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Determining the Extent of Pioneer Mangrove Acidification on Intertidal Oyster Reefs

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ABSTRACT: The Indian River Lagoon (IRL) stretches 251 kilometers along Florida's east coast and is one of the most biodiverse estuaries in North America. Mosquito Lagoon, the northernmost portion of the IRL, is home to mangroves and intertidal oyster reefs that provide numerous ecosystem services. These two habitats are overlapping as climate change drives mangroves poleward. Scientists have documented mangrove expansion and the transition of oyster reef habitat to mangrove islands. Past studies have shown large, adult mangrove stands drive soil acidification. The goal of this study was to understand if stand-alone, or pioneer, *Rhizophora mangle* (red mangroves) and *Avicennia germinans* (black mangroves) acidify intertidal *Crassostrea virginica* (eastern oyster) reef sediment. We collected porewater (i.e., water within sediment) and measured pH with a portable pH meter. Porewater pH was sampled from 0 to 1 meter away from pioneer mangroves in 20 cm increments. Closest to the mangrove trunk, reef sediment pH was significantly more acidic (mean pH of 7.18 for *R. mangle* and 7.02 for *A. germinans*) compared to oyster reef-only control areas with a mean pH of 7.44 (p-value < 0.001 for both mangrove species). By 1 meter away from the mangrove trunk, the pH for both mangrove species was no longer significantly different from the control areas (p-value $= 1.0$), indicating mangrove-driven acidification has a localized effect on oyster reef sediments. Acidification weakens oyster shells, and by understanding the extent of mangroves' acidic effects on oyster reefs, resource managers can use this information to protect declining oyster reef habitat.

KEYWORDS: tropicalization, sediment acidification, oyster reefs, mangrove expansion

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INTRODUCTION

Climate change impacts ecosystems worldwide and can cause rapid ecological changes. Researchers found that between 1960 and 2017 the Earth's average temperature rose approximately 1˚C and will likely continue to increase (IPCC, 2022). An important consequence of this warming is ecological tropicalization. Osland et al. (2021) defines tropicalization as "the transformation of temperate ecosystems by poleward-moving tropical organisms in response to warming temperatures." Scientists have documented the effects of tropicalization and have observed tropical species competing for food and habitat with resident temperate species (Heck et al., 2015; Osland et al., 2021). For example, in the northern Gulf of Mexico, tropical species like herbivorous parrotfish, manatees, and green turtles are consuming seagrass in larger quantities than temperate herbivorous fishes, altering and reducing the structural complexity and nursery role of seagrass habitats in the area (Heck et al., 2015).

Mangroves, a group of tropical and subtropical coastal trees, have expanded poleward over the past few decades into more temperate locations due to tropicalization (Cavanaugh et al., 2014). Globally, researchers have observed that mangrove expansion has resulted in the reduction of salt marsh habitats (Saintilan et al., 2014; Raabe et al., 2012; Hesterberg et al., 2022; Krauss et al., 2011; Cavanaugh et al., 2014). More recently, mangrove expansion, driven by *Avicennia germinans* (black mangroves) and *Rhizophora mangle* (red mangroves), onto intertidal *Crassostrea virginica* (eastern oyster) reefs has become a focus of concern along mangrove's northern range limits in the southeastern United States (McClenachan et al., 2021; Hesterberg et al., 2022).

In Southwest Florida, the Ten Thousand Islands (TTI) that border Everglades National Park changed from oyster reefs to mangrove islands over the course of the past 3,500 years due to sea level rise and progradation (Andres et al., 2019; Parkinson, 1989; Fronczkowski, 2013). This transition in the TTI remains an ongoing trend, as researchers work to restore declining oyster reefs (Volety et al., 2014). In Tampa Bay, 83% of oyster reefs changed to mangrove islands in the past 82 years due to tropicalization (Hesterberg et al., 2022). Furthermore, in the Mosquito Lagoon, there has been an 198% increase in mangrove cover on oyster reefs between 1984 and 2017 (McClenachan et al., 2021). This oyster reef to mangrove island transition can cause ecosystem services to change, affecting many species from small to large.

