis 1982; Lewis 2005). Peterson and Bell (2012) found retention of *A. germinans* propagules in vegetated patches varied with the species of plant present in the patch, with *Sporobolus virginicus* retaining significantly more propagules compared to *B. maritima* and *S. portulacastrum* in a mangrove-upland ecotone. Thus, initial recruitment of halophytes may be an essential first step in the recovery of native wetland communities and further research into the importance of facilitative interactions during early successional stages may provide important applications for wetland restoration.

Over time, competitive interactions with later successional species, such as large mangrove trees, may become more important and lead to a decrease in abundance of early colonizers, particularly in sub-tropical wetlands with a mixed salt marsh-mangrove community (Stevens et al. 2006). In this study, we observed changes in abundances of early colonizers and mangrove species over time. Abundances of all three mangrove species and *B. maritima* increased over time, whereas two of the initial colonizers, *S. perennis* and *D. spicata*, decreased, suggesting a shift in community structure as mangroves and *B. maritima* became larger and more dominant and halophytic grasses and low-growing succulents were competitively excluded.

Recruitment of native vegetation is the initial phase of restoration for this system, as wetlands are a biogenic habitat and food webs are often based on detritus (McKee and Faulkner 2000; Alongi 2009). Thus, colonization by wetland animals may be dependent on the recovery of the plant community. Fiddler crabs were observed within one month of dike removal at restored mosquito impoundment sites and were one of the first animal species observed using newly restored habitat. After restoration, there was a greater number of species of fiddler crabs found at impoundments and initial targets of fiddler crab densities during phase 2 were exceeded in all zones on the restored marsh except for zone 2. However, there was not a significant difference before and after restoration and this could be a result of high variability in fiddler crab densities at each site and throughout the year due to seasonal tidal inundation. Fiddler crabs are an important component of food webs in coastal wetlands because they are detritivores and serve as prey for larger taxa. They also act as ecosystem engineers through their burrowing activities. Fiddler crab burrows can be used by other organisms and can positively change soil conditions by increasing soil drainage, increasing and redistributing soil nutrients, and aerating anoxic wetland soils (Bertness 1985; Duke et al. 1998; Normann and Pennings 1998; Pennings and Bertness 2001; Daleo et al. 2007). The presence of fiddler crabs at all restored impoundments may have increased recruitment and survival of native vegetation by aerating the soil, increasing organic matter (Pennings and Bertness 2001), and trapping propagules in the burrow openings during tidal inundations (M. Donnelly, pers. obs.), serving as an important indicator of the recovery of wetland functioning.

During this study, we observed a total of 25 different bird species using restored sites and control wetlands. Coastal wetlands are an important habitat for a diverse community of bird species, including wading birds, shorebirds, waterfowl, aerial and song birds, and raptors (Brawley et al. 1998; Havens et al. 2002; Alongi 2009; Ma et al. 2010). Presence of foraging birds represents the recovery of important trophic functions at these restored sites. Total number of birds using sites was similar or greater to control wetlands throughout this study and this was similar to observations made at restored wetland sites in Connecticut (Brawley et al. 1998). However, Havens et al. (2002) found bird utilization of a constructed wetland still differed from reference sites after twelve years. Havens et al. (2002) concluded differences in bird utilization were caused by low densities of preferred vegetation. In our study, differences in structural complexity of restored sites over time affected both the types of birds using restored sites and behavior of birds. During the early stages of recovery, shorebirds and wading birds dominated the bird community and foraged among the recovering vegetation. With low vegetation cover and high densities of fiddler crabs and other prey species, these locations were prime feeding grounds for these bird species. In comparison, sites in later stages of recovery with large, mature mangrove trees provided habitat for a different assemblage of bird species and active foraging was observed primarily along the shoreline edge. Thicker vegetation may have decreased foraging area or efficiency in the restored areas. Dense vegetation has been shown to decrease foraging in wetlands in previous studies and many species of birds prefer sparse or unvegetated areas for foraging (Ma et al. 2010). Density and size of vegetation may also affect bird nesting with restored wetlands. We observed nesting by the Wilson plover at one of the restored sites in early stages of recovery. Wilson plovers typically nest on salt flats with low vegetation cover (Bergstrom 1988), thus, the low density vegetation of restored mosquito impoundments may attract nesting by these species during the early stages of recovery; however, older restored sites may be avoided because of greater vegetation cover. Alternatively, pelicans, herons, and egrets typically nest in crowns of mangrove trees in Florida (Odum and McIvor 1990; Alongi 2009), thus, nesting by these species will only occur once mature stands of mangroves have developed. Interestingly, the availability of restored impoundments in different stages of recovery increases the heterogeneity of the estuarine landscape and provided a variety of different habitats for bird use, potentially increasing overall diversity of bird communities within the lagoon. Further investigations into habitat preferences and how they relate to restored wetlands are needed in order to better understand effects of wetland restoration on bird utilization during different successional stages.

After restoration, all three native mangrove species (*R. mangle*, *A. germinans*, *L. racemosa*) recruited to restored mosquito impoundment zones. Mangroves are of special importance to these coastal wetlands as they function as ecosystem engineers and support a highly diverse assemblage of organisms (Alongi 2009). In Florida, approximately 80% of commercially and recreationally important marine species rely on mangroves during some part of their life cycle (Moberg and Ronnback 2003). Ronnback (1999) estimated between 90-280 tons of fish can be produced from one kilometer of mangrove habitat. We documented thirteen species of nekton utilizing restored shorelines with mangroves and halophytic vegetation, including economically important species and important prey sources in coastal wetlands for predatory fish and bird species. Community structure of nekton changed over time and became more similar to control wetlands and this may have been caused by increases in shoreline structure and habitat as restored sites recovered and increased in plant cover. Previous studies have documented restored wetland sites have high abundances and quick recovery of fish populations (Zedler and Callaway 2000). The mobile nature of fish species allows this group of taxa to quickly respond to environmental changes after restoration (Zedler and Callaway 2000). Previous studies of fishes within restored mosquito impoundments in the Indian River Lagoon system has also documented fast recovery of fish populations following reconnection of interior wetlands with estuary (Taylor et al. 1998; Poulakis et al. 2002). Species identified in this study do not represent the entire fish community using these habitats, as Breder traps are limited in the type and size of fishes caught in traps. Large predatory fish species and nekton species potentially avoiding traps or not swimming directly along shoreline would be excluded during this type of sampling. Further studies using multiple trapping methods (i.e. Poulakis et al. 2002) are needed in order to better quantify the full diversity of nekton present in restored coastal wetlands.

Benefits of conserving shoreline wetland vegetation during dike removal

Observations made during site selection for this study in 2006 found abundant mangroves and halophytic vegetation along the anterior shoreline of dikes (M. Donnelly and W. Greening, personal observation). Beginning in 2007, Volusia County Mosquito Control began conserving shoreline vegetation during dike removal when possible. At D-12N, shoreline vegetation was conserved along the full length of the restored dike and ranged between 5 to 15 m in width. At C-8, dikes contained less dredged material and conserved vegetation was not continuous along the shoreline of the dike and was narrower in width (3-7 m), which may explain the slower recovery of C-8 compared to D-12N. The presence of shoreline vegetation at restored mosquito impoundments provided a seed source of native wetland plants directly adjacent to the restored habitat and mangroves and halophytes along the shoreline expanded into zone 1 within one month of dike removal at D-12N and C-8. Conserving shoreline vegetation had a positive effect on the rate of recovery of native plant communities and increases in percent cover compared to previously restored impoundments. Percent cover of D-12N and C-8 after 3 and 3.5 years, respectively, were equal to or greater than percent cover of older impoundments up to eleven years post-restoration at the end of our study. During phase 2, pre-restoration monitoring documented the presence of mangroves and native halophytes along the shoreline and vegetation was conserved during dike removal at all impoundments restored between 2009 and 2010. At these sites we also observed rapid increases in percent cover and mean percent cover values were up to four times our initial targets after only one year.

Importance of abiotic conditions for preventing non-native plant recruitment

At mosquito impoundments, dikes developed a terrestrial plant community invaded by non-native species. A total of three non-native plant species were present on dikes prior to restoration and two of these species, *S. terebinthifolius* and *P. repens*, are classified as Category 1 invasives by the Florida Exotic Pest Plant Council (FLEPPC 2013). *Panicum repens* is an invasive grass species and can form thick monotypic stands which competitively exclude native plant species (Brecke et al. 2001). Highly invasive *S. terebinthifolius* threatens natural areas because it can competitively exclude other native plants (Cuda et al. 2006), chemically inhibit growth and survival of mangroves (Donnelly et al. 2008), and can use water as a secondary dispersal vector in aquatic habitats (Donnelly and Walters 2008). *Schinus terebinthifolius* can tolerate short periods of soil inundation, but does not tolerate frequent or prolonged inundation of soils (Mytinger and Williamson 1987). Mielke et al. (2005) found a decrease in both stomatal conductance and whole plant biomass when *S. terebinthifolius* is exposed to saturated soil conditions. This usually prevents *S. terebinthifolius* from invading wetland habitat, as evidenced by the presence of *S. terebinthifolius* only on dike peaks in pre-restoration monitoring. Spector and Putz (2006) found *S. terebinthifolius* exhibits extensive plasticity in growth forms, including the production of a large crown, which can extend into adjacent areas where it is unable to root. This allows *S. terebinthifolius* to impact plants growing in areas where it would not otherwise be able to compete with the native species (Spector and Putz 2006). During phase 1 monitoring, *S. terebinthifolius* was observed on the restored area of D-12S impoundment. The elevation following restoration at this location was higher (maximum elevation up to 65 cm) than elevations observed at control sites (maximum elevation less than 29 cm) and older restored impoundments (maximum elevation up to 32 cm). Although overall differences were not significantly different, this may be enough to allow the continued growth and survival of this non-native species. Target elevations for phase 2 impoundments were based on areas without *S. terebinthifolius* during phase 1 and no non-native species were documented on the restored area of phase 2 impoundments during two years post-restoration. However, *S. terebinthifolius* remained within interior marshes at some phase 2 impoundments. At these sites, *Schinus terebinthifolius* did not recruit to the restored marsh despite having a readily available seed source adjacent to the restored habitat and showed a decline over time within the interior wetlands, possibly caused by increased inundation once tidal flow was restored. Lugo (1998) argued mangrove habitat can be resistant to invasion by non-native species because abiotic barriers prevent invasion by any species not adapted to wetland conditions. Our results support this argument and suggest the restoration of hydrological conditions on the restored marsh acted as a barrier to invasion by *S. terebinthifolius* and other non-native species, highlighting the importance of appropriate target elevations for the development of native plant communities.

Conclusions

The purpose of this restoration program was to restore hydrology and then allow natural processes to develop native plant and animal communities at restored sites. Dike removal to restore natural elevations and soil conditions was necessary to promote the recruitment and growth of mangrove species, native wetland plants, and increase utilization by wetland fauna. Hydrological restoration is needed when extensive habitat alteration has occurred in coastal wetlands (Lewis 2005). A form of ecological restoration, returning tidal flow to an altered wetland restores natural abiotic conditions necessary to support the diverse assemblage of flora and fauna typical of natural wetlands (Lewis 2005). Here, we documented recovery of native flora and fauna to restored mosquito impoundments during the first eleven years post-restoration. Although plant cover has surpassed our original targets set for this project, it is important to note these areas are far from a fully functioning ecosystem and structural differences were still apparent even in the oldest restored sites. Our study supports the results of other studies showing hydrological restoration of coastal wetlands by removing barriers to tidal influence results in recruitment of halophytic species, developing a diverse plant community without the need for additional planting (Brockmeyer et al. 1997; Turner and Lewis 1997; Lewis 2005; Nilsson et al 2010: Rey et al. 2012). Additionally, we observed facilitative interactions between species may be an important element in wetland succession and further research into the importance of these types of biotic interactions is needed. Applying facilitation concepts to restoration has the potential to increase project success, particularly in systems where physiological stress is high (Bruno et al. 2003; Padilla and Pugnaire 2006; Halpern et al. 2007; Peterson and Bell 2012). An ecosystem-level approach that addresses both biotic and abiotic interactions affecting coastal wetland recovery after restoration is necessary to increase success of restoration projects. With increased anthropogenic activities and threats from future climate change in estuaries, science-based restoration, management, and conservation of coastal wetlands is critical in order to preserve ecosystem services in the future.

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Tables

Table 2.1. Summary of minimal adequate models (glm) comparing maximum elevation, soil moisture, and soil salinity at restored mosquito impoundments and control wetlands (habitat types). Initial model for elevation compared maximum elevation from each transect and included the factor habitat type (restored impoundment (n= 35), unrestored impoundment (n= 5), control wetlands (n= 10, reference value for pairwise comparisons). Initial model for soil moisture and soil salinity included the factors year, habitat type, and zone (10 m from shoreline, 30 m from shoreline). Reference values were control wetlands (habitat type), 2007 (year), 10 m from shoreline (zone) when applicable.

Variable	Minimal Adequate Model	Factor	Estimate	SE	t-value	p-value
Elevation	Habitat Type	Intercept	16.3	4.868	3.349	0.002
		Habitat Type: Unrestored	99.9	8.431	11.849	<0.001
		Habitat Type: Restored	8.814	5.519	1.597	0.117
Soil Moisture	Year + Habitat Type	Intercept	3.926	0.410	9.56	<0.001
		2008	-1.449	0.310	-4.668	<0.001
		2009	0.043	0.379	0.114	0.909
		2010	0.707	0.450	1.57	0.121
		Habitat Type: Restored	-1.003	0.344	-2.912	0.005
Soil Salinity	Year	Intercept	11.59	2.18	5.33	<0.001
		2008	18.06	3.08	5.87	<0.001
		2009	32.39	3.08	10.53	<0.001
		2010	29.90	3.08	9.72	<0.001

Table 2.2. Summary of minimal adequate models (glm) comparing soil moisture and soil salinity for Phase 2 impoundments. Model factors included time since restoration (TSR) and zone (zones 1-4). Reference values were interior wetlands (zone 4) for zone factor.

Variable	Minimal Adequate Model	Factor	Estimate	SE	t value	p value
Soil Moisture	Time Since Restoration*Zone	Intercept	2.317	0.089	26.073	<0.001
		Time Since Restoration (TSR)	0.223	0.006	3.636	<0.001
		Zone 1	-0.230	0.122	-1.886	0.060
		Zone 2	-0.616	0.115	-5.335	0.000
		Zone 3	-0.115	0.124	-0.924	0.356
		TSR*Zone 1	0.018	0.009	2.011	0.045
		TSR*Zone 2	0.029	0.009	3.407	0.001
		TSR*Zone 3	0.012	0.009	1.342	0.180
Soil Salinity	Time Since Restoration	Intercept	21.201	2.137	9.92	<0.001
		Time Since Restoration (TSR)	1.527	0.159	9.616	<0.001

Table 2.3. Scientific names, common names, wetland status, and presence (X) and absence (---) of all plant species observed at mosquito impoundments before and after restoration and control wetlands. P1= Phase 1 impoundments, P2= Phase 2 impoundments

			Before Restoration		After Restoration		Control Wetlands	
Scientific Name	Common Name	Wetland Status[1]	Dike	Interior	Restored	Interior	Shoreline	Interior
Acrostichum danaeifolium	Giant Leather Fern	OBL	X(P2)	X(P2)	---	X(P2)	---	---
Amaranthus australis	Southern Water Hemp	OBL	---	---	X(P2)	X(P2)	---	---
Ambrosia artemisiifolia	Common Ragweed	FACU	---	---	X(P2)	X(P2)	---	---
Andropogon glomeratus	Bushy Bluestem	FACW+	---	---	---	X(P1)	---	---
Avicennia germinans	Black Mangrove	OBL	X(P1,P2)	X(P1,P2)	X(P1,P2)	X(P1,P2)	X	X
Baccharis halimifolia	Groundsel	FAC	X(P1)	---	X(P2)	X(P2)	---	---
Batis maritima	Saltwort	OBL	X(P1,P2)	X(P1,P2)	X(P1,P2)	X(P1,P2)	X	X
Blutaparon vermiculare	Samphire	FACW	---	---	X(P2)	X(P2)	---	---
Borrichia frutescens	Sea Oxeye Daisy	OBL	X(P1,P2)	---	X(P1,P2)	X(P1,P2)	X	---
Cakile lanceolata	Coastal Searocket	FAC	---	---	X(P2)	X(P2)	---	---
Chamaecrista fasciculate	Partridge Pea	FACU	X(P2)	---	---	---	---	---
Chiococca alba	Snowberry	FAC	X(P2)	---	---	---	---	---
Coccoloba uvifera	Sea Grape	FAC	X(P2)	---	---	---	---	---

Scientific Name	Common Name	Wetland Status[1]	Before Restoration Dike	Before Restoration Interior	After Restoration Restored	After Restoration Interior	Control Wetlands Shoreline	Control Wetlands Interior
Conocarpus erectus	Buttonwood	FACW+	X(P1,P2)	X(P2)	X(P2)	X(P2)	---	---
Cyperus ligularis	Swamp Flatsedge	FACW	---	---	X(P2)	X(P1,P2)	X	X
*Cyperus pedunculatus***	Beachstar	FACW	---	---	X(P1)	X(P1)	X	---
Distichlis spicata	Saltgrass	FACW+	X(P1,P2)	X(P1)	X(P1,P2)	X(P1,P2)	X	X
Eustachys glauca	Saltmarsh Fingergrass	FACW	X(P2)	---	---	---	---	---
Forestiera segregate	Florida Swamp Privet	FAC	X(P1)	---	---	---	---	---
Heliotropium angiospermum	Scorpion Tail	FACU	X(P2)	---	---	---	---	---
Heliotropium curassavicum	Seaside Heliotrope	FAC	---	---	X(P2)	X(P2)	---	---
Hibiscus grandiflorus	Marsh Hibiscus	OBL	---	---	X(P2)	X(P2)	---	---
*Indigofera hirsute**	Hairy Indigo	FACU	X(P2)	---	---	---	---	---
Iva frutescens	Marsh Elder	FACW+	---	---	X(P2)	X(P2)	---	---
Juncus roemerianus	Needlerush	OBL	---	X(P2)	---	X(P1,P2)	---	---
Juniperus virginiana	Red Cedar	FACU	X(P1)	---	---	---	---	---

			Before Restoration		After Restoration		Control Wetlands	
Scientific Name	Common Name	Wetland Status[1]	Dike	Interior	Restored	Interior	Shoreline	Interior
Laguncularia racemosa	White Mangrove	FACW+	X(P1,P2)	X(P2)	X(P1,P2)	X(P1,P2)	X	---
Lycium carolinianum	Christmasberry	FACW	---	---	X(P1,P2)	X(P1)	X	X
Myrica cerifera	Wax Myrtle	FAC	X(P2)	---	---	X(P2)	---	---
Opuntia humifusa	Prickly Pear Cactus	UPL	X(P1,P2)	---	---	---	---	---
*Panicum repens**	Torpedograss	FACW	X(P2)	---	---	---	---	---
Poinsettia cyathophora	Painted Leaf	FACU	X(P2)	---	---	---	---	---
Rhizophora mangle	Red Mangrove	OBL	X(P1)	---	X(P1,P2)	X(P1,P2)	X	---
Sabal palmetto	Cabbage Palm	FAC	X(P1)	---	---	---	---	---
Saccharum giganteum	Sugarcane Plumegrass	OBL	X(P2)	---	---	---	---	---
Salicornia bigelovii	Annual Glasswort	OBL	---	---	X(P1,P2)	X(P1,P2)	---	---
Salicornia perennis	Perrenial Glasswort	OBL	X(P1,P2)	X(P1,P2)	X(P1,P2)	X(P1,P2)	X	X
Salix caroliniana	Coastal Plain Willow	OBL	---	---	---	X(P2)	---	---
*Schinus terebinthifolius**	Brazilian Pepper	FAC	X(P1)	---	---	---	---	---

			Before Restoration		After Restoration		Control Wetlands	
Scientific Name	Common Name	Wetland Status[1]	Dike	Interior	Restored	Interior	Shoreline	Interior
Serenoa repens	Saw Palmetto	FACU	X(P1,P2)	X(P1,P2)	---	X(P2)	---	---
Sesuvium portulacastrum	Sea Purslane	FACW	X(P1)	X(P1)	X(P1,P2)	X(P1,P2)	X	X
Spartina alterniflora	Smoothcordgrass	OBL	X(P1,P2)	---	X(P1,P2)	X(P1,P2)	---	---
Spartina bakeri	Baker's cordgrass	FACW	---	X(P2)	---	X(P2)	---	---
Sporobolus virginicus	Seashore Dropseed	OBL	---	X(P2)	X(P1,P2)	X(P2)	---	---
Suaeda linearis	Sea Blite	OBL	X(P2)	---	X(P1,P2)	X(P2)	X	---
Typha latifolia	Broadleaf Cattail	OBL	---	---	X(P2)	X(P2)	---	---
Vigna luteola	Hairypod Cowpea	FACW						

[1] Wetland indicator status: OBL = obligate, FACW = facultative wetland, FAC = facultative, FACU = facultative upland, a positive following FAC categories indicate the species is on the wetter (+) side of the category (National Wetlands Inventory, 1988)

*Non-native species; **Listed as endangered on Florida’s endangered and threatened plant list (Coile and Garland 2003)

Table 2.4. Summary of minimal adequate models (glm, quasipoisson (species richness, plant density), quasibinomial (percent cover) comparing abundance of plant species richness, plant density, and percent cover at restored mosquito impoundments and coastal wetlands (habitat types). Reference values were control wetlands (habitat type), 2007 (year), February (month), zone 4- interior marsh (zone), location (east) when applicable.

Variable	Minimal Adequate Model	Factor	Estimate	SE	t value	p value
Plant Species Richness	TSR + Habitat Type*Zone	Intercept	0.001	0.162	0.008	0.994
		TSR	0.003	0.001	5.452	<0.001
		Habitat Type: Restored	0.645	0.140	4.605	<0.001
		Zone 1	0.103	0.102	1.008	0.314
		Zone 2	0.117	0.102	1.145	0.253
		Zone 3	0.123	0.102	1.206	0.228
		Habitat Type: Restored*Zone 1	-1.082	0.123	-8.801	<0.001
		Habitat Type: Restored*Zone 2	-0.792	0.119	-6.658	<0.001
		Habitat Type: Restored*Zone 3	-0.679	0.118	-5.768	<0.001
Plant Density	TSR + Habitat Type*Zone	Intercept	2.719	0.181	14.989	<0.001
		TSR	0.002	0.001	3.129	0.002
		Habitat Type: Restored	0.313	0.160	1.960	0.051
		Zone 1	0.172	0.119	1.446	0.149
		Zone 2	0.098	0.121	0.812	0.417
		Zone 3	-0.047	0.125	-0.376	0.707
		Habitat Type: Restored*Zone 1	-0.476	0.137	-3.472	<0.001
		Habitat Type: Restored*Zone 2	-0.446	0.139	-3.206	<0.001
		Habitat Type: Restored*Zone 3	-0.224	0.142	-1.572	0.117
Percent Cover	TSR + Habitat Type*Zone	Intercept	3.965	0.149	26.691	<0.001
		TSR	0.003	0.001	4.684	<0.001
		Habitat Type: Restored	0.502	0.126	3.983	<0.001
		Zone 1	0.002	0.083	0.020	0.984

Variable	Minimal Adequate Model	Factor	Estimate	SE	t value	p value
		Zone 2	0.002	0.083	0.020	0.984
		Zone 3	0.002	0.083	0.020	0.984
		Habitat Type: Restored*Zone 1	-1.576	0.108	-14.567	<0.001
		Habitat Type: Restored*Zone 2	-1.265	0.103	-12.262	<0.001
		Habitat Type: Restored*Zone 3	-1.311	0.104	-12.629	<0.001

Table 2.5. Summary of minimal adequate models (glm, negative binomial) comparing abundance of plant species (*Batis maritima, Sarcocornia perennis*, *Distichlis spicata*, *Avicennia germinans*) at restored mosquito impoundments and control wetlands (habitat types). Reference values were control wetlands (habitat type), 2007 (year), February (month), zone 4- interior marsh (zone), location (east) when applicable.

Species	Minimal Adequate Model	Factor	Estimate	SE	z value	p value
Batis maritima	Month + Habitat Type + Year + Zone	Intercept	2.176	0.124	17.529	<0.001
		Month: June	0.096	0.102	0.933	0.351
		Month: October	0.347	0.101	3.433	<0.001
		Habitat Type: Restored	-0.536	0.089	6.010	<0.001
		Year: 2008	-0.411	0.118	-3.480	<0.001
		Year: 2009	-0.137	0.116	-1.184	0.236
		Year: 2010	0.044	0.115	0.388	0.698
		Zone 1	-0.990	0.120	-8.277	<0.001
		Zone 2	-0.432	0.114	-3.792	<0.001
		Zone 3	-0.232	0.113	-2.058	0.040
Sarcocornia perennis	Month + Habitat Type + Year + Zone	Intercept	2.781	0.148	18.734	<0.001
		Month: June	0.068	0.117	0.582	0.561
		Month: October	0.199	0.116	1.719	0.086
		Habitat Type: Restored	-1.145	0.101	11.397	<0.001
Species	Minimal Adequate Model	Factor	Estimate	SE	z value	p value

		Year: 2008	-0.585	0.131	-4.459	<0.001
		Year: 2009	-0.786	0.133	-5.901	<0.001
		Year: 2010	-0.548	0.131	-4.189	<0.001
		Zone 1	-1.289	0.128	-10.039	<0.001
		Zone 2	-1.591	0.132	-12.046	<0.001
		Zone 3	-1.476	0.131	-11.302	<0.001
Distichlis spicata	Month + Year + Zone + Location	Intercept	4.372	0.337	12.982	<0.001
		Month: June	0.163	0.267	0.612	0.541
		Month: October	0.109	0.267	0.407	0.684
		Year: 2008	-0.765	0.303	-2.527	0.012
		Year: 2009	-1.014	0.305	-3.321	<0.001
		Year: 2010	-1.018	0.306	-3.333	<0.001
		Zone 1	-4.138	0.353	-11.711	<0.001
		Zone 2	-0.702	0.284	-2.473	0.013
		Zone 3	-1.644	0.289	-5.688	<0.001
		Location: West	-1.655	0.220	-7.538	<0.001
Avicennia germinans	Month + Habitat Type + Year + Zone + Location	Intercept	1.129	0.105	10.717	<0.001
		Month: June	-0.313	0.078	-4.011	<0.001
		Month: October	-0.165	0.076	-2.185	0.029
		Habitat Type: Restored	-0.642	0.065	9.803	<0.001
		Year: 2008	0.242	0.091	2.658	0.008
Species	Minimal Adequate Model	Factor	Estimate	SE	z value	p value

Year: 2009	0.116	0.093	1.247	0.212
Year: 2010	0.226	0.091	2.478	0.013
Zone 1	-0.304	0.087	-3.512	<0.001
Zone 2	-0.626	0.094	-6.690	<0.001
Zone 3	-0.145	0.084	-1.732	0.083
Location: West	0.391	0.066	5.898	<0.001

Table 2.6. Minimal adequate model results (glm, quasipoisson (fiddler crabs), quasibinomial (percent cover)) for biotic parameters for Phase 2 impoundments. Model factors included time since restoration (TSR) and zone (zones 1-4). Reference values were interior wetland (zone 4) for zone factor.

Variable	Minimal Adequate Model	Factor	Estimate	SE	t value	p value
Percent Cover of Native Plants	Time Since Restoration + Zone	Intercept	1.568	0.183	8.571	<0.001
		TSR	0.022	0.010	2.222	0.028
		Zone 1	-0.352	0.220	-1.600	0.112
		Zone 2	-1.326	0.309	-4.293	<0.001
		Zone 3	-0.398	0.223	-1.782	0.077
Percent Cover of Non-Native Plants	Time Since Restoration + Zone	Intercept	2.443	0.145	16.861	<0.001
		TSR	-0.041	0.012	-3.347	0.001
		Zone 1	-2.645	0.443	-5.977	<0.001
		Zone 2	-2.240	0.367	-6.096	<0.001
		Zone 3	-1.729	0.294	-5.889	<0.001
Fiddler Crab Density	Time Since Restoration + Zone	Intercept	1.568	0.183	8.571	<0.001
		TSR	0.022	0.010	2.222	0.028
		Zone 1	-0.352	0.220	-1.600	0.112
		Zone 2	-1.326	0.309	-4.293	<0.001
		Zone 3	-0.398	0.223	-1.782	0.077

Table 2.7. Presence and absence of fiddler crab species collected on dikes and interior wetlands before restoration and in restored and interior wetlands after restoration. P1= Phase 1 impoundments, P2=Phase 2 impoundments

		Before Restoration		After Restoration	
Scientific Name	Common Name	Dike	Interior	Restored	Interior
Uca pugilator	Atlantic sand fiddler crab	X	X(P1,P2)	X(P1,P2)	X(P1,P2)
Uca pugnax	Atlantic marsh fiddler crab	--	--	X(P1,P2)	X(P1,P2)
Uca rapax	Mudflat fiddler crab	--	--	X(P1,P2)	X(P1,P2)
Uca thayeri	Atlantic mangrove fiddler crab	--	--	X(P1)	X(P1)

Table 2.8. Summary of minimal adequate models (glm, negative binomial) comparing abundance of fiddler crab species (*Uca pugilator*, *Uca pugnax*) at restored mosquito impoundments and control wetlands (habitat types). Reference values were control wetlands (habitat type), 2007 (year), July (month), zone 4- interior marsh (zone), location (east) when applicable.

Species	Minimal Adequate Model	Factor	Estimate	SE	z value	p value
Uca pugilator	Month + Habitat Type + Year +Zone	Intercept	3.590	0.130	28.600	<0.001
		Month: March	-0.450	0.100	-4.470	<0.001
		Month: November	-0.540	0.100	-5.250	<0.001
		Habitat Type: Restored	-0.510	0.100	5.240	<0.001
		Year: 2008	-0.600	0.120	-5.210	<0.001
		Year: 2009	-1.020	0.120	-8.650	<0.001
		Year: 2010	-0.950	0.120	-8.060	<0.001
		Zone 1	-0.290	0.120	-2.490	0.013
		Zone 2	-0.750	0.120	-6.350	<0.001
		Zone 3	-0.460	0.120	-3.960	<0.001
Uca pugnax	Month + Year + Zone + Location	Intercept	0.050	0.310	0.170	0.866
		Month: March	-0.660	0.220	-2.940	0.003
		Month: November	-0.350	0.220	-1.610	0.107
		Year: 2008	1.380	0.280	4.990	<0.001
		Year: 2009	1.670	0.270	6.080	<0.001
		Year: 2010	0.950	0.280	3.370	0.001

Species	Minimal Adequate Model	Factor	Estimate	SE	z value	p value
		Zone 1	0.490	0.250	1.960	0.05
		Zone 2	0.270	0.250	1.060	0.289
		Zone 3	-0.930	0.270	-3.390	0.001
		Location: West	-0.770	0.190	-4.080	<0.001

Table 2.9. Scientific names, common names, residency status in Florida, and presence (X) and absence (--) of all bird species observed at mosquito impoundments after restoration and control wetlands.

			Restored Impoundments							Control Wetlands	
Scientific Name	Common Name	Residency Status	C-8	D-12N	D-12S3	D-12S2	D-12S1	V-1	V-2	D-12R	V-R
Wading Birds											
Ajaia ajaja	Roseate Spoonbill	Resident	--	--	--	--	--	X	X	--	--
Ardea alba	Great White Egret	Resident	X	X	X	X	X	X	X	X	X
Ardea herodias	Great Blue Heron	Resident	X	X	X	X	X	X	X	X	X
Butorides virescens	Green Heron	Resident	--	--	X	--	--	--	--	--	--
Egretta caerulea	Little Blue Heron	Resident	X	X	X	X	X	X	X	X	X
Egretta rufescens	Reddish Egret	Resident	--	--	--	--	X	X	--	--	--
Egretta thula	Snowy Egret	resident	X	X	X	X	X	X	X	X	X
Egretta tricolor	Tricolored Heron	Resident	--	--	--	X	--	--	--	X	--
Eudocimus albus	White Ibis	Resident	X	X	X	X	X	X	X	X	X
Grus canadensis	Sandhill Cranes	Resident	--	--	--	X	--	--	--	--	--
Shorebirds											
Calidris alba	Sanderling	migratory (Aug-April)	--	--	--	--	X	X	--	X	--
Calidris alpina	Dunlin	migratory (Sept.-May)	--	--	X	X	X	X	X	--	X
Charadrius wilsonia	Wilson's Plover	Resident	X	X	X	X	X	X	X	X	X
Larus atricilla	Laughing Gull	Resident	--	--	X	X	--	--	X	X	--
Tringa flavipes	Lesser Yellow Legs	migratory (Aug-May)	--	X	--	X	--	X	--	--	X
Tringa semipalmata	Willet	Resident	--	X	X	X	--	--	X	--	X

			Restored Impoundments							Control Wetlands	
Scientific Name	Common Name	Residency Status	C-8	D-12N	D-12S3	D-12S2	D-12S1	V-1	V-2	D-12R	V-R
Aerial Birds											
Agelaius phoeniceus	Red Wing Blackbird	Resident	X	--	X	X	--	--	X	X	X
Ceryle alcyon	Belted Kingfisher	Resident	--	--	X	X	--	--	--	--	--
Geothlypis trichas	Common Yellowthroat Warbler	resident	X	--	--	X	X	--	--	--	--
Lanius ludovicianus	Loggerhead Shrike	resident	--	X	--	--	--	--	--	--	X
Raptors											
Circus cyaneus	Northern Harrier	migratory (Sept-April)	--	X	--	--	--	--	--	--	--
Pandion haliaetus	Osprey	resident	X	X	X	X	X	X	X	X	X
Water Birds											
Pelecanus erythrorhynchos	White Pelican	migratory (Sept-April)	--	X	--	--	X	--	--	--	--
Pelecanus occidentalis	Brown Pelican	resident	--	--	X	X	X	--	--	--	--
Phalacrocorax auritus	Double-crested Cormorant	resident	X	X	X	--	--	--	--	X	X

Table 2.10. Summary of minimal adequate models (glm, poisson) comparing abundance of bird species (*Eudocimus albus*, *Pandion haliaetus*, *Egretta caerulea*, *Agelaius phoeniceus*) at restored mosquito impoundments and control wetlands (habitat types). Reference values were control wetlands (habitat type), 2007 (year), April (month), location (east) when applicable.

