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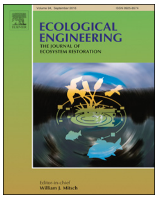

Wood traits and tidal exposure mediate shipworm infestation and biofouling in southeastern U.S. estuaries

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ABSTRACT

Annually, shipworms and other biofouling species cause millions of dollars in damage to wooden marine infrastructure across the world. Given their abundant larval supply and high dispersal potential, bioeroders and biofoulers are ubiquitous threats that shorten the lifespan of wooden docks, piers, boats and shoreline stabilization structures in coastal environments. Despite these impacts, there are no treatments that completely protect wood against shipworms and biofouling. To explore potential approaches for extending the lifespan of wooden shoreline stabilization structures, we conducted two field experiments to evaluate the resistance to shipworms and biofouling of small and large diameter branches of four trees – laurel oak (*Quercus hemisphaerica)*, sweetgum (*Liquidambar styraciflua*), crepe myrtle (*Lagerstroemia* spp.), and black mangrove (*Avicennia germinans*) – positioned at varying distances from the sediment surface in southeastern US estuaries. We discovered that the wood volume lost to shipworm burrows was concentrated near the sediment surface, more prevalent in tree species with lower wood densities, and varied markedly between years. Barnacle fouling was far higher on branches > 30 cm from the surface and on laurel oak and sweetgum branches. In a third field experiment, we tested two chemical and two non-chemical wood treatments and found chemical treatments to be more effective at deterring barnacle fouling and shipworm burrowing of wooden posts, especially beneath the sediment surface. By identifying desirable characteristics of the wood employed and elevations at which the impacts of shipworms and biofouling are especially prevalent, this experimental study informs the design of more durable wooden stabilization structures in coastal environments.

1. Introduction

An important challenge for the functioning and durability of marine infrastructure is biofouling and bioerosion – the growth of barnacles, algae, sponges, and other sessile organisms on or within submerged or partially submerged structures (Richmond and Seed, 1991; Callow and Callow, 2002; Sriyutha Murthy et al., 2009). For instance, biofouling can corrode and degrade metal structures including offshore oil rigs (Edyvean et al., 1988; Stevenson et al., 2011; Yang et al., 2014; Lingvay et al., 2018) and obstruct the optical window of submerged sensors (Sriyutha Murthy et al., 2009). Because this pervasive and widespread problem affects a variety of marine structures and instruments, significant investment continues to be made to combat biofouling (Alberte et al., 1992; Schultz et al., 2011).

One material particularly vulnerable to biofouling is wood. Wooden ships can be adversely affected by the settlement and growth of oysters, barnacles and other sessile invertebrates, and by the infestation of boring bivalve molluscs of the genera *Teredo, Bankia*, and *Lyrodus*, collectively known as shipworms. Barnacles, for instance, increase drag on wooden ships, resulting in increased fuel consumption (Schultz et al., 2011; Lindholdt et al., 2015). In contrast, shipworms bioerode wooden structures with the aid of symbiotic gut bacteria (Rice et al., 1990; Lopez-Anido et al., 2004; Nelson, 2015) and for centuries have posed a problem for humans. In the 1730s, shipworms caused extensive damage to wooden 'wave breakers', which left Dutch dikes and the cities that they protected vulnerable to storm surge and damage (Sundberg, 2015). Likewise, the introduction of *Teredo navalis* into the West Coast of the United States reached epidemic proportions between 1880 and 1920 and caused massive damage to infrastructure due to this shipworm bioeroding wharves, piers, and docks to the point of collapse. The costs of rebuilding and treating structures against future boring and biofouling in San Francisco Bay after this epidemic, along with the economic losses due to lost business from damaged infrastructure, totaled approximately half a billion US dollars (Nelson, 2015). In the US, somewhat outdated estimates (current estimates do not exist to the best of our knowledge) indicate that costs associated with damages to

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infrastructure due to shipworms alone is $205 million US dollars per year (Pimentel et al., 2000), further highlighting the substantial drain on marine and coastal economies that these burrowing molluscs and other biofoulers impose.

Although shipworms and biofouling species are prevalent pests in marine systems, they are especially problematic in coastal and estuarine environments that harbor many wooden structures (e.g. wharves, piers, docks) and significant wooden debris (e.g. fallen trees). Shipworms can tolerate salinities ranging from 5 to 35 ppt, although their boring activity stops at salinities below 10 ppt, and peaks at higher salinities resembling those of the open ocean (Barrows, 1917; Paalvast and van der Velde, 2011a). Optimal water temperature for shipworm growth ranges between 15 and 25 °C (Paalvast and van der Velde, 2011a), however shipworms are able to spawn as soon as temperatures exceed 11–12 °C (Graves, 1928). In addition, females spawn 3–4 times per reproductive season, releasing between 1 and 5 million larvae at a time. These veliger larvae occur in a planktonic stage for up to three weeks before settling on wooden substrates (Grave, 1928; Grave, 1942). During this stage, shipworms have the potential to disperse hundreds of kilometers in currents and ballast water (Scheltema, 1971). Barnacles and oysters, the biofouling taxa observed in this study, exhibit similar life history traits and tolerances to salinity and temperature fluctuations, although they are encrusting, sessile filter feeders rather than wood-consumers (Strathmann et al., 1981; Trager et al., 1990; Qiu and Qian, 1999). Collectively, these life history traits make shipworms, barnacles and oysters well-equipped to survive, persist and damage wooden structures in tropical and temperate estuaries worldwide.

To prolong the lifespan of wooden structures in estuarine environments, humans have employed different methods. Historic accounts show that ancient Egyptians and Chinese protected wooden structures with resin, pitch, and paint (Borges, 2014). Other cultures placed copper or lead plates on wooden ships, as well as used paraffin, tar, and asphalt on piers, wharves, and other structures, to protect against bioerosion and biofouling (Paalvast and van der Velde, 2011b). Creosote – a material derived from the carbonization of coal and one of the most effective protective measures against marine wood borers – has also been applied commonly to marine timber but has been banned or highly regulated in many countries due to its carcinogenic properties (Hoppe, 2002; Ohgami et al., 2015). More modern approaches include treating wood with chromated copper arsenate (CCA), which is relatively effective at deterring biofouling (Weis and Weis, 1992). CCA is widely used to protect wood but remains a controversial approach due to its negative environmental effects (Edwin and Sreeja, 2011; Paalvast and van der Velde, 2011b). Although shipworms, barnacles, and other biofouling organisms have posed a problem for centuries, no method has been developed that is one hundred percent effective at preventing their settlement and growth on wooden structures (Borges, 2014).

The lack of treatment against shipworms and biofouling, and limited understanding of their ecological impacts on various wood types is problematic because wood continues to be a commonly used construction material in estuaries (Borges et al., 2003). In particular, wood is often used in the construction of shoreline stabilization structures, including bulkheads and breakwalls. Breakwalls, also known as groynes in Europe, are composed of wooden piles or fence posts that are filled with brush, branches or small trees. Given their porous nature and construction just offshore, breakwalls are designed to decrease wave or boat wake energy acting on the shoreline edge and facilitate sediment deposition (Herbert et al., 2018). First built in the North Sea in Germany in 1815, breakwalls continued to be constructed today and are preferred over conventional hardened, non-permeable breakwalls because they are less expensive and result in less scouring and erosion of sediment in adjacent unprotected shorelines (Bakker et al., 1984; Orford, 1988; Weichbrodt, 2008; Herbert et al., 2018). For these same reasons, shoreline stabilization and restoration efforts in Germany, the Netherlands, US, and other countries are now adopting more natural approaches including breakwalls (Poff et al., 2004; Borsje et al., 2011; Lippert et al., 2017). In the coming years, the use of wooden shoreline stabilization structures may increase in the face of sea level rise and increased shoreline erosion (Bulleri and Chapman, 2010). Despite the forecasted increase in their use, it remains unclear how their design might be optimized to enhance their longevity in the face of shipworms and other forms of biofouling.