Oysters are suspension-feeding bivalves and are keystone species that offer many vital ecosystem services to estuarine systems. Oysters improve local water quality by filtering out excess nutrients such as algae, phytoplankton, and suspended solids caused by anthropogenic development (e.g., Coen et al., 2007; Grabowski and Peterson, 2007). In doing so, oysters improve water clarity, which allows sunlight to reach subtidal aquatic plants that help provide oxygen to fish and other marine species (Newell & Koch, 2004). Oyster reefs also reduce shoreline erosion caused by storms and sea level rise, create habitat utilized by many important threatened and commercial species, and provide food sources for many coastal organisms (Dexler et al., 2014; Grizzle et al., 2008; Porter et al., 2004; Grabowski et al., 2012). Despite these essential services, shellfish reefs have declined by 85% in the past century (Beck et al., 2011). Oyster reef degradation has been predominately caused by anthropogenic impacts, such as overharvesting, poor water quality, disease, and habitat destruction caused by boat wakes and strikes (Walters et al., 2007; Garvis et al., 2015; Kirby, 2004).

Mangroves are the foundation species of their ecosystems (Ellison, 2019). They provide ecosystem services including sediment stabilization, nutrient cycling, carbon sequestration, shoreline protection, and providing habitat for many species (Sandilyan et al., 2012; Banerjee & Paul, 2022; Nagelkerken et al., 2008). *A. germinans* and *R. mangle* release propagules that can float on the surface of the water for up to 110 days and one year respectively, before becoming established on shorelines (Rabinowitz, 1978; Donnelly & Walters, 2014). Due to tropicalization and a greater number of mangroves present in Florida, there is a high abundance of propagules in estuaries. If these propagules land on oyster reefs or shorelines with their stems upright and are held in place by oyster clusters or other plants, the mangrove propagules can root and transition into a seedling. If individual seedlings survive all the barriers to success (e.g., storms, boat wakes, herbivory), then the mangrove propagules turn into pioneer mangrove trees. Pioneer mangroves are defined here as the first individual trees that colonize and establish themselves in a new location (Corenblit et al., 2015).

Due to their physiology and unique adaptations, mangroves have the potential to cause surrounding

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soil to become more acidic (Middelburg et al., 1996; Marchand et al., 2004; Reef et al., 2010). The soil around mangrove roots undergoes an oxidation process that maintains favorable conditions for the mangrove to grow while creating a byproduct of free hydrogen ions in the soil that contribute to acidic conditions (Thibodeau & Nickerson, 1986). The input of hydrogen ions from decaying leaves and organic matter, as well as from mangroves' storage of carbon dioxide from the atmosphere, leaches into the soil and causes a reaction between water and carbon dioxide to form carbonic acid in surrounding soil (Twilley et al., 1992; Sabine et al., 2004; Aller, 1982). Additionally, mangrove roots release oxygen to the rhizosphere that can mix with sulfur in the soil, creating sulfuric acid (Middelburg et al., 1996). These unique physiological features and the soil chemistry associated with mangroves lead to increased soil acidity in the area surrounding the tree.

Oysters require calcium carbonate to form their shells and attract larval recruits to create oyster reefs (Waldbusser et al., 2011). High acidification can suppress the oyster's shell-building process. Specifically, low pH (i.e., increased acidity) increases the hydrogen ion concentration in the water, which attach to calcium carbonate ions from the surrounding area. This removal of free calcium carbonate ions weakens adult oyster shells and prevents juvenile oysters from forming their shells (Waldbusser et al., 2011; Keppel et al., 2016). One study tested fresh oyster shells, weathered shells, and dredged shells and subjected them to four water treatments with acidic pH. This study determined that oyster shells are subject to increased dissolution rates around a pH of 7.2 (Waldbusser et al., 2011). Benaish et al. (2010) demonstrated that water with low pH minimized the viability of oyster larvae in laboratory trials. In elevated carbon dioxide conditions, which contributed to decreased water pH, juvenile oyster shells were weaker and easily fractured, negatively impacting the oyster's survival.