Species	Minimal Adequate Model	Factor	Estimate	SE	z value	p value
Eudocimus albus	Month + Year + Habitat Type	Intercept	-0.3976	0.5309	-0.749	0.454
		Month: August	-0.3326	0.4691	-0.709	0.478
		Month: December	-1.1639	0.5121	-2.273	0.023
		Year: 2008	0.1687	0.6455	0.261	0.794
		Year: 2009	1.2734	0.5964	2.135	0.033
		Year: 2010	1.255	0.5969	2.102	0.036
		Habitat Type: Restored	1.1925	0.5656	-2.108	0.035
Pandion haliaetus	Habitat Type	Intercept	-1.423	0.224	-6.364	<0.001
		Habitat Type: Restored	-1.290	0.312	4.127	<0.001
Egretta caerulea	Month + Year + Location	Intercept	-0.404	0.342	-1.181	0.237
		Month: August	-0.116	0.226	-0.514	0.607
		Month: December	-0.647	0.263	-2.457	0.014
		Year: 2008	1.000	0.351	2.849	0.004
		Year: 2009	1.063	0.348	3.052	0.002
		Year: 2010	0.824	0.360	2.291	0.022
		Location: West	-0.387	0.201	-1.923	0.051
Agelaius phoeniceus	Month + Habitat Type	Intercept	-1.3404	0.308	-4.352	<0.001
		Month: August	-0.3339	0.317	-1.053	0.292
		Month: December	-2.4849	0.736	-3.376	0.001
		Habitat Type: Restored	-2.0747	0.332	6.248	<0.001

Table 2.11. Scientific names, common names, and presence (X) and absence (--) of all mobile invertebrates and fish species observed at mosquito impoundments after restoration and control wetlands.

		Restored Impoundments							Control Wetlands	
Scientific Name	Common Name	C-8	D-12N	D-12S3	D-12S2	D-12S1	V-1	V-2	D-12-R	V-R
Mobile Invertebrates										
Callinectes sapidus	Blue Crab	X	X	--	--	X	X	--	X	X
Palaemontetes pugio	Grass Shrimp	X	X	X	X	X	X	X	X	X
Panopeus herbstii	Atlantic Mud Crab	X	--	--	--	X	--	--	X	--
Fishes										
Cyprinidon variegatus	Sheepshead Minnow						X			
Fundulus sp.		X	X	--	--	X	X	--	X	X
Gambusia affinis	Mosquitofish	X	X	X	--	--	--	--	X	--
Gobiosoma robustum	Cody Goby	X	X	--	--	--	--	--	--	--
Leiostmus 1anthurus	Spot Croaker	--	--	--	--	X	--	X	--	X
Lucania parva	Rainwater Killifish	--	--	--	X	X	--	--	--	--
Menidia sp.	Silverside	--	X	--	--	--	--	X	X	X
Micropogonias undulatus	Atlantic Croaker	--	--	--	X	X	X	--	--	X
Mugil curema	Mullet	X	X	--	--	--	X	--	X	X

Figures

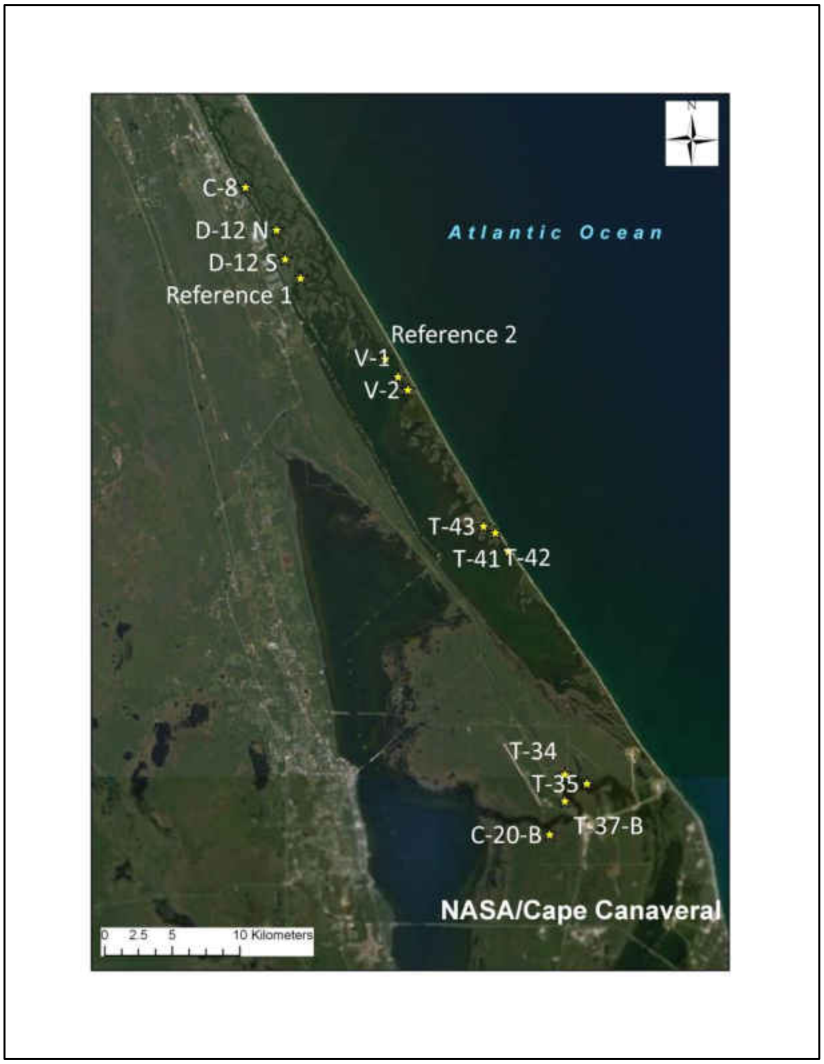

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Figure 2.1. Location of our study was in the northernmost portion of the Indian River Lagoon system in Volusia and Brevard County, Florida, USA. Phase 1 monitoring included C-8, D-12N, D-12S, V-1, V-1, V-2 and reference marshes 1 and 2 (control wetlands). Phase 2 monitoring included T-41, T-42, T-43, C-20B, T-37B, T-34, and T-35.

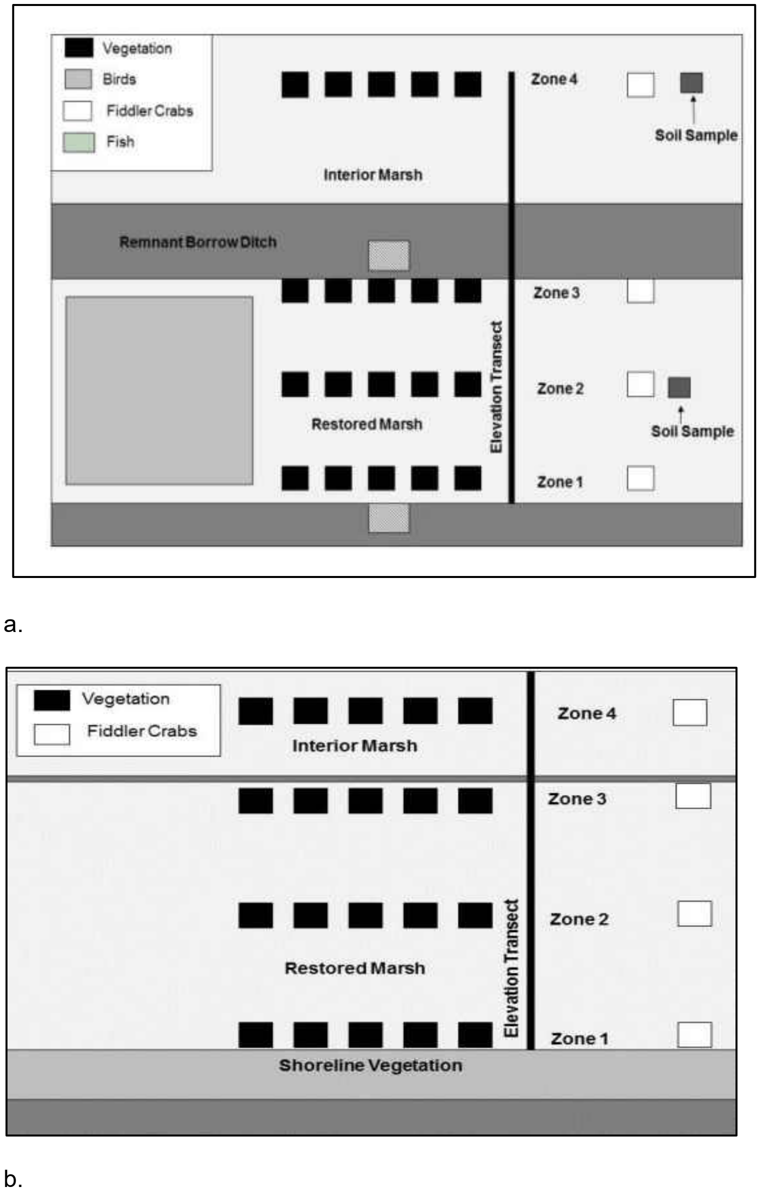


Figure 2.2. Monitoring set-up for each site at mosquito impoundments during phase 1 (a) and phase 2 (c). For phase 1 (a), variables measured at each site were vegetation, birds, fiddler crabs, fishes and mobile invertebrates, elevation, and soil moisture and salinity. Monitoring zones 1,2, and 3 correspond to the restored marsh area of impoundments and zone 4 was located in the interior marsh. During phase 2, vegetation and fiddler crabs were measured in four zones (b), with zone 1 beginning immediately adjacent to remaining shoreline vegetation.

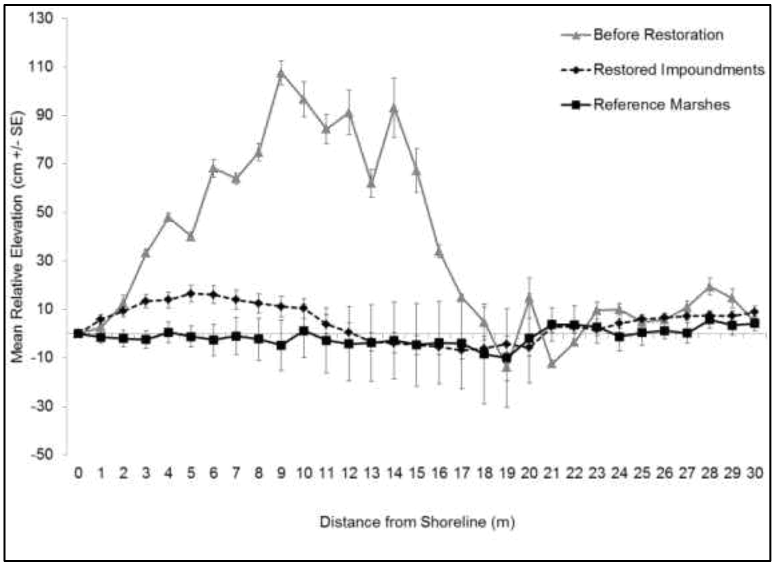


Figure 2.3. The mean relative elevation (cm ± SE) at mosquito impoundments before and after restoration (n= 5, 35 respectively) and reference (control) marshes (n= 10) for phase 1 impoundments. Elevation was measured along a linear transect from MLLW to 30 m landward of shoreline.

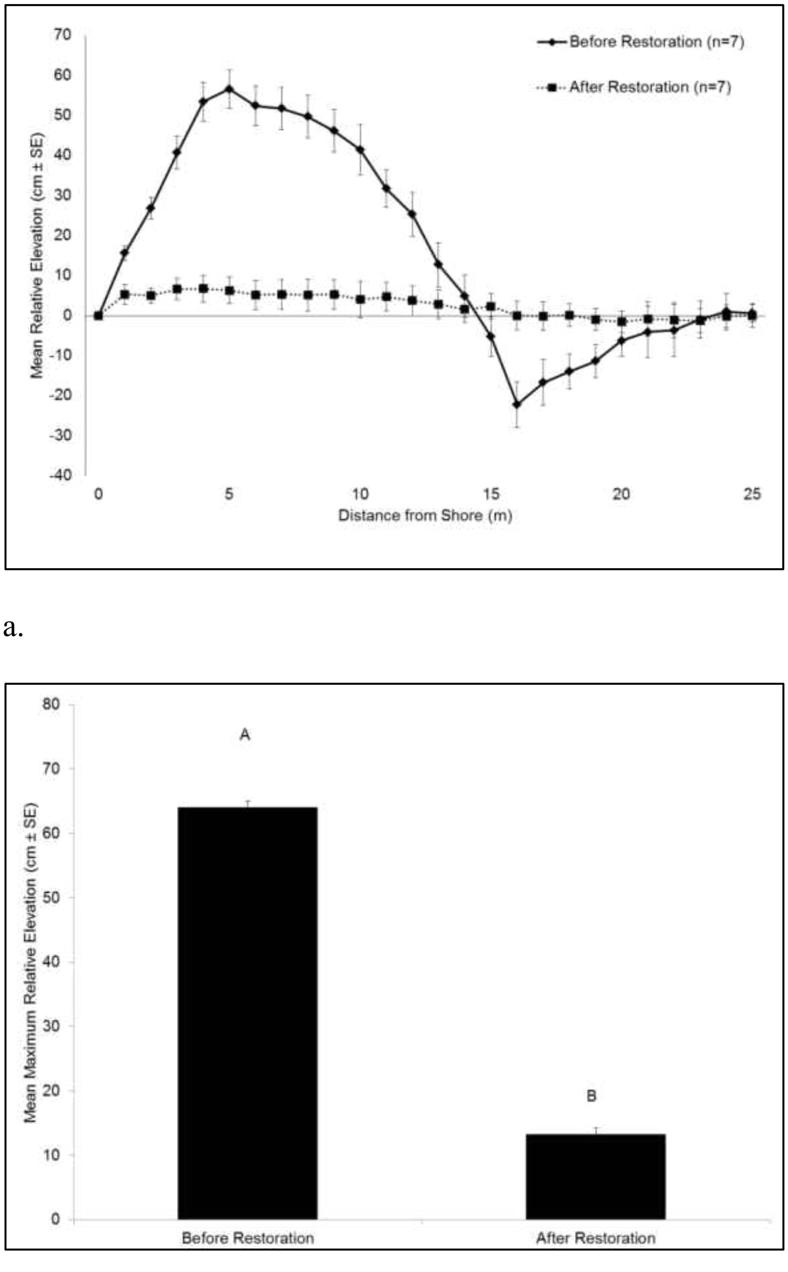
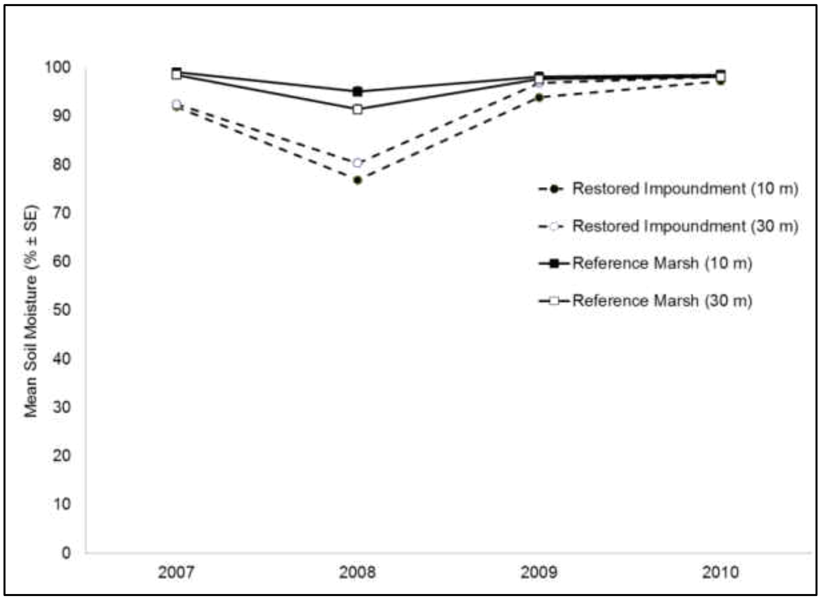


Figure 2.4. The mean relative elevation (cm ± SE) at mosquito impoundments before and after restoration (n= 7) for phase 2 impoundments. Elevation was measured along a linear transect

from MLLW to 25 m landward of shoreline (a) and maximum elevations along each transect (b) was compared using a paired t-test (uppercase letters indicates significant differences).



a.

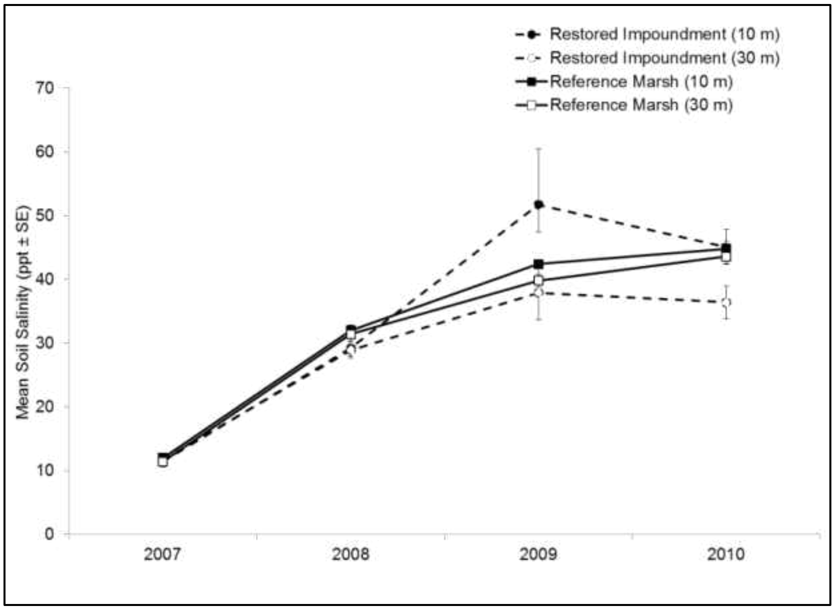
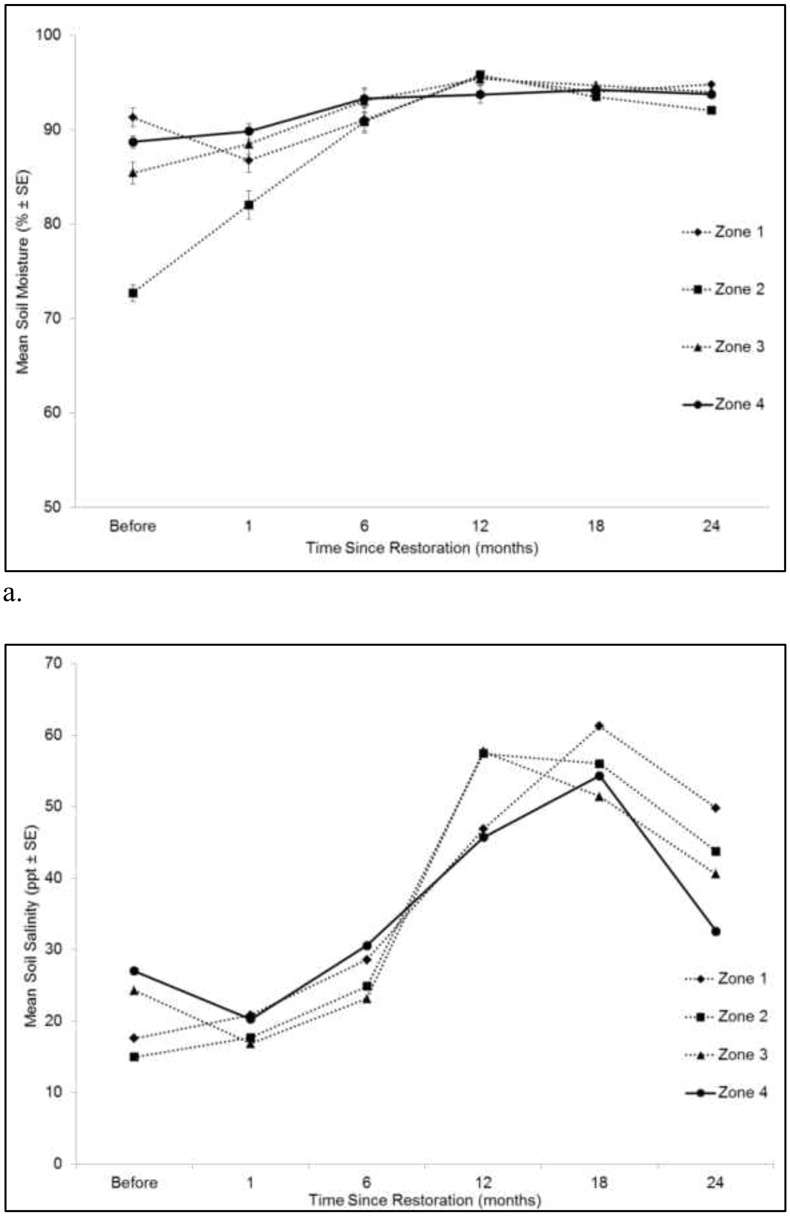


Figure 2.5. Mean soil moisture (% ± SE; a) and soil salinity (ppt ± SE; b) at phase 1 restored impoundments and reference marshes, 10 and 30 m from the shoreline, from 2007 to 2010. Soil moisture was significantly different during 2008 compared to 2007 ($p< 0.001$) and between

restored impoundments and reference marshes ($p = 0.010$). Soil moisture was significantly different during 2008, 2009, and 2010 compared to 2007 ($p < 0.001$ for all comparisons) and between zones 10 m and 30 m from the shoreline ($p = 0.011$).



a.

b.

Figure 2.6. The (a) mean soil moisture (% ± SE) and (b) mean soil salinity (ppt ± SE) of each zone at phase 2 impoundments before restoration through 2 years post-restoration. There was significant variation in soil moisture with time since restoration ($p < 0.001$) and between zones ($p < 0.001$). Soil salinity varied with time since restoration ($p < 0.001$), however, there were no significant differences between zones.

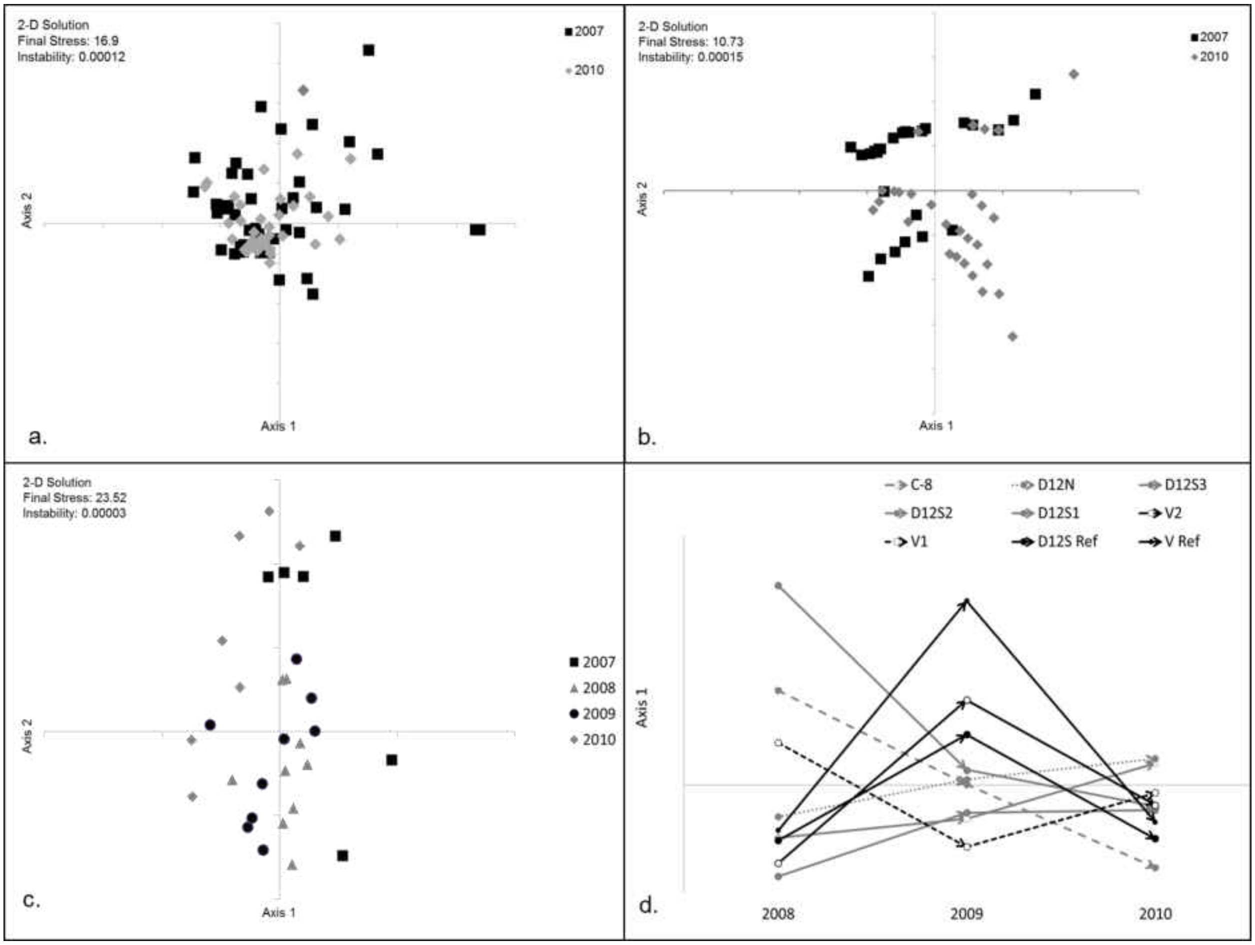


Figure 2.7. Non-metric multidimensional scaling ordination plots for plants (a), fiddler crabs (b), birds (c), and nekton communities at restored impoundments and control wetlands.

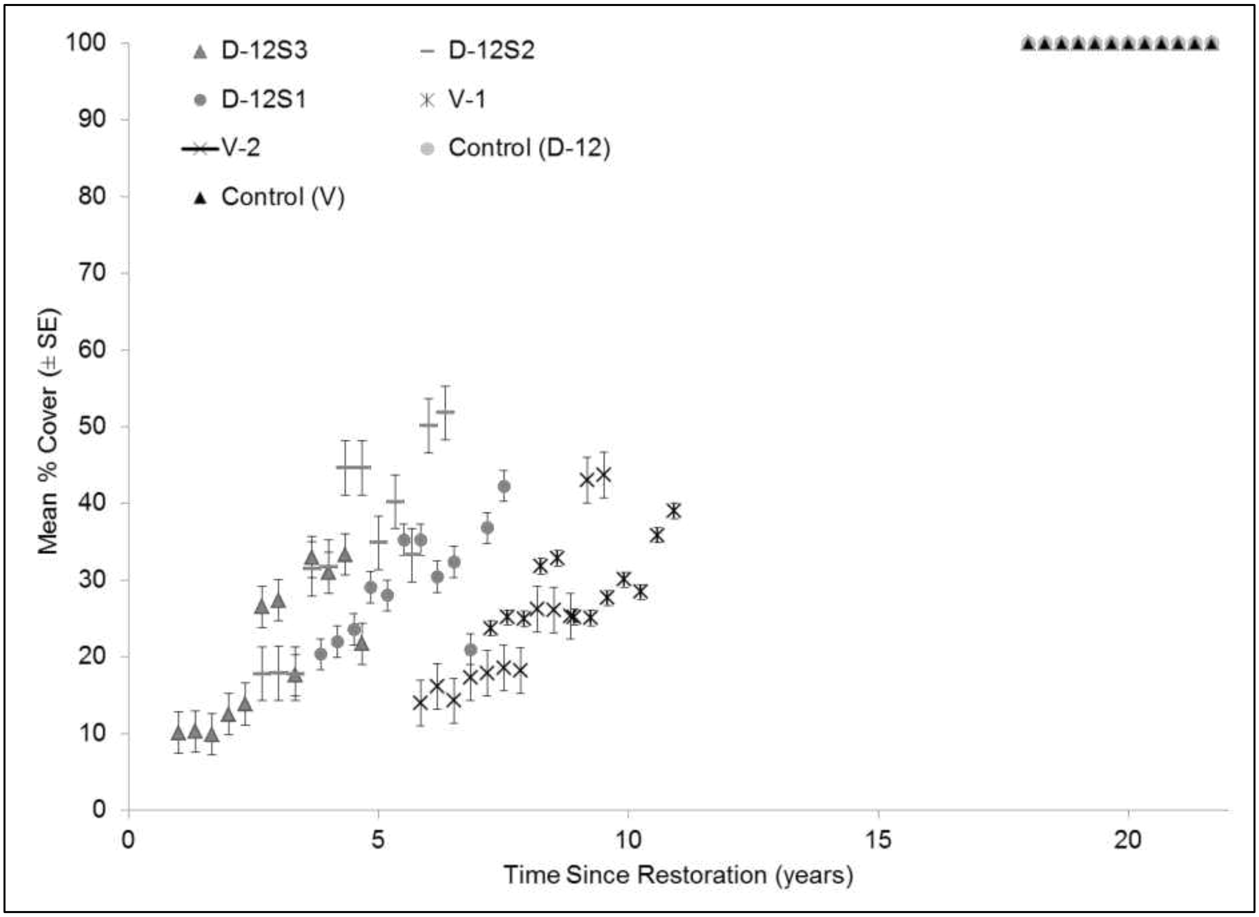
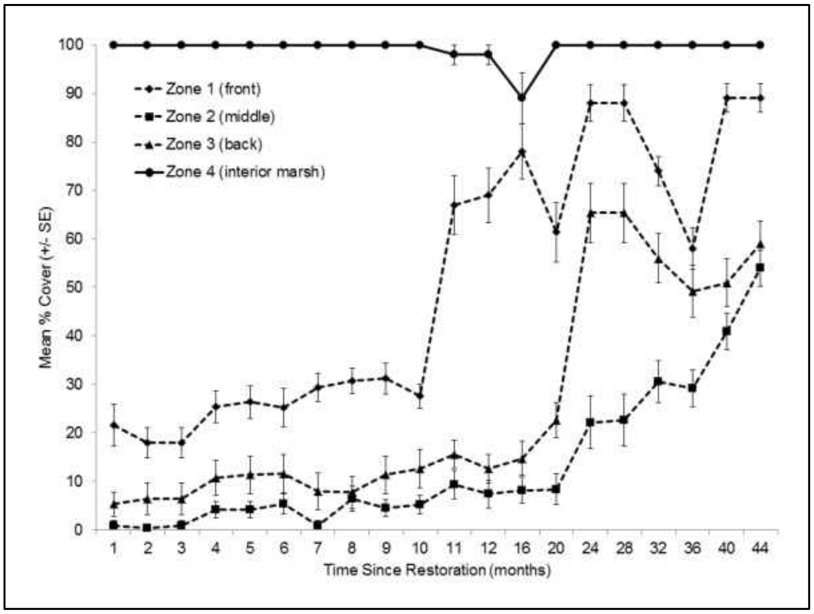
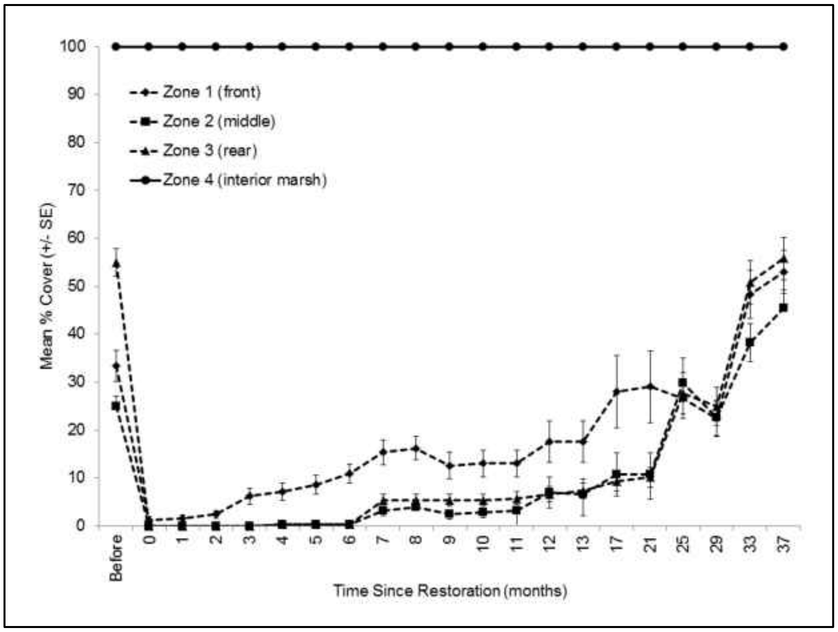


Figure 2.8. Mean percent plant cover (±SE) based on time since restoration at restored impoundments and two control wetlands in phase 1. Time since restoration for control wetlands was based on most recent catastrophic disturbance, freezes in late 1980s, resulting in loss of all tropical vegetation.