To better understand the environmental and substrate characteristics that modulate shipworm infestation and biofouling of intertidal breakwall branches and posts, we conducted a 6-month field experiment to test how distance from the sediment surface, tree species identity, branch diameter, and site interact to mediate shipworm burrow density and percentage of wood volume lost to burrowing in two northeast Florida estuaries (Experiment 1). We then tested how tree species identity and distance from sediment mediate patterns in shipworm infestation and barnacle and oyster settlement across southeastern US estuaries by replicating this experiment for three months in the same two sites and at four additional sites (Experiment 2). Finally, we compared barnacle and oyster colonization as well as shipworm infestation of two non-chemical (tape and silicone wraps) and two chemical techniques (pressure-treated wood and copper-based antifouling paint) meant to protect wooden posts against biofouling and enhance their longevity to unprotected, control posts (Experiment 3).

For Experiments 1 and 2, we hypothesized that: (1) shipworm burrow density and wood volume loss as well as barnacle and oyster density would be highest on branches located close to the sediment surface that are inundated for longest and negligible for branches buried underneath the sediment surface due to anoxic conditions, (2) small branches will lose a higher percentage of wood volume to shipworms, but large branches will have higher shipworm burrow densities, and (3) branches with high wood densities (laurel oak and mangrove) will experience less damage than those with low wood densities (crepe myrtle and sweetgum). For Experiment 3, we hypothesized that chemical treatments would result in wooden posts having fewer barnacles, oysters, and shipworm burrows than non-chemical treatments, but that non-chemical treatments would have less damage than unprotected controls. Together, these three experiments inform the ecologically-engineered design of wooden breakwalls for shoreline protection in the southeastern US, a region where lateral loss of shorelines is pervasive due to boat traffic and high-energy wave environments (Morton, 2003; Herbert et al., 2018).

2. Materials and methods

2.1. Study sites

Experiments 1 and 3 were conducted in two tidal creeks within the Matanzas River Estuary in St. Augustine, Florida, USA (Site 1: 29° 45′ 47.9592″ N, 81° 15′ 46.242″ W and Site 2: 29° 51′ 57.7584″ N, 81° 18′ 48.5316″ W, Fig. 1). These sites are exposed to semidiurnal tides ranging from −0.25 m to 1.25 m above Mean Lower Low Water (MLLW), experience temperatures between 22 and 35 °C in summer and from 4 to 25 °C in winter, and receive an annual average of 113 mm of precipitation per month (NOAA National Centers for Environmental Information 2018). The tidal creeks were surrounded by salt marsh dominated by smooth cordgrass (*Spartina alterniflora*). Black (*Avicennia germinans*) mangroves were also present at both sites and occurred as isolated trees. Eastern oyster, *Crassostrea virginica*, reefs were also common at the lower intertidal margins of the salt marsh habitat. The experiments were deployed approximately 30 cm below the lower elevation of naturally occurring oyster reefs in exposed intertidal mudflats as this elevation is where breakwalls are typically deployed for shoreline stabilization in the region (Herbert et al., 2018).

2.2. Experiment 1: tree species, branch diameter, elevation and site effects

We tested four tree species' susceptibility to shipworm infestation

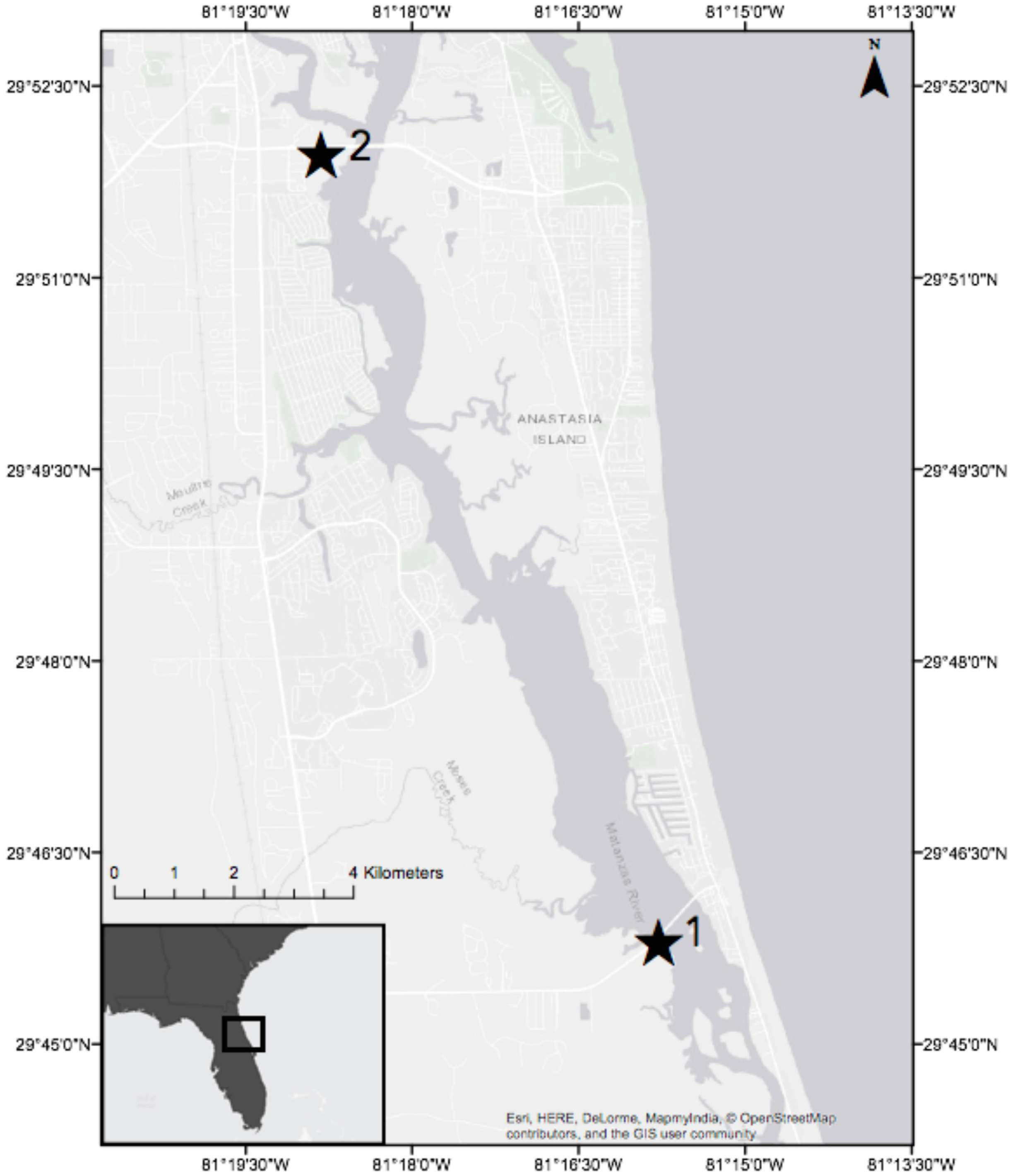

Fig. 1. Map of experimental sites in St. Augustine, FL, United States.

and biofouling: laurel oak (*Quercus hemisphaerica)*, sweetgum (*Liquidambar styraciflua*), crepe myrtle (*Lagerstroemia* spp.), and black mangrove (*Avicennia germinans*). The first three species were selected because of their abundance in the region and thus availability for use in breakwall construction. Laurel oak and sweetgum are native to Florida, while crepe myrtle is an introduced ornamental species that is now well established in the region. Black mangroves are also common in Florida and, due to their natural exposure to shipworms, barnacles and oysters as a result of their intertidal estuarine distribution, we anticipated that this species would be more resistant to shipworm infestation and biofouling. However, mangroves cannot be harvested without a permit and were investigated in this study as a useful comparison from which to gauge the vulnerability of the other tree species to bioerosion and biofouling.

