



Material type affects the community composition and abundance of hard-substrate assemblages in a sedimentary Atlantic estuary

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ABSTRACT: Hard-substrate epibionts have an important role in estuaries; they improve water quality, form habitat, and influence food webs. Coastal urbanization converts natural hard substrates (e.g. oyster reefs and rocky shorelines) into artificial structures, which do not support the same hard-substrate communities. Material composition may be a driving factor behind this difference, so interest is growing in how material type can be used to create marine structures that serve an ecological role. However, this research has mainly been restricted to rocky shorelines. We address this gap by asking how material type affects hard-substrate assemblages in a sedimentary Atlantic habitat. We deployed panels of wood, PVC, and 2 different concrete mixes in Galveston Bay, TX, USA, for 3 mo. Unique communities formed on different materials, which may alter ecosystem services if scaled to large development projects. Material type had a limited effect on richness but strongly affected total cover and biomass, both of which are important metrics for ecosystem function. Across all measures, one concrete mix showed the most potential to serve a beneficial ecological role. Our findings highlight the importance of material type in the design of marine structures in sedimentary Atlantic habitats.

KEY WORDS: Reconciliation ecology · Ecological engineering · Marine construction · Sessile invertebrates · Sedimentary coast

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1. INTRODUCTION

Increasing coastal urbanization threatens marine communities, leaving resource managers with the question of how to respond to environmental concerns and the demands of growing cities. Coastal urbanization has coincided with reduced water quality and severe losses in the abundance of estuary species, including oysters, mussels, other habitat-building invertebrates, mobile invertebrates, and fish (Lotze et al. 2006). Coastal infrastructure is forecasted to expand by 50 to 76% over 25 yr (Floerlet et al. 2021). Artificial structures, including groins, riprap, wharves, pontoons, jetties, breakwaters, seawalls, and bulkheads, already occupy over 50% of the coastline in urbanized estuaries and harbors of Australia, Asia,

Europe, and the USA (Dafforn et al. 2015). These structures form novel habitats for hard-substrate epibiotic assemblages, which include barnacles, bivalves, bryozoans, hydroids, polychaetes, sponges, and tunicates. In unmodified habitats, these assemblages typically form on minerals, such as rocky coastlines, and biogenic materials, such as shells (Davis 2009). Anthropogenic structures replace these natural habitats with plastics, concrete, wood, stone, metals, geotextiles, and fiberglass, which possess unique physical and chemical properties (Bulleri & Chapman 2010). With current engineering practices, artificial structures do not compensate for the loss of natural habitats because they support different communities (Connell 2001, Holloway & Connell 2002, Bulleri & Chapman 2004, 2010, Bulleri 2005). This is

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most prominent on sedimentary coasts where artificial structures may almost entirely replace natural hard substrates. For example, oyster reefs, a valuable hard-substrate habitat in sedimentary coasts, have lost 85% of their historic abundance globally (Beck et al. 2011). In sedimentary coasts, native species can be virtually absent from artificial structures, and non-indigenous species (NIS) are 2 to 3 times more abundant than on rocky coasts (Airoldi et al. 2015).

Changes in the abundance and composition of epibiotic assemblages due to urban sprawl and the loss of natural hard substrate are significant because they may negatively affect the valuable ecosystem functions and services these assemblages perform. Most hard-substrate epibionts are suspension feeders (Riisgård & Larsen 2010). They increase particulate settling rates, modify plankton abundance, and cycle nutrients between the plankton and benthos (Kautsky & Evans 1987, Newell et al. 2005, Grabowski & Peterson 2007, Grabowski et al. 2012). Calcifying epibionts produce persistent, complex habitats for mobile epifauna and sessile epibionts and provide refuge from predation and environmental stress (Gutiérrez et al. 2003, Grabowski & Peterson 2007, Commito et al. 2008, Buschbaum et al. 2009, Grabowski et al. 2012, McQuaid & Griffiths 2014, Bruschetti 2019). Epibiotic assemblages are also an important food source for mobile organisms, including commercially valuable fish and crustaceans (Caine 1987, Lin 1991, Grabowski & Peterson 2007, Grabowski et al. 2012).

There is a growing interest in restoring ecosystem function by designing marine structures that serve an ecological role (Dafforn et al. 2015, Dodds et al. 2022). This goal builds on the principles of reconciliation ecology and ecological engineering. Reconciliation ecology is the restructuring of anthropogenic habitats to increase their use by a range of different species (Rosenzweig 2003, Francis 2009, Francis & Lorimer 2011). Importantly, reconciliation is distinct from habitat restoration and rehabilitation because the human functionality of the space is maintained, and there is no intent to return the habitat to a pre-disturbance state (Francis 2009). Ecological engineering can achieve reconciliation by combining the principles of ecology and engineering to create structures designed to function with a specific habitat (Bergen et al. 2001). Dafforn et al. (2015) expanded on ecological engineering, describing 7 goals for 'multifunctional' marine structures: maintaining local native biota, restoring local biodiversity, maintaining regional biodiversity, providing educational and recreational opportunities, maintaining water quality, facilitating carbon storage, and facilitating aquaculture and food