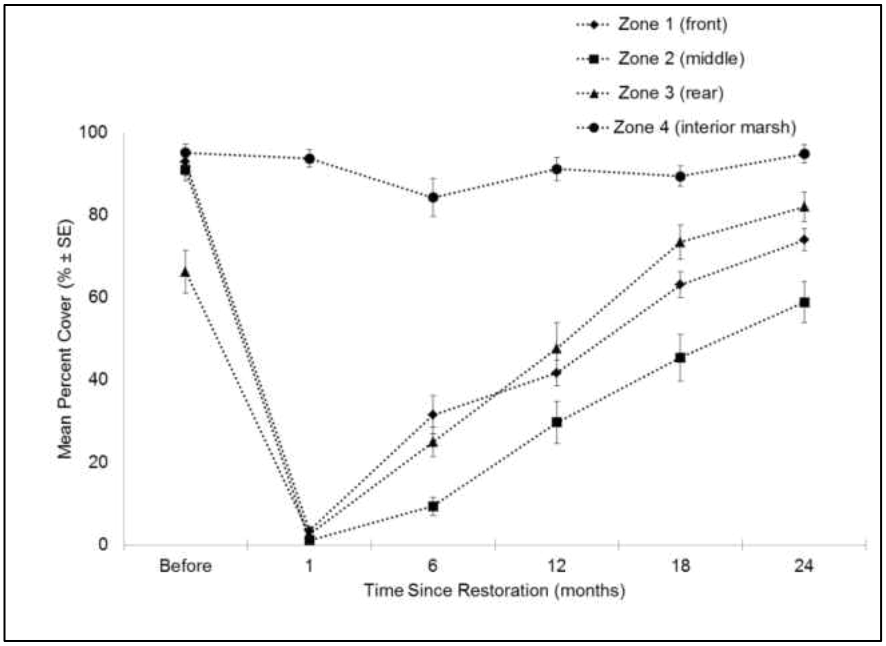


a) D-12N Impoundment

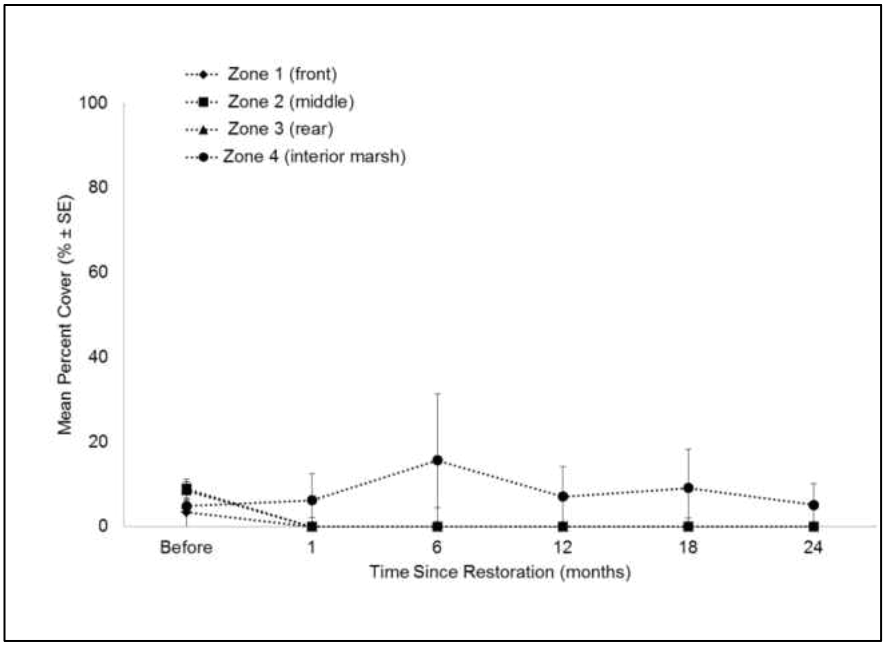


b) C-8 Impoundment

Figure 2.9. Mean percent plant cover (±SE) at restored mosquito impoundments D-12N (a) and C-8 (b) over time since restoration. Both mosquito impoundments were restored in 2007 and monitored monthly for the first year (only C-8 was monitored before restoration).



a.



b.

Figure 2.10. The mean percent plant cover (% ± SE) of native species (a) and non-native species (b) in each zone at phase 2 impoundments before restoration through 2 years post-restoration (n = 7).

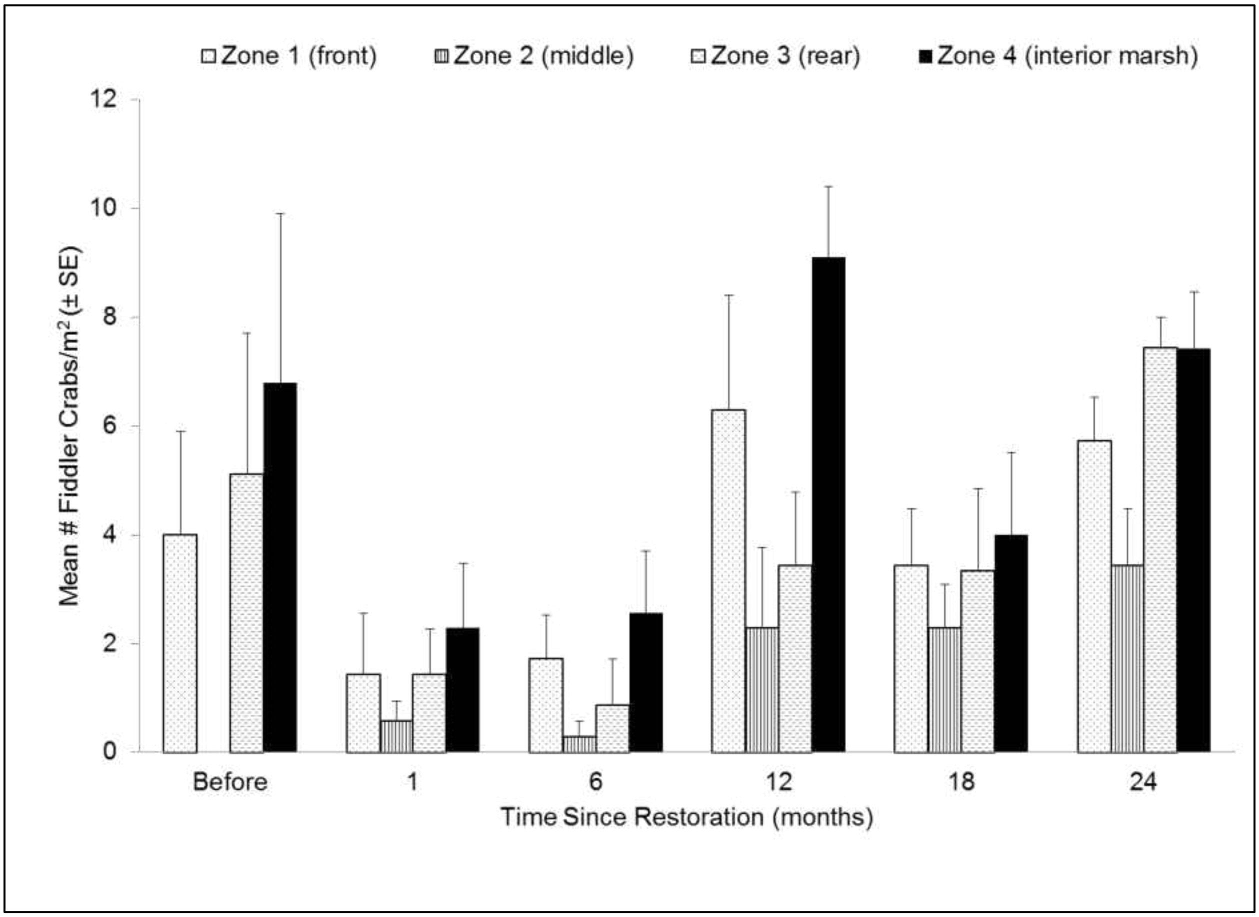


Figure 2.11. The mean number of fiddler crabs m^{-2} (± SE) of each zone at phase 2 impoundments before restoration through 2 years post-restoration.

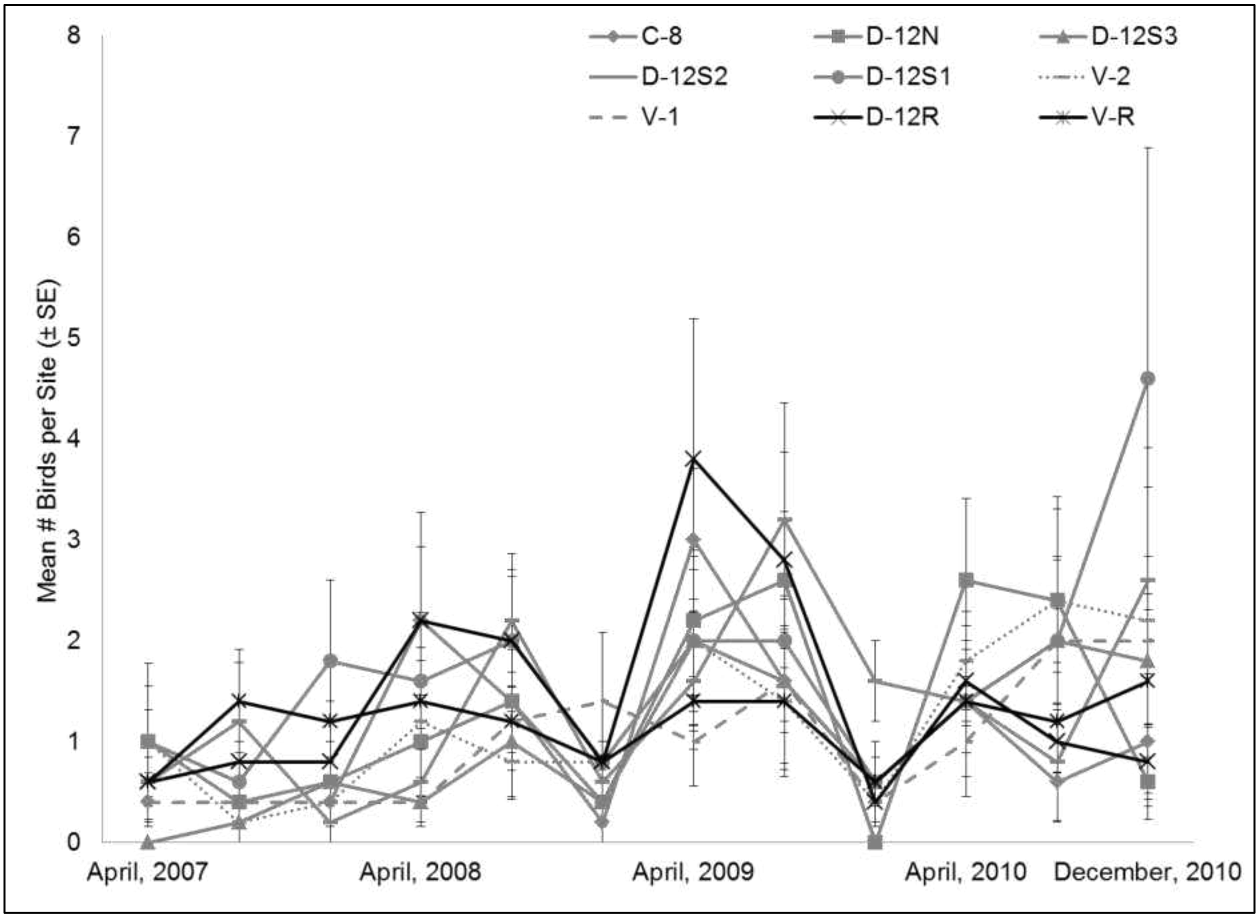


Figure 2.12. Mean total number of birds (± SE) for restored impoundments and control wetlands (D-12R, V-R) for each monitoring period between April 2007 and December 2010.

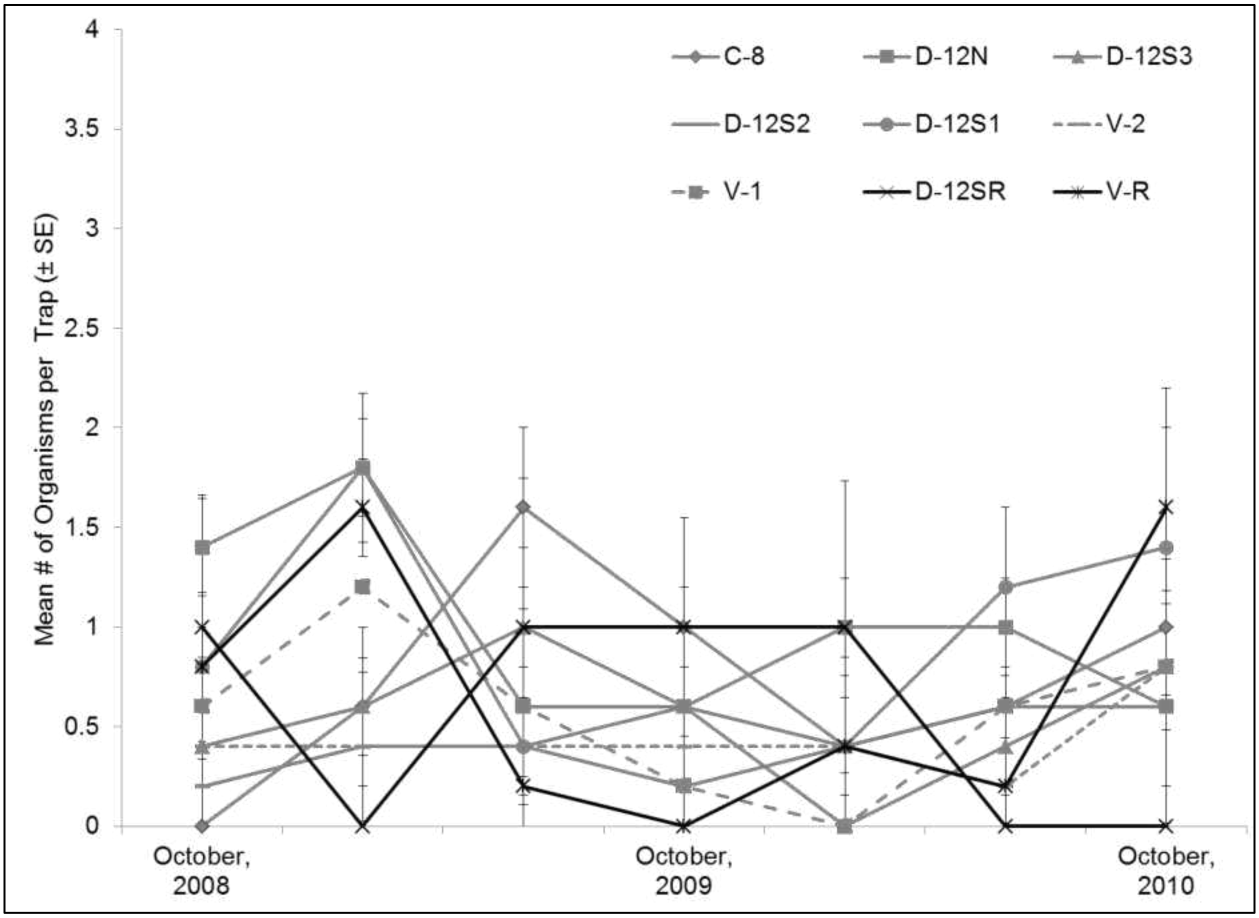


Figure 2.13. Mean total number of organisms (± SE) per trap for restored impoundments and control wetlands (D-12R, V-R) for each monitoring period between October 2008 and October 2010.

CHAPTER 3. TRAPPING OF *RHIZOPHORA MANGLE* BY COEXISTING EARLY SUCCESSIONAL SPECIES

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Abstract

Distributions of mangroves in coastal wetlands are influenced by abiotic conditions and the net effect of biotic interactions, including competition, facilitation and consumer pressure. In coastal wetlands, early successional shrubs, herbs, and grasses may facilitate recruitment of mangroves through multiple mechanisms, including amelioration of environmental conditions, propagule trapping, and structural support. In Mosquito Lagoon, FL, we observed an aggregated distribution of *Rhizophora mangle* propagules along vegetated shorelines with *Batis maritima* and *Sarcocornia perennis* and hypothesized this distribution was a result of propagule trapping by the vegetation. We designed a field experiment to evaluate retention of *R. mangle* propagules on vegetated and unvegetated shorelines in Mosquito Lagoon. Significant differences were found in the retention time of mangrove propagules at each shoreline type, with vegetated shorelines retaining propagules significantly longer than unvegetated shorelines. Results from this study help to define facilitative mechanisms which may be important in successional processes of coastal wetlands and have direct restoration applications. Successful recovery of mangroves at restoration sites may be facilitated by establishment of *B. maritima* and *S. perennis*, when natural propagule sources are available, or through planting mangrove seedlings into existing stands of these halophytes when restoration areas are propagule-limited.

Keywords

Batis maritima; facilitation; mangrove restoration; nurse plants; *Sarcocornia perennis*

Introduction

Mangrove distributions in tropical and subtropical coastal wetlands are influenced by tolerances to abiotic conditions and direct and indirect effects of community interactions, including competition, facilitation and consumer pressure (Odum and McIvor 1990; McKee 1995; Duke et al. 1998; Lacerda et al. 2001; Alongi 2009). In subtropical coastal wetlands, halophytic shrubs, grasses, and herbs can be found growing with mangroves, but the role of positive community interactions on growth, recruitment and distribution of many mangrove species is still largely unknown (Stevens et al. 2006). Positive interactions potentially have an important role in natural regeneration and understanding the biotic processes affecting mangrove species is critical for future conservation, restoration and management of mangrove ecosystems worldwide (Milbrandt and Tinsley 2006; Stevens et al. 2006; Moreno-Mateos et al. 2012; Peterson and Bell 2012).

An estimated 35% of global mangrove area was lost between 1980 and 2000 (Giri et al. 2011), threatening survival of associated organisms and decreasing crucial ecosystem services (Alongi 2009). In response to loss of mangrove habitat, restoration has increased in recent decades; however, mangrove ecosystems are often slow to recover and may require decades before structure and ecosystem function are similar to reference conditions (McKee and Faulkner 2000; Lewis 2005; Moreno-Mateos et al. 2012). One type of facilitation with important applications to ecosystem restoration involves the initial colonization of plant species, which then act as “nurse plants” for other establishing species (Niering et al. 1963; Lewis 1982; Lewis 2005; Padilla and Pugnaire 2006; Lopez et al. 2007; Brooker et al. 2008). The nurse syndrome is a type of facilitation where the seedlings are the beneficiaries of adult plants, the nurse plants, and this type of interaction can be common in early successional communities, creating an aggregated distribution of seedlings associated with the nurse plant (Brooker 2006; Lopez et al. 2007). Nurse plants can help secondary species overcome recruitment limitation and increase success of establishment (Young et al. 2005). Incorporating facilitation into restoration plans is becoming more common in terrestrial ecosystem restoration (Padilla and Pugnaire 2006; Halpern et al. 2007) and inclusion of positive interactions, like nurse effects, can lead to more ecologically-based restoration methods (Padilla and Pugnaire 2006; Brooker et al. 2008). Restoration applications with nurse plants have been beneficial in terrestrial reforestation programs, such as degraded Mediterranean systems (Maestre et al. 2001, Castro et al. 2004, Gomez-Aparicio et al. 2004); however, inclusion of facilitative interactions has been less common in restoration of aquatic systems (Halpern et al. 2007). Identifying co-occurring plant and mangrove interactions and understanding the mechanisms driving these interactions is needed for inclusion in mangrove restoration and management plans.

In coastal wetlands, early successional plants may facilitate recruitment of mangroves through multiple mechanisms, including amelioration of environmental conditions, propagule trapping, and structural support. Milbrandt and Tinsley (2006) found *Batis maritima* significantly increased survival of *Avicennia germinans* seedlings and attributed this positive effect on mangrove survival to greater surface elevation caused by the dense root system of *B. maritima*. McKee et al. (2007) reported positive effects of *Sesuvium portulacastrum* and *Distichlis spicata* on *Rhizophora mangle* in Belize. Both of these species increased establishment of *R. mangle* by propagule trapping, reduction of soil temperature, and improved soil aeration, but only *D. spicata* provided structural support by promoting establishment of propagules in the vertical position (McKee et al. 2007). Mangrove propagules disperse by hydrochory (water dispersal) and stranding and retention in suitable habitat are critical steps for successful establishment after dispersal (Rabinowitz 1978), which can be facilitated through trapping by emergent vegetation in riparian and estuarine habitats (Stevens et al. 2006; McKee et al. 2007; Nilsson et al. 2010; Peterson and Bell 2012). Stevens et al. (2006) found high numbers of propagules dropped by mature mangroves (primarily *A. germinans*) were trapped within 5-15 m of parent trees by vegetation in a subtropical wetland in Florida. The salt marsh grass species *Spartina alterniflora* facilitated propagule retention in Florida wetlands and was particularly beneficial in areas where high wave energy was problematic for mangrove recruitment (Lewis 1982; Lewis 2005). Peterson and Bell (2012) found retention of *A. germinans* propagules in vegetated patches varied with the species of plant present in the patch, with *Sporobolus virginicus* retaining significantly more propagules compared to *B. maritima* and *S. portulacastrum* in a mangrove-upland ecotone. These results suggest location and species-specific characteristics of both the nurse plants and mangrove species can lead to variation in the importance of different mechanisms and the outcome of interactions.

Our study tests the propagule trapping hypothesis with *R. mangle* propagules at a coastal wetland in early stages of recovery following hydrological restoration of mosquito impoundments in Mosquito Lagoon, Florida. *Rhizophora mangle* propagules are large (>30 cm) and retain buoyancy for up to one year (Rabinowitz 1978; Tomlinson 1994); thus, propagule trapping by shoreline vegetation may be important for retaining stranded propagules until initiation of root production, particularly during periods of prolonged flooding. During post-restoration monitoring conducted by authors at this restored mosquito impoundment, we observed higher numbers of *R. mangle* propagules in vegetated patches with initial plant colonizers compared to unvegetated shorelines. The most common shoreline vegetation containing stranded *R. mangle* propagules was a mix of two herbaceous halophytes *B. maritima* and *Sarcocornia perennis*. These commonly co-occurring species are found in coastal wetlands throughout Florida and the Caribbean (Rey 1994; Schmalzer 1995; McKee 1995; Lacerda et al. 2001; Lewis 2005; Rey et al. 2012). Both species are perennial, low-growing (height <1 m), succulent plants that create thick mats of vegetation (Tiner 1993, Taylor 1998) and were commonly the initial plant colonizers at sites monitored within one month of restoration in Mosquito Lagoon. Here, we present results from a field experiment to evaluate the retention of *R. mangle* propagules on vegetated and unvegetated shorelines. We hypothesized mangrove propagules would be retained significantly longer on vegetated shorelines compared to unvegetated shorelines. Identifying biotic interactions between mangroves and associated flora has direct applications to mangrove restoration as well as increasing our understanding of the role of community interactions in structuring ecosystems.

Methods

Study Site

This study was located in Mosquito Lagoon, in Canaveral National Seashore, FL (28° 53’05.81” N, 80°49’44.85” W; Fig 1). Mosquito Lagoon is the northernmost portion of the Indian River Lagoon, a 250 km estuary located on the east coast of Florida that spans the temperate-subtropical climate boundary. Currents in Mosquito Lagoon are primarily wind-driven and north and north-western winds are common during fall and winter months. Water levels in Mosquito Lagoon are microtidal and change seasonally, with high water season occurring in fall and winter (Schmalzer 1995) and coinciding with dispersal time of *R. mangle* propagules. During the high water season, coastal wetlands can be flooded continuously during both high and low tides. In the 1960s, coastal wetlands in Mosquito Lagoon were impounded for mosquito management (Schmalzer 1995; Brockmeyer et al. 1997; Rey et al. 2012). Hydrological restoration began in the 1990s to mechanically level dikes to wetland elevations, followed by natural regeneration of native plant communities (Brockmeyer et al. 1997; Rey et al. 2012). The impoundment where this study was conducted was restored in 2003 (R. Brockmeyer, pers. comm.) and was part of a biodiversity monitoring program documenting recovery of native flora and fauna following hydrological restoration. At the time of this study, the impoundment was seven years post-restoration and supported a patchy distribution of marsh vegetation, which provided researchers with both vegetated and unvegetated patches on shorelines in a similar geographic location (Fig 1).

Experimental Methods

Three trials were conducted and began on the following dates: 11 October 2010 (trial 1), 1 November 2010 (trial 2), and 3 December 2010 (trial 3). The first trial was initiated after the start of seasonal high water and during annual natural *R. mangle* dispersal. Subsequent trials were spaced out to evaluate the effects of propagule trapping over the high water season. Each trial ran for sixteen weeks. Due to overlap in timing of trials to cover the time of *R. mangle* seed dispersal, different shoreline locations along the restored impoundment were used for each trial; thus, the reader is cautioned that the interpretation of the trial date variable is confounded. Locations for each trial were determined during biodiversity monitoring in summer 2010 prior to start of first trial and randomly assigned to one of three trial dates. All locations were low energy shorelines, away from major boating channels, and contained both vegetated and unvegetated areas with a minimum size of 150 m in length parallel to shoreline and 4 m in width for each shoreline type. Post-restoration monitoring included elevation measurements along a perpendicular transect using a laser level and stadia rod. Relative change in elevation from the lowest observed water level to 5 m landward was measured in 0.5 m intervals along four randomly located transects within all study plots. We initially measured seven different locations and selected three locations with similar elevations to control for the effect of elevation on the retention of propagules. All shorelines used in this study had a mean relative elevation between 12.0 and 12.5 cm (-0.5 m NAVD88; Table 1) that gradually sloped landward, increasing by approximately 2% from the lowest observed water level to 4 m landward. The number of days each site were completely flooded during each trial was estimated using relative elevation measurements of restored mosquito impoundment shorelines, field observations of water depth, and minimum tide predications from nearest the nearest tide buoy (Ponce Inlet, http://tidesandcurrents.noaa.gov; Fig 2).

Rhizophora mangle propagules were collected from shorelines (post-dispersal) in non-impounded coastal wetlands in Mosquito Lagoon 24 hrs before start of each trial. Propagules were examined after collection and only those without roots or damage to the hypocotyl were used for this experiment. Propagules were randomly assigned to one of two treatments and painted with different colors (Krylon Interior-Exterior paint): pink (vegetated) and yellow (unvegetated). Prior testing showed spray paint did not decrease survival of propagules (100% of painted and unpainted propagules (n= 15) produced first set of leaves). The length of propagules was measured prior to painting.

The following methods were repeated at each vegetated and unvegetated shoreline for all trials (Fig 1). Study plots with and without vegetation (104 m parallel to shoreline x 4 m perpendicular to shoreline) were established at each location (Fig 1). A linear transect was run parallel to the shoreline in the center of each study plot (Fig 1) and 60 propagules were dropped at randomly generated locations along transect (difference in elevations where each propagule was dropped ranged from 0-3 cm in all study plots). Propagules were dropped in a horizontal position at water's surface (October, November trials) or 5 cm above substrate when sites were dry (December trial). At each location a propagule was dropped, water depth was measured with a meter stick. Vegetated study plots contained a mix of *B. maritima* and *S. perennis* and the percent cover of each species was measured using the point-intercept method in 0.25 m^2 quadrats (10 points per quadrat) centered on each propagule dropped along transects. After two days, a visual search in 2-m wide belt transects on the seaward and landward sides of each initial transect identified locations of retained painted propagules within the 104 m x 4 m study plot (Fig 1). Each *R. mangle* propagule was marked individually with a survey flag (0.9 m in height with 12.7 cm x 12.7 cm orange flag) and ID number. During each monitoring visit, propagules were recorded as retained if present within a 0.25 m^2 quadrat placed on the substrate with the ID flag in the center of the quadrat. Propagule condition (viable or brown/shriveled, consumer damage), propagule orientation (horizontal or vertical), and water depth in each quadrat were also recorded. Initial set-up and all post-deployment monitoring were conducted during low tide. Monitoring occurred every 2 days post-deployment for the first week, and then weekly for a total of sixteen weeks.

Statistical Analysis

The "survreg" function for survival analysis was used to compare the effects of two factors, shoreline type (vegetated, unvegetated) and trial start date (October, November, December), on the retention time of *R. mangle* propagules (R software; R 2.14.1; Crawley 2007).

The final status was defined as either retained or lost, and data was fitted using a Weibull distribution. Simplified models were compared using the ANOVA function to detect significant changes in deviance when terms were removed. For the minimal adequate model, a likelihood-ratio test was used to identify significant effect of factors, using the log-likelihood values given by the "survreg" function. References for contrasts were the vegetated shoreline treatment and December trial because it varied from the first two trials in initial water depth and number of days flooded (see results below). One-way ANOVA was used to compare percent cover of *B. maritima* and *S. perennis* at the initial vegetated quadrats along each transect (n=60 per trial) for the three trial dates (R software; R 2.14.1; Crawley 2007). For all statistical analyses, minimum *p*-value for evaluating significance was 0.05.

Results

The minimal adequate survival model retained the main effects of shoreline type and trial start date and the interaction term (Table 2). The scale was 1.49, indicating hazard (or risk of loss) increased with time in our study and there was a significant effect of factors on propagule retention time (X^2 = 264.8, df = 5, p <0.001). Propagules were lost faster at unvegetated shorelines compared to vegetated shorelines during all trials (estimated effect size= 2.75; p <0.001; Table 2). At all vegetated shorelines, vegetation was emergent at low tide and taller than propagules when in a vertical position (range of propagule lengths= 28-36 cm; Table 1). All vegetated locations had 100% cover in all sixty quadrats and there was no significant difference in percent cover of *B. maritima* and *S. perennis* at the three locations. Mean percent cover ranged between 47% and 51% for *B. maritima* and 49% and 53% for *S. perennis* per location. At the end of the October trial, 44 of the original 60 propagules (73.3%) remained in the vegetated shoreline, compared to one propagule (1.7%) on unvegetated shorelines (Fig 3). In the November trial, 42 propagules (70.0%) were retained on the vegetated shoreline compared to only 6 propagules (10%) at the unvegetated shoreline (Fig 3). At the end of the December trial, 32 propagules (53.3%) were retained in the vegetated area, compared to 1 propagule (1.7%) at unvegetated shorelines (Fig 3).

There were no significant contrasts among trial start dates, but there was a significant interaction for October trial and unvegetated shorelines compared to reference values of vegetated shorelines and December trial (estimated effect size= 4.13; p=0.003, Table 2). Propagules from the October trial at the unvegetated shoreline treatment were lost faster than propagules in the November and December trials: 56 out of 60 propagules (93.3%) were lost after two days (Fig 3). Elevation in study plots was similar for all locations (~12 cm above MLLW; Table 1) and the length of propagules was similar between trial dates (Table 1). The October trial began during the beginning of high water season (initial mean water depth ± SE= 4.7 ± 0.2 cm (vegetated shoreline) and 5.9 ± 0.3 cm (unvegetated shoreline) when propagules deployed; Table 1) and study plots were flooded during both high and low tides for an estimated 33 days throughout the sixteen-week experiment (Table 1). During the November trial set-up, mean water depth ± SE was 4.8 ± 0.3 cm at vegetated shoreline and 5.2 ± 0.3 cm at unvegetated shoreline and study plots were inundated at high and low tide for an estimated 20 total days (Table 1). The December trial began near the end of high water season and vegetated and unvegetated shoreline locations were not flooded during trial set-up (Table 1). The estimated number of days of inundation at high and low tide was 11 days over the sixteen-week trial (Table 1).