To date, mangrove-driven acidification has only been documented for large stands of mangroves (Marchand et al., 2004; Middelburg et al., 1996). In ongoing research in Mosquito Lagoon, large stands of *R. mangle* established on intertidal oyster reefs have been shown to significantly decrease the reef's sediment pH below 7.2 where the rate of oyster shell dissolution increases and reef degradation becomes possible (Harris et al., 2022). However, mangrove recruitment and expansion on oyster reefs starts with a single individual, or pioneer, mangrove. It is unknown whether stand-alone, pioneer mangroves alter the pH of oyster reef sediment. Additionally, the spatial extent of this pH change with mangrove presence is currently unknown. To fill this knowledge gap, the purpose of our research is to address two research questions: 1) Do *Rhizophora mangle* and *Avicennia germinans* pioneer mangroves acidify oyster reef sediment, and 2) What is the spatial extent of sediment acidification extending away from the pioneer mangrove? This information is needed for resource management and for restoration practitioners to determine if the effort involved in removing pioneer mangroves is needed to maintain intertidal oyster reefs.

MATERIALS AND METHODS

Study Site

The Indian River Lagoon (IRL) is an estuary system covering forty percent of Florida's Atlantic coast, extending 251 kilometers in length. The lagoon is a living laboratory for researchers to study multiple ecosystems and species. The IRL is a brackish water system that contains unique and diverse organisms because of its geographic location and supports both temperate and subtropical species (St. Johns River Water Management, 2007). This research takes place in Mosquito Lagoon, the northernmost portion of the IRL. Mosquito Lagoon's salinity ranges from 20 to 35 parts per thousand depending on rainfall. The depth of Mosquito Lagoon is about 1 meter on average and the air temperature in this area ranges from 0 to 32 degrees Celsius (Hall et al., 2001).

Site Selection

This study measured changes in sediment pH over a one-meter distance and compared pH between three treatments: oyster reefs with pioneer *Rhizophora mangle,* oyster reefs with pioneer *Avicennia germinans*, and oyster reef only (no mangroves present; controls) (Figure 1). Due to the limitations of finding a single pioneer mangrove per oyster reef, data was collected at multiple pioneer mangroves on some reefs in which the plants were separated by a minimum of 2 meters. Additionally, for each pioneer mangrove, an oyster reef-only control sample was taken on the same reef but was located at least two meters away from any mangroves. Each site was sampled during low tide to ensure the sediment on the oyster reef was free of surface water inundation. This study focuses on adult mangroves with a minimum height of one meter and used the presence of flowers and

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Figure 1.
Examples of the three reef treatments.

A) Pioneer *Rhizophora mangle* (red mangrove) on an oyster reef. B) Pioneer *Avicennia germinans* (black mangrove) on an oyster reef. C) Oyster reef only (*Crassostrea virginica*) control.

propagules to ensure that the selected mangroves were of reproductive age.

Mangrove Measurements

Transect tape was used to measure mangrove height, distance from the trunk to the farthest extending above-ground root, trunk circumference, and canopy circumference. The number of flowers were counted for both *R. mangle* and *A. germinans* mangrove trees. The number of prop roots were recorded for *R. mangle* and the number of pneumatophores were recorded for *A. germinans*. Additionally, the distance to the reef edge, distance to the nearest mangrove stand, and distance to the closest single mangrove were measured for both mangrove and control sites.

Porewater Collection

Porewater (i.e., water from within the sediment) was collected to measure how sediment pH changed with treatment and distance. This was done using a transect and points in replicate, where porewater pH samples were collected at specific distances for each individual mangrove or control replicate site. For mangrove replicates, a transect line was laid out at the base of the mangrove and extended one meter away from the mangrove trunk out onto the oyster reef. For control replicates, the one meter transect line was placed on an area of an oyster reef with no mangroves present within at least two meters. Transect lines were placed to run parallel to the edges of the reefs. Six porewater samples were taken at intervals of 20 centimeters, beginning at 0 and ending at 100 centimeters. For pioneer *A. germinans,* no porewater was collected at the zero-centimeter distance due to dense pneumatophores and underground roots. Instead, five porewater samples, starting at 20 centimeters, were collected for pioneer *A. germinans*.