production. On rocky coasts, where natural hard substrates are abundant and persistent, ecologically engineered structures may be designed to simply mitigate the impact of urbanization. However, along sedimentary coasts, where hard substrates, such as oyster reefs, were once more abundant, these structures may act as a surrogate habitat. Ecologically engineered structures can meet many of these goals using complex textures, holes, crevices, or pools to mimic natural habitats (Chapman & Blockley 2009, Browne & Chapman 2011, Chapman & Underwood 2011, Evans et al. 2016, Cordell et al. 2017, Strain et al. 2018a,b, 2020, Bishop et al. 2022). Researchers have also tested 'ecologically active' (Perkol-Finkel & Sella 2014) or 'ecologically optimal' (Dodds et al. 2022) materials, such as concrete mixes containing specific aggregates (e.g. shell, mineral, hemp fiber, coral, and crustose coralline algae rubble) or admixtures (e.g. pozzolans) that promote recruitment (Lee et al. 2009, Neo et al. 2009, Huang et al. 2016, Dennis et al. 2018, Natanzi et al. 2021). However, which materials are more or less favorable for any given community and which material traits promote recruitment is not well understood.

Material choice is therefore a significant factor for marine reconciliation ecology. The settlement and survival of epibiont propagules depends on surface characteristics such as micro- and macro-scale topography, color, wettability or polarity, and specific heat capacity (Taki et al. 1980, Young 1983, Raimondi 1988, Rittschof & Costlow 1989, Fletcher & Callow 1992, James & Underwood 1994, Dahlström et al. 2004, Coombes & Naylor 2012, Dobretsov et al. 2013, Myan et al. 2013). Biological effects, such as biofilm presence and composition, gregarious or solitary behaviors, conspecific chemical cues, predation of larvae by other epibionts, changes in topography, and competition with other species can inhibit or facilitate future settlement (Crisp & Ryland 1960, Connell & Slatyer 1977, Dean & Hurd 1980, Dean 1981, Mihm et al. 1981, Navarrete & Wieters 2000, Tamburri et al. 2008). In this way, the materials chosen in marine construction may continue to influence community composition even after colonization.

Despite the number of settlement studies available, more needs to be understood before material type can be utilized when designing ecologically engineered marine structures. Studies have compared settlement on concrete, plywood, fiberglass, and aluminum (Anderson & Underwood 1994); concrete, wood, and sandstone (Glasby 2000); and a variety of other construction and non-construction materials (e.g. Hanson & Bell 1976, McGuinness 1989, Norris 1991, Ma et al.

2017). Meta-analyses of these studies have proved informative for marine ecological engineering (Schaefer et al. 2021, Dodds et al. 2022). However, due to their different goals, many settlement studies only focused on the abundance of one or a few species (Pomeroy & Weiss 1946, Norris 1991, Hills & Thomason 1996, Lee et al. 2009, Neo et al. 2009, Ma et al. 2017). Most were also performed in regions with significant rocky or coral habitats (Hanson & Bell 1976, McGuinness 1989, Glasby 2000, Glasby et al. 2007, Perkol-Finkel & Sella 2014, Ma et al. 2017). Despite being more threatened by coastal urbanization, few studies compare the communities that develop on construction materials in sedimentary habitats (Anderson & Underwood 1994), and in the Atlantic Ocean, we only know of this being performed by surveying preexisting structures (Layman et al. 2014)

We address this knowledge gap by asking how hard-substrate epibiotic assemblages on wood, polyvinyl chloride (PVC), and 2 different concrete mixes differ in their community composition, cover, biomass, and diversity in Galveston Bay, Texas, USA, a heavily urbanized, sedimentary estuary. We hypothesized that each material would develop a unique community, and abundance and diversity would be greatest on more naturalistic materials that epibionts may be better adapted to use as settlement substrates. Therefore, abundance and diversity would be greatest on wood, moderate on concrete, and lowest on PVC because wood occurs commonly as debris, concrete is similar in composition to shells, and PVC is not physically or chemically similar to any natural substrate and is less structurally complex. Such differences might be used to design marine structures that better support reconciliation ecology principles, offering resource managers another tool to improve ecosystem function in urbanized coasts.

2. MATERIALS AND METHODS

2.1. Study site

We conducted our study in West Galveston Bay, Texas, USA (29° 08' 44" N,

95° 02' 49" W). Galveston Bay is a heavily urbanized sedimentary estuary (Fig. 1). The intertidal area is soft sediment, marsh, or armored with artificial structures (e.g. docks, bulkheads, breakwaters). Oyster reefs were once the dominant hard substrate; however, they are significantly degraded and frequently dredged for fisheries. Galveston Bay lacks a natural rocky substrate, but rocky cultch has been added to many oyster reefs to benefit the commercial oyster industry. Rocky riprap is also used to harden the coastline.