At the start of October and November trials, propagules were dropped in a horizontal orientation at water surface, however, propagules shifted to an upright position with the posterior end of the propagule in contact with the substrate when unvegetated locations were flooded at initial set-up. The majority of propagules dropped at vegetated shorelines also shifted into the vertical position in the October and November trials (57 and 53 of the 60 propagules for each trial, respectively). During the set-up of the December trial, propagules remained horizontal when dropped on the unvegetated substrate. In comparison, 41 of the 60 propagules dropped in the vegetation were in a vertical position once in contact with the vegetation. By the end of the three trials, all retained propagules in the vegetated shoreline treatments were in a vertical position and produced two leaves, whereas all propagules remaining in the unvegetated shorelines were in a horizontal position, showed signs of desiccation on the hypocotyl (brown and shriveled), and lacked development of leaves or roots.

Consumer damage to propagules during October and November trials was only observed in the vegetated treatment (32 (53.3%) and 15 (25%) propagules, respectively). Consumer damage was not always fatal in the vegetated shorelines and 14 damaged propagules in the October trial and 10 damaged propagules in the November trial were retained and produced leaves by the end of the trial. Consumer damage during the December trial was observed on 12 (20%) propagules in the vegetated shoreline and on the one remaining propagule in the unvegetated shoreline. Damage to the propagules on the vegetated shoreline during final weeks of December trial (when locations were experiencing less frequent periods of complete inundation) resulted in propagules broken into multiple sections.

Discussion

Facilitation by nurse plants through propagule trapping and support can have a positive effect on mangroves by increasing retention until rooting occurs at shorelines with frequent flooding, particularly in locations where the habitat is recovering from natural or anthropogenic disturbances (Lewis 1982; McKee et al. 2007). Our study found the presence of *B. maritima* and *S. perennis* on shorelines had a significant positive effect on retention time of *R. mangle* propagules, supporting a hypothesis that vegetation can increase retention time as a mechanism of facilitation by propagule trapping. In addition, only mangrove propagules in the vegetated treatments were in a vertical position, did not show signs of desiccation, and produced roots and initial leaves by the end of our study. We also observed natural recruitment of three native mangrove species (*R. mangle*, *A. germinans*, and *Laguncularia racemosa*) in the vegetated study plots during all three trials. Although propagules from the three species were also observed stranded in the unvegetated plots, we did not see any propagules develop into seedlings during our trials. Recruitment and growth of pioneer halophytes able to trap and support mangrove propagules may be a critical first step in secondary succession and recovery of mangrove communities at disturbed or restored coastal wetlands.

Mangrove dispersal in Mosquito Lagoon coincides with seasonal high water and mechanisms increasing retention of propagules when shorelines are inundated can positively affect mangrove recruitment. There was a significant interaction between trial date and shoreline type, with the largest difference in time of retention observed in the October trial when propagules were subjected to an estimated 33 days of flooding at both high and low tides, compared to 20 and 11 days during the November and December trials, respectively (Fig 2; Table 1). Although study plots were flooded during the set-up of both the October and

November trials (Fig 2; Table 1), higher retention of propagules during the November trial may have been caused by the decrease in number of days study plots were inundated over the entire tidal cycle. The orientation of shorelines for the October and November trials was different from the December trial (Fig 1) and differences in currents and wave energy may also account for some of the variation between trials. However, all sites were in a low-energy location, away from major boating channels, and the similarities in elevations of the sites (Table 1) suggest wave energy and rates of erosion were similar among sites.

Mangrove propagules initiated root production and produced a first set of leaves when locations were experiencing frequently flooded conditions at vegetated shorelines. Our study suggests propagules released from parental trees at the beginning of the high water season will particularly benefit from trapping in vegetation due to the extended inundation period; however, this mechanism may be less critical during the dry season in this microtidal estuary. In mesotidal estuaries with daily tidal fluctuations, the effect of propagule trapping may be greater due to more frequent inundation periods and increased chance of removal by tides after stranding; thus, comparative studies between mesotidal and microtidal wetlands would be useful in order to understand the effect of propagule trapping under different hydrodynamic conditions. The importance of facilitative interactions may increase as coastal wetlands experience effects of sea level rise, assuming nurse plants will be able to tolerate rises in sea level (Gilman et al. 2008; Alongi 2009; McKee et al. 2012). Plant-plant interactions have a significant effect on plant community dynamics and may mediate some environmental changes caused by climate change or other anthropogenic threats (Brooker 2006; Padilla and Pugnaire 2006; Brooker et al. 2008). Climate changes can also interrupt some community interactions or intensify others, such as competition (Brooker 2006), and research evaluating synergistic effects of climate change and community interactions is needed to understand the role interactions have in the resistance and resilience of mangrove systems.

Propagule trapping specifically assists with retention of propagules during the post-dispersal stranding phase of a mangrove's life cycle; however, vegetation may have both direct and indirect effects on mangroves and may change with developmental stage. For example, vegetation may provide an indirect benefit to stranded propagules by shading them from direct sunlight and reducing mortality from desiccation (McKee et al. 2007). We found propagules retained on the unvegetated shorelines suffered from desiccation, leading to the loss of viability by the end of trials when water levels decreased and sites were exposed to longer dry periods. In comparison, propagules on the vegetated shorelines did not show signs of desiccation, despite dry conditions at the end of the trials. McKee et al. (2007) also observed signs of desiccation in *R. mangle* propagules planted in bare patches in a recovering wetland in Belize. In addition to the benefits of shading to the propagules, vegetation also shades the soil and decreases rates of evaporation during dry periods (Bruno et al. 2003; Young et al. 2005), further reducing potential of desiccation to propagules and creating more favorable abiotic conditions once the propagules becomes rooted.

Growth and survival of mangrove seedlings once established on the shoreline will be affected by tolerances to local abiotic conditions and amelioration of limiting soil conditions by initial colonizers, which may indirectly facilitate survival of seedlings (McKee et al. 2007). We compared vegetated shorelines to unvegetated shorelines in order to test a hypothesis of propagule trapping; however, the differences in plant distribution could have been caused by local conditions within the patches on the shorelines. At our study site, initial recruitment of *B. maritima* and *S. perennis* occurred through seed and fragment dispersal and extension of vegetative runners from the interior portion of the restored mosquito impoundment. Plant cover increased over time through vegetative propagation, resulting in vegetated patches surrounded by bare patches. Both species are halophytes with a high tolerance for salinity (Davy et al. 2006; Debez et al. 2010) and these two early successional species have been observed colonizing bare patches where salinity can increase to over 70 ppt during the dry season (soil salinities average 28 ppt year-round; unpublished data, Donnelly et al.). After colonization, vegetated areas at restored mosquito impoundments have significantly lower soil salinities (10-20 ppt less) compared to unvegetated areas (unpublished data, Donnelly et al.). This was similar to findings by McKee et al. (2007) in Belize where decreased soil salinity and temperature was observed in vegetated patches compared to bare patches. Once established, long-term survival of mangroves seedlings will also be affected by other biotic interactions, including competition for light and nutrients with neighboring plants (McKee 1995; Bruno et al. 2003; Young et al. 2005; Stevens et al. 2006; McKee et al. 2007). Our study focused on the effect of vegetation on initial establishment of mangroves at restored locations and ended after sixteen weeks, therefore, long-term effects of early colonizing species on mangrove survival after the establishment phase is beyond the scope of our study and additional studies are needed to further investigate the role of facilitative interactions in coastal wetlands succession.

Negative biotic interactions, such as damage by crabs, insects, and other consumers, also strongly influence mangrove seedling establishment and distribution within a coastal wetland (Robertson et al. 1990; Rey 1994; McKee 1995; Minchinton and Dalby-Ball 2001; Stevens et al. 2006). Although not a primary objective for this study, we observed herbivore damage to mangrove propagules in the vegetated shorelines, including bite marks, entrance and exit holes of suspected Lepidopteran larvae, and propagules broken into multiple pieces. Propagule damage was only observed on the one remaining propagule in the unvegetated treatment during the December trial, but this difference can be a result of the short time period most propagules were retained rather than a difference in shoreline type. However, nurse plants may serve as refugia for consumers (Padilla and Pugnaire 2006) and propagule damage was a cause of mortality at the vegetated shorelines. Consumer damage did not prevent establishment of seedlings at vegetated shorelines and the overall effect of vegetation on propagule retention and establishment was positive in all trials. In comparison, the small number of propagules retained in the unvegetated treatments did not transition to the seedling stage despite lack of damage by consumers.

Our results support a hypothesis of propagule trapping as an important facilitative mechanism for recruitment of *R. mangle* to subtropical coastal wetlands following water dispersal and also identify additional questions for future research. First, longer studies are needed to investigate the effect of early successional species on *R. mangle* after seedling establishment and the long-term effect on coastal wetlands succession. Second, the size of propagules may influence success of propagule trapping, however, we did not tag propagules prior to deployment in the field and we could not include the propagule length in our statistical analysis as a potential factor on retention time. Third, our method of dropping propagules into the middle of the study plots was chosen because it mimics methods used by restoration practitioners. Thick patches of vegetation may impede mangrove propagules from moving into vegetation with tides (Peterson and Bell 2012); however, we observed natural dispersal of mangrove propagules into the interior portion of the vegetation patches during this study, possibly as a result of stranding during high tides when vegetated shorelines were completely submerged. Studies using a more natural method of introducing propagules would be helpful to further investigate the effects of propagule trapping on naturally dispersing propagules. Fourth, species present in different locations may have different effects on mangrove propagule trapping. In contrast to the trapping of *R. mangle* propagules by *B. maritima* documented in this study, Peterson and Bell (2012) found *B. maritima* did not have a positive effect on retention of smaller *A. germinans* propagules. McKee et al. (2007) also found differences in the effects of nurse plant species in Belize and these results suggest species-specific characteristics may be important in evaluating the importance of propagule trapping on mangrove species. Finally, the positive effect of vegetation on mangroves, particularly those occurring during the initial colonization and establishment stages, has direct applications to coastal wetland restoration and studies combining facilitative interactions and coastal wetland restoration applications are needed.

Our study documented over 50% of propagules dropped into the vegetated area were retained and survived to the seedling stage, which is a higher survival rate of propagules than many other mangrove restoration projects where survival and retention of propagules and small seedlings often ranges between 1% to 20% (Gilman and Ellison 2007; Salgado Kent and Lin 1999; Lewis 2005; Samson and Rollon 2008; Kamali and Hashim 2011). Applying facilitation concepts to restoration has the potential to increase project success, particularly in systems where physiological stress is high (Bruno et al. 2003; Padilla and Pugnaire 2006; Halpern et al. 2007; Peterson and Bell 2012). In riparian and wetland habitats, restoration methods utilizing natural dispersal through hydrochory can be applied to larger areas, completed with lower project and labor costs, and maintain local genetic variation and adaptations (Nilsson et al. 2010). Hydrological restoration of coastal wetlands by removing barriers to tidal influence has been shown to promote growth of halophytic species and natural dispersal of mangrove propagules, developing a diverse plant community without the need for additional planting (Brockmeyer et al. 1997; Turner and Lewis 1997; Lewis 2005; Nilsson et al 2010: Rey et al. 2012). When natural regeneration is not possible due to recruitment limitations, planting propagules or seedlings in existing vegetation may increase establishment compared to planting in unvegetated locations (Young et al. 2005; Milbrandt and Tinsley 2006; Peterson and Bell 2012). An ecosystem-level approach that addresses both biotic and abiotic interactions affecting mangrove recruitment, survival, and growth is necessary to increase success of mangrove restoration projects and conserve remaining mangrove ecosystems.

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Tables

Table 3.1. Means (± SE) for initial propagule length (cm), elevation of study plots (cm), water depth at start of trial (cm), and the estimated number of days sites were submerged at both high and low tides for each trial date and shoreline treatment.

Trial Start Date	Mangrove Dispersal Season	Shoreline Type	Mean Length of Propagules (cm ± SE)	Mean Relative Change in Elevation (cm ± SE)	Mean Water Depth at Start of Trial (cm ± SE)	Time Sites Submerged for Full Tide Cycle (days)
11 October 2010	Early Dispersal Season	Vegetated	30.5 ± 0.2	12.3 ± 2.1	4.7 ± 0.2	33
		Unvegetated	30.7 ± 0.3	12.5 ± 2.2	5.9 ± 0.3	33
1 November 2010	Mid-Dispersal Season	Vegetated	30.7 ± 0.3	12.0 ± 2.1	4.8 ± 0.3	20
		Unvegetated	31.3 ± 0.3	12.1 ± 1.8	5.2 ± 0.3	20
3 December 2010	Late Dispersal Season	Vegetated	31.3 ± 0.4	12.3 ± 1.2	0.0 ± 0.0	11
		Unvegetated	30.9 ± 0.3	12.4 ± 1.3	0.0 ± 0.0	11

Table 3.2. Model summary of survival analysis comparing retention time of *Rhizophora mangle* propagules between shoreline types (vegetated, unvegetated) and trial start dates (October, November, December). Reference values were December trial and vegetated shoreline treatment.

	Value	SE	z	p
Intercept	5.63	0.29	19.31	<0.001
Trial- October	0.13	0.42	0.31	0.76
Trial- November	-0.02	0.41	-0.05	0.96
Shoreline Type- Unvegetated	-2.89	0.36	-8.07	<0.001
October: Unvegetated	-1.50	0.50	-2.99	0.003
November: Unvegetated	0.09	0.50	0.18	0.86
Log(scale)	0.40	0.05	8.52	<0.001

Model: Trial Start Date + Shoreline Type + Trial Start Date*Shoreline Type

Figures

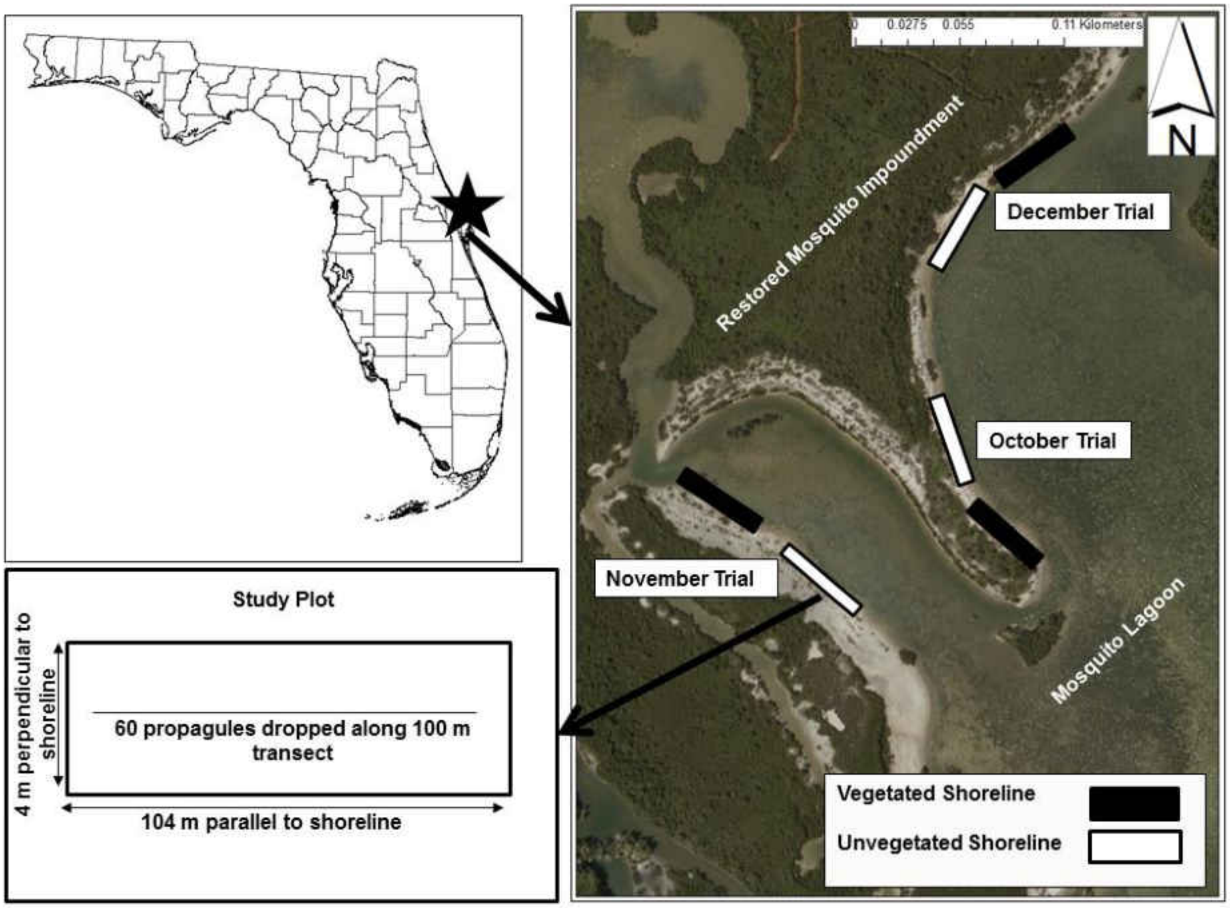

Figure 3.1. Study location was a restored mosquito impoundment in Mosquito Lagoon, on the central east coast of Florida. Three pairs of study plots were established prior to start of experiment and randomly assigned to trial start dates (October, November, December). Each study plot (vegetated, unvegetated) was 104 m in length parallel to shoreline and 4 m in length perpendicular to shoreline. (Florida map: Florida County Boundaries- Florida Statewide July 2011 layer downloaded from http://www.fgdl.org/metadataexplorer/explorer.jsp; Aerial photography was provided by St. Johns River Water Management District)

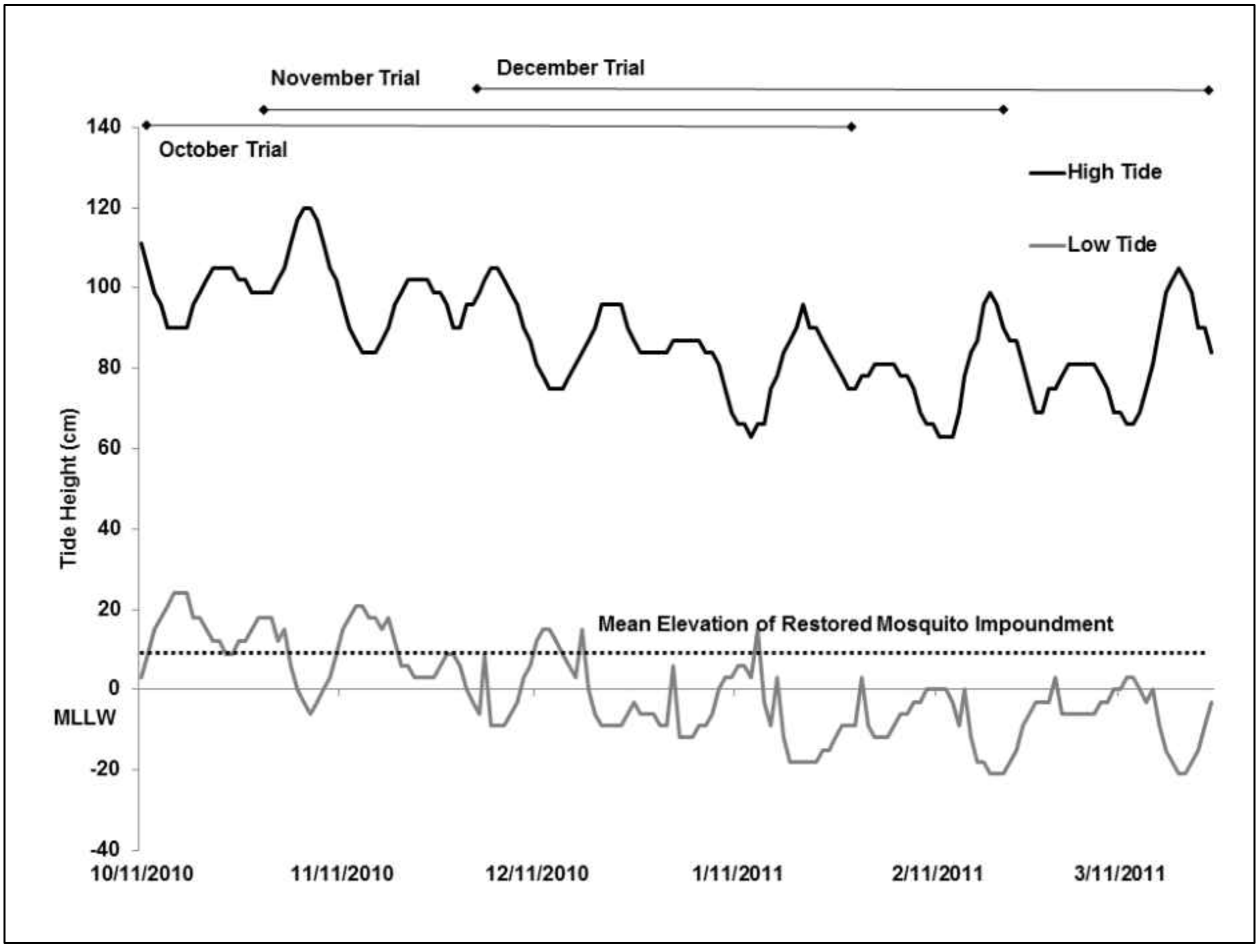

Figure 3.2. The maximum tide height (cm; solid black line) and minimum tide height (cm; solid gray line) during the October, November, and December trials. The mean elevation of the mosquito impoundment where study was conducted is shown with the black dotted line. Tidal data was derived from predicted tidal heights for the Ponce Inlet, New Smyrna station and was retrieved from http://tidesandcurrents.noaa.gov.

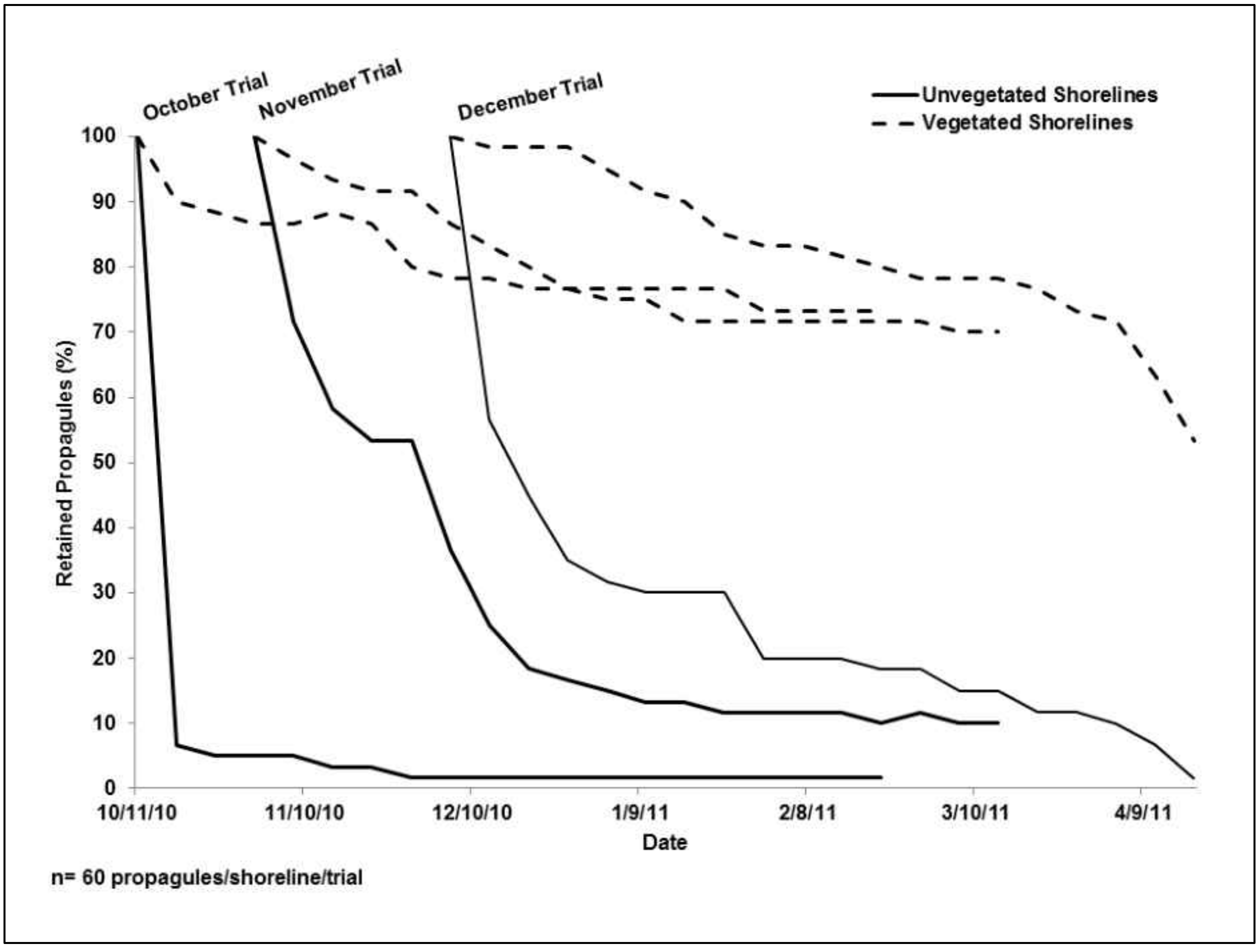

Figure 3.3. Percent of *Rhizophora mangle* propagules retained at unvegetated shorelines (solid line) and vegetated shorelines (dashed lines) for trials initiated on 11 October 2010 (trial 1), 1 November 2010 (trial 2), and 3 December 2010 (trial 3). For each trial date, 60 propagules were dropped on day1 at each shoreline type (vegetated, unvegetated). There was a significant effect of factors on the retention of propagules (survival analysis: X^2 =264.8, df = 5, p < 0.001).

CHAPTER 4. EFFECT OF PRE-DISPERSAL DAMAGE ON BOUYANCY OF MANGROVE PROPAGULES IN FLORIDA

Abstract

Damage to mangrove propagules has been shown to affect dispersal, recruitment, survival, establishment, and growth in tropical and subtropical coastal wetlands around the world. The purpose of this study was to use observational and experimental methods to evaluate the frequency and type of pre-dispersal propagule damage and the effect of damage on propagule buoyancy for *Avicennia germinans*, *Rhizophora mangle*, and *Laguncularia racemosa* in Mosquito Lagoon, Florida. The overall frequency of pre-dispersal damage was significantly greater for *R. mangle* propagules, compared to *A. germinans* and *L. racemosa*, and showed variation in annual collections between 2006 and 2010. Types of damage on mangrove propagules were identified as three general categories (scrapes, bite marks, holes). Scrapes were the most common damage type for all three species. Holes were more frequent in *A. germinans* and *L. racemosa* propagules compared to *R. mangle*. A variety of insects were found inside of mangrove propagules, including ants, beetles, spider mites, fly larvae and lepidopteran larvae. Damaged propagules floated for significantly less time compared to undamaged propagules for all mangrove species, suggesting pre-dispersal damage could decrease dispersal capabilities and affect long-distance propagule supply, recruitment, and regeneration of disturbed sites. Results from this study increase our understanding of the role of biotic interactions in the structure and function of coastal wetlands and have potential applications for future management, conservation, and restoration of ecologically important mangrove species.

Keywords: *Avicennia germinans,* herbivory, *Laguncularia racemosa, Rhizophora mangle*

Introduction

Mangroves are halophytic plants and a dominant component of sub-tropical and tropical coastal wetlands (Alongi 2009). Historically, the primary factors controlling mangrove structure and function in coastal wetlands were expected to be abiotic factors, such as tidal inundation and salinity, which acted as bottom-up controls on mangrove populations (Odum and McIvor 1990, Cannicci et al. 2008, Alongi 2009). Although the importance of physiologically stressful abiotic conditions of mangrove habitat cannot be overlooked (Odum and McIvor 1990, McKee 1995, Elster et al. 1999, Alongi 2009), an increasing amount of research has documented the importance of biotic factors on mangrove populations through positive and negative interactions (Cannicci et al. 2008, Alongi 2009, Feller et al. 2010). Biotic interactions with flora and fauna, including competition, facilitation, and herbivory, can directly and indirectly affect mangrove growth, survival, and reproduction (Robertson et al. 1990, McKee 1995, Elster et al. 1999, Minchinton and Dalby-Ball 2001, Cannicci et al. 2008, Alongi 2009, Feller et al. 2010).

Herbivory can occur on leaves, stems, roots, and reproductive structures of mangroves, with rates and severity of damage varying by location, species of mangroves and consumers, and abiotic factors (Robertson et al. 1990, McKee 1995, Elster et al. 1999, Cannicci et al. 2008). Primary consumers of mangroves were previously thought to play a minor role in the flow of energy and nutrients through mangrove ecosystems, which is usually classified as a detritus-based system with the majority of primary productivity moved through tidal action (Odum and McIvor 1990, Cannicci et al. 2008; Alongi 2009, Feller et al. 2010). However, studies have documented herbivory levels were similar in mangrove forests compared to temperate and tropical terrestrial forests (Burrows 2003). Herbivory in mangrove systems potentially affects numerous ecosystem processes, including primary production, energy flow, and nutrient cycling (Cannicci et al. 2008, Alongi 2009, Feller et al. 2010).

Mangroves produce viviparous propagules which can remain on parent trees for a few months to a year, depending on the species and location, before dispersing via hydrochory (Rabinowitz 1978, Tomlinson 1986). Damage to propagules can affect dispersal, recruitment, survival, establishment, and growth in coastal wetlands around the world (Snedaker and Lahmann 1988, Smith et al. 1989, McKee 1995, McGuiness 1997, Duke et al. 1998, Minchinton and Dalby-Ball 2001, Sousa 2003, Minchinton 2006). Propagule damage can occur pre-dispersal, during maturation on trees, and post-dispersal, when the propagules are stranded after dispersal period (Duke et al. 1998, Minchinton and Dalby-Ball 2001, Cannicci et al. 2008). Propagules contain nutrient-rich, buoyant tissue to support the developing seedlings during dispersal and establishment phases; this can also be an important food source for animal species (Alongi 2009). Crab species can cause significant post-dispersal damage that affects recruitment, distribution and survival of mangrove propagules and seedlings (Snedaker and Lahmann 1988, Smith et al. 1989, McKee 1995, McGuiness 1997), particularly those of the genus *Rhizophora* and *Avicennia* (Smith et al. 1989, McKee 1995, Duke et al. 1998).

Insects, primarily beetles and caterpillars, are common causes of damage to mangrove propagules before and after dispersal (Onuf et al. 1977, Robertson et al. 1990, Farnsworth and Ellison 1997, Elster et al. 1999, Minchinton and Dalby-Ball 2001, Sousa et al. 2003, Devlin 2004). Survival of *Avicennia germinans* was decreased by damage from insects in mangrove forests in Colombia, with caterpillars causing up to 100% loss of propagules and seedlings (Elster et al. 1999) Pre-dispersal damage by the boring beetle *Coccotrypes rhizophorae* decreased propagule viability (Onuf et al. 1977) and resulted in mortality of up to 89% of *Rhizophora mangle* seedlings in closed-canopy gaps after dispersal (Sousa et al. 2003). In Australia, Robertson et al. (1990) found 3% to 92% of propagules from twelve mangrove species were damaged by insects while attached to parent trees. Insect damage significantly reduced survival, height, and biomass of seedlings from damaged propagules, but overall effects varied with mangrove species (Robertson et al. 1990). Consumers can directly cause damage by eating all or part of the propagule and indirectly through consumption of algae or insects living in or on the mangrove propagule. Insects which bore into propagules increased propagule mortality more than herbivores that only damage the outer tissues (Robertson et al. 1990, Farnsworth and Ellison 1997, Elster et al. 1999, Minchinton and Dalby-Ball 2001, Sousa et al. 2003).

Pre-dispersal damage to propagules can significantly impact the early life history of mangroves once they are released from the parent tree (Robertson et al. 1990, Minchinton and Dalby-Ball 2001). Minchinton and Dalby-Ball (2001) found establishment of *A. marina* propagules was not significantly affected by damage occurring pre-dispersal because insects only consumed the cotyledons of propagules but did not damage embryonic axis. However, loss of cotyledons decreased resources available to the developing seedling and resulted in shorter seedlings with lower leaf production compared to seedlings from undamaged propagules (Minchinton and Dalby-Ball 2001). Another potential consequence of pre-dispersal damage to mangrove propagules was an effect on the buoyancy of propagules (Minchinton 2006). The dispersal distance of propagules in water currents is directly affected by the length of time buoyancy is retained (Rabinowitz 1978) and any factor influencing buoyancy will also affect dispersal capabilities and movement of propagules to long distance locations (Minchinton 2006).

Infestation by larval insects was shown to have a positive effect on buoyancy of propagules of *Avicennia marina*, as holes increased air within the propagule and increased the likelihood the propagule would float after losing the pericarp (Minchinton 2006). In addition, larvae inside of propagules can survive immersion in seawater (Robertson et al. 1990, Minchinton 2006). Propagule infestation of *A. marina* served as an effective dispersal vector for fly and moth species, but propagule viability decreased over time, with fewer viable propagules found at long-distance dispersal sites (Minchinton 2006). This can have a significant effect on wetland community structure as dispersal acts as an ecological filter on local species diversity and effects successional processes and recovery of disturbed and restored sites (Neff and Baldwin 2005, Nilsson et al. 2010). While numerous post-dispersal studies exist, research investigating the effects of pre-dispersal damage on buoyancy of other mangrove species is needed in order to better understand the strength of this interaction on mangrove reproductive success.