For each tree species, we tested two branch diameter classes relevant for filling breakwalls given their availability and ease of handling, large and small. Because of the natural distribution of branch sizes, diameter classes differed slightly among species. Laurel oak had a small diameter class ranging from 1 to 2.5 cm and a large diameter class ranging from 2.5 to 5 cm. Crepe myrtle and sweetgum had a small diameter class ranging from 1 to 2 cm and a large diameter class ranging from 2 to 4 cm. Mangrove branches had a small diameter class ranging from 1 to 1.5 cm and a large diameter class ranging from 1.5 to 3.5 cm.

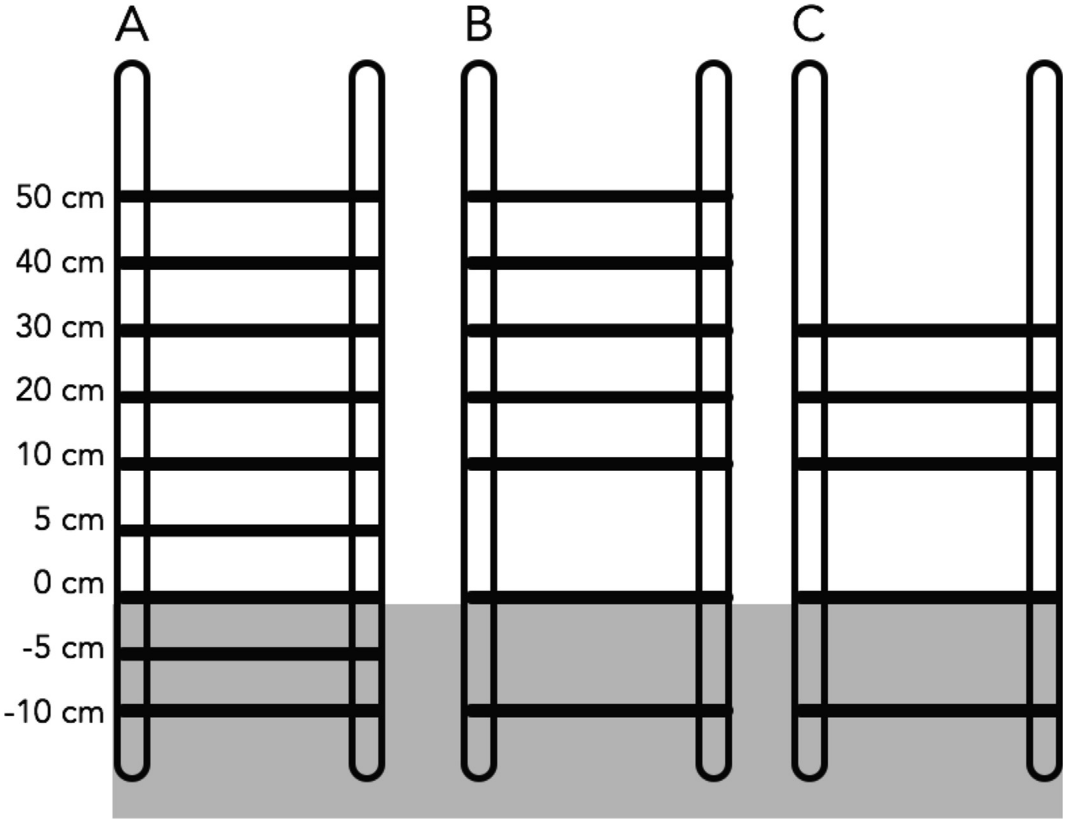

Fig. 2. Experimental design of ladders. Rungs represent tree branches positioned at the shown distances from the sediment, which is represented by the gray shading: (a) design of small ladders for crepe myrtle, sweetgum, and laurel oak branches; (b) design of large ladders for crepe myrtle, sweetgum, and laurel oak branches; (c) design for both small and large mangrove ladders.

To compare shipworm infestation and biofouling prevalence between tree species, diameter classes, and distances from the sediment surface, we built 'ladders' using PVC poles as the ladder sides and tree branches as rungs (Fig. 2). Each ladder from the small diameter class had a total of nine, 50 cm-long branch rungs secured to the PVC pipes with cable ties at distances of −10, −5, 0, 5, 10, 20, 30, 40, and 50 cm from the sediment surface. Each ladder in the large diameter classes had a total of seven, 50 cm-long branches secured at distances of −10, 0, 10, 20, 30, 40, and 50 cm from the sediment; note that the −5 and 5 cm rungs were omitted from large branch ladders due to space constraints. Five replicate ladders were built for each study site and diameter class for laurel oak, sweetgum, and crepe myrtle branches. However, due to a lack of available tree branches and legislation in Florida restricting mangrove trimming, small and large diameter mangrove ladders had only 5 branches each, positioned at −10, 0, 10, 20, and 30 cm from the sediment (N = 5 small diameter and N = 4 large diameter class ladders). In July 2016, the ladders were driven by hand into the sediment at a spacing of 1 m in the intertidal mudflat and 2–3 m from the salt marsh shoreline edge at each study site. The elevations of the ladders were −0.57 to −0.73 m and −0.51 to −0.59 m above mean low water at sites 1 and 2, respectively. These locations were selected to mimic the location where breakwalls are typically built to stabilize eroding shorelines. The ladders were retrieved six months later in January 2017.

In the lab, number of barnacles and oysters were counted on each branch to evaluate biofouling. Oysters were rarely observed on branches, averaging only 0.5 oysters per branch across the 562 branches deployed, so are not discussed further in the main text (see Appendix A1 for summary of results). We then measured the length and diameter of each branch in order to calculate the initial wood volume by multiplying the cross-sectional area of the branch times its length. We then cut each branch into 5 cm-long segments and, for each segment, counted the number of shipworm burrows. Using calipers, we then measured the diameter and depth of 10 burrows per segment. If less than 10 burrows were observed, all burrows were measured. We used the burrow diameter and depth to calculate the volume of each of these 10 burrows by multiplying the area of the burrow opening times the burrow depth. We then averaged these volumes, multiplied this value by the number of burrows per segment, and summed these values across each branch to estimate the total wood volume lost to shipworm burrowing. Finally, we calculated the percent of branch wood volume lost to shipworms by dividing the total volume of wood lost to shipworm burrowing by the initial wood volume.

2.3. Experiment 2: regional study of tree species, elevation and site effects

To evaluate potential spatial variation across the region and assess interannual variability in shipworm infestation rates and biofouling at the two sites evaluated in Experiment 1, we repeated this experiment in June 2017 in the same two sites used in Experiment 1 and deployed ladders at 4 additional sites along the southeastern US coast (Cedar Key, FL, Withlacoochee Bay, FL, Suwannee River, FL, and Sapelo Island, GA). Based on results from Experiment 1, we used only small diameter laurel oak and sweetgum ladders with branches positioned at distances from 0 to 30 cm above the sediment in 10 cm intervals as these tree species varied in their vulnerability to shipworms and biofouling, and these diameter class and positions were most vulnerable to shipworms and thus best suited for assessing spatial and interannual variation in bioerosion and biofouling rates. At each site, we deployed 5 replicates of each ladder in June 2017 and retrieved them September 2017. Branches were brought back to the lab and analyzed in the same way as branches in Experiment 1 – barnacles and oysters were counted on each branch and branches were cut into 5-cm segments and inspected for shipworm burrows. Similar to Experiment 1, oysters were relatively rare and only reported on further in Appendix A2.