Our study site was a shallow (approximately 2 m deep), sheltered marina in a residential area far from

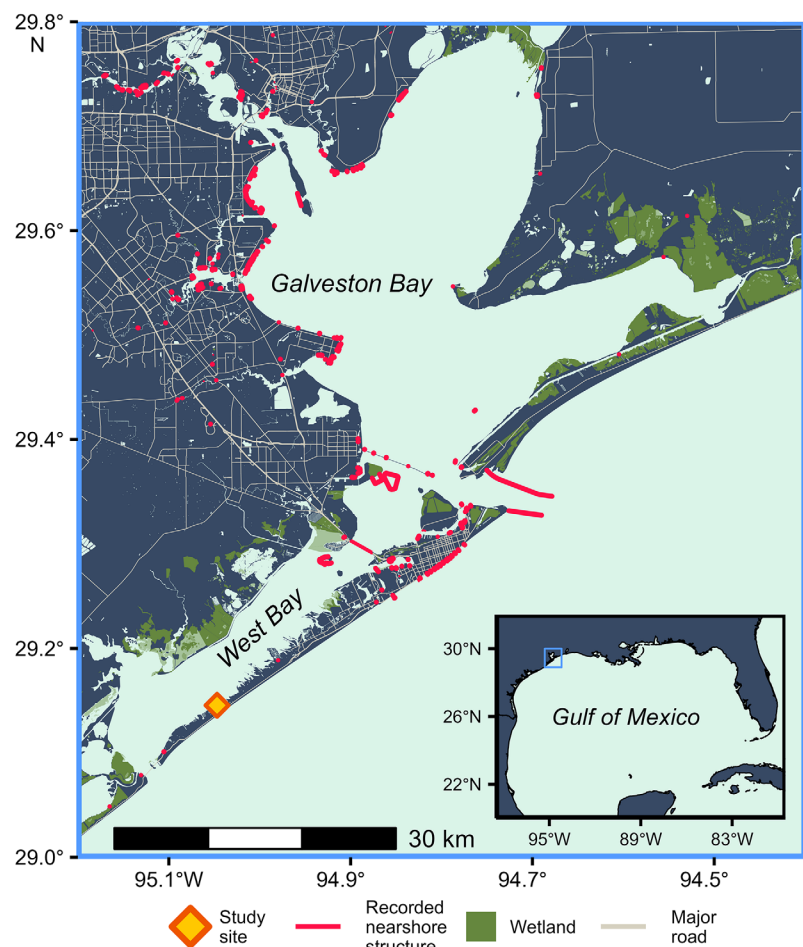


Fig. 1. Study region in Galveston Bay, TX, USA. The blue box in the inset indicates the location within the northern Gulf of Mexico. The study site (yellow and orange diamond) was located in West Galveston Bay. A subset of large-scale nearshore structures, including breakwaters, groins, piers, bridges, marinas, boat launches, and docks, are shown in red (note that other, less well-recorded structures, including bulkheads, are not depicted). The coastline and bodies of water were retrieved from the 2021 US Census Bureau data using the 'tigris' package in R (Walker 2016). The locations of roads, wetlands, and recorded nearshore structures were retrieved from OpenStreetMap™ using the 'osmdata' package in R (Padgham et al. 2017)

any natural or restored oyster reefs. The waterfront included wooden pilings, concrete bulkheads, and aluminum sheet piling, so the local larval supply came from an urbanized area constructed with mixed material types.

2.2. Panel fabrication

We fabricated panels (14×14 cm, $n = 6$ for each material) from untreated, solid pine wood, grey PVC, and 2 different concrete mixes. We then sanded the panels with an orbital sander twice, using a progressively finer grit to control for differences in texture. Although we did not examine the surfaces microscopically (which likely varied based on their different chemical and physical properties), their apparent surface textures were comparable. We chose wood due to its use in pilings and bulkheads and PVC for its use in pile wrappings and sheet pilings for bulkheads. We prepared concrete mix 1 (CM1) using city and state-level construction specifications for bridge substructures and precast concrete, such as dock pilings. We then used the designs of environmentally friendly marine concretes to prepare concrete mix 2 (CM2; Perkol-Finkel & Sella 2014, Huang et al. 2016, Dennis et al. 2018). CM1 contained 10% silica fume, 25% class F fly ash, and 65% type I/II Portland cement by mass. CM2 contained 50% ground granulated blast-furnace slag (GGBS) and 50% type I/II Portland cement by mass. Our concrete mixes did not contain aggregate, sand, or other admixtures to ensure that texture and rugosity were comparable between all materials.

2.3. Sampling

We suspended the panels from a covered, fixed dock from June to September 2021. The panels hung from a weighted line at a depth of 1 ± 0.5 m and ≥ 1 m from neighboring panels to ensure they stayed submerged at low tide, did not touch the seabed, and would not scrape against one another. The panels faced downward to limit algal growth and prevent sediment build-up. This ensured that the communities were dominated by hard-substrate epibionts.

After 3 mo, we collected the panels and analyzed species composition under a high-resolution stereo microscope to assess species richness, diversity, and community composition. We identified organisms to the lowest taxonomic level possible and measured abundance, using guides to visually estimate the

proportion of live cover (Anderson 1986, Dethier et al. 1993). For estimates < 0.01 (1%), we assigned a value of 0.001 (0.1%) to indicate presence. When totaled, the proportion of cover was > 1 (100%) due to organisms growing over one another. We measured wet biomass to the nearest gram by taking the difference in weight before and after scraping the front clean.

2.4. Analysis of community composition

We constructed a 2-dimensional, non-metric multidimensional scaling (2D-nMDS) plot to visualize differences in community composition by material. We tested the effect of material on community composition using a permutational multivariate analysis of variance (PERMANOVA) in PRIMER-e version 7 (Anderson 2017). Prior to running the PERMANOVA with 9999 permutations, we fourth-root transformed the proportion of cover for each taxon to adjust for differences between sparse and dominant taxa, generated a Bray-Curtis dissimilarity matrix, and used a permutational multivariate analysis of dispersion (PERMDISP) test to confirm multivariate homogeneity of variance. We used a similarity percentage (SIMPER) analysis to determine the percent contribution of taxa toward community composition dissimilarities. Data were untransformed to more accurately represent the contributions of the most dominant taxa.