At each distance along the transect line, a 2.5-centimeter diameter PVC pipe was hammered ten centimeters into the oyster reef sediment in areas with no overlaying surface water. Ten centimeters was previously determined to be the average burial depth of oysters on Mosquito Lagoon's intertidal oyster reefs (Walters et al., 2021). The sediment core (i.e., the sediment within the PVC pipe) was removed and discarded. Within minutes, porewater seeped into the hole. To collect the porewater, a sipper apparatus was constructed using a 10-milliliter plastic syringe, rubber tubing, and a 10-millimeter glass pipette (Roman et al., 2001; Taillardat et al., 2018). Both the sipper and the 20-milliliter collection vial were rinsed three times with porewater to reduce any chance of contamination. The final porewater sample was then extracted using the sipper and added to the vial, which was capped and labeled.

All porewater samples were tested immediately after collection with an Oakton pH 6+ Handheld Meter. This pH meter included automatic temperature compensation to account for temperature differences in the samples. Each device was calibrated using a three-point calibration with pH buffer solutions before each fieldwork day. Between each sample, the pH probe and temperature component of the pH meter were rinsed with deionized water to ensure there was no contamination. This process was conducted for all samples.

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Statistical Methods

Statistical methods were conducted using R (R Core Team, 2022) and RStudio (RStudio Team, 2022). We used a general linear mixed effect model (GLMM) with Akaike information criterion (AIC) model selection to determine which variables best predicted porewater pH. To account for the repeated replicate points along each transect as well as the locations of the sites, we tested the individual random effects of replicates and reef sites, as well as the nested random effect of replicates and reef sites in the model selection. The best model used porewater pH as the response variable and the interactive effect between distance along the transect and treatment type as the predictors and used the random effect of replicates on the intercept. With the ggeffects package in RStudio (Ludecke, 2018), the ggpredict function was used to compare and plot model predictions for each site and further confirm that no specific site skewed the overall porewater pH values. To determine the pairwise comparisons between different treatments at each distance, a contrast matrix was created using the marginal effects package in RStudio (Arel-Bundock, 2022). The contrast matrix used a prediction hypothesis model, that allowed the model to predict comparisons for *A. germinans* at zero centimeters based on the other distance interval data collected for these mangroves. Comparisons in the contrast matrix were taken independently of each other. To reduce any Type I Error associated with this method, a sequential Bonferroni correction was applied to the p values from the contrast matrix.

RESULTS

Mangrove Metrics and Measurements

In total, 19 *R. mangle* and 8 *A. germinans* mangroves were included in the study. For each mangrove, there was one adjacent control site that consisted of oyster reef only (N = 27). The mean measurements for each mangrove treatment are listed in Table 1. All mangroves were determined to be adults of reproductive age due

Table 1.
Rhizophora mangle and *Avicennia germinans* Mean Measurements

Mangrove Metrics	*Rhizophora mangle*	*Avicennia germinans*
Height (m)	1.38 ± 0.07	1.9 ± 0.15
Canopy Circumference (m)	4.68 ± 0.47	11.32 ± 1.08
Trunk Circumference (cm)	22.58 ± 2.97	23.25 ± 3.33
Number of Above Ground Roots	32.00 ± 3.44	All had over 100 pneumatophores
Farthest Extending Above-Ground Roots from Trunk (cm)	73.00 ± 6.68	163.00 ± 38.87
Farthest Above-Ground Root along the Transect Line (cm)	44.00 ± 5.71	55.00 ± 5.11

Note: Average measurements ± standard error. N =19 for *R. mangle*, and N = 8 for *A. germinans.*