2.4. Experiment 3: anti-fouling techniques for wooden substrates

We tested five wood protection treatments against biofouling: CCA pressure-treated fence posts, Rust-Oleum 207,012 Marine Flat Boat Bottom commercial copper anti-fouling paint, 1.5-cm thick silicone wraps made with Smooth-On Mold Max silicone mold-making rubber, Gorilla duct tape, and an untreated control (Appendix B). The pressure-treated fence posts were 8.9-cm diameter by 1.5 m long, livestock fence posts that are often used in groyne, breakwall, seawall and bulkhead construction, while the other three treatments were applied to 5.08 cm × 5.08 cm by 1.5 m long untreated spruce pine fir wooden posts. The treatments were applied to the middle 1 m of the post, which was then driven into the ground making sure that 0.5 m of treated surface was underground and 0.5 m was above the sediment. The copper paint, silicone wrap and duct tape were utilized as treatments because all three are easy to acquire and/or inexpensive and easy-to-apply materials. Five replicates of each treatment were deployed in July 2016 in sites 1 and 2 (same sites as in Experiment 1). They were retrieved on January 2018, after 18 months, and brought to the laboratory for processing. Biofouling was assessed for each post by counting all barnacles and oysters per post and dividing this number by the surface area of each post to standardize these values. Shipworm damage was quantified by cutting each post at the −10, −5, 0, 5, 10, and 20 cm mark and estimating the percent of the cross-sectional area burrowed by shipworms. These posts were left in the ground for significantly longer than the branches from Experiments 1 and 2 to explore the potential long-term efficacy of these protective treatments in reducing the rate of biofouling and bioerosion on wooden breakwalls. (See Table 1 for summary of all three experiments.)

2.5. Statistical analyses

To evaluate the significance and relative importance of site, distance from the sediment surface, tree species, and diameter in explaining variation in the number of barnacles per branch, the number of oysters per branch (Appendix A), percent wood volume lost, and shipworm burrow density in Experiment 1, we developed a regression tree using the analysis of variance (ANOVA) method of recursive partitioning for each response variable. We then pruned over-fitted trees using k-fold cross-validation (see Gittman et al., 2015 for details). Regression trees were made using R version 3.2.2 and the R package “rpart” (Therneau et al., 2018). We utilized regression trees to both facilitate identification of the relative importance of the four fixed factors (i.e. the factors that explain the most variation in each response metric are found at the base of the regression tree) and overcome challenges associated with interpreting complex, multi-factor interactions that can arise from four-factor ANOVA. However, because the regression tree revealed branch diameter to be of little significance ($p > 0.5$) in predicting the number of barnacles per branch, we simplified our analytical approach and evaluated the effect size and significance of site, distance from the sediment, and tree species on this specific response variable with a three-way ANOVA. Post hoc analyses were performed using Tukey HSD test.

For Experiment 2, we used a three-way site * distance from the sediment * tree species ANOVA to evaluate the effect size and significance of these fixed factors and their interactions on the number of barnacles per branch. Due to the lack of shipworm burrows obtained in Experiment 2 (3 total burrows in 240 branches), no statistical analyses were run for the percent wood volume lost and shipworm burrow density response variables.

To evaluate the significance and relative importance of site and wood protection treatment on the number of barnacles and oysters (Appendix A) per unit surface area of post and percent area burrowed by shipworms on wooden posts in Experiment 3, two-way ANOVAs were run with these two variables as fixed factors. Separate ANOVAs were run for the percentage of area burrowed by shipworms and the number of barnacles per branch at each distance from the sediment (i.e.

Table 1
Objective, study species, branch diameters, distance from sediment, treatments, site, and duration of experiments 1, 2, and 3.

Experiment	Experimental factors	Tree Species	Branch diameter	Distances from the sediment	Sites	Duration
1	Site, distance from sediment, tree species identity, and branch diameter	Crepe myrtle (*Lagerstroemia* spp.), Laurel oak (*Quercus hemisphaerica*), Sweetgum (*Liquidambar styraciflua*), Mangrove (*Avicennia germinans*)	Small (1–2.5 cm) and Large (2.5–5 cm)	−10, −5, 0, 5, 10, 20, 30, 40, 50 cm	Saint Augustine Sites 1 and 2	6 months (July 2016 – Jan. 2017)
2	Site, distance from sediment, and tree species	Laurel oak (*Quercus hemisphaerica*), Sweetgum (*Liquidambar styraciflua*)	Small (1–2.5 cm)	0, 10, 20, and 30 cm	Saint Augustine Sites 1 and 2, Cedar Key, Withlacoochee Bay, Suwannee River, and Sapelo Island	3 months (June 2017 – Sep. 2017)
3	Chemical and non-chemical wood treatment methods	Treated (pressure-treated, tape, silicon, copper paint) and untreated wooden posts	Pressure treated wood post dimensions: 8.9 cm diameter × 1.5 m long. All other post dimensions: 1.5 m × 5.08 cm × 5.08 cm	−10, −5, 0, 5, 10, and 20 cm	Saint Augustine Sites 1 and 2	6 months (July 2016 – Jan. 2018)