We used R version 4.1.2 to perform all univariate analyses. Before each comparison, we used Levene's test and the Shapiro-Wilk test to determine if the data met the assumptions of homogeneity of variance and normality. We analyzed the effect of material type (factor) on the proportion of cover for 3 functional groups (response variable). Each functional group contained only the species revealed by the SIMPER analysis to contribute $> 5\%$ of the dissimilarities between the assemblages on different materials. The 3 functional groups and species included were: soft-bodied suspension feeders (the kamptozoan or entoproct *Bartensia* sp. and the soft-bodied bryozoan *Amathia imbricata*), calcifying suspension feeders (the barnacles *Amphibalanus eburneus* and *A. improvis*), and mixed-strategy feeders (the polychaete spionid *Polydora cornuta*, which alternates between deposit and suspension feeding). We chose these functional groups based on differences in lifestyle and the ecosystem functions and services they provide. For all 3 comparisons, Levene's and Shapiro-Wilk tests indicated that the data were non-normal

and heteroscedastic. This was not resolved via transformation, so we used a Kruskal-Wallis test to compare the proportion of cover between materials. For significant results ($p < 0.05$), we used a post-hoc Dunn test with a Bonferroni correction (to avoid type 1 errors) to test for differences in cover between factors.

2.5. Analysis of abundance and diversity

We used an ANOVA to test for differences in univariate indices of overall abundance (total proportion of cover and biomass) and diversity (species richness and Shannon-Wiener diversity) between materials. Levene's and Shapiro-Wilk tests showed that the data were normal and homoscedastic for all comparisons of abundance and diversity. For significant results, we tested for differences between factors using a post hoc Tukey's honestly significant difference (HSD) test.

3. RESULTS

3.1. Community composition

Across all panels, we identified 14 hard-substrate taxa, including kamptozoans (entoprocts), bryozoans, barnacles, spionids, mussels, oysters, shipworms, and serpulids. We also observed multiple mobile organisms such as nudibranchs, polychaetes, amphipods, and crabs, although their abundance was not considered for the analysis. Visualization of the data via a 2D-nMDS plot indicated large differences in community composition between materials. Communities on CM2 were very similar to one another as suggested by the limited spread of the points in Fig. 2, and CM2 communities appeared most similar to those on PVC and CM1. The PERMANOVA indicated that community composition differed between materials (data 4th-root transformed, pseudo- $F_{3,20} = 6.8$, $p(\text{perm}) < 0.001$). All pairwise comparisons of community composition between materials differed, excluding that of CM1 against CM2 ($p = 0.089$) and CM2 against PVC ($p = 0.28$, Table 1).

In the SIMPER analysis (data untransformed), 5 taxa contributed $> 5\%$ toward the dissimilarity in community composition between materials: *Bartensia* sp., *Amathia imbricata*, *Amphibalanus eburneus*, *A. improvisis*, and *Polydora cornuta* (Table 2). These species also tended to be the most dominant taxa on all panels.

In univariate analyses, the proportion of cover for each functional group differed between materials

(Fig. 3, Table 2). Soft-bodied suspension feeders (*Bartensia* sp. and *A. imbricata*) covered a greater area of CM1 and CM2 panels than wood (Kruskal-Wallis, $\chi^2 = 19.94$, $df = 3$, $p < 0.001$). Calcifying suspension feeders (*A. eburneus* and *A. improvisis*) covered a greater area of CM1 panels than CM2 (Kruskal-Wallis, $\chi^2 = 8.79$, $df = 3$, $p = 0.032$). Mixed-strategy feeders (*P. cornuta*) covered a greater area

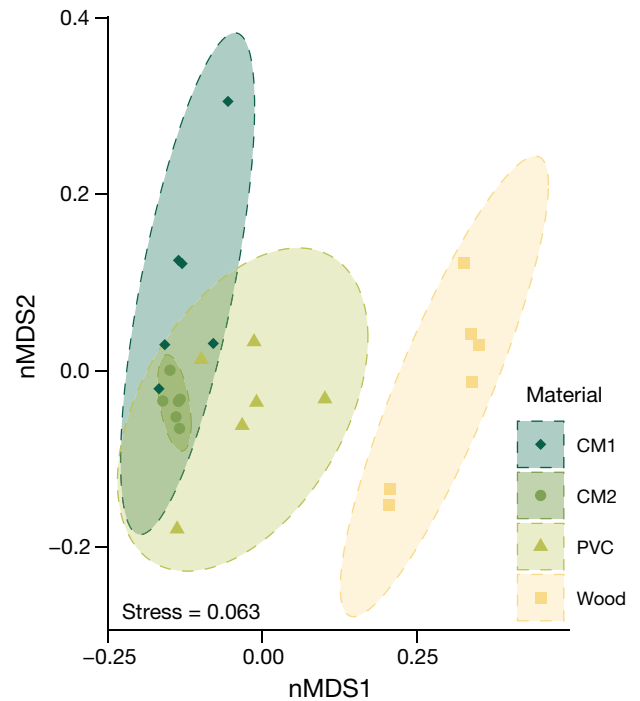


Fig. 2. Two-dimensional, non-metric multidimensional scaling (2D-nMDS) plot showing the ordination of hard-substrate community composition in relation to material type. The closer 2 points are, the more similar their community compositions are. This plot is based on an untransformed Bray-Curtis dissimilarity matrix of the proportion of cover of each taxon. $n = 6$ for all materials; CM1 (CM2): concrete mix 1 (concrete mix 2; see Section 2.2 for details)