The purpose of this study was to use observational and experimental methods to evaluate the frequency and type of pre-dispersal propagule damage and the effect of damage on propagule buoyancy on three species of mangroves in Florida. Our study site was Mosquito Lagoon, a 250 km estuary spanning the temperate-sub-tropical climate boundary on the east coast of Florida and northernmost portion of the Indian River Lagoon system. In this transitional zone, coastal wetlands are a mixed saltmarsh-mangrove community with three native species of mangroves, *Laguncularia racemosa* (L.) C.F. Gaertrn (white mangrove), *Rhizophora mangle* L. (red mangrove), and *Avicennia germinans* (L.) L. (black mangrove). Propagules from each species vary in size, structure, length of time attached to the parent tree, and vivipary. *Laguncularia racemosa* produces ovoid-shaped propagules in the summer months in Florida that are retained on the tree for up to six months. This species produces the smallest propagules of the three Florida mangrove species (1-2 cm) and differs from *R. mangle* and *A. germinans* because propagules are cryptoviviparous, completing germination during the dispersal stage (Tomlinson 1986). The propagule consists of an embryo covered by a pericarp (McKee 1995), with cotyledons and radicle developing during the dispersal period (Rabinowitz 1978). Pericarps make the propagule buoyant for hydrochory and are not shed until rooting in substrate occurs post-dispersal (Rabinowitz 1978). *Rhizophora mangle* produces rod-shaped propagules with a long hypocotyl (McKee 1995) up to 30 cm in length that remain on the tree for nine months to a year in Florida (Odum and McIvor 1990). *Rhizophora mangle* propagules retain buoyancy longer than other Florida mangroves, with some propagules retaining buoyancy for over a year (Tomlinson 1986). *Avicennia germinans* produces small (2-4 cm), elliptical-shaped propagules with four succulent-like cotyledons and hypocotyl encased in a pericarp (Rabinowitz 1978, McKee 1995). Propagules begin to form during early summer in Florida and are retained on the tree for up to six months (Tomlinson 1986). Pericarps are shed during the first few days of dispersal and the entire embryo retains buoyancy for over 100 days (Rabinowitz 1978).

Methods

Damage to *A. germinans*, *R. mangle*, and *L. racemosa* propagules was quantified by collecting propagules once a month during September, October, and November in 2006 through 2010 for each species. All mangrove propagules from this study were collected from Mosquito Lagoon within Canaveral National Seashore in New Smyrna Beach, FL (28° 53’05.81” N, 80°49’44.85” W). Propagules were collected pre-dispersal from twenty trees of each species with mature propagules at time of collection. For each tree, ripe propagules were collected by shaking five branches for one minute and collecting propagules dropped from the branches into a bucket (Clarke and Myerscough 1991, Minchinton 2006). Propagules were visually examined and the number of damaged and undamaged propagules was recorded. For collections from 2008-2010, damaged propagules were sorted into damage categories (bite marks, scrapes, and holes) based on descriptions of herbivory damage to propagules and leaves from previous studies (Robertson et al. 1990, Feller et al. 2013). Scrapes were shallow (depth< 2 mm), superficial marks on outer layer of propagule epidermis or pericarp that did not penetrate into internal tissues. The bite mark category consisted of propagule damage irregular in shape, greater than 2 mm in depth, penetrating the epidermis or pericarp, and included damage to internal tissues or developing cotyledons. Damage categorized as holes was round, symmetrical and included damage to the inner tissues or developing cotyledons. All holes observed on propagules were less than 1 mm in diameter. During the last collection of each year, length and mass of twenty propagules from each damage type were measured and the level of damage was assessed by estimating the proportion of propagule length with damage (low = < 25%, medium = 25% to 50%, and high = >75%) for bites and scrapes or counting number of holes (low= 1 hole, medium= 2 holes, high= 3+ holes). Propagules were then cut open to evaluate internal damage and to identify presence of insect larvae or other organisms. In addition, twenty propagules each year from *A. germinans* and *L. racemosa* with holes (indicating possible presence of larvae) were placed into small plastic cups with 3 cm of soil and three mangrove leaves and covered with cheesecloth to allow larvae to complete their life cycles for identification.

Rhizophora mangle, *A. germinans*, and *L. racemosa* mangrove propagules with different types of damage were used to test the effect of damage on length of time propagules retain buoyancy. Three trials were conducted for each mangrove species. Propagules for each species were randomly selected from propagule collections made during fall 2009 and buoyancy trials began 24 hrs after each propagule collection. Initial trial dates were 27 September 2009 for trial 1, 30 October 2009 for trial 2, and 27 November 2009 for trial 3. There were four damage types for *A. germinans* and *L. racemosa* trials: holes, bite marks, scrapes, and undamaged (control). *Rhizophora mangle* trials had three damage types: bite marks, scrapes, and undamaged (control). Propagules of *R. mangle* rarely had holes and this damage type was not included in buoyancy trials because of insufficient number of replicates. Propagules were kept in aquariums to evaluate the length of time buoyancy was retained (Rabinowitz 1978, Donnelly and Walters 2008). Fifty propagules of each damage type were randomly assigned to one of five replicate 38-L aquariums for each trial (10 propagules per damage type per aquarium). Different aquariums were used for each mangrove species. Initial length and mass of all propagules was recorded prior to start of experiment. Aquariums were equipped with individual flow-through filters to simulate moving water and filled with 34-L of 30 ppt saltwater (natural salinity of Mosquito Lagoon). The number of propagules retaining buoyancy was recorded daily. Trials lasted until all propagules lost buoyancy with *L. racemosa* and *R. mangle* propagules. In trials with *A. germinans*, propagules remained buoyant for 100+ days and trials were terminated when floating propagules produced roots and first set of leaves.

The frequency of pre-dispersal predation was compared between mangrove species and years of collection (2006-2010) with general linear model selection (quasibinomial, logit) for proportion data (Crawley 2005; R 2.12.2). Models and significant model factors were compared using analysis of deviance tests (Crawley 2005; R 2.12.2). Frequency of damage types was compared between mangrove species and years of collection (2008-2010) with general linear model selection (quasibinomial, logit) and analysis of deviance tests for proportion data

(Crawley 2005; R 2.12.2). The first year of collection (2006) and mangrove species *R. mangle* were selected *a priori* for pairwise contrasts if respective factors were significant. The number of propagules infested with larvae was summed across year and damage type to calculate total numbers of infested propagules for each mangrove species and Fisher's exact test for count data was used to compare infestation with larvae among three mangrove species (Crawley 2005; R 2.12.2). The effects of damage on length and mass of propagules were compared for each mangrove species using two-way ANOVAs (damage type x collection year) (R 2.12.2). ANOVA assumptions were checked with boxplots and homogeneity of variance tests (R 2.12.2). The length of time propagules remained buoyant for each species by damage type was compared using the "survreg" function with the time variable representing number of days propagule remained floating (R 2.12.2). The final status was defined as either floating or sunk, and data was fitted using a Weibull distribution. For the minimal adequate model, a likelihood-ratio test was used to identify significant effect of factors, using the log-likelihood values given by the "survreg" function. The initial model included damage as a main effect, trial and tank as nested variables, and mass and length of propagules as covariates. Model selection was used to compare models with variables removed in a stepwise manner (R 2.12.2) with final model retaining only significant variables with p-value < 0.05. Simplified models were compared using the ANOVA function to detect significant changes in deviance when terms were removed.

Results

The total number of propagules examined for collections from 2006 to 2010 was 18,885 for all three mangrove species, with variations for each species per year, based on propagule availability (Table 4.1). Frequency of pre-dispersal propagule damage varied significantly between years ($p = 0.04$) and mangrove species ($p<0.001$), with means ranging between 14.5% for *L. racemosa* in 2007 to 73.7% for *R. mangle* in 2008 (Table 4.2; Figure 4.1). The interaction term in the model (year*mangrove species) was not significant and the minimal adequate model was year + mangrove species (Table 4.2). Percent of propagules with pre-dispersal damage from collections in 2008 (27.7% *L. racemosa*, 31.4% *A. germinans*, 73.7% *R. mangle*) and 2010 (30.3% *L. racemosa*, 59.5% *A. germinans*, 44.0% *R. mangle*) was significantly higher than in 2006 (20.9% *L. racemosa*, 16.6% *A. germinans*, 34.1% *R. mangle*) (2008: $p = 0.02$, 2010: $p<0.001$, Figure 4.1). The overall frequency of pre-dispersal damage was significantly greater for *R. mangle* propagules, compared to *A. germinans* ($p = 0.01$) and *L. racemosa* ($p<0.001$; Figure 4.1). Pre-dispersal damage ranged from 34% to 73% for *R. mangle* between 2006 and 2010, with an overall frequency of 51.6% of propagules. The frequency of damage of *A. germinans* propagules was between 16.6% and 59.5% of propagules collected (overall frequency= 35.8%). *Laguncularia racemosa* had the least amount of pre-dispersal predation on propagules, ranging between 14.5% and 30.3% (overall frequency= 23.5%).

The length of scrapes ranged between 2% to 90% of total propagule length, with the majority of scrapes for all species classified as the low damage category (Table 4.3). Scrapes left a scar on the propagules with thicker tissue that covered the damage on the epidermis or pericarp. In the laboratory, we found artificial scrapes created with a dissection needle on *R. mangle* propagules were repaired within 24-36 hours (M. Donnelly, pers. obs.). Bite marks could span up to 80% of propagule length, however, the majority of bite marks for all mangroves were in the low damage category (Table 4.3). Single holes were found in *R. mangle* propagules collected during 2009 (11 propagules) and 2010 (4 propagules) (Table 4.3). The number of holes in *Avicennia germinans* and *L. racemosa* propagules ranged between 1 and 6 holes per propagule; the majority of propagules, however, had 1 hole per propagule (Table 4.3).

Multiple types of insects and larvae were found inside of mangrove propagules, including ants, beetles, spider mites, fly larvae and lepidopteran larvae. For all three mangrove species, insects were only found inside of damaged propagules and no insects or signs of internal damage were observed in propagules without damage. Propagules with scrapes had the lowest amounts of internal damage and larva was found in one propagule with a scrape from *L. racemosa*. The boring beetle *C. rhizophorae* was found in three *R. mangle* propagules with bite marks from the 2008 collection, but was not observed in propagules collected in 2009 and 2010 or in propagules of other mangrove species. Lepidopteran larvae were most common in *L. racemosa* and *A. germinans* propagules and were the only group found in all three species of mangroves' propagules. There was a significant difference in number of propagules infested with larvae for the three mangrove species ($p = 0.006$), with *R. mangle* propagules having the least number of infested propagules. Larvae were most common in propagules with bite marks and holes. Larvae were present in 15% to 80% of *A. germinans* propagules with holes and between 5% and 20% of propagules with bite marks (Table 4.4). The percentage of *L. racemosa* propagules with holes and larval infestation ranged between 15% and 80% of propagules (Table 4.4). *Laguncularia racemosa* propagules with bite marks and larval infestation ranged between 10% and 40% of propagules (Table 4.4). Larvae were found in 5% or less of *R. mangle* propagules with bite marks in the three years of propagule collections (Table 4.4). *Rhizophora mangle* propagules with holes collected during 2009 had larvae in two out of 11 propagules and one out of four propagules contained larvae in 2010. Larval infestation of *L. racemosa* and *A. germinans* propagules caused extensive internal damage. In 20% to 40% of the *L. racemosa* and *A.*

germinans propagules examined with holes each year, complete consumption of developing cotyledons and damage to embryonic structures was observed and no green tissue was present when the propagules were cut open. For all three mangrove species, propagules with holes tended to have minimal damage when viewed from the outside. However, evidence of larvae (i.e. frass, feces) and internal damage to cotyledons was observed even if living larvae were not present in the propagules. The only Lepidopteran larvae to develop into moths during 2008-2010 were from *L. racemosa* propagules and were identified as the moth *Nola laguncularia*e.

The frequency of damage types (bite marks, scrapes, holes) did not vary significantly by year. The interaction between mangrove species and damage type was also not significant and both factors were removed, with the minimal adequate model including the additive effects of mangrove species and damage type (Table 4.5). The frequency of undamaged propagules was over 50% for all three mangrove species and significantly greater than frequency of bite marks, scrapes and holes ($p<0.001$ for all three damage types; Table 4.5; Figure 4.2). The overall percentage of *R. mangle* propagules damaged with bite marks and scrapes was 26% and 23%, respectively. Scrapes were the most common damage type of *A. germinans* and *L. racemosa* and bite marks were the least common damage type for both species (Figure 4.2). The frequency of holes was less than 1% of *R. mangle* propagules (Figure 4.2). In comparison, holes were found in 13% of *A. germinans* propagules and 10% of *L. racemosa* propagules (Figure 4.2).

Length and mass of mangrove propagules were significantly different between years and damage types for all three mangrove species (Table 4.6). Year of collection ($p< 0.001$) and damage type ($p= 0.002$) were both significant factors on length of *Avicennia germinans* propagules, however, there was not a significant interaction between the two factors ($p= 0.30$). Length of propagules was significantly smaller in 2010 compared to 2008 and 2009 (Table 4.6;

Figure 4.3a). Propagules with scrapes were significantly smaller in length than undamaged propagules ($p<0.001$) and propagules with bite marks ($p= 0.01$) (Figure 4.3a). Mass of *A. germinans* propagules was also significantly different between years of collection ($p<0.001$) and damage type ($p= 0.005$; Table 4.6; Figure 4.3b). Mass of propagules was significantly less in 2010 compared to 2008 and 2009 ($p<0.001$ for both years; Figure 4.3b). Undamaged propagules had significantly more mass than propagules damaged by scrapes ($p<0.001$) and holes ($p= 0.009$). *Rhizophora mangle* propagule lengths were significantly different between years ($p<0.001$), with propagules in 2009 smaller than propagules collected in 2008 ($p<0.001$) or 2010 ($p= 0.002$) (Table 4.6, Figure 4.4a). There was no significant difference in length of *R. mangle* propagules between damage types (Table 4.6, Figure 4.4a). There was a significant interaction between year of collection and damage type on the mass of *R. mangle* propagules. The mass of undamaged propagules was smaller compared to propagules with bite marks and scrapes in 2008 and 2010 (Figure 4.4b). There was a significant interaction between year and damage type for both length ($p<0.001$) and mass ($p= 0.002$) of *L. racemosa* propagules (Table 4.6; Figure 4.5). Propagules with scrapes and holes tended to be smaller in length and mass compared to undamaged propagules and propagules with bite marks (Figure 4.5).

Mean mass (± SE) and length (± SE) of mangrove propagules used in buoyancy trials varied by species (Table. 4.7) and was included in initial models to compare buoyancy of propagules with different damage types. Overall, buoyancy of mangrove propagules was significantly affected by damage type and the minimal adequate survival model retained the main effects of damage type and nested variable of trial for all three mangrove species (Tables 4.8-4.10). Mass of propagules had a significant effect on the buoyancy of *A. germinans* and was retained in the final model (Table 4.8). Mass and length were both non-significant on the amount of time *R. mangle* propagules floated and were removed from the final model (Table 4.9). Both covariates had a significant effect on buoyancy of *L. racemosa* propagules and were retained in the final model (Table 4.10). There was a significant effect of damage on propagule buoyancy for *Avicennia germinans* propagules (Table 4.8; Figure 4.6a). Trials ran for 133 days and some propagules with all types of damage retained buoyancy for the entire duration of trials (Figure 4.6a). However, both bites and scrapes had a significant negative effect on the length of time propagules remained buoyant compared to undamaged propagules ($p<0.001$, Table 4.8, Figure 4.6a). There was also variation among trials with *A. germinans*, with undamaged propagules and propagules with holes in trial 2 and all propagules with all damage types in trial 3 floating significantly less time compared to reference values of trial 1 and undamaged propagules (Table 4.8, Figure 4.6a). In buoyancy experiments with *R. mangle* propagules, there was a significant effect of damage on propagule buoyancy ($p<0.001$, Table 4.9; Figure 4.6b). Undamaged propagules retained buoyancy significantly longer compared to propagules with bite marks ($p=0.05$, Table 4.9) and scrapes ($p<0.001$, Table 4.9) in all three trials and the maximum time propagules remained buoyant was 79 days in trial 1, 164 days in trial 2, and 151 days in trial 3 (Figure 4.6b). In comparison, the maximum number of days a propagule with scrapes retained buoyancy was 43 days in trial 1, 95 days in trial 2, and 96 days in trial 3 (Figure 4.6b). Propagules with bite marks retained buoyancy longer than propagules with scrapes and the maximum number of days propagules remained buoyant was 75 days in trial 1, 144 days in trial 2, and 135 days in trial 3 (Figure 4.6b). *Laguncularia racemosa* propagules without damage retained buoyancy longer than damaged propagules in all three trials, however, there was only a significant main effect for propagules with bite marks and scrapes ($p<0.00$; Table 4.10; Figure 4.6c). In all three trials, undamaged propagules retained buoyancy for 50 days or more and scrapes lost buoyancy at a faster rate than undamaged propagules (Figure 4.6c). In trial 3, a proportion of propagules with bite marks retained buoyancy for over 50 days, however, all propagules with scrapes and holes had sunk by 22 days and 44 days, respectively (Figure 4.6c).

Discussion

Damage to propagules while attached to trees can potentially affect early life stages, influencing recruitment of seedlings and distribution and abundance of mangrove communities (Onuf et al. 1977, Robertson et al. 1990, Minchinton and Dalby-Ball 2001). In our study, pre-dispersal damage had negative effects on propagule growth, buoyancy, and potential viability, however, frequency and damage type varied between mangrove species. We identified three general types of damage, scrapes, bite marks, and holes, and all types of damage were created by multiple species of consumers. *Rhizophora mangle* had the highest frequency of damage (34% to 73% per year) and *L. racemosa* had the lowest (14.5% to 30.3% per year), but *L. racemosa* and *A. germinans* had a greater frequency of damage by boring insects compared to *R. mangle*. These insects caused the most damage to propagules and caused extensive loss of developing structures, potentially decreasing viability. Pre-dispersal propagule damage significantly decreased number of days propagules retained buoyancy compared to undamaged propagules for all three mangrove species (Table 5; Figures 12-14). Our results document pre-dispersal damage effects dispersal capabilities of mangroves and add to the growing body of research supporting the importance of biotic interactions in mangrove systems. In addition, significant temporal variation in frequency of damage and propagule size observed in this multi-year study provides research questions for future study of interactions between abiotic and biotic factors and how these interactions may be affected by future climate change.

Our study found overall frequency of pre-dispersal damage ranged between 24% and 51%, depending on species, and was comparable to frequency of propagule damage reported from other mangrove forests around the world (Robertson et al. 2990, Clarke 1992, Farnsworth and Ellison 1997, Minchinton and Dalby-Ball 2001). Scrapes were the most common damage type for all three species. This was also the most ambiguous category and possibly included damage not caused by consumers, such as mechanical abrasion caused by movement against a branch or barnacles growing on prop roots, or accidental damage by consumers, such as damage caused by molluscs feeding on algae or other organisms (Murphy 1990). Scrapes caused the least amount of damage to propagules from all three species, particularly propagules from *A. germinans* and *L. racemosa* which have an exterior pericarp protecting developing structures. Although scrapes caused minimal internal damage to propagules, propagules with scrapes were significantly smaller than undamaged propagules for *A. germinans*.

Bite marks were found on all three species of mangroves. Bite marks caused greater internal damage than scrapes, however, pericarps of *A. germinans* and *L. racemosa* offered some protection to the internal structures and internal damage from bite marks was often limited to the outer surface of folded cotyledons. This category of damage could have been caused by consumers feeding on the propagule or indirectly through feeding on other organisms. Larger bite marks may have been caused by predators attracted by the presence of insects inside the mangrove propagules. Whereas the presence of insects may not directly kill the mangrove propagule, damage by crabs or other predators trying to consume the internal insects could result in mortality of the propagule when cotyledons and embryonic structures are damaged (M. Donnelly, personal observation). Compared to scrapes and holes, bite marks did not affect the size of propagules and had larger mean length and mass than other damage types and undamaged propagules for all three species in most years. This could be related to the time propagule was on the tree prior to collection, since the longer propagules are on a tree, the more opportunity for damage by consumers. The smaller sizes of *R. mangle* undamaged propagules compared to propagules with bite marks and scrapes may also be a result of younger propagules with less time exposed to consumers.

Holes caused by boring insects were an important type of damage for *A. germinans* and *L. racemosa*, however, were rarely found in *R. mangle* propagules. This type of damage can often have the greatest negative effect on propagule survival and damage to cotyledons and other structures observed in this study is similar to the findings from other locations (Farnsworth and Ellison 1997, Elster et al. 1999, Minchinton and Dalby-Ball 2001, Sousa et al. 2003). Internal damage was most severe in *L. racemosa* propagules with holes and, in some cases, internal tissue was completely consumed or remaining tissue was brown, shriveled, or rotting. Although Lepidopteran larvae were found in all three species, the only species we were able to identify was *Nola laguncularíae* from *L. racemosa* propagules because it was the only larvae to develop to the adult stage. No moths developed from *A. germinans* propagules, preventing identification, and future research identifying insect species utilizing *A. germinans* propagule is needed to understand the effect of these consumers on reproductive success.

Our study documented damage to mangrove propagules while attached to the tree can have a negative effect on buoyancy, potentially limiting dispersal capabilities through hydrochory. The length of time a fruit remains buoyant is a major limiting factor to the distance seeds may disperse (Rabinowitz 1978) and varies by species. The maximum floating times observed for our three study species had the same pattern observed by Rabinowitz (1978) in Panama, where propagules of *R. mangle* floated for the longest (104 days), followed by propagules of *A. germinans* (82 days) and *L. racemosa* (3-55 days). Longer dispersal times are advantageous for dispersing in water currents, increasing the potential of propagules to reach appropriate habitat for establishment (Rabinowitz 1978). If initial stranding occurs in unsuitable habitat, retention of buoyancy can lead to reintroduction of propagules to water currents and increase opportunities for stranding in a more suitable location (Rabinowitz 1978). Pre-dispersal damage decreasing buoyancy limits potential for long distance dispersal and decreased the likelihood of establishment into suitable habitat, however, overall effects of damage varied by damage type and between mangrove species. Scrapes had a significant negative effect on buoyancy of propagules for all three mangrove species, suggesting even minimal exterior damage to propagules can decrease length of time propagules float during dispersal. Exterior damage potentially increased rate of water logging of inner tissues or changed floating characteristics when damaged tissue was repaired. Bite marks decreased buoyancy time for all three mangrove species and this type of pre-dispersal damage also potentially limits dispersal capabilities of mangrove propagules caused by increased saturation of interior tissues. Holes had less of an effect on the buoyancy of propagules compared to scrapes and bite marks. Insect holes may provide a dispersal advantage to propagules due to the presence of air bubbles within the propagule (Minchinton 2006). In addition, propagules with holes tended to be smaller and lighter compared to undamaged propagules and this may also lead to increased buoyancy (Minchinton 2006).

Increasing buoyancy time of propagules may be advantageous to internal insects using propagules as a mode of dispersal; however, studies with *A. marina* have shown presence of internal larvae can decrease the likelihood of viability of propagules once buoyancy is lost (Minchinton 2006). In our study, internal larvae were expelled from propagules when pericarps fell off of *A. germinans* propagules during buoyancy trials, limiting the dispersal of insects to only a few days and minimizing damage to propagules during dispersal period. In comparison, pericarps of *L. racemosa* are retained throughout the dispersal period, serving as a potential long distance dispersal mechanism for larvae but also increasing loss of viability of propagules. During buoyancy trials with *L. racemosa*, undamaged propagules and propagules with scrapes and bite marks completed germination while floating as evidenced by the extension of the radicle out of the pericarp (Rabinowitz 1978), however, only 10% or less of propagules with holes were observed with a radicle. This observation combined with the observed internal damage suggests damage by boring insects has the greatest negative effect on *L. racemosa* propagule viability.

We found the years 2008 and 2010 had significantly different frequencies of damage compared to 2006, which had the lowest proportion of damaged propagules. Two possible reasons for significant differences between years are variation in the abundance and identity of propagule consumers, which are strongly affected by climate variables. In Mosquito Lagoon, tropical mangroves are nearing the northern limit of distribution, thus, many common tropical herbivores are nearing their northern limit as well. In 2008, damage to *R. mangle* propagules was the highest (73%) frequency of damage observed during this study. The second highest observed frequency of damage was in 2010 when 59.5% of *A. germinans* propagules were damaged. The variety in types of damage and insects inside of propagules suggests a diverse group of potential consumers in Mosquito Lagoon, but temperature may strongly affect local community diversity. Wetlands in Florida on the temperate-sub-tropical boundary may have a different group of consumers compared to more tropical locations, including a mix of both temperate and tropical species. Annual fluctuations in temperature will potentially influence growth, reproduction, and survival of the herbivore community, causing annual variability in the proportion of propagules damaged. For example, the tropical boring beetle *C. rhizophorae* was found in *R. mangle* propagules during 2008, however, was not observed in propagules collected in 2009 and 2010. Temperatures went below freezing during winters in 2009 (5 days minimum temperature < 0°C) and 2010 (17 days minimum temperature < 0°C), whereas mean monthly minimum temperatures were greater than 9°C during 2006 through 2008 and no days had temperatures below freezing (temperature data from nearest weather station at Ponce Inlet, Florida, http://www.ncdc.noaa.gov/cdo-web/). Cold temperatures may have caused a decline in the population of *C. rhizophorae* as well as other tropical consumers, leading to a lower frequency of damage of *R. mangle* propagules after the peak in 2008. Previous studies have shown *C. rhizophorae* infestations occurring prior to dispersal can have a negative effect on *R. mangle* propagule viability (Onuf et al. 1977) and annual variations in beetle abundances caused by temperature fluctuations may indirectly effect annual seedling recruitment in sub-tropical-temperate systems.

Variation in frequency of damage between three mangrove species may be caused by presence or absence of predators in mangrove canopies. For example, *Aratus pisonii*, an arboreal crab, inhabits trees of all three species (Beever et al. 1979, Erickson et al. 2012, M. Donnelly, personal observation). However, studies in the west coast of Florida have found *A. pisonii* consumed more leaves from *R. mangle* than *A. germinans* and *L. racemosa* (Erickson et al. 2003, Erickson et al. 2012), suggesting trophic interactions with *A. pisonii* could be more important for *R. mangle*. *Aratus pisonii* is a generalist omnivore and eats a variety of insects and other herbivores living in mangrove trees (Erickson et al. 2003, Lopez and Conde 2013, Riley et al. 2014). Food sources for crabs were shown to vary with mangrove forest structure and season in

Venezuela due to variation in nutritional content of mangrove leaves or other factors influencing feeding behaviors, such as presence of crab predators (Lopez and Conde 2013). Therefore, strength of interactions between mangroves and crabs may also be highly variable under different environmental conditions and limiting factors on crab populations could affect frequency of propagule damage. Beever et al. (1979) found a negative correlation between abundance of crabs and moth species, *Phocides pygmalion*, known to consume *R. mangle*. Crabs may be part of a trophic cascade with propagule consumers and mangroves, providing an indirect positive benefit to mangroves by decreasing the abundance of herbivores in the canopy. Biotic interactions often contain both negative and positive components and the outcome is based on the relative "costs" versus "benefits" of the interaction. For example, *A. pisonii* consumes a high percentage of leaves and can indirectly damage propagules by consuming boring insects, potentially outweighing any indirect positive effects from preying on consumers. Additional research to identify insect consumers and relationships with predators is needed in order to further evaluate interactions between temperature, insect diversity and abundance, and propagule damage.

Another potential defense for mangroves against herbivores is a mutualistic relationship with ants (Cannicci et al. 2008, Francini and Rovati 2011). Extrafloral nectaries attracting ants have been identified for *R. mangle* (Primack and Tomlinson 1978) and *L. racemosa* (Franciso et al. 2009, Francini and Rovati 2011). *Laguncularia racemosa* had the lowest frequency of propagule damage; however, we found boring insects had the greatest effect on propagule viability compared to other mangrove species. Presence of nectaries on leaves of *L. racemosa* to attract ants may be an important mechanism against infestation by boring insects, resulting in lower frequencies of damage and protect propagule viability. Future research investigating interactions between ants, herbivores and *L. racemosa* (Francini and Rovati 2011) as well as other mangrove species in Florida is necessary to understand the importance of these interactions.

Annual variation in abiotic factors may also explain differences in sizes of propagules between years. *Rhizophora mangle* had significantly smaller propagules in 2009 and *A. germinans* and *L. racemosa* had significantly smaller propagules in 2010 for all damage types. Freezing temperatures during winter months caused all three species of mangroves to lose leaves (M. Donnelly, pers. obs.) and replacing this lost biomass may have decreased energy available for reproduction later in the year. Additionally, herbivory on leaves has been shown to influence reproductive output as resources may be depleted replacing leaf biomass (Anderson and Lee 1995, Tong et al. 2003, Cannicci et al. 2008); thus, variations in leaf herbivory related to temperature control on consumer populations may also effect size of propagules. Multi-year studies are beneficial for identifying variation in these types of interactions, which may not be apparent in short-term observations over a single reproductive season.

Results from our study have applications to mangrove restoration and identify future research questions. Acting as ecosystem engineers, mangroves provide habitat for a diverse assemblage of organisms and numerous services, including shoreline stabilization, carbon sequestration, and water filtration. As mangrove habitat continues to be degraded and threatened by future changes in climate, the need for restoration and conservation has increased and understanding biotic interactions has multiple applications to management of this ecologically important habitat. Our study identified negative effects of pre-dispersal damage on propagule buoyancy, potentially limiting long-distance dispersal. Hydrological restoration of mangroves by removing tidal barriers has been shown to promote natural recruitment of mangrove propagules from adjacent areas without the need for additional planting (Brockmeyer et al. 1997; Turner and Lewis 1997; Lewis 2005; Nilsson et al 2010; Rey et al. 2012). Based on the results from our study, dispersal of propagules to restored sites may be limited when frequency of pre-dispersal damage is high. When natural regeneration is not possible due to recruitment limitations, planting propagules or seedlings is often used to speed up recovery of damaged systems (Field 1999). Examination of propagules for damage prior to planting in the field or greenhouse could be important precaution for improving survival and growth of seedlings, however, long-term evaluation of seedling survival is needed to determine importance for individual species (Minchinton and Dalby-Ball 2001). Results from this study suggest multi-species interactions may be an important biotic control on mangroves and trophic link between primary production and flow of energy and nutrients through mangrove ecosystems. Additional studies are needed to identify consumers and investigate the strength of positive and negative interactions between crabs and herbivores in the mangrove canopy. In addition, understanding effects of temperature and inundation frequency on these interactions has important implications for evaluating effects of climate change on mangrove systems. Biotic interactions between mangroves, other plant species, and fauna will potentially change under different climate conditions (Alongi 2009; McKee et al. 2012, Guo et al. 2013) and influence structure and function of mangrove systems in the future. As warmer winters allow for expansion of mangroves into more temperate areas (Osland et al. 2013), potential consumers of propagules will also change as mangroves come into contact with new consumers or escape herbivory from tropical species. An ecosystem-level approach that addresses both biotic and abiotic interactions affecting mangrove propagule production, dispersal and viability is necessary to increase success of mangrove restoration projects and conserve remaining mangrove ecosystems.

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Tables

Table 4.1. The total number of propagules collected during September, October, and November from 2006 to 2010 for *A. germinans*, *R. mangle*, and *L. racemosa*.

Year of Collection	Month of Collection	*Avicennia germinans*	*Rhizophora mangle*	*Laguncularia racemosa*
2006	September	375	291	375
2006	October	463	256	362
2006	November	166	209	498
2007	September	134	225	1458
2007	November	351	501	1282
2007	October	291	279	1221
2008	September	293	79	592
2008	October	399	181	947
2008	November	127	238	806
2009	September	156	108	407
2009	October	229	131	613
2009	November	222	141	453
2010	October	359	133	1094
2010	November	281	301	719
2010	December	227	109	803

Table 4.2. Model summary of comparisons between percent propagules with damage by year (2006-2010) and mangrove species (*R. mangle*, *A. germinans*, *L. racemosa*). Reference values were 2006 for year and *R. mangle* for mangrove species.

