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Red mangrove (*Rhizophora mangle*) roots serve as additional valuable habitat for the eastern oyster (*Crassostrea virginica*) in a subtropical estuary

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ARTICLE INFO	A B S T R A C T				
Keywords: Bivalve Facilitation Intertidal Predation Seascape Coexistence	Occasionally, two foundation species co-exist within seascapes, where one is nested within, or near, the other. However, we often lack an understanding of interactions between co-existing foundation species and how such interactions may affect their demographic rates. Oysters and mangroves are foundation species that often co- occur in subtropical estuaries, with oysters assembled into reefs found near mangrove-rimmed shorelines or oysters growing attached to mangrove prop roots. We evaluated demographics and potential ecological mech- anisms affecting eastern oysters (<i>Crassostrea virginica</i>) living on intertidal reefs compared with those growing on red mangrove roots (<i>Rhizophora mangle</i>) using a series of field surveys and by measuring evaporation rates as proxy for desiccation. We found that total oyster density on mangrove roots was over two times higher per unit sample area compared to intertidal reefs. This difference occurred despite slightly higher oyster settlement rates to reefs than mangrove roots, suggesting higher post-settlement mortality in reefs compared to roots. Higher oysters and greater abiotic stress on oysters on reefs versus mangrove root habitats. The comparative demog- raphy of oysters on reefs and mangrove roots provides insight into mechanisms by which mangrove roots represent valuable habitats for eastern oysters. Moreover, these findings suggest that future oyster restoration efforts may benefit by considering restoring oyster reefs in close proximity to red mangroves given their addi- tional source of potential ovster settlers.				

1. Introduction

Foundation species create habitats that can influence communities in multiple ways (Bertness and Callaway, 1994; Stachowicz, 2001; Ellison et al., 2005; Angelini et al., 2011). For example, the habitat created by foundation species can serve as shelter, modify abiotic factors, or provide substrate for settlement, all of which may influence biodiversity, complexity of food webs, predator-prey interactions, and/or ecosystem productivity (Dayton, 1972; Bruno and Bertness, 2001; Aquino-Thomas and Proffit, 2014). In some cases, two foundation species can co-exist, where one is nested within or in close proximity to the other (Bruno and Bertness, 2001; Angelini et al., 2011; Bishop et al., 2012). However, we often lack an understanding of how co-existing foundation species interact with each other and how such interactions may affect demographic rates of these species. Understanding the dynamics of co-existing foundation species and the mechanisms that influence

abundance has the capacity to broaden our understanding of interhabitat relationships and may improve our ability to protect or restore habitats and associated biodiversity in the face global climate change (Bishop et al., 2009).

Oysters and mangroves are two foundation species that occupy intertidal zones and can co-occur, although species coexistence is not obligate. In selected subtropical settings, oyster reefs are found in close proximity to mangrove-rimmed shorelines within estuarine seascapes. In the subtropical and tropical western Atlantic region, eastern oysters (*Crassostrea virginica*) and both red and black mangroves (*Rhizophora mangle* and *Avicennia germinans*, respectively) often co-occur along an intertidal stress gradient (Aquino-Thomas and Proffit, 2014; Chacin, 2019). Studies often focus on oyster reefs because they are the predominant oyster habitat, however some effort has been directed at oysters when they are epibiont on mangrove roots (Drexler et al., 2014). In Australia, oysters associate with mangrove (*Avicennia marina*)

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pneumatophores, which trap fucoid algae and provide settlement substrate for the oyster, *Saccostrea glomerata* (Bishop et al., 2012). Although oysters and mangroves form important habitats for many taxa and perform a variety of ecological roles (Krauss et al., 2008; Booth and Heck Jr., 2009; North et al., 2010), there remains limited understanding of the interactions between these two foundation species, including the demographic consequences for oysters growing on a reef versus mangrove root habitat.