Table 1. Results of the pairwise permutational multivariate analysis of variance (PERMANOVA) comparing community composition (fourth root transformed taxa coverage) between different construction materials in a sedimentary Atlantic habitat. CM1 (CM2): concrete mix 1 (concrete mix 2; see Section 2.2 for details)

Comparisons	t	$p(\text{perm})$	Unique perms
CM1 vs. CM2	1.69	0.089	462
CM1 vs. PVC	1.83	0.026	462
CM1 vs. Wood	4.025	0.002	461
CM2 vs. PVC	1.15	0.28	462
CM2 vs. Wood	3.048	0.002	461
PVC vs. Wood	3.19	0.002	462

Table 2. Results of the similarity percentage (SIMPER) analysis using the untransformed community composition (taxa coverage), and the mean \pm SE proportion of cover for taxa that contributed $>5\%$ to the dissimilarity between materials. Taxa were grouped into functional groups: soft-bodied suspension feeders, calcifying suspension feeders, and mixed-strategy feeders for further comparisons. CM1 (CM2): concrete mix 1 (concrete mix 2)

	— Soft-bodied suspension feeders —		— Calcifying suspension feeders —		Mixed-strategy feeders
	Bryozoan <i>Amathia imbricata</i>	Kamptozoan <i>Bartensia sp.</i>	Barnacle <i>Amphibalanus eburneus</i>	<i>Amphibalanus improvisis</i>	Spionid <i>Polydora cornuta</i>
Percent contribution					
CM1 vs. CM2	28.08	23.2	23.1	17.1	—
CM1 vs. PVC	24.15	36.37	16.5	12.3	8.68
CM1 vs. Wood	32.24	42.11	9.86	7.68	6.79
CM2 vs. PVC	38.95	24.59	13.53	9.59	8.96
CM2 vs. Wood	46.61	33.91	8.54	—	6.28
PVC vs Wood	45.57	31.34	12.09	5.09	5.06
Mean \pm SE					
CM1	0.4 \pm 0.022	0.49 \pm 0.024	0.083 \pm 0.012	0.033 \pm 0.011	0.04 \pm 0.0
CM2	0.45 \pm 0.0	0.45 \pm 0.0	0.045 \pm 0.005	0.0083 \pm 0.0065	0.035 \pm 0.0034
PVC	0.4 \pm 0.022	0.41 \pm 0.015	0.053 \pm 0.011	0.015 \pm 0.0072	0.02 \pm .0026
Wood	0.27 \pm 0.011	0.32 \pm 0.01	0.062 \pm 0.016	0.0035 \pm 0.0033	0.012 \pm 0.0059

of CM1 panels than PVC and wood (Kruskal-Wallis, $\chi^2 = 15.24$, $df = 3$, $p = 0.002$).

3.2. Abundance and diversity

Abundance and diversity also differed between materials (Fig. 4). Assemblages on CM1 and CM2 covered a greater total proportion of the panel than PVC and wood (ANOVA, $F_{3,20} = 95.22$, $p < 0.001$), and the wet biomass of CM1 panels was greater than all other materials (ANOVA, $F_{3,19} = 6.89$, $p = 0.003$). CM1 communities were richer than those on wood (ANOVA, $F_{3,20} = 3.65$, $p = 0.03$), but there was no difference in the Shannon-Wiener index.

3.3. Non-indigenous and nuisance species

We identified 3 non-indigenous species (NIS), all below 1% cover when present. These included the bryozoan *Hippoporina indica* and the serpulids *Ficopomatus enigmaticus* and *F. uschakovi* (Fofonoff et al. 2023). *H. indica* was present on 1 of 6 CM1 panels, and *F. enigmaticus* was present on 1 of 6 CM2 panels. We found *F. uschakovi* on all CM1, 2 CM2, and 3 PVC panels. No serpulids, native or non-indigenous, were found on wood panels.

Shipworms were present on 4 of 6 wood panels with a cover below 1%. At the time of recovery, the shipworms were too small to extract from the wood for identification. It is unknown if the shipworms found

were non-indigenous; however, as borers of marine structures, they are generally considered a destructive nuisance species.

4. DISCUSSION

This is the first settlement study we are aware of to test how hard-substrate epibiotic communities vary on different construction materials in a sedimentary Atlantic habitat. We compared communities on untreated, solid pine wood, PVC, and 2 different concrete mixes. CM1 contained silica fume and class F fly ash, and CM2 contained GGBS. Our results show that material type greatly affected community composition, the abundance of 3 functional groups, total cover, and biomass, but not richness or diversity. This suggests that material type may be an important factor when designing structures in sedimentary Atlantic habitats to support reconciliation ecology goals.