	Estimate	SE	t	p
(Intercept)	-0.48	0.31	-1.53	0.14
Year(2007)	0.25	0.34	0.74	0.47
Year(2008)	0.86	0.35	2.45	0.02
Year(2009)	0.48	0.39	1.23	0.23
Year(2010)	1.04	0.35	2.99	<0.001
Mangrove(*A. germinans*)	-0.78	0.30	-2.60	0.01
Mangrove(*L. racemosa*)	-1.34	0.26	-5.10	<0.001

Model= Year + Mangrove Species

Table 4.3. The number of propagules in each damage level for *R. mangle*, *A. germinans*, and *L. racemosa* examined during 2008-2010 (total number of propagules examined = 20 propagules for each mangrove species per category for each year, except *R. mangle* hole category in 2009 (n = 11) and 2010 (n = 4). The level of damage was based on the proportion of the propagule length with damage (low = < 25%, medium = 25% to 50%, and high = >75%) for bites and scrapes or number of holes (low= 1 hole, medium= 2 holes, high= 3+ holes). N/A= no propagules

		Bite			Scrape			Hole		
Mangrove Species	Year	Low	Medium	High	Low	Medium	High	Low	Medium	High
Rhizophora mangle	2008	12	4	4	12	2	6	N/A	N/A	N/A
	2009	11	6	3	14	4	2	11	N/A	N/A
	2010	15	2	3	12	5	3	4	0	0
Avicennia germinans	2008	10	4	6	9	6	5	13	4	3
	2009	12	6	2	10	5	5	15	3	2
	2010	9	7	4	11	7	2	9	7	4
Laguncularia racemosa	2008	10	6	4	12	5	3	14	3	3
	2009	12	5	3	10	6	4	15	4	1
	2010	9	7	4	11	5	4	13	4	3

Table 4.4. Percentage of propagules with each damage type infested with Lepidopteran larvae from collections in 2008, 2009, and 2010 (n= 20 for each damage type per year except hole category for *R. mangle* in 2009 (n=11) and 2010 (n=4)). N/A= no propagules collected with damage type.

		% Propagules with Internal Damage			% Propagules Infested with Larvae		
Mangrove	Damage Type	2008	2009	2010	2008	2009	2010
Avicennia germinans	Bite	65	60	75	5	20	10
	Hole	85	95	85	15	80	65
	Scrape	10	5	5	0	0	0
	Undamaged	0	0	0	0	0	0
Rhizophora mangle	Bite	100	100	100	5	0	0
	Hole	N/A	100	100	N/A	18	25
	Scrape	5	20	15	0	0	0
	Undamaged	0	0	0	0	0	0
Laguncularia racemosa	Bite	40	70	25	0	40	10
	Hole	25	80	90	15	60	80
	Scrape	15	5	5	5	0	0
	Undamaged	0	0	0	0	0	0

Table 4.5. Model summary of comparisons between percent of propagules for mangrove species (*R. mangle*, *A. germinans*, *L. racemosa*) and damage types (undamaged, bite, hole, scrape). Reference values were *R. mangle* for mangrove species and undamaged for damage type.

	Estimate	SE	T	P
(Intercept)	0.46	0.36	1.28	0.21
A. germinans	0.02	0.42	0.04	0.97
L. racemosa	-0.20	0.37	-0.54	0.60
Bite	-2.56	0.37	-6.84	p<0.001
Hole	-2.67	0.39	-6.90	p<0.001
Scrape	-1.96	0.32	-6.05	p<0.001

Model= Mangrove species + damage type

Table 4.6. Results of two-way ANOVAs (year x damage type) comparing length and mass of *Avicennia germinans*, *Rhizophora mangle*, and *Laguncularia racemosa* propagules.

Mangrove	Variable	Source	Type III SS	Df	MS	F	p
Avicennia germinans	Length	Year	19.94	2	9.97	37.93	< 0.001
		Damage Type	4.05	3	1.35	5.13	0.002
		Year*Damage	1.90	6	0.32	1.21	0.302
		Error	79.37	302	0.26		
		Total	2312.14	314			
	Mass	Year	25.75	2	12.87	13.56	< 0.001
		Damage Type	12.26	3	4.09	4.30	0.005
		Year*Damage	9.10	6	1.52	1.60	0.147
		Error	286.77	302	0.95		
		Total	1948.26	314			
Rhizophora mangle	Length	Year	5412.70	2	2706.35	12.41	< 0.001
		Damage Type	229.35	2	114.68	0.53	0.591
		Year*Damage	485.82	4	121.46	0.56	0.694
		Error	56502.35	259	218.16		
		Total	223132.93	268			
	Mass	Year	4546.56	2	2273.28	88.79	< 0.001
		Damage Type	119.05	2	59.53	2.33	0.099
		Year*Damage	292.60	4	73.15	2.86	0.024
		Error	6630.88	259	25.60		
		Total	75933.89	268			
Laguncularia racemosa	Length	Year	14.02	2	7.01	160.98	< 0.001
		Damage Type	1.18	3	0.39	9.00	< 0.001
		Year*Damage	1.23	6	0.21	4.73	< 0.001
		Error	14.10	324	0.04		
		Total	813.91	336			
	Mass	Year	2.70	2	1.35	135.45	< 0.001
		Damage Type	0.38	3	0.13	12.55	< 0.001
		Year*Damage	0.20	6	0.03	3.39	0.002
		Error	3.23	324	0.01		
		Total	41.88	336			

Table 4.7. The mean (± SE) mass (g) and length (cm) of propagules from *R. mangle, A. germinans,* and *L. racemosa* from buoyancy experiment.

				Mass (g)		Length (cm)	
Mangrove	Trial	Damage Type	N	Mean	SE	Mean	SE
Rhizophora mangle	1	Undamaged	50	15.52	0.70	24.16	0.21
		Bite	50	15.91	0.74	22.72	0.22
		Scrape	50	14.09	0.70	21.99	0.16
	2	Undamaged	50	13.87	0.62	22.17	0.23
		Bite	50	18.05	0.82	26.17	0.26
		Scrape	50	15.25	0.83	23.04	0.20
	3	Undamaged	50	13.82	0.68	22.30	0.32
		Bite	50	18.49	0.80	26.16	0.26
		Scrape	50	15.38	0.75	22.45	0.23
Avicennia germinans	1	Undamaged	50	2.24	0.11	2.50	0.01
		Bite	50	2.22	0.13	2.47	0.04
		Hole	50	1.52	0.11	2.15	0.03
		Scrape	50	1.58	0.12	2.02	0.03
	2	Undamaged	50	1.43	0.11	2.09	0.02
		Bite	50	1.46	0.10	2.16	0.01
		Hole	50	1.14	0.09	2.06	0.02
		Scrape	50	1.18	0.11	1.94	0.05
	3	Undamaged	50	2.13	0.09	2.51	0.02
		Bite	50	1.92	0.12	2.39	0.06
		Hole	50	1.89	0.13	2.32	0.02
		Scrape	50	1.94	0.09	2.37	0.20
Laguncularia racemosa	1	Undamaged	50	0.31	0.02	1.44	0.20
		Bite	50	0.22	0.01	1.28	0.20
		Hole	50	0.20	0.01	1.17	0.00
		Scrape	50	0.24	0.01	1.28	0.20
	2	Undamaged	50	0.27	0.02	1.38	0.01
		Bite	50	0.24	0.01	1.37	0.20
		Hole	50	0.20	0.01	1.21	0.01
		Scrape	50	0.19	0.01	1.24	0.01
	3	Undamaged	50	0.19	0.01	1.32	0.20
		Bite	50	0.14	0.01	1.11	0.01
		Hole	50	0.13	0.01	1.05	0.01
		Scrape	50	0.14	0.01	1.19	0.01

Table 4.8. Model results for length of time *A. germinans* propagules with different types of damage remained buoyant using survival analysis. Final model was Damage + Damage(Trial) with mass as a covariate. Reference values were undamaged for damage type and trial 1 for trials.

	Value	SE	z	p
(Intercept)	5.87	0.55	10.76	<0.001
Mass	0.51	0.12	4.37	<0.001
Bite	-2.10	0.58	-3.59	<0.001
Hole	-1.02	0.61	-1.66	0.10
Scrape	-4.87	0.56	-8.77	<0.001
Undamaged(Trial 2)	-3.82	0.55	-6.95	<0.001
Bite(Trial 2)	-0.61	0.42	-1.43	0.15
Hole(Trial 2)	-2.76	0.45	-6.14	<0.001
Scrape(Trial 2)	0.74	0.35	2.08	0.04
Undamaged(Trial 3)	-2.24	0.54	-4.11	<0.001
Bite(Trial 3)	-0.87	0.41	-2.12	0.03
Hole(Trial 3)	-3.27	0.45	-7.32	<0.001
Scrape(Trial 3)	2.31	0.35	6.54	<0.001
Log(scale)	0.55	0.03	16.03	<0.001

Table 4.9. Model results for length of time *R. mangle* propagules with different types of damage remained buoyant using survival analysis. Final model was Damage + Damage(Trial). Reference values were undamaged for damage type and trial 1 for trials.

	Value	SE	z	P
Intercept	3.90	0.14	28.11	<0.001
Bite	-0.39	0.20	-1.99	0.05
Scrape	-1.04	0.20	-5.30	<0.001
Undamaged(Trial 2)	0.42	0.20	2.13	0.03
Bite(Trial 2)	0.05	0.20	0.28	0.78
Scrape(Trial 2)	0.61	0.20	3.10	<0.001
Undamaged(Trial 3)	0.43	0.20	2.19	0.03
Bite(Trial 3)	-0.04	0.20	-0.18	0.86
Scrape(Trial 3)	0.57	0.20	2.89	<0.001
Log(scale)	-0.02	0.04	-0.55	0.58

Table 4.10. Model results for length of time *L. racemosa* propagules with different types of damage remained buoyant using survival analysis. Final model was Damage + Damage(Trial) with mass and length as covariates. Reference values were undamaged for damage type and trial 1 for trials.

	Value	SE	z	P
Intercept	1.79	0.24	7.48	<0.001
Mass	1.67	0.44	3.77	<0.001
Length	0.64	0.19	3.34	<0.001
Bite	-0.44	0.15	-3.03	<0.001
Hole	0.11	0.15	0.73	0.46
Scrape	-0.51	0.15	-3.47	<0.001
Undamaged(Trial 2)	-0.61	0.14	-4.27	<0.001
Bite(Trial 2)	-0.32	0.14	-2.21	0.03
Hole(Trial 2)	-0.34	0.14	-2.37	0.02
Scrape(Trial 2)	-0.33	0.14	-2.25	0.02
Undamaged(Trial 3)	-0.05	0.15	-0.35	0.73
Bite(Trial 3)	-0.08	0.14	-0.59	0.56
Hole(Trial 3)	-0.45	0.14	-3.14	<0.001
Scrape(Trial 3)	-0.43	0.15	-2.96	<0.001
Log(scale)	-0.34	0.03	-11.10	<0.001

Figures

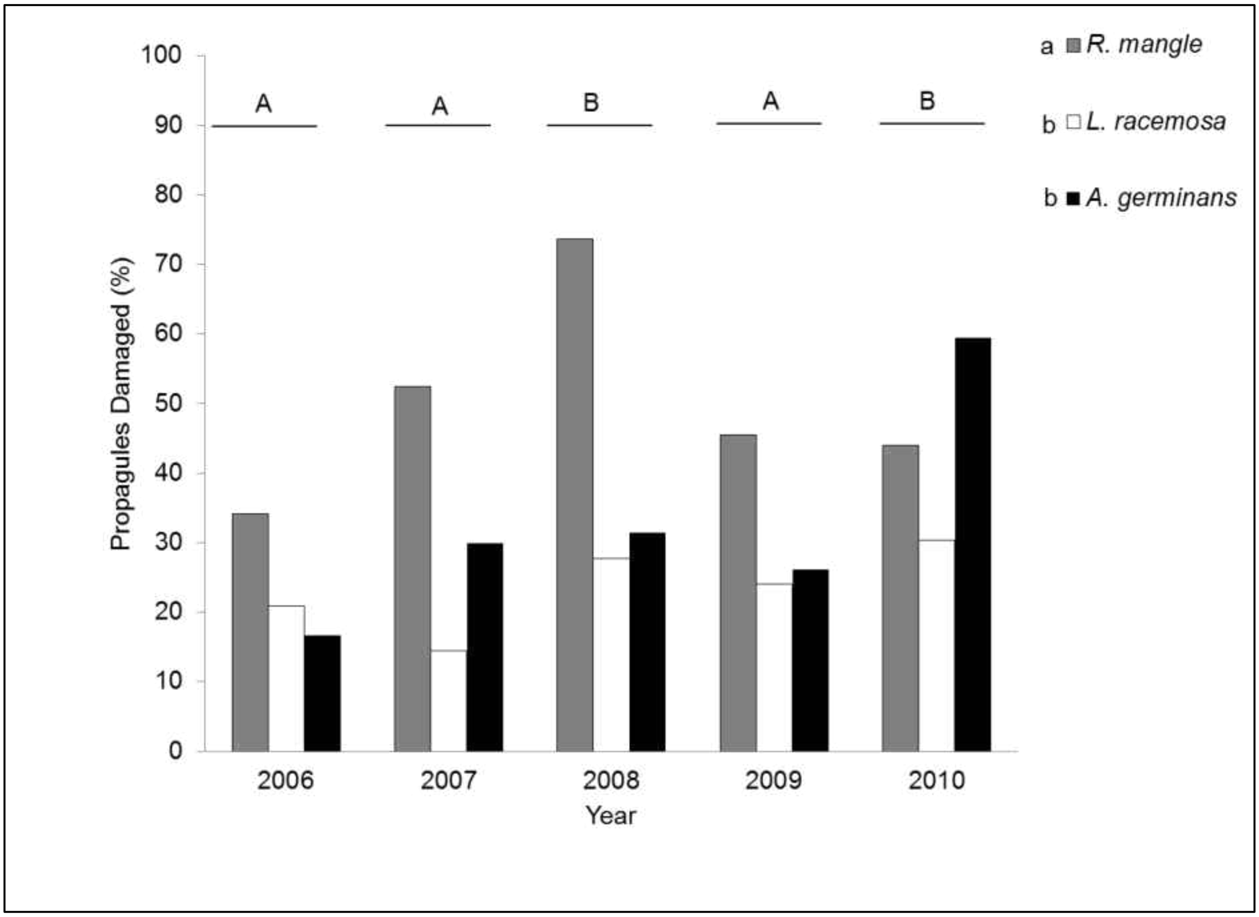


Figure 4.1. The percentage of mangrove propagules with pre-dispersal damage (all damage types combined) for each year of collection (2006-2010) for *R. mangle*, *L. racemosa*, and *A. germinans*. Uppercase letters represent significant differences between years and lowercase letters represent significant differences between mangrove species.

Figures

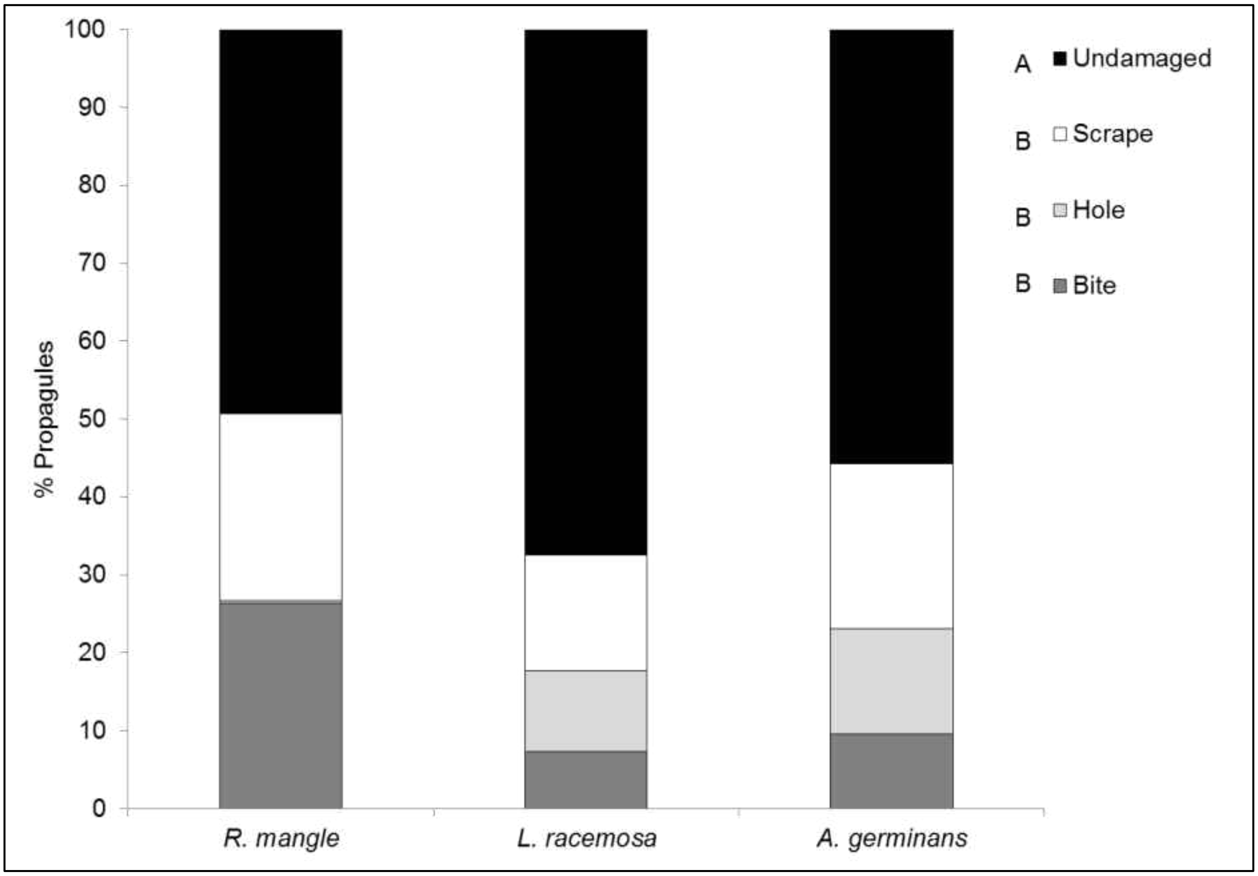
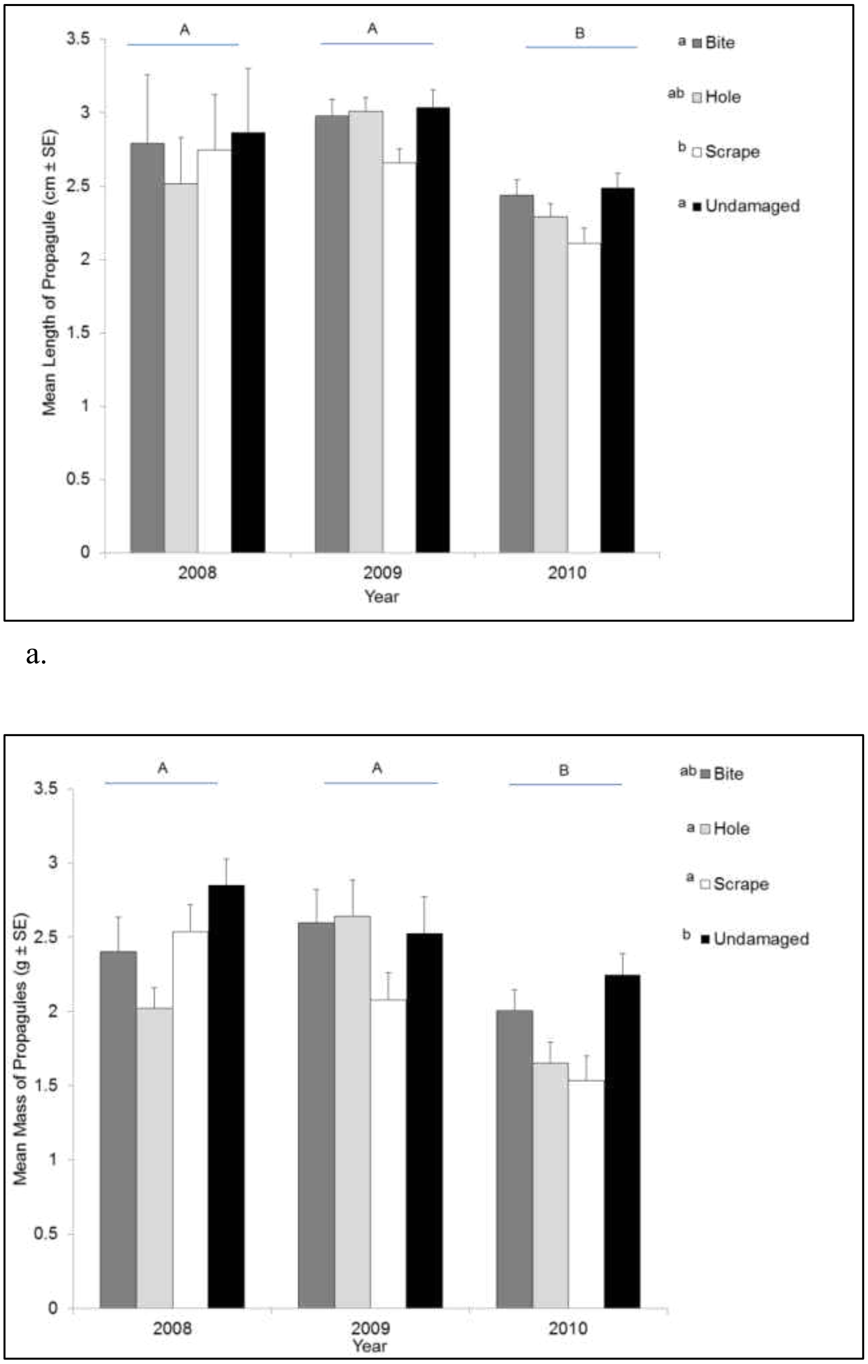


Figure 4.2. The percent of propagules with each type of damage for the total number of propagules collected for *R. mangle*, *L. racemosa*, and *A. germinans* between 2008 and 2010. Uppercase letters represent significant differences between damage types.

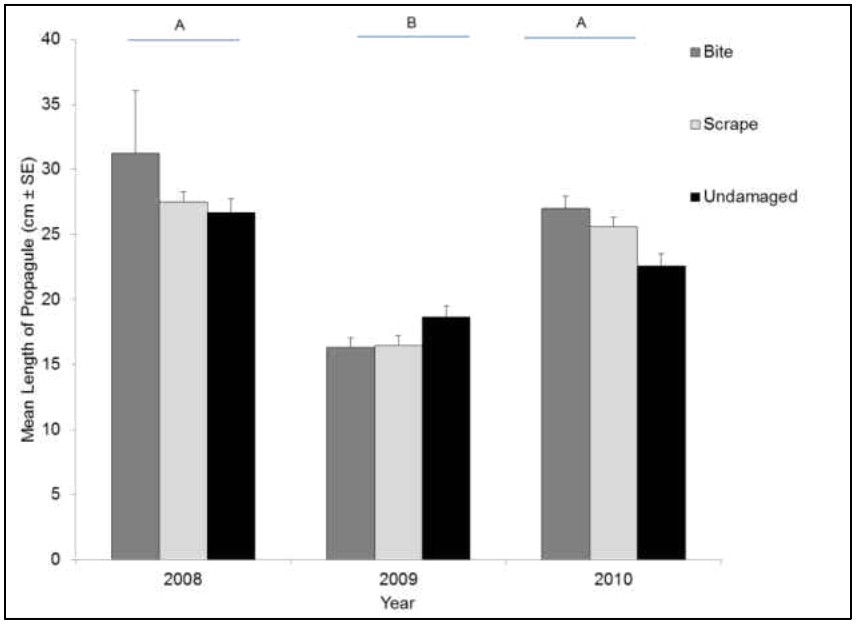


a.

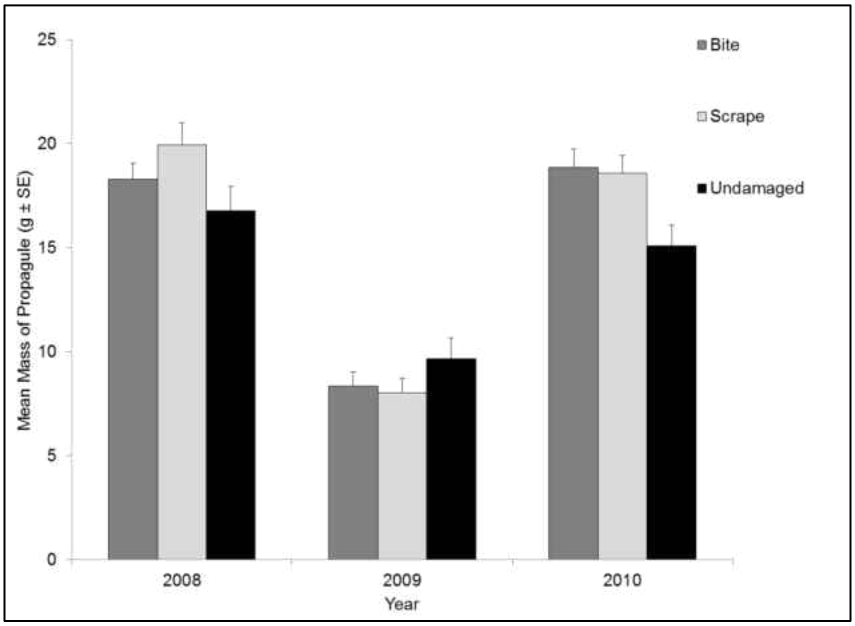
b.

Figure 4.3. Mean (a) length (±SE) and (b) mass (±SE) of *Avicennia germinans* propagules with each type of pre-dispersal propagule damage. Two-way ANOVAs (year x damage type) were

used to compare length and mass of propagules and significant differences are represented by uppercase letters for years and lowercase letters for different damage types.

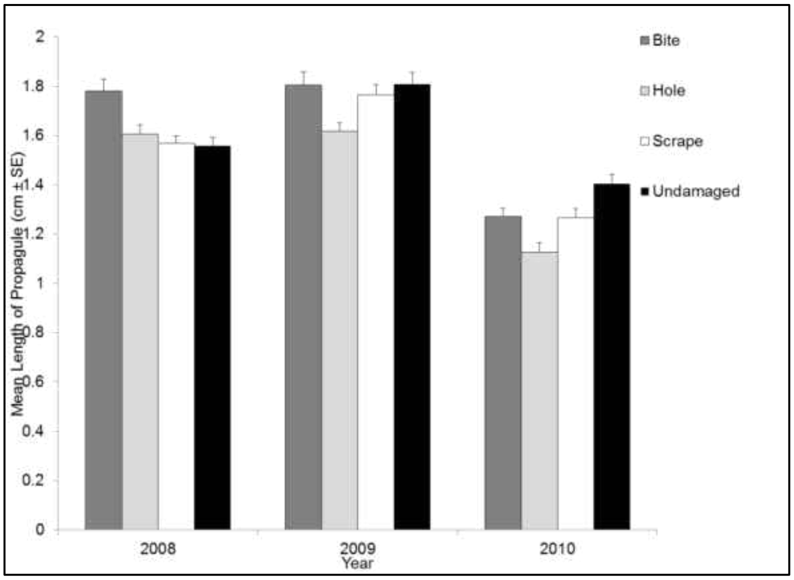


a.

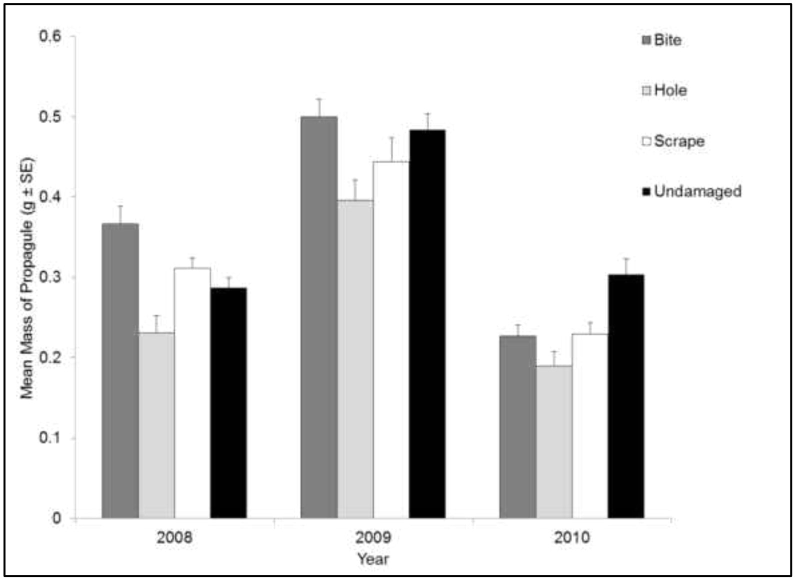


b.

Figure 4.4. Mean (a) length (±SE) and (b) mass (±SE) of *Rhizophora mangle* propagules with different types of pre-dispersal propagule damage. Two-way ANOVAs (year x damage type) were used to compare length and mass of propagules and significant differences are represented by uppercase letters for years.

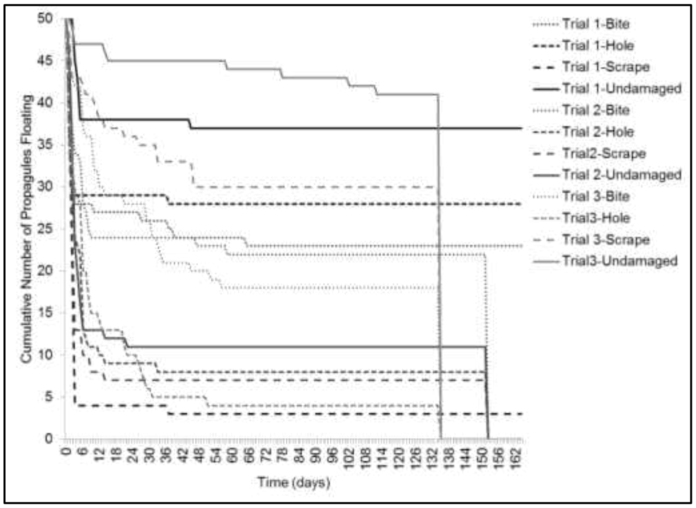


(a)

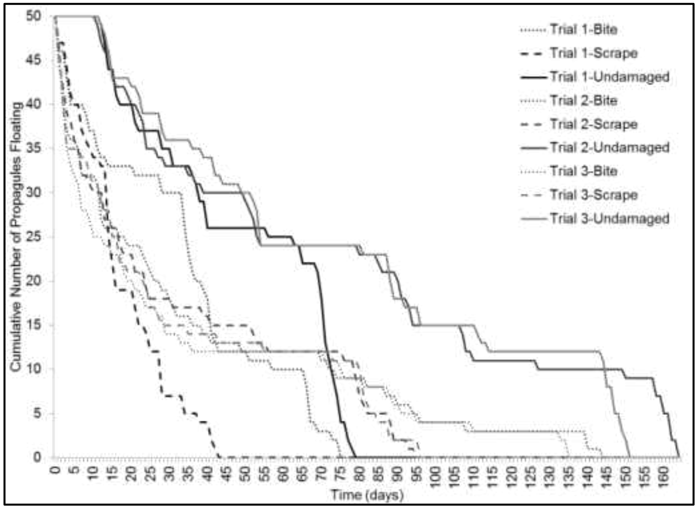


(b)

Figure 4.5. Mean (a) length (±SE) and (b) mass (±SE) of *Laguncularia racemosa* propagules with different types of pre-dispersal propagule damage. Two-way ANOVAs (year x damage type) were used to compare length and mass of propagules and there was a significant interaction between factors for both length and mass ($p<0.001$ for both variables).



(a) *Avicennia germinans*



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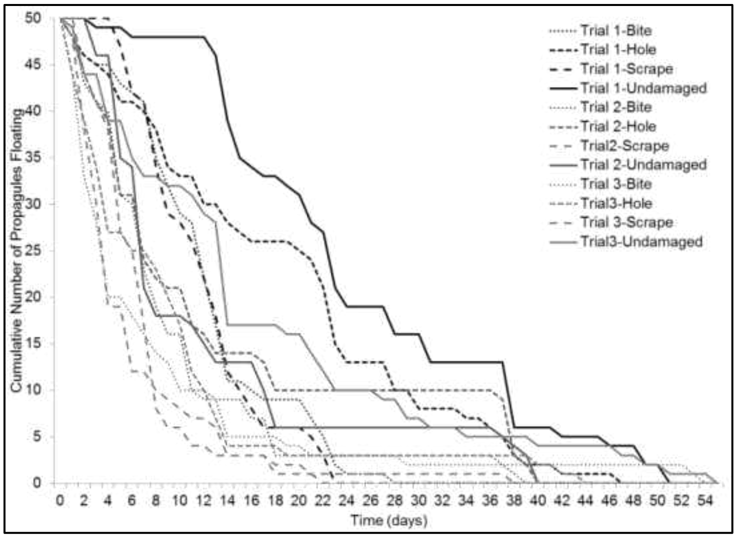
(b) *Rhizophora mangle*



(c) *Laguncularia racemosa*

Figure 4.6. Cumulative number of floating propagules per day for *Rhizophora mangle* (a), *Avicennia germinans* (b), and *Laguncularia racemosa* (c) with each damage type during trial 1 (black lines), trial 2 (dark gray lines), and trial 3 (light gray lines) of buoyancy experiment. The following types of damage were compared: bites (small dots), holes (small dashes), scrapes (large dashes), undamaged (control, solid). There was a significant interaction between mass of propagule, damage type, and trial for all three mangrove species.