Factors that affect oyster population establishment and growth in reef versus mangrove settings may markedly differ. For example, when oyster reefs are adjacent to mangroves, oyster predators may use the mangrove root structures as refugia thereby enhancing their safe access to benthically-attached oyster prey (Aquino-Thomas and Proffit, 2014; Chacin, 2019). Conversely, oysters suspended on mangrove roots unattached to the benthic substrate may experience less gastropod predation (e.g. Pusack et al., 2018) or have higher survival or stability due to protection from sedimentation or storms (Schutte and Byers, 2017; Colden and Lipcius, 2015; Aquino-Thomas and Proffit, 2014). Oysters on mangrove prop roots may experience lower desiccation stress than those on reefs due to shading by the mangrove canopy. Shading by mangrove canopy may reduce internal temperatures in oysters and allow them to retain more moisture relative to ovsters on reefs, which are fully exposed to the sun. Similarly, depending upon the sampling design, higher abundances of oysters have been observed on mangroves roots when compared to oysters on reefs (Drexler et al., 2014). Despite the documented positive associations between oysters and mangroves, not all mangroves in estuarine systems host oyster epibionts on their roots. This raises the question of whether certain mechanisms could render some mangroves unsuitable as ovster habitat. Much remains unknown but, our study aimed to further investigate the oyster-mangrove relationship and gain insights into potential mechanisms such as predation, settlement, and water loss, which could contribute to these associations.

We compared and contrasted oysters growing on intertidal reefs with those living as epibionts on mangrove roots using field surveys and a field experiment. We asked: 1) Do the densities of oysters differ between those on reefs versus mangrove prop roots?, 2) Does oyster settlement differ between the two habitats?, and 3) Are there any abiotic (i.e., evaporation rates) and biotic factors (i.e., predator abundance) that may affect oyster demography on the two habitats? We focused this study in the eastern Gulf of Mexico, where the eastern oysters have experienced severe population declines and mangroves are undergoing poleward expansion in distribution (Snyder et al., 2021). This location presents a useful model system for examining interactions between two foundation species that are important habitats for many other marine organisms of ecological and economic importance (Searles et al., 2022; Grabowski and Peterson, 2007; Hutchison et al., 2014; Peters et al., 2015).

2. Methodology

2.1. Study organisms

The eastern oyster inhabits estuarine and coastal habitats along the east coast of North and South America from the Gulf of St. Lawrence to southern Florida, throughout the Gulf of Mexico and Caribbean to the Yucatan Peninsula of Mexico, and along the coasts of Venezuela, Brazil, and Argentina (Galtsoff, 1964; NOAA Fisheries Eastern Oyster Biological Review Team, 2007). A variety of ecological services and economic benefits are offered by the eastern oyster including provision of food and habitats for many estuarine organisms, nutrient transfer between the benthos and the water column, erosion reduction, shoreline stabilization, and water quality improvement (Bahr and Lanier, 1981; Lenihan and Peterson, 1998; Beck et al., 2011). Before Europeans arrived in North America, the eastern oyster was harvested for consumption (MacKenzie et al., 1997) and it continues to support commercial and recreational fisheries along the Gulf and Atlantic coasts of the United States (Drexler et al., 2014).

Red mangroves occur in estuarine systems throughout the tropics and subtropics, can form very productive forests in the intertidal zone, and support diverse assemblages of organisms (Rodriguez and Stoner, 1990; Torres-Pratts and Schizas, 2007; Tunnell and Withers, 2009; Peters et al., 2015). Aerial prop roots (or stilt roots) originate from the trunk or branches of the red mangrove and extend towards the sediment surface. Ramification of mangrove prop roots produces a structurally complex arching system (Gill and Tomlinson, 1971; Brooks and Bell, 2002). This complex set of roots provides extra support for the mangrove, additional access to oxygen in anoxic sediments, and offers substrate for sessile epibenthos such as sponges, mussels, algae, tunicates, anemones, and barnacles. The eastern oyster is found attached to prop roots in selected estuarine areas, often where oyster reefs co-occur (Odum et al., 1982; Krauss et al., 2008; Aquino-Thomas and Proffit, 2014).

2.2. Study sites

We conducted this study in Tampa Bay, Florida, USA (Fig. 1), a large estuary with a mean depth of <5 m and a surface area of ~1000 km² (Chen et al., 2007). We selected three study sites (Upper Tampa Bay Park, Clam Bayou, and Ft. De Soto State Park) that contained both oyster epibionts on mangrove prop roots and oyster reefs. This scenario presented the ideal seascape composition to examine how the demographics of one foundation species (oysters) was influenced by the coexistence of another (mangroves), in both nested (oysters growing on prop roots) and in close proximity contexts (oyster growing on reefs nearby mangroves within 5–10 m).