As predicted, material type strongly affected the community composition and biomass of hard-substrate epibionts. Differences in community composition and biomass may be directly tied to ecosystem functions that are considered highly desirable in habitat reconciliation and ecological engineering, such as supporting trophic exchange and fisheries, increasing habitat structure, and maintaining water quality (Francis 2009, Layman et al. 2014, Dafforn et al. 2015, O'Shaughnessy et al. 2020). All 3 functional groups that contributed toward dissimilarities in community composition — soft-bodied suspension feeders

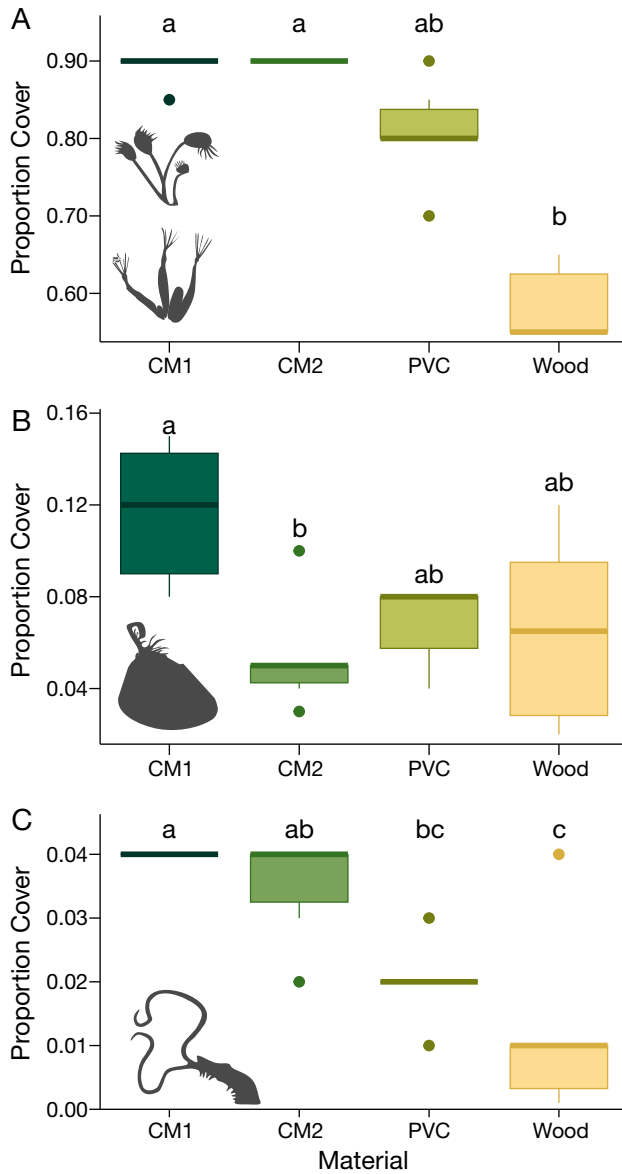


Fig. 3. Proportion of cover of the 3 functional groups: (A) soft-bodied filter feeders (*Bartensia* sp. and *Amathia imbricata*), (B) calcifying filter feeders (*Amphibalanus eburneus* and *A. improvisis*), and (C) mixed-strategy feeders (*Polydora cornuta*), found to contribute $>5\%$ to dissimilarity in the similarity percentage (SIMPER) analysis. Bar: median; box: interquartile range (IQR); whiskers: max./min. value within $1.5 \times$ IQR above/below box; points: outliers. Within each plot, the letters above boxplots indicate a significant difference in cover between materials (Dunn's post hoc with Bonferroni correction, $p < 0.05$). All materials had $n = 6$ replications

(the kamptozoan *Bartensia* sp. and the soft-bodied bryozoan *Amathia imbricata*), calcifying suspension feeders (the barnacles *Amphibalanus eburneus* and *A. improvisis*), and mixed-strategy feeders (the polychaete spionid *Polydora cornuta*) — were more abundant on CM1 than on at least one other material.