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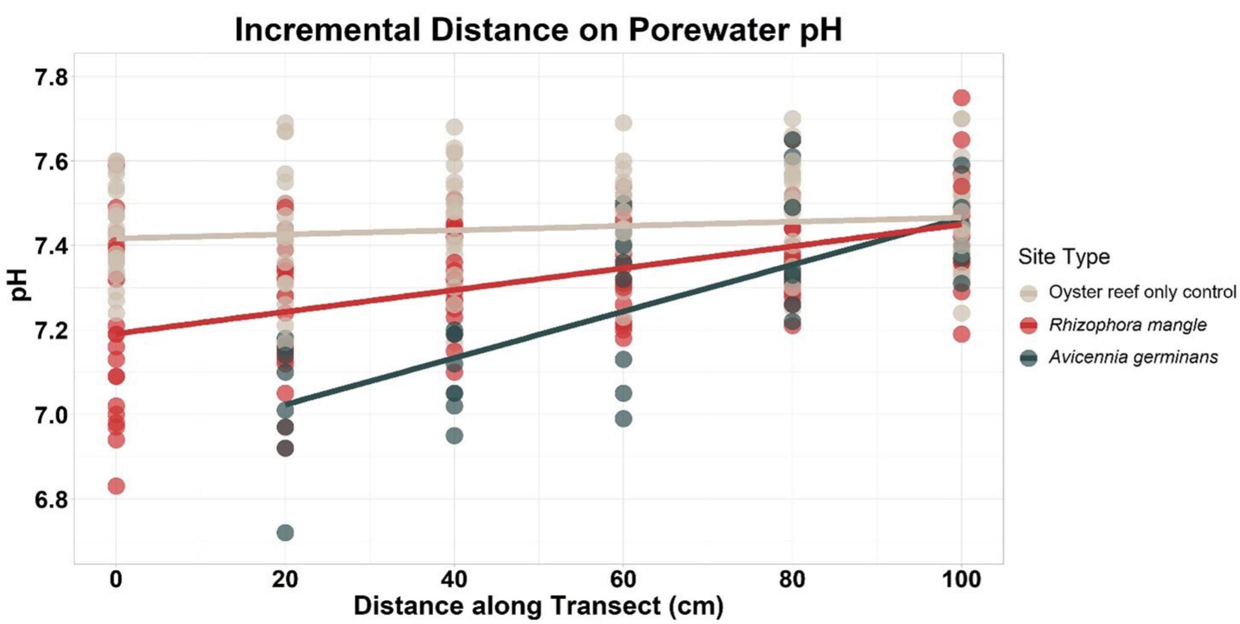
Table 2.
Average Distances for *Rhizophora mangle*, *Avicennia germinans*, and Oyster Reef Only Controls

Distances	*Rhizophora mangle*	*Avicennia germinans*	Control
Distance to Reef Edge (m)	8.24 ± 4.16	2.53 ± 0.61	3.89 ± 0.48
Distance to Nearest Mangrove Stand (m)	8.57 ± 2.48	20.19 ± 6.66	14.05 ± 2.84
Distance to Closest Single Mangrove (m)	2.66 ± 0.45	5.08 ± 2.01	7.83 ± 1.44

Note. Mean distances ± standard error. N = 19 for *R. mangle,* N = 8 for *A. germinans,* and N = 27 for controls.

Figure 2.
Porewater pH with Distance Plot



Note. Porewater pH values plotted with distance along the transect for each treatment. The linear regression line demonstrates the change in pH from 0 – 100 cm with increasing distance away from the mangrove trunk for pioneer *R. mangle* and *A. germinans*. N = 19 for *R. mangle*, N = 8 for *A. germinans*, N = 27 for controls. *A. germinans* were unable to be sampled at 0 cm due to pneumatophore density.

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to the presence of reproductive structures, including flowers and propagules. The mean pioneer *A. germinans* were taller, had more above-ground roots that extended farther away from the mangrove trunk, and had a larger canopy circumference than the mean pioneer *R. mangle* (Table 1). Furthermore, mean pioneer *A. germinans* were farther away from mangrove stands and other single mangroves on the oyster reef but were closer to the reef edge compared to both pioneer *R. mangle* and control treatments (Table 2).