2.3. Oyster demography and predators

On reefs, we measured the density of oysters at each site within 0.25 m^2 quadrats. We selected three tidal zones within oyster reefs to examine patterns of oyster zonation in June through November 2018. We sampled at the top zone on the crest of the reef above mean water level, at the middle zone found in the slope of the reef (half-way distance between top and bottom) approximately at mean water level, and at the bottom edge of the reef, which was the area at which the oyster cover became sparse (below mean water level). In each quadrat, we excavated oysters to a depth at which no live oysters were found, collected all oysters, and counted them in the laboratory.

To measure the density of oysters on an equivalent surface area on mangrove prop roots at each of the three sampling sites, we approximated the curved surface area of a cylinder:

surface area = $2\pi r \times h$

where 'r' is the radius ($\sim 2 \text{ cm} = 0.02 \text{ m}$) and 'h' is the height (31.5 cm = 0.315 m) of prop root sampled. We selected 6 prop roots of ~4 cm diameter of the same mangrove to reach the $\sim 0.24 \text{ m}^2$ per sample (Fig. 2). The height of 31.5 cm was decided based upon preliminary random surveys where we measured the lengths (cm) of 21 prop roots covered by oysters from the lowest to the highest point, relative to tidal elevation. Based on the mean length 29.6 \pm 1.4 cm (\pm standard error), we designated the extent of the intertidal habitat to be surveyed for oyster abundance along root surfaces to be 31.5 cm. Furthermore, within the targeted intertidal area of mangrove prop roots as identified from preliminary analyses (above), we established three subzones of equal length within the 31.5 cm intertidal section of each root: bottom, middle, and top, representing 10.5 cm height increments. Next, we quantified the density of oysters along each intertidal section of the 6 prop roots of the same mangrove tree. Each survey selected a different mangrove tree. In total, 11 mangroves and 9 reefs were surveyed across study sites.

In each survey (reef quadrat or prop roots), we quantified spat (< 25 mm in shell height) as well as seed and adults (≥ 25 mm in shell height),



Fig. 1. Map of Tampa Bay with the three study sites indicated by the stars.



Fig. 2. Sampling design used to quantify oyster density in the two intertidal habitats. We measured the density of oysters at each site within 0.25 m² quadrats. We selected three tidal zones within oyster reefs to examine patterns of oyster zonation. To measure the density of oysters on an equivalent area on mangrove prop roots at each of the three sampling sites, we approximated the curved surface area of a cylinder: surface area $= 2\pi r \times h$, where '*r*' is the radius ($\sim 2 \text{ cm} = 0.02 \text{ m}$) and '*h*' is the height (31.5 cm = 0.315 m) of prop root sampled. We selected 6 prop roots of $\sim 4 \text{ cm}$ diameter of the same mangrove to reach the $\sim 0.24 \text{ m}^2$ per sample. Within the targeted intertidal area of mangrove prop roots as identified from preliminary analyses (see methods for more details), we established three subzones of equal length within the 31.5 cm intertidal section of each root: bottom, middle, and top, representing 10.5 cm height increments. Next, we quantified the density of oysters along each intertidal section of the 6 prop roots of the same mangrove tree.

which allowed us to calculate the total number of oysters (spat + seed and adults). We estimated oyster mortality of collected individuals within each sample by counting the number of gaping shells; i.e., two valves still attached at the hinge, open and with no remaining tissue (Ford et al., 2006; Jordan, 1995). We also enumerated all xanthid crabs (*Panopeus* spp.) and crown conchs (*Melongena corona*), important predators of oysters (Kimbro et al., 2017), encountered within each collected oyster sample.

We also deployed seventy-two clean and bare ceramic tiles (116.6 cm²) across both habitat types and intertidal zones (bottom, middle, top) in each of the three study sites to quantify settlement and survival of oyster settlers during the spawning season May–July 2018 (Bahr and Lanier, 1981; Burrell, 1986). We placed the tiles on six roots and six reefs in the middle zone at all three study sites (n = 36). Due to logistical constraints such as limited field assistance and length of tidal cycles, the conditions allowed for limited amount of work, thus we were able to deploy only three tiles to each of the bottom (n = 18) and top intertidal zones (n = 18) at the study sites. We then counted all oyster settlers on the ceramic tiles one-month post-deployment.

To quantify oyster settler survival, we deployed seventy-two additional clean tiles in the same design as the settlement tiles above at the three study sites. After a month of deployment, we removed and blotdried the tiles and circled the first five oysters counted clockwise that had settled on the tile with a permanent black marker. For logistical reasons, we limited the number of tracked oysters to five per tile. Any additional oysters were removed from the tiles. We then redeployed the tiles for another month, after which we quantified survivorship of marked individuals. We calculated survival as the proportion of settlers alive out of the total initially marked over the one-month period. Any new settlers during the second month of deployment were not included in this analysis.