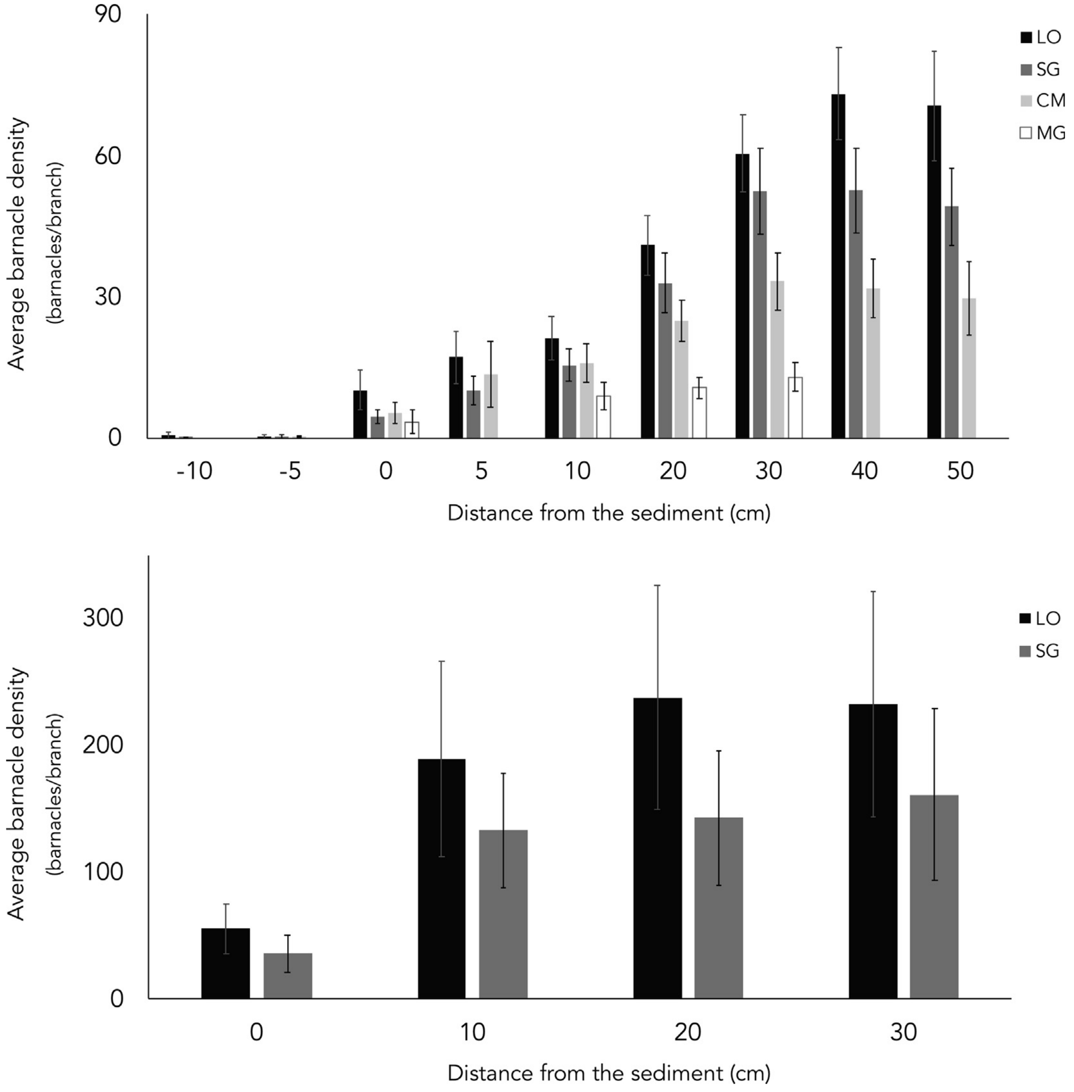

Fig. 3. Mean (± standard error) number of barnacles per branch for laurel oak (LO), sweetgum (SG), crepe myrtle (CM), and mangrove (MG) branches at each distance from the sediment in (a) Experiment 1 and (b) Experiment 2.

−10, −5, 0, 5, 10, and 20 cm from the sediment surface).

3. Results

3.1. Biofouling

3.1.1. Experiment 1

Interactions between distance from the sediment and tree species and between distance from the sediment and site, as well as the main effects of distance from sediment, tree species and site (all: $p < 0.0001$) significantly affected barnacle fouling of branches in Experiment 1 (Fig. 3A). At farther distances from the sediment (≥ 30 cm), the number of barnacles per branch increased dramatically, reaching > 50 barnacles per branch, on laurel oak and sweetgum branches, but remained below 30 barnacles on crepe myrtle and mangrove branches (distance from sediment * tree species: $F_{3,546} = 15.4$, $p < 0.0001$). At distances close to the sediment (i.e. between −10 and 10 cm), all tree species had few barnacles per branch, densities that steadily increased with increasing distance from the sediment (distance from sediment * site: $F_{1,546} = 16.7$, $p < 0.0001$), especially at site 2 where approximately 50% more barnacles were observed (site: $F_{1,546} = 23.7$, $p < 0.0001$). In general, branches positioned ≥ 30 cm supported significantly more barnacles than those positioned at lower distances (distance from the sediment: $F_{1,546} = 348.2$, $p < 0.0001$) and barnacle density was considerably higher on laurel oak (36 ± 3 barnacles per branch, mean ± SEM here and below), sweetgum (27 ± 3 barnacles per branch) and crepe myrtle (18 ± 2 barnacles per branch) than mangrove (7 ± 1 barnacles per branch, tree species: $F_{3,546} = 20.7$, $p < 0.0001$, Fig. 3, Table 2, Appendix C).

3.1.2. Experiment 2

For Experiment 2 in which ladders with laurel oak and sweetgum branches spanning heights from 0 to 30 cm were deployed across six estuaries, the interaction between distance from the sediment and site ($F_{5,216} = 14.4$, $p < 0.0001$), as well as the main effects of these fixed

Table 2
Summary of ANOVA results for barnacle biofouling in Experiment 1.

		Barnacle Density (# per m^2)	
Variable	df	F value	p value
Distance from sediment	1, 546	348.2	< 0.0001
Tree species	3, 546	20.7	< 0.0001
Site	1, 546	23.7	< 0.0001
Distance from sediment * tree species	3, 546	15.4	< 0.0001
Distance from sediment * site	1, 546	16.7	< 0.0001

Table 3
Summary of ANOVA results for barnacle biofouling in Experiment 2.

		Barnacle Density (# per m^2)	
Variable	df	F value	p value
Distance from sediment	1, 216	14.5	< 0.0002
Tree species	1, 216	4.6	< 0.05
Site	5, 216	55.2	< 0.0001
Distance from sediment * site	5, 216	14.4	< 0.0001

factors (distance from sediment: $F_{1,216} = 14.5$, $p < 0.0002$; site: $F_{5,216} = 55.2$, $p < 0.0001$) influenced barnacle fouling of branches. While we observed significantly higher barnacle densities on branches positioned 10, 20 and 30 cm above the sediment at Cedar Key, the site where the most barnacles were observed, this pattern was the opposite at Withlacoochee. At the other sites, barnacle densities were relatively low and did not vary much with distance from the sediment (Table 3, Appendix C). Across sites, laurel oak branches were fouled by more barnacles than sweetgum ($F_{1,216} = 4.6$, $p < 0.05$), a pattern consistent with results from Experiment 1.

3.1.3. Experiment 3

Although barnacle density did not differ between sites for posts treated with copper paint, silicone, or duct tape in experiment 3, pressure-treated fence posts and control posts were fouled by more barnacles at Site 1 (0.75 and 0.17 barnacles cm^{-1}, respectively) than at Site 2 (0.25 and 0.03 barnacles cm^{-1}, respectively, treatment * site: $F_{4,40} = 3.40$, $p < 0.02$). Significantly higher densities of barnacles colonized pressure-treated fence posts than all other treatments with an average of 0.5 barnacles cm^{-1}. In contrast, zero barnacles were observed on silicone-treated posts and only 0.03–0.1 barnacles cm^{-1} were observed on the copper paint, duct tape, and control post treatments (treatment: $F_{4,40} = 12.97$, $p < 0.0001$). Barnacle density was also more than 2-times higher at Site 1 (0.2 barnacles cm^{-1} on average) compared to Site 2 (0.07 barnacles cm^{-1} on average, site: $F_{1,40} = 7.36$, $p < 0.01$, Table 4).

3.2. Shipworm damage

3.2.1. Experiment 1

Despite sites 1 and 2 having a number of branches with evidence of shipworm boring (75 of 278 branches with at least one shipworm burrow at Site 1 and 79 of 284 branches at Site 2), damage, measured both in terms of burrow density and wood volume lost, differed between the two sites. Regression tree analyses explained 99.9 and 94.4% of the variation in the percent of wood volume lost (Fig. 4A, tree root node error = 0.015) and burrow density (Fig. 4B, tree root node error = 5.56), respectively, and revealed that site was the strongest driver of both shipworm damage metrics. While on average 2.6% of wood volume loss to burrows was observed at Site 2, only 0.4% wood volume loss was observed at Site 1. Similarly, while 10 burrows were observed per branch on average at Site 2, only 1 burrow per branch was observed at Site 1. Shipworm burrowing also varied significantly with distance from the sediment at both sites and across the four species. While we detected shipworm burrows at all distances, the percent of wood volume lost peaked in branches located between 0 and 20 cm from the sediment layer. Specifically, regression trees for both shipworm damage metrics (Fig. 4) identified −2.5 cm (i.e. 2.5 cm below the sediment surface) to be the lower limit and 25 cm to be the upper limit of the zone at which most shipworm damage occurs. Within this zone, between 3.7 and 5% of wood volume was lost to shipworm burrows compared to only 0.4% wood volume loss outside this area. Similarly, shipworm burrow densities ranged between 14 and 19 burrows per branch if the branch was positioned within this zone versus 1–2 burrows per branch if the branch was positioned further into the sediment or higher in the water column.

Tree species was the third most important factor mediating variation in shipworm burrow damage such that sweetgum and crepe myrtle branches experienced > 2.5-times higher percent wood volume loss and 3-times higher shipworm burrow density than laurel oak and mangrove branches (Figs. 4 and 5). While branch diameter had no significant effect on the percentage of wood volume lost, it did explain variation in burrow density such that large diameter branches had almost three times more burrows than small diameter branches (Fig. 4B, Table 5).