Porewater pH Results

All sites had six pH samples collected at 20-centimeter intervals along the one meter transect, except for *A. germinans* which had five samples since the zero-centimeter distance was not able to be collected due to dense pneumatophores and underground roots. Porewater pH at the pioneer mangrove treatments changed with distance along the transect, extending away from mangrove trunk (Figure 2). The overall mean porewater pH for each treatment was 7.24 for the *A. germinans*, 7.32 for the *R. mangle*, and 7.44 for the oyster reef controls.

Distance had a significant effect on porewater pH ($z = 10.21$, $p < 0.001$), with pH values increasing (becoming less acidic) with increasing distance from a pioneer mangrove (Figure 2). The interaction between distance and treatment was also found to be significant ($z = -4.87$, $p < 0.001$). To understand where these significant differences with distance and treatment occurred, the contrast matrix was used to return p values to correspond with pairwise treatment comparisons for each distance. Comparisons between the treatments at each distance are shown in Table 3. At 0 centimeters along the transect

Table 3.
Pairwise Comparisons for each Treatment with Distance

Distance (cm)	Treatment Comparison	p value
0	Control vs. *R. mangle*	< 0.001
0	*R. mangle* vs. *A. germinans*	< 0.001
0	Control vs. *A. germinans*	< 0.001
20	Control vs. *R. mangle*	< 0.001
20	*R. mangle* vs. *A. germinans*	< 0.001
20	Control vs. *A. germinans*	< 0.001
40	Control vs. *R. mangle*	< 0.001
40	*R. mangle* vs. *A. germinans*	0.001
40	Control vs. *A. germinans*	< 0.001
60	Control vs. *R. mangle*	0.004
60	*R. mangle* vs. *A. germinans*	0.086
60	Control vs. *A. germinans*	< 0.001
80	Control vs. *R. mangle*	0.283
80	*R. mangle* vs. *A. germinans*	1.000
80	Control vs. *A. germinans*	0.086
100	Control vs. *R. mangle*	1.000
100	*R. mangle* vs. *A. germinans*	1.000
100	Control vs. *A. germinans*	1.000

Note. GLMM contrast matrix output for the pairwise comparisons of treatment at each distance along the transect; the p values were adjusted using sequential Bonferroni correction. N = 19 for *R. mangle*, N = 8 for *A. germinans*, N = 27 for oyster reef only controls.

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line, the closest distance to the mangrove trunk, all treatments were significantly different from each other ($p < 0.001$ for all). At 60 centimeters, pioneer *R. mangle* and *A. germinans* were no longer significantly different ($z = -2.51$, $p = 0.086$), but both were significantly more acidic than control sites ($z = -3.46$, $p = 0.004$ for *R. mangle*; and $z = -5.18$, $p < 0.001$ for *A. germinans*). All three treatments were similar at 80 cm ($p > 0.1$ for all), indicating that by this distance away from the trunk of a pioneer mangrove, at least 1-meter tall, porewater pH returns to a range typical to that of an oyster reef-only area.

DISCUSSION

Pioneer Mangrove Impact on Porewater pH

In recent decades mangroves have been expanding poleward and increasing in abundance on oyster reefs (McClenachan et al., 2021; Hesterberg et al., 2022). Oyster shells are prone to dissolution in acidic conditions and, as mangroves are drivers of sediment acidification, it is essential to quantify whether mangroves are acidifying oyster reef sediment (Waldbusser et al., 2011; Middelburg et al., 1996; Marchand et al., 2004; Harris et al., 2022). Our research found that pioneer mangroves (*Rhizophora mangle* and *Avicennia germinans*) can acidify surrounding oyster reef sediment extending 60 cm away from the mangrove trunk.