In addition to predation, desiccation stress is an important abiotic mechanism of mortality in intertidal systems (Foster, 1971; Hamilton and Gosselin, 2020) and may affect oysters differently depending on the habitat settings they grow (Fig. 3). To examine this potential mechanism, we conducted an experiment to test whether evaporative water loss differed between the area under the canopy of red mangroves versus oyster reefs at low tide. We placed 10×15 cm semitransparent white mesh bags filled with 10 g of vermiculite in both habitat types during February (Funo et al., 2019). We placed 15 bags on the top intertidal zone on mangrove prop roots and 15 on the top of oyster reefs (3 bags \times 5 reefs) for 2.5 h during low tide. During deployment, bags were completely exposed with no risk of being splashed by waves and no precipitation occurred during the experiment. Prior to the initiation of the experiment, we submerged all the bags in seawater until reaching a constant weight (g), and weighed each bag immediately before they



Fig. 3. Average density \pm standard error of seed and adult, juvenile (spat), and total oysters on oyster reefs and mangrove prop roots. Sites were sampled from June through November 2018. Densities on mangrove prop roots were for all observed oysters, including those that became dislodged during sampling.

were placed onto prop root or reef. After the experimental period, we transferred each semitransparent bag to a second plastic bag that we sealed and stored in a dark cooler and weighed again upon return to land.

2.3.1. Challenges in measuring and comparing oyster densities

We encountered several challenges with the methods we used to approximate equivalent areas between habitats. We conducted oyster density sampling at three intertidal zones by subdividing the mangroves roots into smaller areas, leading to unequal sampling areas compared to those in reef intertidal zones. Thus, although we compared oyster densities between these two habitats, it would be inappropriate to do so at the habitat*intertidal zones level. Instead, we cautiously focused on broader patterns.

Additionally, we faced difficulties when transporting samples of prop roots with oysters to the lab for quantification. All prop roots from the same sample were placed in a mesh bag, during which some oysters became dislodged from the roots, making it impossible to assign them to a specific intertidal zone. Across samples, the mean (standard error) proportion ovsters that became dislodged were 0.18 (0.03) for juveniles, 0.24 (0.03) for adults, and 0.20 (0.03) for the combined size classes. We assumed that this effect occurred consistently across our sampling of mangrove prop roots. Although these dislodged oysters were included in the habitat-level calculations, they were excluded from the intertidal zone-level calculations and as such a discrepancy of oyster densities was observed between the habitat level and intertidal zones. Moreover, while we refined our oyster sampling methodology on prop roots, sampling was initiated in oyster reefs, thus resulting in a time lag between habitat types in our survey timeline. We recognize that this discrepancy and methodological challenges may have influenced our results. To address these limitations, we recommend that future studies further refine methods to enable consistent sampling of oysters across both habitats at multiple time points throughout the year. This approach would help capture seasonal and temporal variations more accurately, enhancing comparability between habitats.

2.4. Statistical analyses

We compared oyster densities between habitat types and across intertidal zones using generalized linear mixed models (GLMMs). We ran separate models for the densities of spat, seed and adult (combined), and total oysters as response variables. For all three models, habitat type (reefs and roots) and intertidal zones (bottom, middle, and top) were fixed effects and site was included as a random effect. Although we did not consider site as a variable of interest in this study, we included it as a random factor to control for variability introduced by sampling in different sites of Tampa Bay (Chacin et al., 2016). We used a quasi-Poisson distribution for the non-integer data and conducted the models using the *MASS* package (Venables and Ripley, 2002) in the *R* statistical environment (R Core Team, 2021).