3.2.2. Experiment 2

Of 240 branches deployed across six sites in Experiment 2, only one sweetgum branch deployed at Site 2 was burrowed by shipworms. A total of three burrows were found in this branch, accounting for approximately a 1% wood volume loss in the branch.

3.2.3. Experiment 3

Two-way ANOVAs performed to assess variation in the percent of wooden post volume lost to shipworms at each distance from the sediment found treatment and site to have significant effects on this metric of shipworm damage, but only at −10 cm (Treatment: $F_{4,36} = 4.45$, $p < 0.01$, Site: $F_{1,36} = 10.09$, $p < 0.005$) and −5cm distances (Treatment: $F_{4,36} = 4.58$, $p < 0.005$, Site: $F_{1,36} = 7.53$, $p < 0.01$). At −10 and −5cm, shipworm burrowing was significantly higher on control posts (28% and 32% of post area lost to burrows, respectively) and significantly lower on copper paint and duct tape treated posts (0% wood volume lost at both distances) (Table 4, Appendix D).

Similar to the branch ladders (see Experiment 1 results above), wooden posts deployed at Site 2 experienced significantly higher burrowing at −10 and −5 cm from the sediment (17% and 19% of area burrowed, respectively) than those deployed at Site 1 at those same distances (1.9% and 3.7% of area burrowed, respectively). At the 10 cm distance, control posts experienced significantly higher burrowing (23% of area burrowed) than all other treatments (< 15% of area burrowed). At all other distances, shipworm damage ranged from 0 to 27% area burrowed but did not differ between treatments or sites.

4. Discussion

In this experimental field study, we discovered spatial complementarity in wood vulnerability to biofouling and bioeroding organisms whereby branches and posts located at greater distances from the sediment (≥ 30 cm) were more susceptible to biofouling by barnacles, while those at elevations close (0–20 cm) to the sediment surface

Table 4
Summary of ANOVA results for barnacle and shipworm biofouling in Experiment 3.

		Barnacle Density (# per cm^2)		Shipworm burrow percent cover at −10 cm		Shipworm burrow percent cover at −5 cm	
Variable	df	F value	p value	F value	p value	F value	p value
Treatment	4, 40	12.97	< 0.0001	4.45	< 0.01	4.58	< 0.005
Site	1, 40	7.36	< 0.01	10.09	< 0.005	7.53	< 0.01
Treatment * Site	4, 40	3.40	< 0.02	2.1	< 0.1	1.6	< 0.5

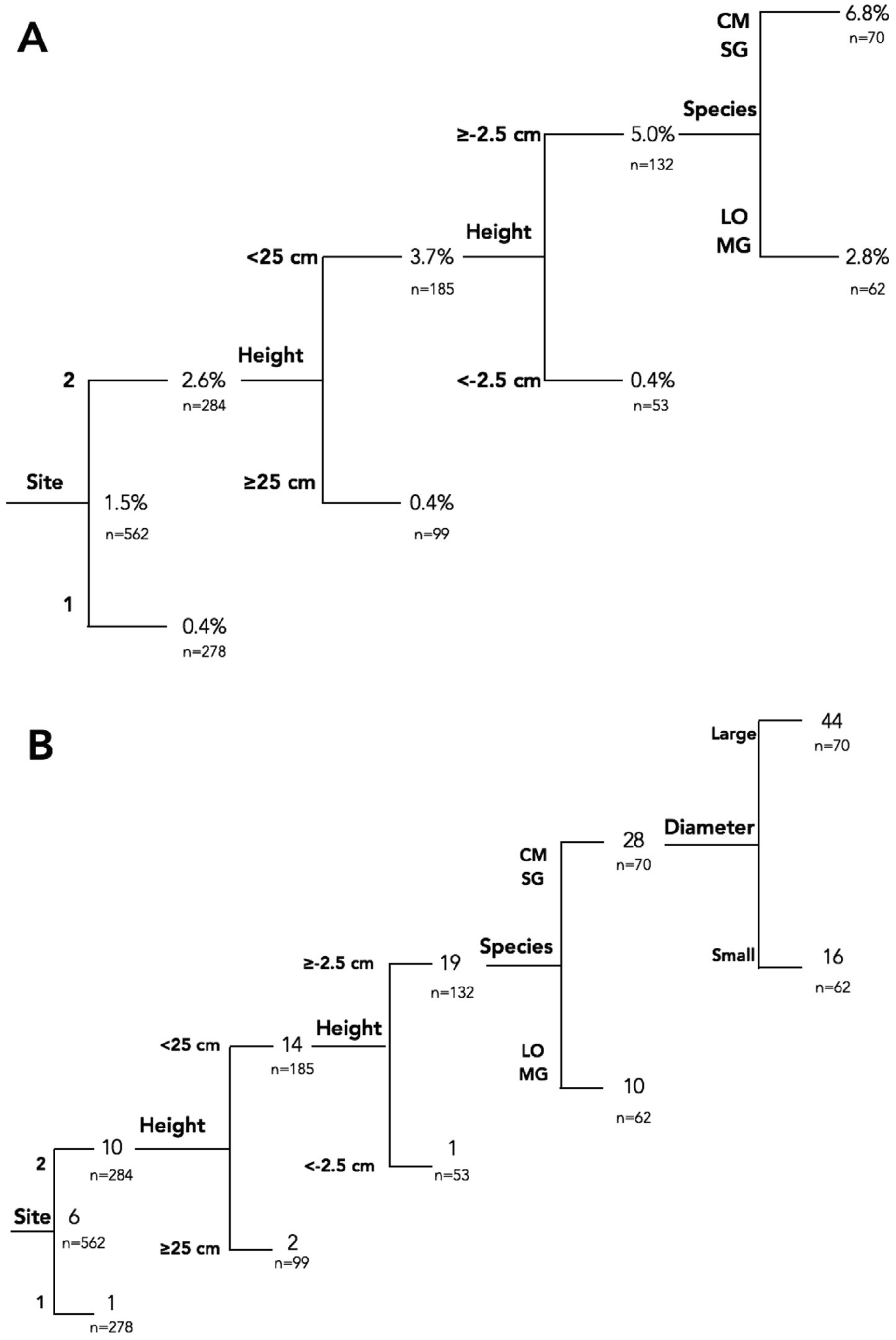

Fig. 4. Experiment 1 regression trees revealing the relative importance of site, distance from the sediment surface, tree species and branch diameter in mediating: (a) the percent wood volume lost and (b) the number of shipworm burrows per branch. In both panels, the mean percent wood volume lost in (a) or number of burrows per branch in (b) is indicated after each split along with the number of branches (n) included in the analysis.

were more intensively damaged by shipworms. In addition, we found that trees with lower wood and tannin densities – i.e. sweetgum and crepe myrtle – were more vulnerable to shipworm burrowing than higher wood density tree species and that copper-based paint and duct tape offered the greatest protection against barnacles and shipworms for wood in intertidal environments. Together, these results indicate that biofouling and bioerosion of wooden marine infrastructure can be reduced through the strategic use of certain tree species and easy-to-implement treatments that interfere with the settlement and growth of these biota.