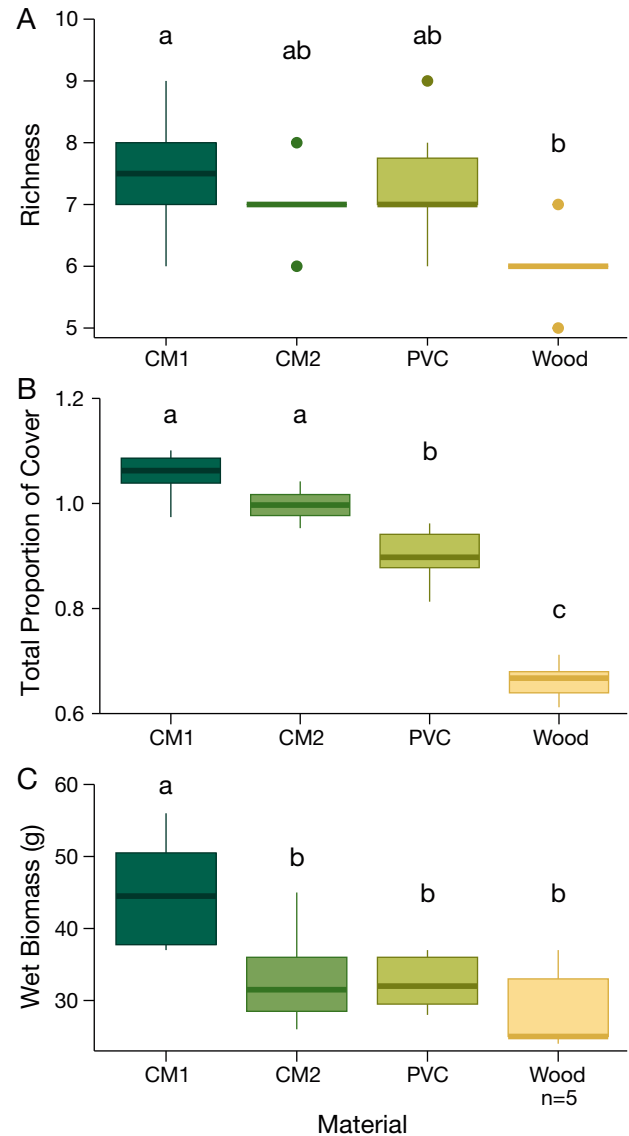


Fig. 4. Comparisons of (A) richness, (B) the total proportion of cover, and (C) wet biomass between materials. Boxplot parameters as in Fig. 3. Within each plot, the letters above boxplots indicate a significant difference between materials (Tukey's honestly significant difference test, $p < 0.05$). $n = 5$ for the wet biomass of wood; $n = 6$ for all other materials and comparisons

Bryozoans and kamptozoans are the primary prey for many small mobile invertebrates, such as nudibranchs, pycnogonids (and other small arthropods), turbellarians, polychaetes, and nematodes, so they may help to support trophic exchange (Canning & Carlton 2000, Lidgard 2008). Spionids experience frequent sublethal predation, which constitutes a significant portion of the diet of many fishes and macroinvertebrates, so their presence may support fisheries at larger scales (De Vlas 1979, Woodin 1982). The persistent struc-

tures produced by barnacles also form critical habitat for mobile organisms in sedimentary coasts (Barnes 2000, Mendez et al. 2015). Additionally, all 3 functional groups filter the water, suggesting that structures made from CM1 may support a greater water filtration capacity than the other materials we tested (Bullivant 1968, Frithsen & Doering 1986, Zhukova 2000, Riisgård & Larsen 2010). This is consistent with surveys of preexisting dock pilings in a sedimentary Atlantic estuary (Florida, USA) by Layman et al. (2014), who found that unique communities formed on different materials, and communities on concrete filtered a greater quantity of water than those on PVC and wood. Although we did not quantify filtration rates, biomass, an indicator of the productivity or metabolic activity of a community, was also greater on CM1 panels than on all other materials, meaning CM1 assemblages may have converted a greater quantity of plankton and particulate organic matter into benthic animal biomass (Whittaker 1965, Wilson 1991, Chiarucci et al. 1999, Malerba et al. 2019). Our results suggest that material type may impact the productivity of mobile communities, habitat structure, and water filtration capacity at larger scales.

Material type had a weak effect on species richness and no effect on biodiversity. This is consistent with a meta-analysis by Dodds et al. (2022), which found that material type impacts the abundance but not the richness of assemblages. However, material type did affect species coverage and may have affected NIS presence, both important traits for maintaining local biodiversity, which is valued in ecological engineering (Dafforn et al. 2015). To maintain biodiversity, populations must persist over time (Groves et al. 2002). Many hard-substrate epibionts experience a mate-finding Allee effect, meaning reproductive success may be seriously reduced on materials with low population densities. Gametes become increasingly dilute as they diffuse away from broadcast spawners, and species with internal fertilization may require a conspecific nearby to reproduce (Levitán & McGovern 2005, Gascoigne et al. 2009, Velazquez-Castro & Eichhorn 2017). For example, the barnacle *Amphibalanus improvisus*, which reproduces via internal fertilization, was only present on 2 wood panels and 2 CM2 panels, with an average cover below 2% when present. This species may only be able to reproduce through self-fertilization when on wood and CM2 structures (Furman & Yule 1990, Velazquez-Castro & Eichhorn 2017). Materials with higher species coverage, like CM1, may be more likely to produce a greater quantity of genetically diverse larvae (another valuable dimension of diversity), which can settle on other

structures or contribute back to the native population, thus maintaining local biodiversity. However, this level of interconnectedness can be problematic if it assists the invasion of NIS. Although richness was greater on CM1 than on wood, after removing NIS, there was no difference in local richness. NIS occurred more frequently on concrete and PVC than wood in a pattern consistent with Dodds et al. (2022). However, the abundance of NIS in our study may be too low (<1% cover) to draw a strong connection between NIS presence and material type. NIS are generally prevalent on infrastructure in sedimentary coasts (Airoldi et al. 2015) but have a low abundance in Galveston Bay (Jurgens et al. 2022). The high variability in salinity and temperature in this region may prevent NIS from becoming established despite the frequent vessel transit (Jurgens et al. 2022). The effect of material type on NIS prevalence should be considered more closely, especially in other more vulnerable sedimentary Atlantic systems. Our results indicate that material type may be important for maintaining biodiversity or limiting NIS presence.