We conducted three additional analyses to better understand potential mechanisms that could explain the observed oyster densities. We compared differences in number of gaping oyster shells, across habitat types using permutation-based, non-parametric t-tests and across intertidal zones (three levels) using permutation-based, non-parametric analysis of variances (np-ANOVAs) in MATLAB and the Fathom toolbox (Jones, 2017; permutations = 1000). We conducted similar analyses for predator densities as well as settler survival across habitats and intertidal zones. Pairwise comparisons were included for the tests involving intertidal zones. We verified homogeneity of dispersion with the function np-disp, which is equivalent to Levene's test (Anderson, 2006), and, when needed, we square-root transformed the data. All statistical tests were conducted using a significance threshold (α) of 0.05. Recognizing that ecological significance may not always align with statistical significance given the high natural variability and complexity of ecological data and that in field-based ecological studies sample sizes are limited by logistical constraints, we also considered for interpretation results with *p*-values approaching, but not exceeding, 0.085 (Martinez-Abrain, 2008; Smith, 2020). Using a slightly higher alpha can make statistical tests more sensitive to weak but potentially meaningful effects that would otherwise be missed and can also help to counteract the reduced statistical power associated with small sample sizes. These near-significant values were examined for their potential influence on the observed ecological patterns. Lastly, we calculated the differences in bag weights in the evaporative water loss experiment (weight (g) at beginning – weight (g) at conclusion) to derive estimates of percent water loss/2.5 h. We then compared these estimates using non-parametric *t*-tests.

3. Results

Using different methodologies to sample oysters in two intertidal habitats, we found that total oyster density was 67 % higher on mangrove prop roots than on oyster reefs ($t_{34} = 6.06$, p < 0.001) and these results were consistent for spat ($t_{34} = 7.44$, p < 0.001) and seed and adults ($t_{34} = 2.97$, p < 0.001, Fig. 3). On reefs, the densities of spat did not differ from seed or adults ($t_{51} = 0.46$, p = 0.88). On prop roots, the density of spat was 57 % higher than seed and adults ($t_{21} = 5.02$, p = 0.001).

Within-habitats, oyster density varied across intertidal zones, but in different ways between reefs and roots. The total, spat, and seed plus adult densities on reefs were similar between the middle and top zones, and both supported higher oyster densities than the bottom zone (Table 1; Fig. 4A). In comparison, the density of total oysters on prop roots was significantly higher in the middle intertidal zone compared to the bottom and top zones, which did not differ from each other (Table 1; Fig. 4B). These patterns were consistent for both spat and seed plus adult oyster densities on roots (Table 1; Fig. 4B).

The percentage (\pm SE) of gaping oysters, indicative of mortality, was over two times higher on oyster reefs (15.6 \pm 3.0 %) than mangrove

Table 1

Model summaries of the relationships between oyster densities and intertidal zones on mangrove prop roots and on oyster reefs. Significant p values are bolded.

Intertidal zone	Coefficient	Standard error	DF	t	р
Oyster reefs					
Total oyster density					
Bottom (Intercept)	4.89	0.28	22	17.26	< 0.001
Middle	1.10	0.21	22	5.10	< 0.001
Тор	1.22	0.21	22	5.74	< 0.001
Juvenile (spat) oyster					
density					
Bottom (Intercept)	4.25	0.34	22	12.53	< 0.001
Middle	0.99	0.25	22	4.00	< 0.001
Тор	1.18	0.24	22	4.92	< 0.001
Seed and adult oyster					
density					
Bottom (Intercept)	4.10	0.33	22	12.27	< 0.001
Middle	1.22	0.27	22	4.44	< 0.001
Тор	1.27	0.27	22	4.63	< 0.001
Mangroves					
Total oyster density					
Bottom (Intercept)	5.36	0.15	28	35.77	< 0.0001
Middle	0.51	0.19	28	2.74	0.01
Тор	-0.29	0.22	28	-1.28	0.21
Juvenile (spat) oyster					
density					
Bottom (Intercept)	5.03	0.17	28	30.13	< 0.0001
Middle	0.51	0.21	28	2.44	0.02
Тор	-0.19	0.25	28	-0.75	0.45
Seed and adult oyster					
density					
Bottom (Intercept)	4.26	0.15	28	28.35	< 0.0001
Middle	0.46	0.19	28	2.42	0.02
Тор	-0.54	0.24	28	-2.19	0.03

prop roots (6.6 ± 0.9 %; $t_{36} = 3.06$, p = 0.02; Fig. 5). The percentage of gaping oysters on reefs was similar among the intertidal zones ($F_{2, 24} = 2.20$, p = 0.09). We observed the highest mortality at the bottom zone, consistent with lowest densities of oysters observed among reef intertidal zones (Fig. 4A). Although not significant at the alpha 0.05 level, the probability that there were no differences in mortality across intertidal zones on mangrove prop roots was very low ($F_{2, 30} = 2.15$, p = 0.06). The percentage of gaping oysters on roots was higher in the middle (~ 8 %) compared to the top zone (~ 4 %; $t_{21} = 1.68$, p = 0.042), and similar between the bottom and middle zones ($t_{21} = 0.27$, p = 0.92;). The probability that mortality did not differ between the bottom and top of prop roots was also low ($t_{21} = 1.58$, p = 0.07).