Similar barnacle biofouling results were found in Experiments 1 and 2, with the number of barnacles per branch increasing with increasing height (Fig. 3). This pattern of enhanced barnacle colonization of higher elevation surfaces is consistent with that reported in the literature for intertidal barnacles (e.g. Grosberg, 1982; Wethey, 1983; Raimondi, 1988) and is thought to be driven both by larval behavior (e.g. barnacle larvae are buoyant, responsive to light, and favor low-pressure environments found near the water surface) and by enhanced vulnerability of barnacles, once settled, to predation at lower intertidal elevations (Connell, 1970). In Experiment 2, we also found barnacle abundance to be relatively high in Cedar Key but did not differ between the other five sites, variability that we suspect was driven by higher barnacle larval delivery to this more open-water rather than estuarine site (Minchinton and Scheibling, 1991), although variation in predation

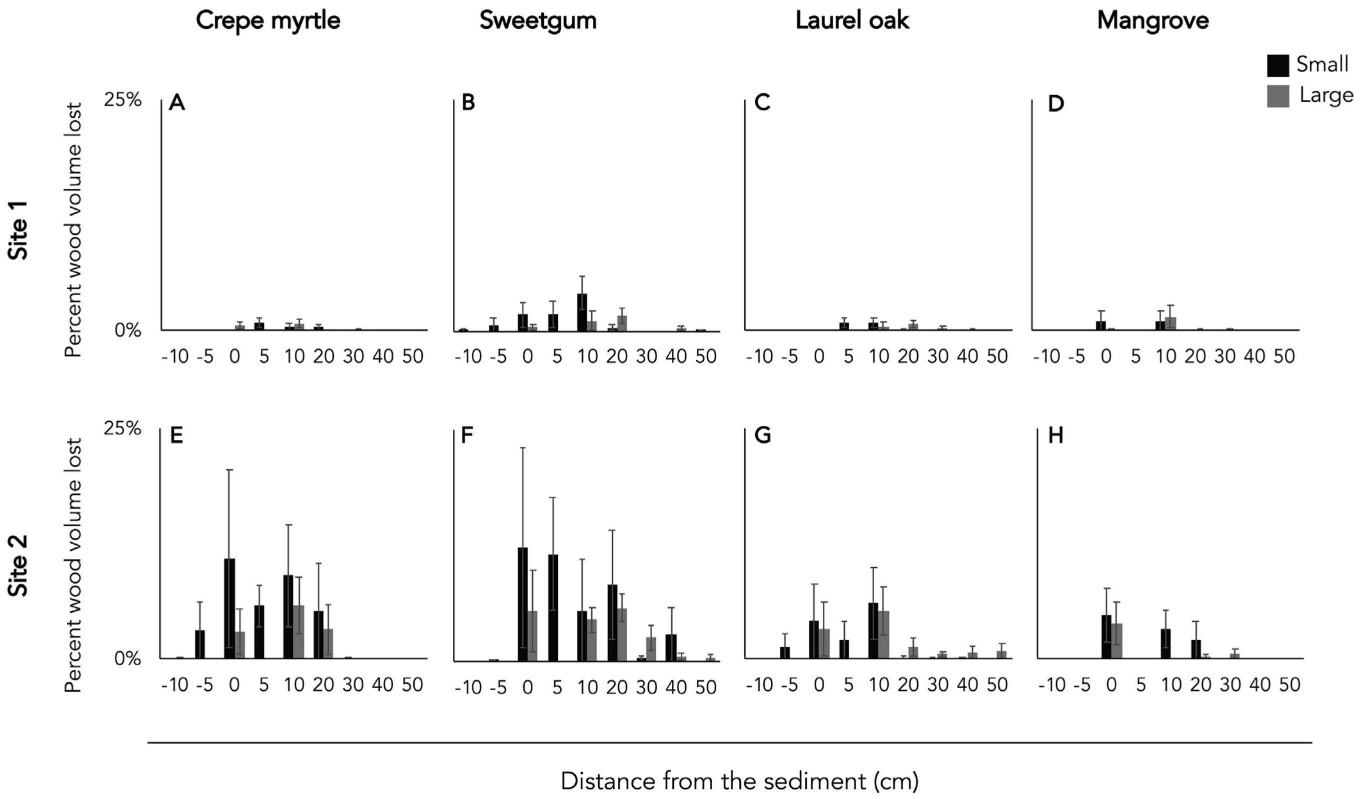

Fig. 5. Percent wood volume lost from (a) crepe myrtle (b) sweetgum, (c) laurel oak and (d) mangrove branches in Site 1 and (e) crepe myrtle (f) sweetgum, (g) laurel oak and (h) mangrove branches in Site 2. Small and large diameter branches are shown as black and gray bars, respectively. Data are shown as mean ± standard error for five replicates at each site, species, and diameter class.

Table 5
Summary of statistical results for shipworm biofouling in Experiment 1.

		% Wood Volume Lost	Burrows per branch
Site	Site 1	0.4 ± 0.1%	1 ± 0.2
	Site 2	2.6 ± 0.4%	10 ± 1.6
Distance from sediment	> 0 cm	0.4 ± 0.3%	1 ± 0.9
	0–20 cm	5 ± 0.8%	19 ± 3.2
	< 25 cm	0.5 ± 0.2%	2 ± 1.0
Tree Species	Crepe myrtle	6.1 ± 1.7%	28 ± 9.4
	Sweetgum	7.6 ± 2.0%	27 ± 6.0
	Laurel oak	3.1 ± 1%	12 ± 4.0
	Mangrove	2.4 ± 0.8%	6 ± 2.0
Branch diameter	Small	NSD	16 ± 4.5
	Large	NSD	44 ± 11.0

pressure cannot be ruled out as a contributing factor to the observed variation.

When considering potential treatments against barnacle biofouling in Experiment 3, we found silicone to be the most effective (i.e. no barnacles settled on silicone-treated posts), and pressure-treated wood to be the least effective. Savoya and Schwindt (2010) quantified barnacle settlement on substrates of varying texture in supporting and found rough-textured substrates to be most suitable for barnacle growth. These results might explain why no barnacles were observed on silicone: its surface texture is very smooth. In contrast, the relative ineffectiveness of pressure-treated wood in warding off barnacles could be due to both the rougher surface of these posts promoting colonization as well the amount of time these posts were in the water in our experiment (18 months). Weis and Weis (1996) and Edwin and Sreeja (2011) found that when pressure-treated wood is submerged, it leaches copper, chromium, and arsenic (CCA) into the water such that, after two months, these chemicals are no longer in high enough concentrations to deter biofoulers. Thus, it is possible that, although the pressure-treated posts initially supported little to no barnacle growth, their anti-fouling capacity was diminished by the end of the experiment. Viewed in the context of wooden marine infrastructure, these results suggest that barnacles are likely to induce the largest drag and ecological effects (e.g. forming a physical barrier to shipworm larval settlement (Singh and Sasekumar, 1996)) on the rough-surfaced, upper sections (≥30 cm) of wooden break walls and posts that do not emit strong chemical deterrents in coastal environments.

Shipworms and other marine borers have been attacking wood for centuries (Nicholas, 1982) and, in response, many techniques (e.g. fish-, coconut-, cashew-oils as coatings or application of sand, cement, black tar, and copper chromate arsenate) to deter shipworms have been employed (Nagabhushanam, 1997). The average and maximum percent wood volume lost to shipworms recorded in our study was < 7% and 55%, respectively, over six months (Fig. 4). Although generally low, this level of damage can be enough to compromise the structural integrity of wooden structures, especially those exposed to high and/or frequent wave and wake loading (Charles et al., 2016). Most importantly, the shipworm infestation patterns observed across site, distances from the sediment, and tree species give an indication of when and how often wooden structures, like breakwalls and bulkheads, will need maintenance. In particular, the bottom of walls and walls built from less dense sweetgum and crepe myrtle branches – species that lost the most wood volume to shipworms (Fig. 5) – are likely to need more maintenance, especially at sites experiencing high shipworm recruitment. Our results correspond to previous studies that also found tree species to vary in resistance to borers depending on certain traits; for example, resistance to marine borers has been shown to increase with wood silica and alkaloid contents (Nicholas, 1982; Roszaini and Salmiah, 2015).