Based on the results, pioneer mangroves, at least one meter tall and of reproductive age, did contribute to acidification of oyster reef sediment. There was a negative correlation between acidity and distance from the mangrove trunk, where porewater in the sediment became more acidic with closer proximity to a pioneer mangrove. Pioneer mangroves of both species significantly reduced porewater pH at the mangrove trunk and extending up to 60 cm away, when compared to oyster reef only controls. This demonstrates that a single, pioneer mangrove can acidify oyster reef sediment, however this effect is localized.

There were key differences between *R. mangle* and *A. germinans* pioneer mangroves in this study. The predicted pairwise comparison demonstrated that porewater pH between the mangrove species was significantly different from 0 to 40 cm, with *A. germinans* having significantly lower pH values. These differences in pH may be related to differences in growth dynamics between *R. mangle* and *A. germinans*. In our study, *A. germinans* had larger canopy circumferences and had more above ground roots that extended farther from the trunk compared to *R. mangle* (Table 1). *A. germinans* also have a lower cold tolerance (≤ -6.6 ˚C) than *R. mangle* (≤ -4 ˚C) (Cavanaugh et al., 2014). The last major freeze event with temperatures around -4 ˚C in Mosquito Lagoon occurred in 1995 and caused a reduction in *R. mangle* mangrove abundance (McClenachan et al., 2021). These growth disparities between the mangrove species suggest *A. germinans* may be more established on oyster reefs, possibly having survived the last major freeze event. *A. germinans* larger canopy circumference likely contributes to greater leaf litter and organic matter decomposition driving increased carbonic acid input to the reef surface (Aller, 1982). Additionally, the abundance and extent of *A. germinans* pneumatophores could support greater amounts of gas exchange and oxidation below ground, compared to *R. mangle*, that could acidify the rhizosphere (Thibodeau & Nickerson, 1986).

Impact to Oyster Reefs

As pioneer mangroves continue to grow and tropicalization allows for new mangrove recruitment to oyster reefs each year following propagule release, the impact of mangrove-driven acidification will increase and may have vast implications for oyster reef habitats. Oyster shells are prone to increased dissolution rates in a pH around 7.2 and lower (Waldbusser et al., 2011). In this study, many porewater pH values fell below 7.2 within 60 cm of the mangrove trunks, including the lowest pH value of 6.72 under pioneer *A. germinans* (Figure 2). These values indicate that mangroves may contribute to faster oyster shell dissolution. Increased acidity on oyster reefs prevents oysters from forming shells and weakens already formed shells (Waldbusser et al., 2011; Keppel et al., 2016; Beniash et al., 2010). Localized mangrove-driven acidification could lead to shell dissolution and may increase the degradation of oyster reef habitats.

Mangrove roots are a driving force in sediment acidification, as roots promote oxidation reactions in the soil that leads to acidic conditions (Thibodeau & Nickerson, 1986; Middelburg et al., 1996). Along the transect line where porewater pH was sampled, mangrove aboveground roots extended out to an average of 44 cm for *R. mangle* prop roots and 55 cm for *A. germinans* pneumatophores. These distances correspond to the pairwise pH comparisons, where within 60 cm of the mangrove trunk porewater is significantly more acidic than oyster reef control area. As these mangroves grow, increased mangrove root density and root spatial extent

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could enlarge mangroves' acidification impact (Thibodeau & Nickerson, 1986).

Additionally, increased mangrove abundance on oyster reefs will likely result in more organic matter present in the form of leaf litter. This organic matter can lead to an additional release of carbonic acid to oyster reef sediment (Reef et al., 2010; Twilley et al., 1992; Sabine et al., 2004). A study in the Southern Caribbean found that leaf litter and wood remaining after *A. germinans* logging, promoted porewater acidification as the organic matter decomposed. This acidification effect led to a significant increase in shell corrosion for a species of gastropod in the area (Amortegui-Torres et al., 2013). Higher amounts of organic matter from mangrove leaf litter on oyster reefs may lead to further dissolution and corrosion of oyster shells.