There was a suggestive evidence that the number of oyster settlers differed between reef and root habitats ($t_{68} = 3.38$, p = 0.06; Table 2). Settlement was higher on the bottom and middle zones compared to the top in both mangrove and reef habitats (Table 2, Fig. 6). Likewise, following one-month post-settlement, there was suggestive evidence that overall survivorship of these oyster settlers was higher in mangrove prop roots versus oyster reefs ($t_{42} = 1.77$, p = 0.08), but this difference was mainly driven by settler survival in the top zone of mangrove prop roots being approximately three times higher than that on reefs (t = 2.95, p = 0.02; Fig. 7). Survival of oyster settlers did not differ among zones for either habitat (all p > 0.05).

The density (mean \pm SE) of xanthid crabs did not differ between habitats (mangroves = 31 \pm 6 crabs/0.25 m², reefs = 43 \pm 5 xanthid crabs /0.25 m²; $t_{36} = 1.21$, p = 0.22), nor among the intertidal zones on reefs (bottom = 35 \pm 6, middle = 57 \pm 9, top = 35 \pm 8; $F_{2, 24} = 2.18$, p = 0.08). The density of crown conchs on oyster reefs was 0.7 conchs /0.25 m² (\pm 0.2) and did not differ among intertidal zones ($F_{2, 24} = 1.09$, p = 0.388). Crown conchs were not present on the mangrove prop roots sampled.

The percentage of water loss from experimental bags was lower underneath the canopy on the mangrove prop roots (13.02 \pm 0.67 %) compared to the top of reefs (22.26 \pm 0.94 %; *t* = 7.87, *p* = 0.001).

4. Discussion

Through a combination of field surveys and water evaporative loss measurements, we observed notable differences in eastern oyster demography between oysters on intertidal reefs and those living as epibionts on mangrove prop roots. We recognize that the structural differences between these two habitats made it difficult to standardize the sampled areas and timing of sampling, which necessitates caution in interpreting the results due to methodological differences. Despite these limitations, we observed that total oyster density was over two times higher per unit sample area on mangrove root habitats compared to intertidal reefs. This difference in density occurred despite 30-40 % higher settlement rates to reefs, indicating that post-settlement mortality was greater in oyster reefs compared to mangrove prop roots. Higher post-settlement mortality on reefs was consistent with our observations of more predators (xanthid crabs and crown conchs), higher percentage of gaping oysters, and greater abiotic stress on reef compared to mangrove root habitats. The results of this study suggest that mangroves roots can serve as additional valuable habitats for the eastern oyster.

The densities of both oyster spat, and seed plus adult were higher on red mangrove prop roots than on oyster reefs despite the 30–40 % higher supply of larval settlement recorded on tiles on intertidal oyster reefs. Although not statistically significant at the 0.05 alpha level, short-term survival was highly variable and appeared to be more than twice as high on both the bottom and top of mangrove roots compared to oysters reefs, which may contribute to the higher oyster densities observed on mangroves. Other studies have suggested that oyster larvae may select substrates shaded by mangroves for settlement as higher densities of larvae have been observed in mangrove roots compared to other nonshaded larval collectors (Funo et al., 2019). Greater total abundance of oysters on mangrove roots were largely a result of higher numbers of



Fig. 4. Average density \pm standard error of total (juveniles + seed and adults), juveniles (spat), and seed and adult oyster density per sample across intertidal zones (bottom, middle, top) on oyster reefs (A) and mangrove prop roots (B). Note that because we were unable to assign intertidal zones to oysters that became dislodged from mangrove prop roots during sampling, the densities used in the right panel (B) include only those that remained intact. Thus, the densities displayed for intertidal zones on mangrove prop roots are necessarily lower than those presented in Fig. 3.



Fig. 5. Percentage of gaping oysters (\pm standard error) in the two different habitats.

Table 2

Model summaries of the relationships between oyster settlement and intertidal zones on mangrove prop roots and on oyster reefs.