Contrary to our prediction, there was no apparent association between the naturalness of a material and the abundance and diversity of hard-substrate epibionts. The mechanisms behind this observation are not fully understood. Despite being common as debris, wood had the lowest cover and biomass of any material. The reason for this is not well studied as much more effort has been put into antifouling research than determining what properties wood may have that limit recruitment (Treu et al. 2019). The low surface energy of PVC (the low intermolecular force of attraction between the surface of PVC and other materials) or hydrophobicity may have contributed to the decreased recruitment of certain species (Rittschof & Costlow 1989, Dahlström et al. 2004, Li et al. 2016), and leachates from PVC are also more toxic than those from other plastics (Bejgarn et al. 2015, Li et al. 2016, Hermabessiere et al. 2017, Sarker et al. 2020, Gewert et al. 2021). PVC is 15–50% phthalate by weight (Gilbert 2001). Phthalates, a plastic additive, are not chemically bound to the polymer, leach easily, and act as endocrine disruptors even at low concentrations (Oehlmann et al. 2009, Net et al. 2015). Concrete may have been a more favorable substrate because of its similarity in composition to shell or stone, but each concrete mix did not perform equally well. Calcium hydroxide in concrete may act as a settlement cue for calcifying organisms, but the coverage of calcifying suspension feeders only differed between CM1 and CM2 (Anderson 1996). It has been proposed that admixtures affect recruitment by

decreasing the pH of concrete (Dooley et al. 1999). However, the pH of standard concrete does not differ from that of seawater after 3–6 mo (Dooley et al. 1999), and when only the pH of concrete is altered, there is no difference in the community composition, cover, or richness of epibiotic assemblages (Hsiung et al. 2020). Admixtures also change the profile and abundance of toxic metals leached from concrete. McManus et al. (2018) reported that, at equal replacement levels, GGBS concrete (like CM2) leached more zinc than fly ash concrete (like CM1) and standard concrete. At replacement levels comparable to our own, Togerö (2006) found that GGBS concrete leached more zinc and copper than fly ash concrete. Zinc and copper are toxic to hard-substrate invertebrates and larvae, which may explain the differences in recruitment (Clarke 1947, Rainbow 1985, Devi 1995). However, there are many caveats to this conclusion. (1) Metal content and leachability vary considerably between admixture sources, so we cannot confirm if it played a role here (Togerö 2006, Müllauer et al. 2015, McManus et al. 2018). (2) Metal ion speciation is more significant in determining bioavailability and toxicity than the total abundance of a metal (van Veen et al. 2001). (3) The copper and zinc leaching rate of GGBS concrete is orders of magnitude lower than that of antifouling paints, so given adequate tidal exchange, concretes are less likely to form a toxic boundary layer at the water–surface interface (Togerö 2006, Ytreberg et al. 2010, Lagerström et al. 2018, Lindgren et al. 2018). (4) Since most metal leaching occurs at the surface of concrete, differences in metal concentrations become insignificant over time (Hillier et al. 1999, Lagerblad 1999, Jain & Neithalath 2009, McManus et al. 2018). Metal leaching is also an inadequate explanation for the difference in the cover of calcifying suspension feeders between CM1 and CM2 because *A. eburneus* and *A. improvisis* are early colonizers of failing metal-based antifouling paints (Weiss 1947). Material traits may also interact with a variety of environmental qualities such as season, salinity, dissolved oxygen, pollutant presence, temperature, and alkalinity to affect hard-substrate communities (Mook 1980, Mayer-Pinto & Junqueira 2003, Jewett et al. 2005, Brown et al. 2016, Lord 2017). Future studies considering which material and environmental traits drive differences in epibiont settlement would be useful to further inform reconciliation-focused engineering.

Potential caveats to this study include the duration and relatively modest sample size ($n = 6$ per material). A larger sample size may have revealed a stronger effect of material type on richness or other commu-

nity variables. Our experiment of 3 mo was also comparatively short, although many of the study organisms can experience multiple life cycles over a single season. Assemblages on different construction materials have been observed to converge relatively quickly (e.g. 4–5 mo; Anderson & Underwood 1994) or maintain their differences for longer periods (Glasby 2000). However, our results were comparable to Layman et al. (2014), who surveyed preexisting structures of various ages in a sedimentary Atlantic estuary. This suggests that material type may have a persistent effect on hard-substrate assemblages in this ecosystem. If materials follow separate successional trajectories, material type may be used to select communities most similar to the natural habitat. However, it is unlikely that any of the materials we tested had a similar composition to the natural community. Although we did not make comparisons between panels and natural hard-substrate habitats, 2 species common on oyster reefs in Galveston Bay had a notably low abundance or were absent from panels: the dark false mussel *Mytilopsis leucophaeata* and the sea-grape tunicate *Molgula manhattensis*. This may be caused by the intense predation pressure these species experience in this region (Jurgens et al. 2022). This emphasizes that material type alone is unlikely to achieve a community that mimics the natural habitat, and it should be used in combination with more complex structural designs that provide refugia.

Despite these limitations, our findings indicate that material type may affect community composition and abundance, multiple ecosystem functions, and the maintenance of local biodiversity. Of the materials tested, CM1 showed the greatest potential for use in ecological engineering. We recognize that marine structures cannot be used as a replacement for healthy natural habitats and may facilitate the spread of NIS (Airoldi et al. 2015). However, as urbanization continues to convert the coastline into artificial structures, we highlight the potential for resource managers to select materials that provide the greatest ecological benefit.

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