Further Impacts of Mangrove Expansion

All mangroves in this study were adults of reproductive age; however, mangrove height was below two meters for all trees indicating that the trees were still young and will continue to grow. Growth of the mangroves can lead to increased sediment stabilization, salt excretion, and below-ground gas exchange creating a more suitable habitat for other mangroves (Srikanth et al., 2015). Based on the biogeomorphic succession model, mangroves in this study are in the "pioneer phase" as the first recruits to a new habitat (Corenblit et al., 2015). This model describes the process of physical and biological transition that occurs as plants colonize new areas. Over multiple decades established pioneer mangroves will create ideal conditions for additional mangrove recruitment and lead to the "ecological phase" of the model where the habitat has been changed completely to a mangrove stand. Furthermore, in low nutrient, calcareous soils, plants actively acidify the soil via root exudates to promote better nutrient uptake (Dakora and Phillips, 2002). As oyster shells are made of calcium carbonate, reef sediment is likely calcareous in nature promoting mangrove-driven acidification. Over time, mangrove acidification will create more ideal soil conditions for new mangrove recruitment further lending to the biogeomorphic succession model (Corenblit et al., 2015). As more pioneer mangroves begin to expand onto oyster reefs, their collective release of acids into the sediment will have a significant impact on the overall pH of the reef.

Oysters are a keystone species that provide multiple significant ecosystem services (Keppel et al., 2016). The surrounding estuarine ecosystem may drastically change if mangroves replace oyster reef habitats. Species that require oyster reefs for food, habitat, protection, and attachment substrate would be impacted the most. As filter feeders, oysters improve local water quality and clarity allowing for sunlight to reach submerged aquatic vegetation, such as seagrass beds (Grabowski et al., 2012). Therefore, other coastal habitat types may diminish along with oyster reef decline. Poor water quality also decreases predator populations and causes increased populations of lower trophic species, impacting the overall food web (Qiang & Silliman, 2019). Various ecological functions, biodiversity, and food web disturbances may occur as more temperate species that inhabit oyster reefs are impacted by tropicalization and increased mangrove abundance (Aquino-Thomas et al., 2014).

Future Directions

As habitats transition due to tropicalization, it will be important to document the associated impacts of these shifts. Research is needed to understand if mangrove-driven acidification is actively causing oyster shell dissolution and to predict rates of mangrove expansion to farther poleward oyster reefs in the decades to come. Installing trail cameras on oyster reefs with mangrove presence could provide insight into how biodiversity is impacted on these reefs. In addition, understanding how oysters' attachment to *R. mangle* prop roots affect the abundance, physiology, and viability of both mangroves and oysters is essential to understanding how this will impact the distributions of these species in the future. Lastly, oyster reef restoration plays a vital role in re-establishing oyster reef functionality in Mosquito Lagoon and many other locations (Walters et al., 2020; Grabowski and Peterson, 2007). Mangrove expansion has the potential to greatly impact restoration projects. Research is needed to determine if removing mangrove propagules from restored reefs is worthwhile to prevent mangrove expansion at these sites to allow restored reefs to become established.

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CONCLUSION

Based on its geographic location, Mosquito Lagoon is one of the first points of contact between temperate and subtropical species impacted by tropicalization (St. Johns River Water Management, 2007). Studying habitat transitions in this area may help predict future global habitat shifts that will become more common with the progression of climate change.

Due to tropicalization, mangroves have been expanding onto oyster reef habitats, with potentially negative effects for oysters (McClenachan et al., 2021; Hesterberg et al., 2022). Oyster reefs are threatened globally by multiple factors and understanding how mangrove expansion plays a role in reef degradation is key to developing productive restoration efforts to protect and conserve oyster reefs. Our data determined that pioneer *R. mangle* and *A. germinans* significantly acidify oyster reef sediment from 0 to 60 cm near the base of the trees. The acidic conditions observed in our research warrants cause for concern. Low sediment pH can increase the risk of oyster shell dissolution and may harm oysters' viability, reproductive success, and population abundance, posing a direct threat to the surrounding ecosystem. This study provides necessary insight as to how individual, pioneer mangroves impact oyster reefs and can be used to improve conservation of all these important species.

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