Habitat	Coefficient	Standard Error	DF	t	р	
Oyster settlement						
Mangroves (Intercept)	2.50	0.74	68	3.38	0.001	
Reefs	0.38	0.20	68	1.89	0.06	
Oyster settlement reefs						
Bottom (Intercept)	3.23	0.75	31	4.32	< 0.001	
Middle	-0.24	0.25	31	-0.99	0.33	
Тор	-1.08	0.38	31	-2.82	0.008	
Oyster settlement						
mangroves						
Bottom (Intercept)	2.92	0.73	31	3.98	< 0.001	
Middle	-0.19	0.33	31	-0.58	0.57	
Тор	-1.42	0.60	31	-2.38	0.02	

seed and adults at middle and top survey locations on roots compared to reefs. Post-settlement mortality in benthic marine communities can be influenced by predation, competition for space, parasites and in the case of intertidal habitats, abiotic stress (e.g., Dayton, 1971; Paine, 1974; Bertness and Hacker, 1994; Bruno and Bertness, 2001; Alberti et al., 2010; Batchelor et al., 2023). Studies that target oyster survivorship of subadults on both reefs and roots, especially across depths, are logical follow-ups to elucidate further any contrasting demographic patterns



Fig. 6. Number of oyster settlers (\pm standard error) on the settlement tiles in the two different habitats and across intertidal zones (bottom, middle, and top).



Fig. 7. Survival of oyster recruits \pm standard error on the settlement tiles at different intertidal zones (bottom, middle, and top) on oyster reefs and mangrove prop roots. Only settler's survival was significantly higher at the top intertidal zone in mangroves compared to reefs as indicated by asterisk.

between habitats.

We observed some differences in predator abundance between reefs and roots. The crown conch, one of south Florida's predominant oyster predators (Wilber and Herrnkind, 1982; Garland and Kimbro, 2015),

was absent in our prop root oyster samples, but present on oyster reefs, representing a source of mortality dependent on habitat (e.g. Chamberlain et al., 2014; Carroll et al., 2015; Chacin and Stallings, 2016; Booth et al., 2018). Xanthid crab predator densities did not differ significantly between reef and mangrove root habitats. However, xanthid crabs were on average, 10 % more abundant on oyster reefs compared to mangrove prop roots, which may have influenced oyster survival rates on reefs (Pusack et al., 2018). Given that xanthid crab size is crucial in assessing their potential of being oyster consumers (Bisker and Castagna, 1987), we encourage future research focus on measuring size variations to determine if they vary between reefs and oyster epibionts on mangroves. These predator abundance patterns may have been related to habitat structural differences between the prop roots and reefs. For instance, the structural complexity created by the prop roots may have reduced foraging efficiency of predators or hindered predator access to oyster epibionts, thus contributing to higher abundance of oysters on mangroves. Habitat complexity has been shown to influence predation in many soft (salt marsh; Eggleston et al., 1992; seagrass; Heck Jr and Wetstone, 1977, Horinouchi, 2007; Chacin and Stallings, 2016) and hard benthic environments (coral reefs; Graham et al., 2009; Hines et al., 1990; Seitz et al., 2001; Stoner, 2009; ovster reefs; Grabowski and Powers, 2004; artificial reefs; Wall and Stallings, 2018) and it may have played a similar role in our study system. Lastly, a suite of predators that was not quantified in our survey such as birds (e.g., oyster catcher; Brush et al., 2017) and fishes (e.g., sheepshead) may also feed disproportionately more on oysters on intertidal reefs than on mangrove roots, leading to higher mortality in accessible reefs.

Our finding of higher density of oysters on prop roots compared to reefs is consistent with other studies in the region. Drexler et al. (2014) reported higher density of oysters on mangrove prop roots than on reefs in Tampa Bay. Similarly, oysters were more abundant on prop roots than on oyster clumps found on the benthos in the Indian River Lagoon, Florida (Aquino-Thomas and Proffit, 2014). Our results differed substantially (in terms of magnitude) from these other studies, which could be attributed to differences in methods. We found oyster densities on prop roots to be approximately twice (922 oysters per 0.25m²) that observed by Drexler et al. (2014) and nearly five times that reported by Aquino-Thomas and Proffit, 2014; (187.5 oysters per 0.25 m²). Thus, at the local scale, a consistent pattern existed of higher densities of oysters on mangrove roots than on reefs or ground oyster clumps, and at broader scales, high differences in oyster abundance were observed. Yet, given that mangrove roots can serve as habitats for oysters, additional studies are needed to better understand their contribution to population dynamics, ecological processes, and ecosystem services.