CHAPTER 5. INTERACTIONS BETWEEN *RHIZOPHORA MANGLE* AND SALTMARSH FLORA AND FAUNA OVER ENVIRONMENTAL GRADIENTS

Abstract

Interactions between two species may have both positive and negative components, such as direct negative effects from competition between neighboring individuals and indirect positive effects from decreased environmental stressors. For plants in coastal wetlands, distributions are controlled by the species' tolerances to abiotic factors associated with the intertidal region and the outcome of community interactions with co-occurring flora and fauna, which can vary over environmental gradients. In Mosquito Lagoon, on the east coast of central Florida, coastal wetlands support a diverse group of plant and animal species, with numerous potential community interactions. We designed a mesocosm experiment to test the effects of water level, co-occurring plant species (*Sarcocornia perennis*, *Batis maritima*), and fiddler crab species (*Uca pugilator*) on the survival and growth of the red mangrove, *Rhizophora mangle*. In addition, we conducted a field experiment to examine effects of biotic interactions on *R. mangle* over natural environmental gradients at restored and natural coastal wetlands in Mosquito Lagoon, FL. Our mesocosm study found abiotic conditions related to water level had the strongest effect on *R. mangle* survival and growth compared to biotic factors during the first year of the mangrove's life-cycle. The net effect of neighboring plants on *R. mangle* was species specific, with interactions with *B. maritima* having a negative net effect on mangrove survival. In comparison, there was no significant effect of *S. perennis* on mangrove survival or growth during the first year. There were no significant effects of fiddler crabs on the survival or growth of *R. mangle* seedlings, suggesting the net effect of interactions between mangrove and fiddler crabs was neutral in this study. Our field study had low survival of *R. mangle* propagules at all sites. At natural wetlands, only one *R. mangle* propagule at one site survived to the end of the study. At restored sites, two *R. mangle* propagules at one site survived to the end of the study. Evaluating the outcome of community interactions improves our understanding of the role these interactions have in structuring natural communities, influencing successional processes, and guiding ecological restoration practices.

Keywords

Batis maritima, coastal wetlands, competition, facilitation, fiddler crabs, mangrove, *Sarcocornia perennis*, *Uca pugilator*

Introduction

Coastal wetlands are characterized by the halophytic plant species colonizing the physiologically stressful habitat of the intertidal zone of low energy shorelines (Pennings and Bertness 2001). Plant diversity and distribution in coastal wetlands is controlled by the species' tolerances to abiotic factors and the outcome of community interactions with co-occurring flora and fauna (Bertness1991; Pennings and Bertness 2001; Zhang et al. 2008; Malkinson and Tielborger 2010). Plant and animal interactions can be classified as negative (competition, herbivory), positive (facilitation), or neutral and occur through both direct and indirect mechanisms (Callaway and Walker 1997; Olofsson et al.1999; Tielborger and Kadmon 2000; Brooker et al. 2007). Interactions between two species may have both positive and negative components, such as the direct negative effect from competition and indirect positive effects by decreased environmental stressors (Malkinson and Tielborger 2010). The relative influence of these factors on a plant's fitness can vary over environmental gradients and the stress-gradient hypothesis predicts the importance of facilitative interactions relative to negative interactions may increase with increasing levels of abiotic stress (Bertness and Callaway 1994; Malkinson and Tielborger 2010). For an individual plant, the net effect of direct and indirect community interactions over an environmental gradient can be positive, negative, or neutral depending on the outcome of each individual interaction and the species' tolerances to abiotic stressors. This net effect of community interactions influences plant distribution, abundance, and successional processes (Malikinson and Tielborger 2010), affecting the structure and function of the biogenic coastal wetland system; thus, understanding the role of these interactions is important for coastal wetland management, conservation, and restoration (Milbrandt and Tinsley 2006; Stevens et al. 2006; Moreno-Mateos et al. 2012).

In Mosquito Lagoon, the northernmost estuary of the Indian River Lagoon system on the east coast of central Florida, coastal wetlands support a diverse group of plant and animal species (Schmalzer 1995), with numerous potential community interactions. Here, the temperate and sub-tropical climate boundaries overlap and fast growing salt marsh grasses, herbs, and shrubs dominate during early successional stages following a disturbance, such as a freeze, but can be out-competed by mangroves once established (Stevens et al 2006; Raabe et al. 2012). However, periodic freezes and other natural and anthropogenic environmental factors often maintain a heterogeneous habitat in these subtropical wetlands (Stevens et al. 2006; Raabe et al. 2012). Salt marsh plant species and mangroves have complex relationships involving both competitive interactions for resources and facilitative interactions through indirect effects on environmental conditions (Stevens et al. 2006). Mangroves can also be facilitated by salt marsh vegetation trapping propagules in the intertidal region, preventing removal during tidal inundation and wave activity and increasing the likelihood of rooting and establishment of mangrove propagules

(Lewis 1982; Lewis 2005; Stevens et al. 2006; Donnelly and Walters 2014). In northeastern coastal wetlands, succession of species occurs through multiple interactions involving both facilitative and competitive interactions (Bertness 199, Hacker and Bertness 1995). *Spartina patens* and *Distichlis spicata* initially invaded bare patches, decreasing the salinity of the hypersaline soil conditions for later colonization by *Juncus gerardi*, which then competitively excludes the initial colonizers (Bertness 1991). *Juncus gerardi* decreased soil salinity and increased soil oxygen levels and facilitated establishment of another marsh species, *Iva frutescens*, into lower marsh habitats it would otherwise not be able to survive (Hacker and Bertness 1995).

Studies documenting effects of neighboring plants in mangrove- dominated wetlands have found evidence of facilitation through multiple mechanisms (Milbrandt and Tinsley 2006; McKee et al. 2007). Milbrandt and Tinsley (2006) documented improved survival for *Avicennia germinans* seedlings in southwest Florida when planted with the common marsh halophyte *Batis maritima* and suggested an increase in soil elevation had a positive effect on mangrove survival in southwest Florida. McKee et al. (2007) reported positive effects of two halophytes, *Sesuvium portulacastrum* and *D. spicata*, on the establishment of *Rhizophora mangle* in a recovering clear-cut forest in Belize by multiple mechanisms, including propagule trapping, reduction of soil temperature and salinity, improved soil aeration, and structural support (*D. spicata* only). The facilitation of a young seedling by a mature plant, known as the nurse syndrome, can be common in early successional stages and can have both a facilitative and competitive component (Lewis 1982; Lewis 2005; Lopez et al. 2007; Brooker 2006). The positive effects must outweigh the negative effects for the interaction to be beneficial to the seedling and this may be one explanation why these types of interactions are more common in areas with physiologically stressful abiotic conditions (Brooker 2006; Lopez et al. 2007).

Plant-animal interactions in coastal wetlands can also range from positive to negative. Herbivory on plants by insects and grapsid crabs can have a negative effect on plant growth and survival, affecting recruitment and distribution of mangroves (Robertson et al. 1990; Rey 1994; McKee 1995; Minchinton and Dalby-Ball 2001; Stevens et al. 2006; Alongi 2009). Plants can also benefit from interactions with fauna and the presence of burrowing crabs has been shown to increase soil aeration, drainage, and decomposition of plant debris, decrease soil salinity, and improve nutrient levels through waste deposition (Bertness 1985; Duke et al. 1998; Normann and Pennings 1998; Lacerda et al. 2001; Pennings and Bertness 2001; Daleo et al. 2007; Smith et al. 2009). Research on the mangrove species *Laguncularia racemosa* in Florida documented increased growth when fiddler crabs (*Uca* sp.) were present (Smith et al. 2009). Fiddler crabs are often one of the first species to colonize recently disturbed or newly restored habitat (Smith et al. 2009) and may be an important facilitator of plant recruitment through amelioration of abiotic conditions during early stages of recovery of coastal wetland plant communities (Smith et al. 2009). However, changes in soil characteristics and the resulting effect on plant species can be the result of numerous interactions among conspecifics, neighboring plant species, and fauna, making it difficult to isolate the mechanisms and individual effects of each interaction in the field.

The purpose of this study was to experimentally test the net effects of water level and co-occurring plant and animals from coastal wetlands on the survival and growth of seedlings of the red mangrove *Rhizophora mangle*. In Mosquito Lagoon, we have been involved with a monitoring program documenting natural regeneration of coastal wetlands following hydrological restoration of mosquito impoundments since 2005. Early colonizers of restored sites include the plant species *Sarcocornia perennis* (perennial glasswort) and *Batis maritima* (saltwort) and the fiddler crab *Uca pugilator*. *Batis maritima* and *S. perennis* are halophytic succulent plant species found in coastal wetlands throughout Florida and the Caribbean (Rey 1994; Schmalzer 1995; McKee 1995; Lacerda et al. 2001; Lewis 2005; Rey et al. 2012). Both species are perennial, low-growing (height: <1 m) plants that expand in cover through production of runners, creating thick mats of vegetation (Tiner 1993, Taylor 1998). Recruitment of mangroves was observed to follow colonization by these early successional species, often resulting in an aggregated distribution of mangroves in vegetated patches with fiddler crabs and burrows. We designed a mesocosm experiment to test the effects of water level, *S. perennis*, *B. maritima*, and *U. pugilator* on the following variables: 1) survival of *R. mangle* seedlings, 2) growth of *R. mangle* seedlings, and 3) soil characteristics. In addition, we conducted a field experiment to examine effects of biotic interactions on *R. mangle* over natural environmental gradients at restored and natural coastal wetlands in Mosquito Lagoon. If facilitative interactions were stronger than competitive interactions, we hypothesized there would be a positive net effect on survival and growth of *R. mangle*. Alternatively, a negative net effect on *R. mangle* would occur if competitive interactions were stronger than facilitative interactions. Studies evaluating positive and negative interactions improve our understanding of the role these interactions have in community structure and their application to conservation and restoration of natural systems (Brooker et al. 2007).

Methods

Mesocosm Experiment

A full factorial design was used to test all possible combinations of the following treatments on *R. mangle* seedlings in mesocosms: four plant treatments (*B. maritima*, *S. perennis*, mimic plants, or no plants (control)), three fiddler crab treatments (*U. pugilator*, mimic fiddler crab burrows, or no fiddler crabs or burrows (control)), and two water levels (low, high) (Table 5.1). A total of 24 treatment combinations were tested, with 17 replicates for each combination (408 total mesocosms). Each individual mesocosm was created by inserting an 11 L plastic nursery pot (25.5 cm diameter and 26 cm deep) into an 18 L bucket (30 cm diameter; 37 cm deep). The plastic nursery pots were filled with artificially created substrate in a 1:1 ratio of topsoil (Earthgro®) and sand (KolorScape® all-purpose play sand). Height of substrate in pots was 23 cm. Buckets were drilled with four 1-cm holes at either 10 cm (low water treatment) or 20 cm (high water treatment) to maintain water depths and filled with 30 ppt saltwater (Instant Ocean salts and tapwater) to mimic natural conditions in Mosquito Lagoon, FL where mangrove propagules were collected. Water depths and salinities were monitored every two days and water and salt (Instant Ocean) were added as needed.

Mesocosms were randomly assigned one of 24 possible treatment combinations and experimental treatments were set-up using the following methods for plant and fiddler crab treatments during November 2009, prior to addition of *R. mangle* propagules. Mesocosms were planted with either one cutting (15-20 cm in length) of *B. maritima* or *S. perennis*, one mimic plant (15 cm *Ambulia* plastic plant; Tetra Wonder Works), or no plants (plant control). Plastic aquarium plants were used to test the effect of shading on soil conditions without the presence of living aboveground or belowground biomass. For fiddler crab treatments, mesocosms received either two fiddler crabs (*U. pugilator*, range of carapace length: 0.5 cm to 1.5 cm), three mimic fiddler crab holes, or no fiddler crabs. Artificially created fiddler crab burrows were used to test the effects of burrows without the presence of fiddler crabs. Three mimic fiddler crab burrows per mesocosm were created using tubing (10 cm deep, 1.5 cm diameter) and were recreated weekly. During preliminary tests with mesocosms in summer 2009, two fiddler crabs made between 2-4 holes per mesocosm during the one month trial and 3 holes were chosen as the experimental density for mimic fiddler crab burrow treatments. In the same preliminary trial, diameters of 20 holes were measured with electronic calipers and the mean diameter (± SE) of the holes was 1.3 ± 0.1 cm. To provide food for fiddler crabs, one sheet of dried marine algae (Ocean Nutrition Green Algae) was added to all mesocosms before the addition of fiddler crabs and one half of a sheet was added each month for the first three months. Fiddler crabs usually exited burrows during filling of water and this allowed confirmation of survival of crabs. If fiddler crabs were not observed during three consecutive fillings, the crab was assumed dead and replaced.

Rhizophora mangle propagules were collected from ten locations in Mosquito Lagoon during December 2009. Propagules from different locations were combined and kept in buckets filled with 30 ppt saltwater from collection until planting time. Freezing temperatures during January and February 2010 delayed planting of propagules in mesocosms until March 2010. Propagules were planted in mesocosms by inserting the lower 5 cm of the propagule into substrate, with one propagule per mesocosm. During holding time in buckets, propagules began root production and all propagules planted in mesocosms had roots at start of experiment, however, no leaves were present at planting time. Initial height of propagules (from soil surface to apical meristem) was measured after planting and propagules were monitored every two days for opening of initial leaves. Mangrove height, number of leaves, and number of branches was then measured every three months until end of the experiment in April 2011.

To compare the effects of plant and fiddler crab treatments on soil conditions in mesocosms, soil temperature, porewater salinity, soil moisture and soil drainage were monitored monthly in each mesocosm from March 2010 to April 2011. Porewater salinity was measured using a syringe to remove water at a depth of 5 cm and measured with a handheld refractometer. Soil moisture and temperature were measured using a combination moisture and temperature soil probe (Aquaterr M-300) at a depth of 5 cm. Soil drainage was measured by inserting a 10 mL plastic pipette (with the bulb removed) five centimeters into the substrate, adding 10 ml of 30 ppt saltwater to the pipette, and measuring the amount of time for 10 ml of water to drain (Bertness 1985). To minimize one test from influencing the results of another test, soil characteristics were collected over a two-day period, with porewater salinity, soil moisture and soil temperature measured on day one, and soil drainage measured on day two. Holes created by probes and instruments were filled in by hand immediately following completion of test.

Field Experiment

This field study complements the mesocosm experiment and compared mangrove survival, growth, and susceptibility to propagule predation over a range of natural biotic and abiotic conditions at restored and reference locations. The following methods were repeated at six locations in Mosquito Lagoon, three restored coastal wetland sites where dikes built for mosquito management were mechanically removed (V-1, D-12S, and D-12N) and three neighboring reference marshes. At each impoundment or reference marsh, one location was randomly chosen along the shoreline using ArcGIS (permanent monitoring sites from Chapter 1 were excluded). At this location, an x-y grid system was created using transect tapes running parallel to the shoreline for 100 m and perpendicular to the shoreline for 15 m (average width of restored area of impoundments). Twenty-five quadrats (0.5 m x 0.5 m) were randomly distributed across the grid, using randomly generated pairs of numbers in Microsoft Excel as x and y coordinates for the location of each quadrat. Within each quadrat, one *R. mangle* propagule was planted and presence of salt marsh flora and fiddler crabs was recorded and water and soil characteristics were measured (methods described in detail below).

Within each quadrat, one *R. mangle* propagule was planted by inserting the lower portion of the propagule into the marsh surface. Prior to deployment, the length and mass of all propagules were recorded. Propagules were checked for survival, leaf production, and damage monthly for thirteen months (May 2010-June 2011). After thirteen months, remaining propagules were measured for height and number of leaves for each plant was recorded.

During initial planting, all plants present in the quadrat were identified to species and percent cover by species was estimated. Number of fiddler crab holes was counted and any fiddler crabs visible were recorded. Water depth, water salinity (refractometer), and water temperature (digital thermometer) was recorded for each location with standing water. In areas without standing water, soil moisture and temperature were measured using an Aquaterr combination soil probe at depths of 10 cm. Soil samples were taken with a soil probe of the upper 10 cm of substrate and returned to the lab for soil salinity analysis. Samples were air dried for one to three weeks, depending on moisture content, and soil salinity was then estimated by mixing distilled water and soil (2:1 ratio), allowing it to settle for 24 hrs and measuring the salinity of the supernatant with a handheld refractometer. Percent cover, plant species present, fiddler crabs, and water and soil characteristics were measured each month when mangrove propagule data was collected.

Statistical Analysis

The “survreg” function for survival analysis was used to compare the effects of plant, fiddler crab, and water level treatments on survival of *R. mangle* propagules (R software; R 2.14.1; Crawley 2007). Initial model included all interactions of treatments and data was fitted using a Weibull distribution. Simplified models were compared using the ANOVA function to detect significant changes in deviance when terms were removed. For the minimal adequate model, a likelihood-ratio test was used to identify significant effect of treatments, using the log-likelihood values given by the “survreg” function. References for pairwise contrasts were the controls for plant and fiddler crab treatments and high for water level treatment. Separate MANOVAs were used to compare differences in growth variables of surviving *R. mangle* seedlings (change in height, number of leaves, number of branches, number of days to first leaves, covariate= initial height) and differences in abiotic conditions (soil salinity, soil temperature, soil temperature, drainage) between water level, plant, and fiddler crab treatments. Initial model included all interactions of the treatments (R software; R 2.14.1; Crawley 2007). Simplified models were compared using the ANOVA function to detect significant changes in deviance when terms were removed. In the field experiment, minimal survival of *R. mangle* prevented statistical analysis of results. For all statistical tests, a p-value of 0.05 or less was considered significant.

Results

Mesocosm Experiment

In total, 336 *R. mangle* propagules established in the mesocosms, producing leaves and transitioning to the seedling stage, and survived until the end of the 13-month experiment (Figure 5.1). The minimal adequate model for survival of *R. mangle* seedlings retained the main effects of water level and plant treatment and the interaction term, with a significant effect of treatments on survival ($X^2 = 26.8$, df= 7, $p < 0.001$; Table 5.2). There were no significant effects of fiddler crab treatments on survival of *R. mangle* propagules in our study and this factor was removed from the survival model. The scale was 0.88, indicating hazard (risk of death) decreased with time in our study. The low water treatment had a significant negative effect on survival ($p = 0.01$; Table 5.2), with 158 total surviving mangroves in the low water treatment compared to 178 mangroves in the high water treatment at the end of the experiment. Within the plant treatments, plant mimics and *B. maritima* had a significant negative effect on mangrove survival ($p = 0.04$ and $p = 0.01$, respectively; Table 5.2; Figure 5.1); however, there was not a significant effect of *S. perennis* on mangrove survival compared to the control. There was a significant interaction between low water level and plant mimic treatments, with a significant positive effect on survival compared to the reference values of high water and control plant treatment ($p = 0.01$; Table 5.2; Figure 5.1).

The minimal adequate model for biotic variables retained the main effect of water level ($p < 0.001$) and there was a significant difference between the high and low water level treatments (Table 5.3). Individual responses showed significant differences between water levels on change in height, number of leaves and number of branches ($p < 0.001$ for all three variables).

There were no significant effects from plant or fiddler crab treatments and these factors were removed from the final model. The mean change in height ranged between 15.1 and 17.3 cm for treatment combinations in the low water level group, compared to a range of 15.8 to 19.7 cm in the higher water level treatments (Figure 5.2). In the low water level treatment, the mean number of leaves ranged between 8.2 and 13.6 leaves, compared to 17.6 and 24.0 leaves in the high water treatment combinations (Figure 5.3). The mean number of stems ranged between 1.40 and 2.40 stems in the low water treatment, compared to 3.0 to 4.2 stems in the high water level treatment combinations (Figure 5.4). The mean number of days until initial leaves opened ranged between 34.0 and 56.7 days for the low water treatments and 33.6 to 56.3 days for the high water treatments (Figure 5.5).

The minimal adequate model for soil characteristics retained the main effect of water level ($p< 0.001$; Table 5.4). Individual responses shows significant differences between water levels on soil moisture ($p= 0.014$) and soil drainage ($p< 0.001$). There were no significant effects from plant or fiddler crab treatments and these factors were removed from the final model. Mean soil moisture was ~10% higher in the high water treatment compared to the low water treatments (Figure 5.6). Mean soil drainage was faster in the low water treatment (means ranged between 33.4 seconds and 36.4 seconds per treatment combinations) compared to the high water treatment (means ranged between 57.8 and 66.0 per treatment combinations; Figure 5.7). The mean soil temperature and porewater salinity was similar for all treatment combinations. Mean porewater salinity ranged between 5.7 ppt and 8.1 ppt for all treatment combinations (Figure 5.8). Mean soil temperature ranged between 28.9°C and 30.2°C for all treatment combinations (Figure 5.9).

Field Experiment

A total of three *R. mangle* seedlings survived at all sites in the field experiment. At reference wetlands near V-1 and D-12S, all propagules were lost or dead by the end of the experiment. One propagule survived until the end of the study at the reference wetland near D-12N and was 33.5 cm in height and had four leaves. At the restored mosquito impoundment sites, all propagules were lost or dead at V-1 and D-12S. Two propagules survived until the end of the study at D-12N. One seedling was 34.6 cm in height and had six leaves. The second propagule was 38.7 cm in height and had four leaves. At reference marshes, 64% of total propagules (75 total propagules, 25 propagules per site at 3 sites) were not retained in quadrats, 14.7% were retained and were brown and shriveled, and 20% of propagules suffered from damage by herbivores. At restored impoundments, 73.3% of total propagules (75 total propagules, 25 propagules per site at 3 sites) were not retained in quadrats, 20.0% were retained and were brown and shriveled, and 4.0% of propagules suffered from damage by herbivores. The two propagules surviving until the end of study at restored sites were in quadrats with greater than 60% plant cover.

Discussion

In subtroptical and tropical coastal wetlands, mangroves are affected by interactions between abiotic factors, plants, and animals and the effect of mangrove interactions with these factors can influence recruitment, distribution, and abundance. We tested the effects of water level and co-occurring plant and animals on the survival and growth of *R. mangle* seedlings during the first year of development. In our mesocosm study, we found water level had the strongest significant effect on mangrove survival and growth, with the low water treatments having lower survival and growth compared to the high water treatment. The net effect of neighboring plants on *R. mangle* was species specific. Interactions between mangroves and *B. maritima* had a negative net effect on mangrove survival but did not affect mangrove growth parameters. In comparison, there were no significant effects of *S. perennis* on mangrove survival or growth, suggesting the net effect was neutral for this species. There were no significant effects of fiddler crabs on the survival or growth of *R. mangle* seedlings, suggesting the net effect of interactions between mangrove and fiddler crabs was neutral in our study. In the field experiment, minimal survival of *R. mangle* propagules was observed at all sites. At both sites, the majority of propagules were lost from the quadrats and the final survival of these propagules was unknown. At reference sites, propagule damage by herbivores was common and resulted in mortality of propagules. At restored sites, frequency of propagule damage was lower and these propagules appeared to suffer more from desiccation (brown, shriveled propagules).

A defining characteristic of coastal wetlands is the physiologically stressful conditions of the intertidal habitat. Frequent tidal flooding with saltwater results in saturated, anoxic soils and introduces high amounts of salts to the substrate (Odum and McIvor 1990; Pennings and Bertness 2001). Plant distribution in coastal wetlands is strongly affected by a species' tolerance to inundation and salinity (Bertness 1991; Ward et al. 2006; Alongi 2009). *Rhizophora mangle* typically inhabits the lower intertidal zone and is adapted to prolonged periods of inundation and soil salinities up to 60 ppt (Tomlinson 1994). The low water level treatment with decreased soil moisture and water availability was a limiting factor for *R. mangle* seedlings in this study and had a stronger effect on survival and growth compared to the biotic factors in our study. Porewater salinity was not a source of abiotic stress in the mesocosms because measured values were low (mean porewater salinity ≤ 8.18 ppt) in all treatment combinations compared to the upper tolerance of *R. mangle*. Porewater salinity was also lower than the conditions of coastal wetlands in Mosquito Lagoon, where porewater salinity can be 30 ppt or more, depending on frequency of tidal inundation.

The balance between positive and negative interactions may vary across environmental gradients, with plant interactions more likely to have a positive net effect in stressful environments compared to negative interactions when growing in less stressful areas (Bertness and Callaway 1994; Tielborger and Kadmon 2000; Brooker et al. 2007; Valiente-Banuet and Verdu 2008; Zhang et al. 2008). The only significant interaction over our artificial environmental gradient of water level in our study was a positive effect of plant mimics on *R. mangle* survival when growing in the low water level treatment. We tested plant mimics in an attempt to separate out positive effects from shading the substrate and decreasing evaporation rates from negative effects of competition between two plants, as seen in the negative effect of *B. maritima* on *R. mangle* survival. The plant mimic had a positive effect in the low water level treatment compared to the high water level treatment, suggesting shading did potentially have a positive effect in the absence of competition. In comparison, there was not a significant interaction between our abiotic treatment of water level and the presence of *B. maritima* or *S. perennis* on *R. mangle* survival or growth, suggesting the net effect of the plant-plant interactions did not vary under the two water levels tested. Results from studies in northeastern marshes from Maine to Rhode Island had predicted the positive effect of neighbors shading the substrate and reducing porewater salinities may be more important in low latitude marshes with higher evapotranspiration rates compared to high latitude marshes (Bertness and Leonard 1997; Pennings et al. 2003). However, neighbor removal experiments in Georgia and Alabama did not support this prediction (Pennings et al. 2003). Plants in southern marshes responded positively to the removal of neighbors, despite an increase in porewater salinities, suggesting competition was the primary plant-plant interaction (Pennings et al. 2003). Plants common in low latitude marshes may have higher salinity tolerances as an adaption to higher rates of evapotranspiration, decreasing the importance of facilitative interactions (Pennings et al. 2003). Thus, the outcome of community interactions in coastal wetlands can be strongly influenced by the species-specific tolerances and adaptations to the abiotic conditions in the system.

Positive interactions between burrowing crabs and plants provide benefits to both groups of taxa, creating a facultative mutualism between crabs and plants (Bertness 1985; Normann and Pennings 1998; Bortulus et al. 2002). In our study, we did not observe a significant positive or negative effect of fiddler crabs on growth or survival of *R. mangle* or on any of the measured soil characteristics related to our water level treatments. The density of fiddler crabs in the mesocosms (2 crabs; 3 burrows) was relatively low compared to densities in coastal wetlands in Mosquito Lagoon, where densities can be as high as 10 crabs and 30 burrows in a 0.25 m^2 plot. We chose *U. pugilator* because it is the most common fiddler crab in Mosquito Lagoon wetlands and is the first fiddler crab species to utilize restored sites, however, this species can be aggressive and our preliminary trials found more than 2 crabs in a mesocosm resulted in mortality of the crabs. The low density of crabs and burrows could have minimized the effect on mangrove growth and survival in our study. Stevens et al. (2009) found a positive correlation between fiddler crab burrow density and height, trunk diameter, and leaf production of *Laguncularia racemosa* (white mangrove) in wetlands in Tampa Bay, FL. The non-significant effect of our fiddler crab treatments could also have been due to the lack of complete inundation in our mesocosms. A common benefit of the presence of burrowing crabs in frequently flooded wetlands comes from aeration of the anaerobic soils (Normann and Pennings 1998; Daleo et al.

2007; Stevens et al. 2009). Increased oxygen availability can have a direct positive effect on mangroves and other co-occurring plants (Normann and Pennings 1998); however, Daleo et al. (2007) reported the increased growth of *Spartina densiflora* near crab burrows in coastal Argentina was due to the colonization of roots with mycorrhizal fungi. The increased production of plant species growing in the presence of burrowing crabs may be due to this indirect facilitation through mycorrhizal fungi, rather than a direct effect of fiddler crabs on plant growth, and additional research is needed in order to identify the facilitative mechanisms between plants and burrowing crabs (Daleo et al. 2007).

Our study found abiotic conditions had the strongest effect on *R. mangle* survival and growth compared to biotic factors during the first year of the mangrove's life cycle. Mesocosms can be useful for identifying specific effects of plant and animal interactions by removing some of the stressors and confounding factors experienced by plants in the natural environment. However, the artificial set-up of mesocosms may also be limited in detecting the effects of complex interactions resulting from the numerous factors affecting plants in a natural setting. Within the mesocosm experiment, we had high rates of survival in all treatments, but our complementary field study had extremely low rates of survival at all sites, suggesting the complex interactions in the field strongly influence mangrove survival in natural systems. Our mesocosm experiment only tested two static water levels, compared to fluctuating inundation regimes of natural coastal wetlands, and porewater salinities remained low compared to natural wetlands. In addition, we focused on factors affecting *R. mangle* seedlings in their first year of growth. The relative effects of biotic interactions may change over different stages in the life cycle of the plant and understanding these effects has direct applications for coastal wetland restoration. Restoration programs have often focused on planting one species of mangrove, often ignoring the complex biotic interactions between flora and fauna and influences of abiotic factors in the system (Lewis 2005). Applying facilitation concepts to restoration is becoming more common and has the potential to increase project success, particularly in systems where physiological stress is high (Bruno et al. 2003; Padilla and Pugnaire 2006; Halpern et al. 2007). Evaluating the outcome of community interactions improves our understanding of the role these interactions have in structuring natural communities, influencing successional processes, and guiding ecological restoration practices, and studies in the field are needed to further investigate the complex relationship between biotic and abiotic factors on long-term survival of mangroves in coastal wetlands.

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Tables

Table 5.1. A full factorial design was used to test all possible combinations of the following plant, fiddler crab, and water level treatments in the mesocosm experiment.

Treatments	Experimental Factors	Total Factors/Treatment
Plant	Glasswort, Saltwort, Mimic Plants, None	4
Fiddler Crabs	Fiddler Crabs, Mimic Holes, None	3
Water Level	High, Low	2

Total Treatment Combinations: 24

Number of replicates/treatment combination: 17 mesocosms

Total number of mesocosms: 408

Table 5.2. Model summary of survival analysis comparing survival of *Rhizophora mangle* between treatments. The minimal adequate model retained main effects of water level and plant treatments and interaction terms. Reference values were high water treatment and plant treatment control (no plants or plant mimics).

	Value	SE	Z	P
Intercept	8.86	0.70	12.60	<0.001
Water Level- Low	-1.76	0.70	-2.52	0.01
Plant Treatment- *S. perennis*	-0.38	0.81	-0.47	0.64
Plant Treatment- Mimic	-1.43	0.71	-2.02	0.04
Plant Treatment- *B. maritima*	-1.71	0.70	-2.44	0.01
Low:*S. perennis*	0.77	0.90	0.86	0.39
Low:Mimic	2.04	0.84	2.44	0.01
Low:*B. maritima*	1.40	0.77	1.83	0.07
Log(scale)	-0.12	0.11	-1.10	0.27

Table 5.3. Results of minimal adequate MANOVA model comparing differences in growth variables of surviving *R. mangle* seedlings (change in height, number of leaves, number of branches, number of days to first leaves, covariate= initial height) between experimental treatments.

	Df	Pillai approx.	F	p-value
Initial Height	1	0.028	3.220	0.023
Water Level	1	0.204	28.251	<0.001
Residuals	333			

Table 5.4. Results of minimal adequate MANOVA model comparing differences in abiotic variables of mesocosms with surviving *R. mangle* seedlings (soil salinity, soil moisture, soil temperature, drainage) between experimental treatments.