According to regression tree analyses, site was the most important factor mediating shipworm burrow density and amount of wood volume lost (Fig. 4). One might expect that ladders at lower elevations, given their longer inundation time, to be exposed to shipworm-infested waters for a longer and thus suffer higher shipworm damage. This rationale cannot explain our results in Experiment 1, however, since Site 1 ladders, positioned at an average elevation of −0.65 m above sea level, experienced less damage than those at Site 2 which were positioned higher in elevation at −0.59 m above sea level. Additionally, one might also expect proximity to a saltwater source to correspond to shipworm damage given shipworms' preference for higher salinities (Barrows, 1917). However, we found average salinities during the study period to be nearly the same at the two sites according to nearby water quality monitoring stations (34.8 vs. 34.1 ppt at Sites 1 and 2, respectively) despite variation in site proximity to tidal inlets to the open ocean (Site 1 and 2 are 8.3 and 6.5 km, respectfully, away from the closest tidal inlet to the Atlantic Ocean). Given that Site 1 consisted of a narrow, meandering creek surrounded by denser vegetation, while Site 2 consisted of a wider creek that was closer and had a wide, unvegetated connection to the main channel, it is possible that local geomorphology drove the significant variation in shipworm damage between the sites. Specifically, it is likely that a greater water volume was exchanged per tidal cycle at Site 2 relative to Site 1, resulting in higher delivery of shipworm larvae, based on Leonard and Reed's (2002) finding that creek vegetation reduced water flow speed and on Roegner's (2000) calculations that narrow creeks transport a lower volume of water than wider creeks.

The second most important indicator of shipworm boring was distance from the sediment surface. Results from Experiment 1 show shipworm damage to be concentrated in the top 20 cm above the sediment layer, consistent with findings from Tuente et al. (2002) who also found that shipworm burrow densities on wooden piles in German harbors increase with decreasing height above the sea floor. Scheltema and Truitt (1956) found similar results in Maryland's coastal waters, with higher shipworm densities on wooden panels positioned closer to the sediment surface over a range of depths from 0 to 2.1 m. Finally, Paalvast and van der Velde (2011a) similarly report a negative correlation between shipworm burrowing and distance from the sea floor at depths of 0–1 m. This general pattern of high shipworm colonization of wood close to the sediment surface likely arises because shipworms cannot access and survive within branches found deep in the substrate (-5 and −10 cm) due to anoxic conditions and because branches at the upper limits (≥30 cm) are inundated, and thus exposed to shipworm larvae, for less time. Given these dynamics, shipworm activity would be expected to be more prevalent closer to the sediment and would explain patterns seen in this and previous experiments.

Finally, tree species identity also influenced the extent of shipworm bioerosion (Fig. 5). These differences may be due to tree species' differing hardness, with shipworm burrows being more prevalent in softer branches that require less energy investment to burrow into than in harder branches (Paalvast and van der Velde's, 2011a). One measure of tree hardness is wood density, which is typically calculated by the ratio of dry weight of wood divided by its green volume (Zobel and Jett ,1995). In our first experiment, we found significantly more shipworm damage on sweetgum and crepe myrtle branches, which have wood densities of 0.42 and 0.55 $\mathrm{g\,cm^{-3}}$, respectively (Holbrook and Putz, 1989; Reyes et al., 1992). In contrast, black mangrove and oak species – those that experienced less shipworm damage – have higher wood densities of 0.87 and 0.70 $\mathrm{g\,cm^{-3}}$, respectively (Reyes et al., 1992; Saenger, 2002). These shipworm burrowing patterns are consistent with Paalvast and van der Velde's (2011a) who also found higher shipworm damage in softer fir than in harder oak panels. In addition, oak and mangrove trees produce tannins, a compound known to limit protein availability to organisms consuming their bark and leaves (Hathway, 1958; Robbins et al., 1987; Kimura and Wada, 1989), potentially limiting digestibility of these wood types in shipworms. These results suggest that the tree species used can be a significant driver in the long-term vulnerability of wooden structures in coastal environments.

From the regional study carried out during the second year of this experiment we can see that there can be interannual variability in shipworm activity. One possibility is that patterns seen from one year to the next are a result of the time the experimental branches was deployed. The ladders were in the field for six months (July-January) in experiment 1 and three months (June-September) due to logistical constraints in experiment 2. In their field experiment conducted in Port of Rotterdam, Netherlands, Paalvast and van der Velde (2011a) report that although shipworm larvae were present in the water from April-November, they did not observe infestations in their wooden panels before September. This suggests that shipworm larvae might have been present but the wood was not in the water long enough for larvae to grow, develop, and cause significant, visible damage. These findings also importantly suggest that the timing of when wood gets placed in the water matters. Structures, such as wooden breakwalls, might have a longer life span if they are strategically built around the period of minimum reproductive activity to minimize their larval exposure and thus reduce shipworm boring.

However, as stated previously, shipworms prefer high-salinity environments. This may have also influenced our regional study results given that 2016 experienced higher drought levels and coincident salinity levels in our study sites than 2017. During the 2016 study period, the Palmer Drought Severity Index ranged from −2.73 to −2.06, while during 2017 it ranged from −0.76 to 2.48 (Appendix E1) in this region. Salinities between the two years differed mainly in the minimum values reached. Sites 1 and 2 experienced minimum salinities of 28.6 and 23.2 ppt in 2016, respectively, but these values dropped to 16.2 and 9.7 ppt in 2017 (Appendix E1). It is important then to consider how climate change and other anthropogenic drivers interact to affect the severity and duration of drought, thus creating conditions for persistent shipworm activity.

5. Conclusions: enhancing wooden structure longevity in coastal environments

Barnacle biofouling and shipworm boring preferences seen here can be used to inform the construction of wooden structures in coastal environments, such as wooden breakwalls used as living shorelines techniques. Particularly, understanding how shipworm burrowing varies across different tree species can help identify the optimal building materials that will prolong the life span of these structures. For instance, when selecting filling for wooden breakwalls, choosing tree species with higher wood densities and high tannin content may result in structures that are more resistant to shipworm damage and that may not require as much maintenance compared to lower wood density species. In addition, knowing where shipworm burrowing and biofouling are concentrated along the water column can help predict which will be the most vulnerable areas of wooden structures. With this knowledge, priority can be given to the bottommost 20 cm of wooden structures when maintenance to combat bioerosion is required. Furthermore, being aware of the spatial variability in shipworm boring and biofouling, and of characteristics such as larval delivery to a site, can help determine how long wooden structures will last in a particular area. Knowing if a site has high or low larval delivery can indicate the extent of shipworm damage that can be expected and thus inform the timing of potential maintenance. Also, being aware of the environmental conditions (e.g. drought, decreased river discharge, warmer temperatures) that can create a hospitable environment for shipworms can help coordinate the timing of the deployment of new structures in order to maximize their life span or can dictate maintenance efforts for wooden structures already installed in coastal areas. Finally, treating wooden marine infrastructure at strategic locations (e.g. parts of the structure found near the sediment surface or underground) with easy-to-use materials with minimal environmental risk (e.g. inexpensive adhesive wraps or concrete slurries that prevent biofouling organisms from adhering or burrowing into the surfaces of posts or pilings) can protect areas key to maintaining structural stability. Ultimately, shipworms will be a persistent threat to wood in coastal environments, but a better understanding of the conditions under which shipworm boring occurs can promote a smarter approach to prolonging the life span of wooden structures. Knowing the areas that are vulnerable to shipworm damage and addressing these vulnerabilities through innovative techniques such as combinations of natural and manmade materials can help build more resistant and longer-lasting structures.

Declaration of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2019.03.008.

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