We experimentally recorded less water evaporation on mangrove roots compared to oyster reefs, suggesting oysters in these habitats experience different levels of desiccation stress during intertidal exposure. Such differences in desiccation stress may have also contributed to the observed differences in oyster density between the habitats. Mangrove canopy cover availability is one unique feature that differs between these habitat types. Mangrove canopies can extend up to 35 m in height and form a complex branching structure (Proffitt and Travis, 2010) that provides shade to the oysters growing on the prop roots. Accordingly, increased shade could lower desiccation stress of oysters on roots and facilitate oyster survival in these habitats. Additionally, the canopy may help to buffer against extreme temperatures, thus ameliorating desiccation stress and improving thermoregulation by oysters. It is also possible that the vertical orientation of oysters on mangroves may enhance their capacity to ameliorate temperature and desiccation stress compared to oysters with more horizontal orientation such as in oyster reefs (McAfee et al., 2018). Combined, these findings suggest that red mangroves may serve as a potential physiological refuge for oysters through alteration of microclimate by the canopy. Our study is the first to examine one of the possible mechanisms driving the differences in oyster densities between mangroves and oyster reefs; additional studies would be required to explore these relationships over longer time

periods, especially during summer months. Overall, our results identify environmental conditions within red mangroves that make the prop roots suitable habitat for eastern oysters.

4.1. Oysters and mangroves: Looking forward

Oyster reefs provide important ecosystem services such as shoreline stabilization and fish habitat (Coen et al., 1999; Coen and Grizzle, 2007; Grabowski and Peterson, 2007; Beck et al., 2011; Grabowski et al., 2012; Pierson and Eggleston, 2014; Ridge et al., 2015). Therefore, the worldwide decline of oysters has instigated an enormous amount of effort allocated to oyster restoration, especially in the Gulf and Atlantic coasts of the United States (Beck et al., 2011; Theuerkauf et al., 2015; Kimbro et al., 2020). Mangrove roots may not only serve as an additional habitat for oysters, but may also provide a subsidy of oyster settlers for oyster reefs. Prop roots "overgrown" with oysters can eventually break off (Aquino-Thomas and Proffit, 2014, S. Bell, personal observations) possibly serving as an initial point of settlement for reef formation. Consequently, future oyster restoration efforts may benefit by considering restoring oyster reefs near red mangroves.

As mangroves continue to expand their habitat range poleward in response to climate change (Cavanaugh et al., 2014; Cavanaugh et al., 2019), interactions between mangroves and other systems found at higher latitudes will become more common (Feher et al., 2017; Saintilan et al., 2014). Indeed, replacement of salt marsh habitats by the expansion of mangroves has garnered much recent attention (Cavanaugh et al., 2014; Osland et al., 2013; Rodriguez et al., 2016). Although the eastern oyster has a cold temperature tolerance that allows them to exist at higher latitudes than mangroves, the continued expansion of these intertidal trees suggests we should expect to see increased co-occurrence of these two foundation species. Accordingly, understanding the relationship between mangroves and oysters will allow us to predict ecosystem-level effects and better shoreline management of our estuaries. Interestingly, the positive relationship we observed mangroves to have on oyster demography could be likely dependent on species and on temporal scale. For example, in Australia, despite different biotic and abiotic conditions on rocky shores and mangrove forests, Lee et al. (2012) found similar Sydney rock oyster (Saccostrea glomerata) settlement and post-settlement mortality between habitats. It is also possible for mangroves to ultimately have a longer-term, negative effect on oysters. Intertidal oyster reefs can trap mangrove propagules (McClenachan et al., 2020), and in due time, become mangrovedominated islands (Hesterberg et al., 2022). Colonization rates of intertidal oyster reefs by mangroves in the Mosquito Lagoon, Florida have doubled since 1943 (McClenachan et al., 2020), but the short- and long- term effects on oysters and associated biodiversity are unclear, meriting further research. Moreover, not all intertidal oyster reefs are colonized by mangroves, nor do all red mangrove prop roots host epibiont oysters. We advocate for more work that focuses on this exciting area of research to better understand the patterns, mechanisms, and interplay of positive and negative interactions between these organisms and the habitats they form.

CRediT authorship contribution statement

Dinorah H. Chacin: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Susan S. Bell:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Christopher D. Stallings:** Writing – review & editing, Supervision, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial

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interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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