	Df	Pillai approx.	F	p-value
Water Levels	1	0.564	106.437	<0.001
Residuals	332			

Figures

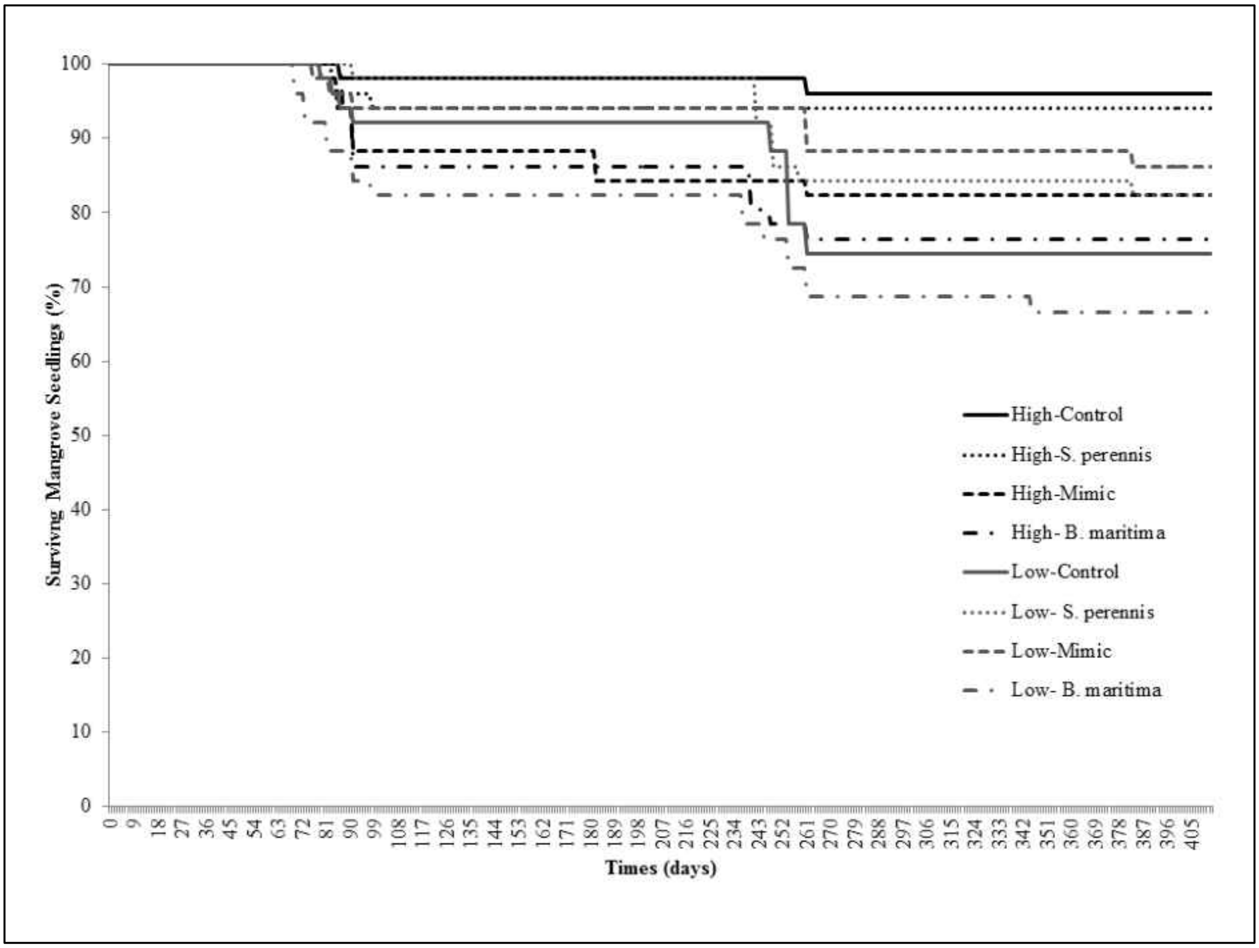

Figure 5.1. Survival of *Rhizophora mangle* seedlings in plant treatment combinations grown under low (gray lines) and high (black lines) water level conditions.

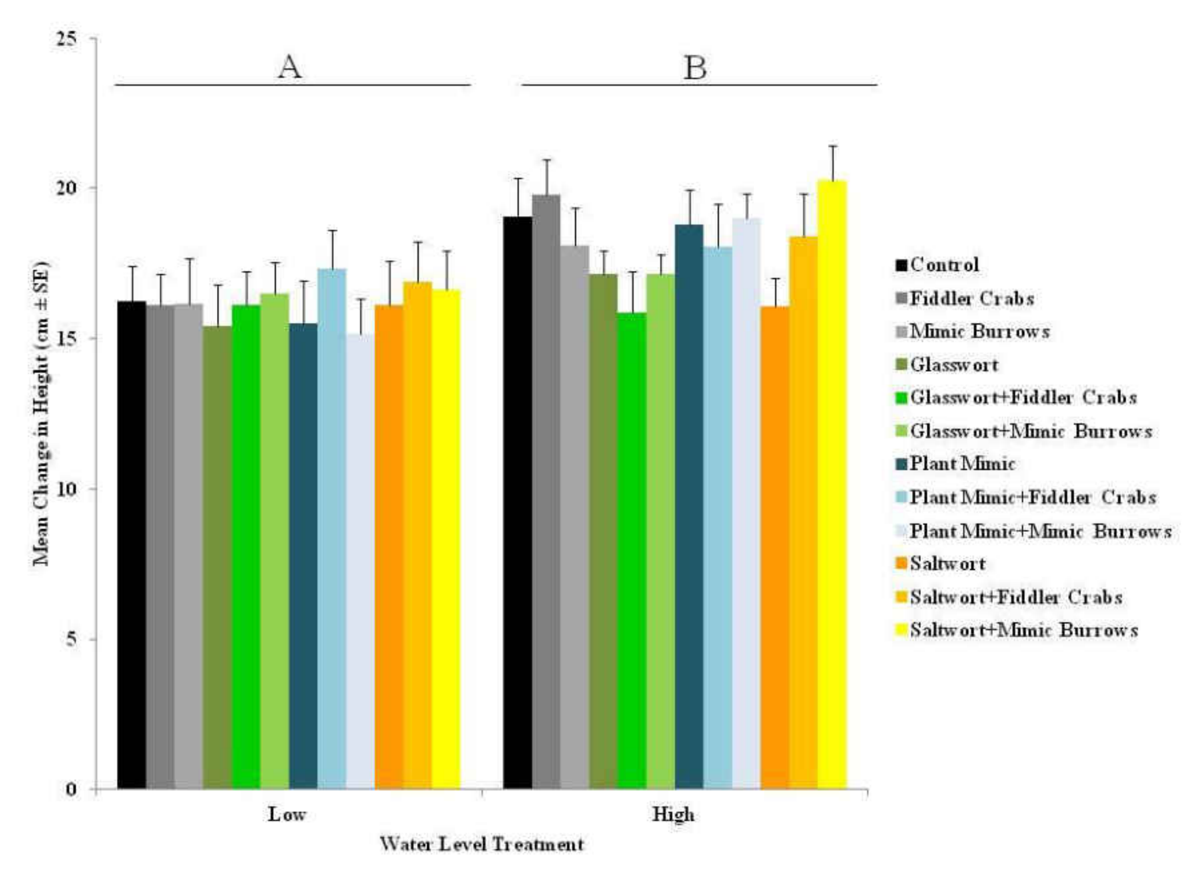

Figure 5.2. Mean change in height (cm ± SE) for all surviving *R. mangle* (n = 336). Significant differences between water levels based on individual responses from MANOVA analysis are represented by uppercase letters.

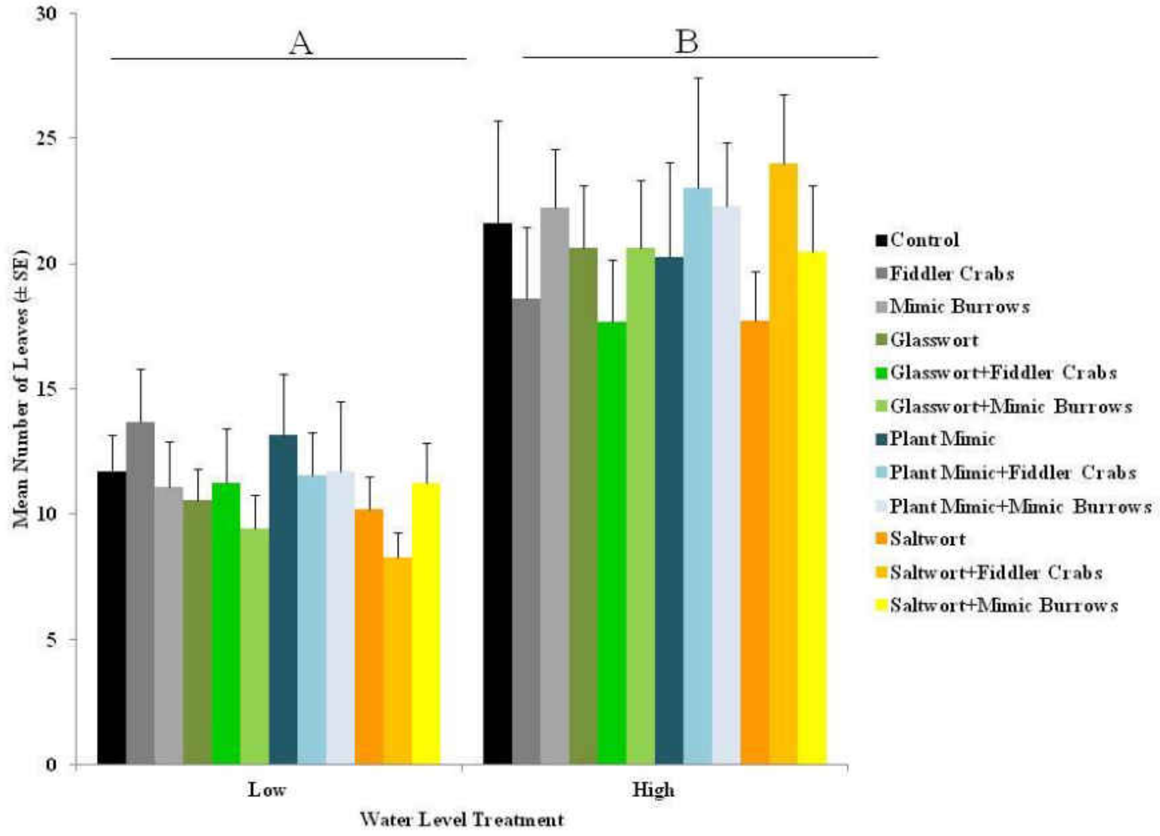

Figure 5.3. Mean number of leaves (± SE) for all surviving *R. mangle* (n = 336). Significant differences between water levels based on individual responses from MANOVA analysis are represented by uppercase letters.

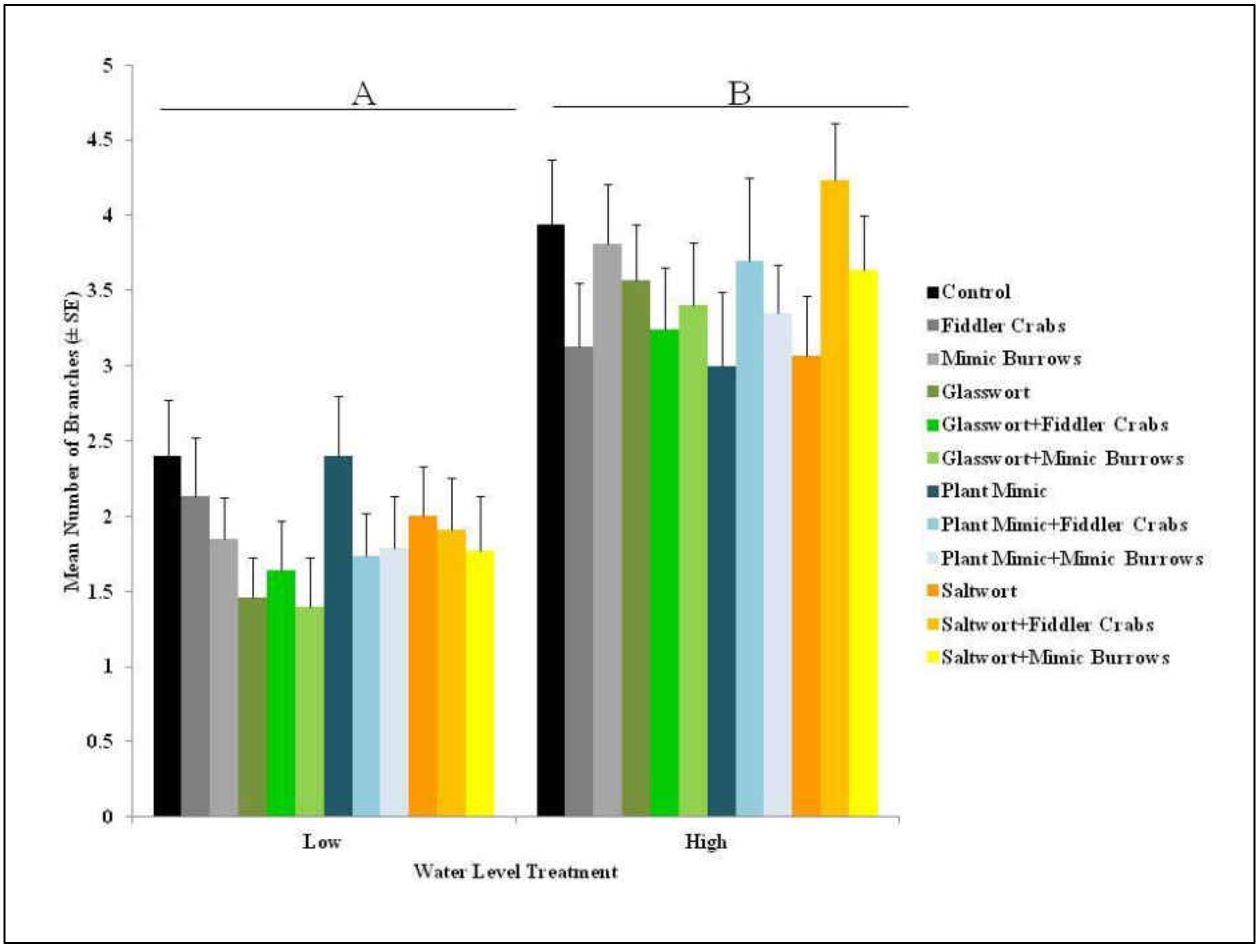

Figure 5.4. Mean number of branches (± SE) for all surviving *R. mangle* (n = 336). Significant differences between water levels based on individual responses from MANOVA analysis are represented by uppercase letters.

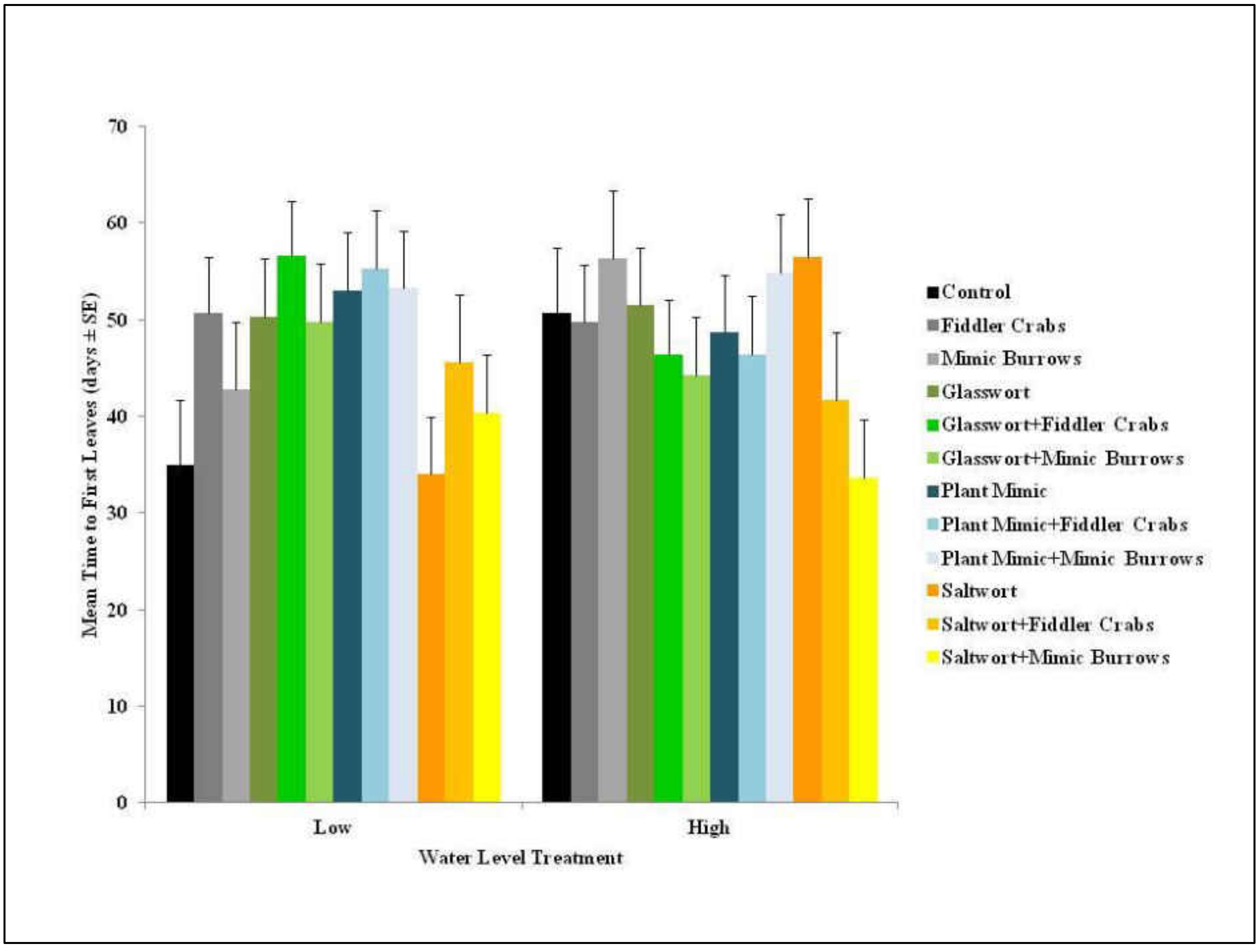

Figure 5.5. Mean time to first leaves (days ± SE) for all surviving *R. mangle* (n = 336).

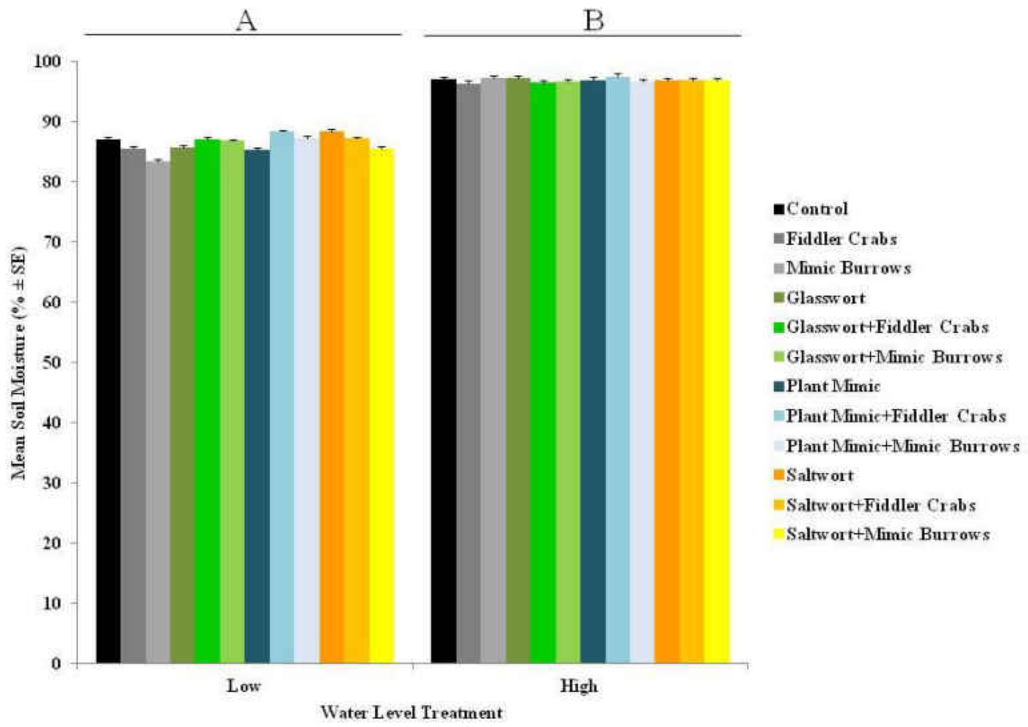

Figure 5.6. Mean soil moisture (% ± SE) of mesocosms with surviving *R. mangle* seedlings (n = 336). Significant differences between water levels based on individual responses from MANOVA analysis are represented by uppercase letters.

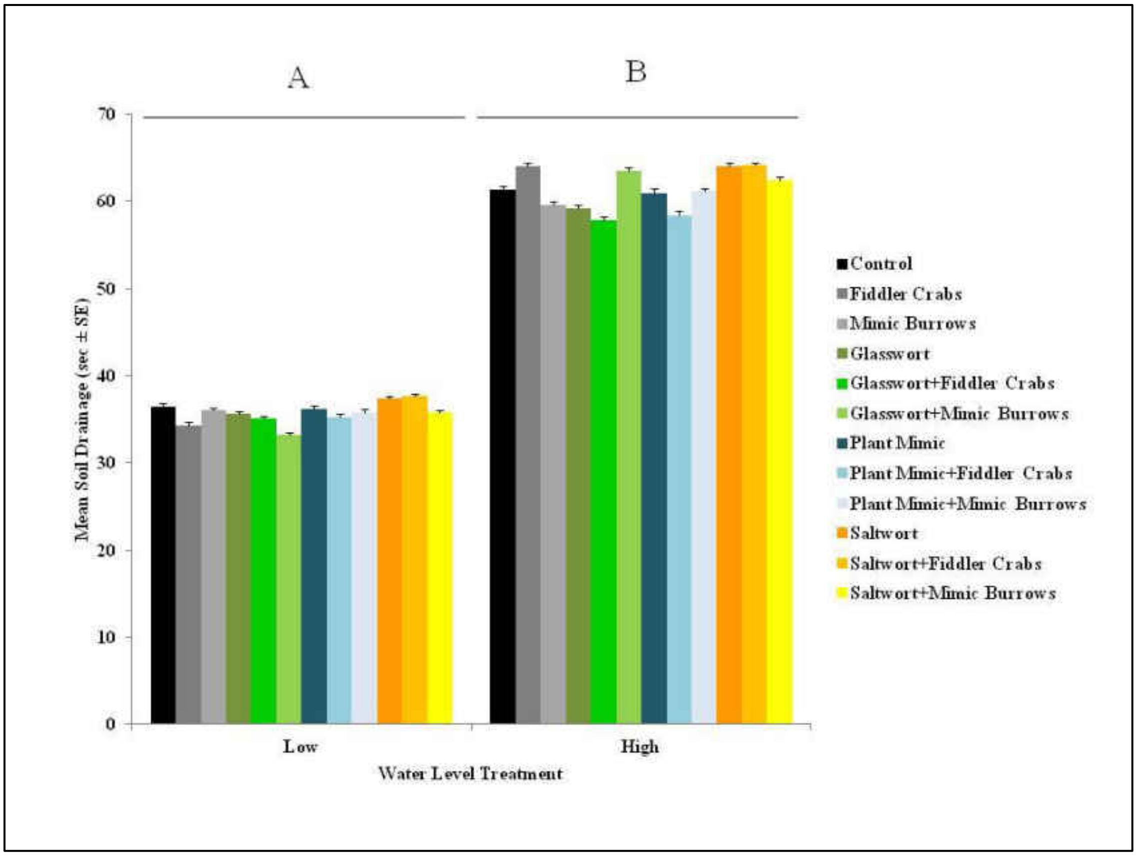

Figure 5.7. Mean soil drainage (sec ± SE) in mesocosms with surviving *R. mangle* seedlings (n = 336). Significant differences between water levels based on individual responses from MANOVA analysis are represented by uppercase letters.

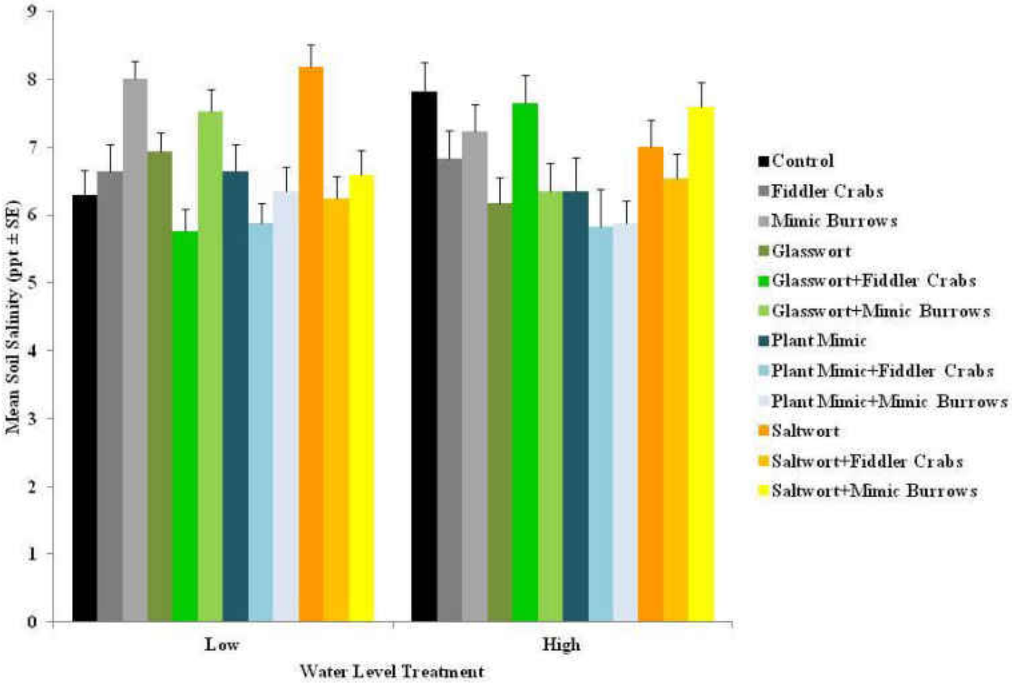

Figure 5.8. Mean soil salinity (ppt ± SE) of mesocosms with surviving *R. mangle* seedlings (n = 336).

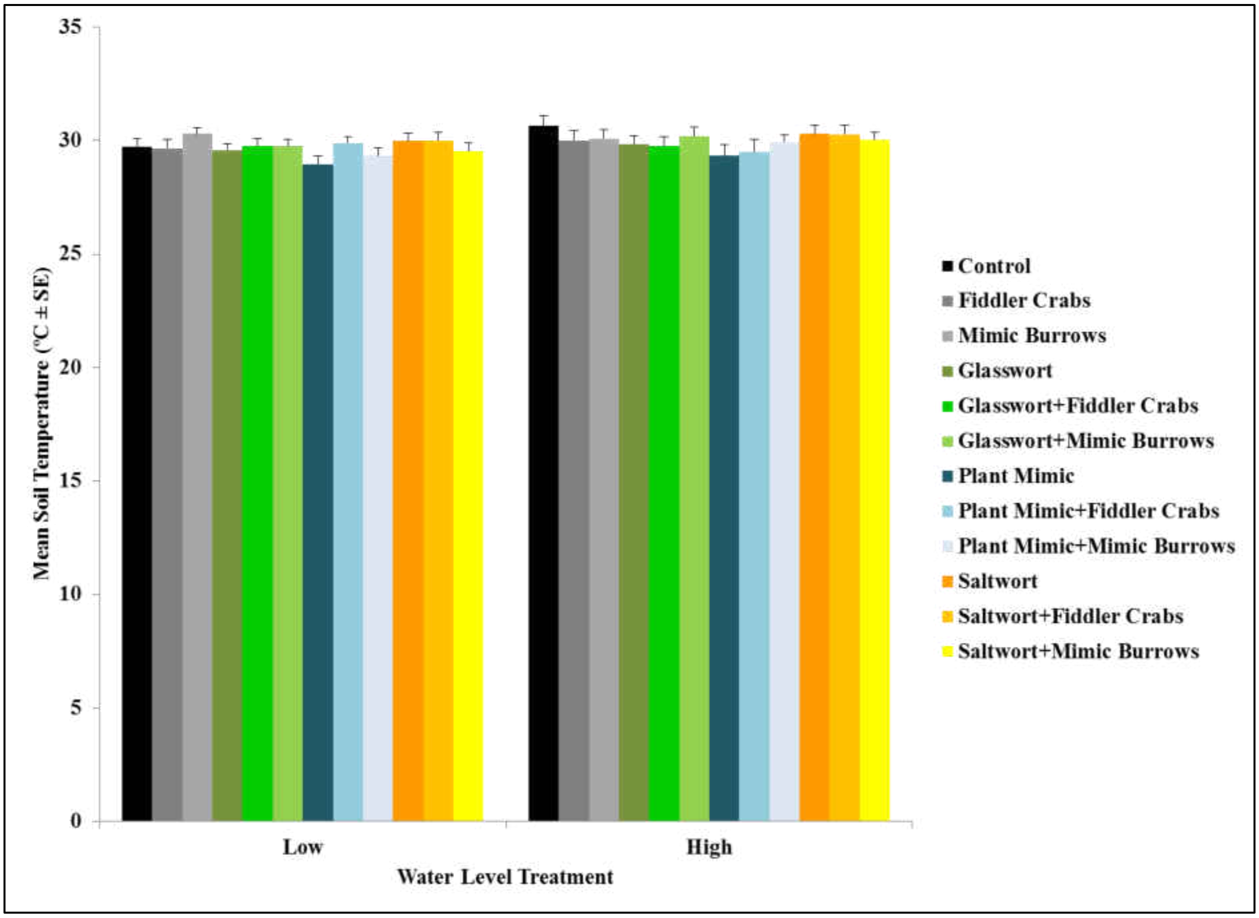

Figure 5.9. Mean soil temperature (°C ± SE) of mesocosms with surviving *R. mangle* seedlings (n = 336).

GENERAL CONCLUSIONS

My dissertation used a combination of observational studies and manipulative experiments to investigate the role of biotic interactions on native Florida mangroves and coastal wetland communities. First, I monitored the natural regeneration of coastal wetlands following hydrological restoration at mosquito impoundments. Dominant plant species found in the control wetlands have established at all restored sites and abundance of the non-natives have been significantly reduced. Initial recruitment of plants occurred within one month of restoration, facilitated by leveling which left native wetland vegetation at the shoreline intact to serve as a seed source for recruitment into the leveled areas. Fiddler crabs were found at all restored sites, supporting the initial recovery of food web processes at restored mosquito impoundment sites. The observation of a variety of wading birds and shorebirds foraging on the restored surface and nekton utilizing the shoreline further indicates the recovery of food web processes at restored sites. This observational study provided numerous applications for future coastal wetland restoration, including:

1) Target elevations of 15 cm were effective at restoring natural hydrological properties by allowing tidal flow across the marsh surface during high water season and retaining high soil moisture during low water season when wetlands were not inundated.

2) Natural regeneration of vegetation following dike leveling occurred at all restored impoundment sites within one-year of restoration and was a viable restoration technique in areas where substantial numbers of seeds and propagules were available.

3) Preservation of shoreline vegetation enhanced the rate of plant recovery on leveled portion of dike by serving as a nearby seed and propagule source and promoting vegetative propagation of halophytes into the restored marsh zone within one month of dike removal.

4) Abiotic conditions can act as a natural barrier to prevent non-native plant recruitment and restoring hydrological conditions was an effective method for reducing non-natives in coastal wetlands.

In addition to management recommendations, monitoring at restored mosquito impoundments identified potential biotic interactions which may be important for community recovery and are applicable to future restoration, including the importance of positive interactions between co-occurring flora and mangroves and effects of propagule herbivory on mangrove dispersal and recruitment. Manipulative experiments were conducted to test hypotheses related to these biotic interactions. Results from the propagule trapping experiment supported our hypothesis of initial colonizers facilitating recruitment of *R. mangle* by increasing potential for retention. In addition, this experiment also documented propagule damage after dispersal as a potential limiting factor to *R. mangle* recruitment. Results from our field surveys of pre-dispersal propagule damage found yearly variations in frequency of damage, which may be related to annual fluctuations in temperature and water levels and effects on herbivore populations. Results from this study suggest multi-species interactions may be an important biotic control on mangroves and trophic link between primary production and flow of energy and nutrients through mangrove ecosystems. In buoyancy trials, we found pre-dispersal propagule damage had a significant negative effect on length of time propagules floated once released from the tree, which could limit dispersal to restored areas relying on natural regeneration from neighboring locations. Mesocosm experiments highlighted the importance of water levels on growth of *R. mangle*, further supporting the need for hydrological restoration in areas where habitat alterations have decreased tidal inundation and changed abiotic conditions.

In summary, coastal wetland diversity and functions are strongly affected by both abiotic and biotic processes within the ecosystem and successful restoration needs to address both aspects of the system. Whereas restoration projects often focus on effects of abiotic conditions, the inclusion of biotic processes, particularly facilitative interactions can potentially benefit restoration efforts, especially in systems where physiological stress is high (Bruno et al. 2003; Padilla and Pugnaire 2006; Halpern et al. 2007; Peterson and Bell 2012). In riparian and wetland habitats, restoration methods utilizing natural dispersal through hydrochory can be applied to larger areas, completed with lower project and labor costs, and maintain local genetic variation and adaptations (Nilsson et al. 2010). Hydrological restoration of coastal wetlands by removing barriers to tidal influence has been shown to promote growth of halophytic species and natural dispersal of mangrove propagules, developing a diverse plant community without the need for additional planting (Brockmeyer et al. 1997; Turner and Lewis 1997; Lewis 2005; Nilsson et al 2010: Rey et al. 2012). Alternatively, when natural regeneration is not possible due to recruitment limitations, planting target species within existing vegetation may increase establishment compared to planting in unvegetated locations (Young et al. 2005; Milbrandt and Tinsley 2006; Peterson and Bell 2012). Biotic interactions between mangroves, other plant species, and fauna will potentially change under different climate conditions (Alongi 2009; McKee et al. 2012, Guo et al. 2013) and influence structure and function of mangrove systems in the future. As warmer winters allow for expansion of mangroves into more temperate areas (Osland et al. 2013), biotic interactions will also change as mangroves come into contact with new consumers or escape herbivory from tropical species. An ecosystem-level approach that addresses both biotic and abiotic interactions affecting recruitment, survival, and growth of mangroves and other wetland vegetation is necessary to increase success of coastal wetland restoration projects and improve management and conservation of these diverse and productive ecosystems.