

Artificial structures versus mangrove prop roots: a general comparison of epifaunal communities within the Indian River Lagoon, Florida, USA

Dean S. Janiak^{1,*}, Richard W. Osman², Christopher J. Freeman¹, Valerie J. Paul¹

¹Smithsonian Marine Station, Ft. Pierce, Florida 34949, USA

²Smithsonian Environmental Research Center, Edgewater, Maryland 21037, USA

ABSTRACT: Urbanized coastal landscapes are becoming increasingly widespread throughout the world, and as a result, essential habitat is being replaced with artificial structures. Mangroves are threatened globally, and crucial ecosystem functions are being lost (e.g. habitat/refuge for associated species). There remains a lack of understanding of how artificial structures function as habitat compared to natural substrates, particularly those being lost, such as mangrove prop roots. The objectives of this study were to compare benthic epifaunal communities on artificial structures to those on mangrove prop roots across a large spatial scale and to assess seasonal trends of colonizing species within each habitat. Identified species were also classified as either native or non-native to assess whether artificial structures harbor more non-natives compared to mangroves. Results indicated that community composition differed significantly between habitat types, as did richness and diversity. More species were found and in higher percent cover on artificial structures. Only a few species were dominant throughout the study and were present in both habitats, and these species varied in their abundance across sites and time. Colonization at all sites was continuous throughout each season, particularly for those dominant species. Non-native species richness made up 30–50% of the community composition in each of the habitats and was significantly higher on artificial structures. Overall, artificial structures appeared to provide a functional, unique surface for both dominant and rare species and could act as a buffer to biodiversity loss in mangroves, a globally threatened habitat.

KEY WORDS: Artificial structures · Mangroves · Indian River Lagoon · Non-native · Epifauna

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INTRODUCTION

Over the last several decades, humans have drastically altered the coastal marine landscape (Bulleri & Chapman 2010, Gittman et al. 2015). With nearly one-third of the human population living within 100 km of the shoreline, rapid urban sprawl is resulting in concomitant losses of vital natural habitat and ecosystem services (Gittman et al. 2016). Such losses are not habitat-specific and include seagrass beds (Orth et al. 2006), oyster reefs (zu Ermgassen et al. 2012), coral reefs (Bellwood et al. 2004), and mangrove forests (Alongi 2002), with much of the damage resulting

from anthropogenic influences. Of these threatened ecosystems, mangrove forests are a unique foundational species found along the coastal shore throughout the tropics, supporting marine and terrestrial biodiversity at all trophic levels (Kathiresan & Bingham 2001). Mangroves are globally threatened by a variety of human activities, including aquaculture construction, timber harvesting, and coastal development (Alongi 2002). Over the past 4 decades, there has been a steady global decline in mangrove forests, with an estimated loss of 35% (Valiela et al. 2001). The worldwide destruction of mangrove forests is a major concern because they offer a diverse set of eco-

*Corresponding author: janiakd@si.edu

system provisions, including raw materials for humans, coastal protection from storms, and habitat for a variety of terrestrial and marine species in shallow water environments (Barbier et al. 2011). Specifically, prop roots and pneumatophores of some species extend into the water column and provide a complex, 3-dimensional hard substrate for a diverse suite of invertebrates and a vital refuge for many juvenile fish species (Nagelkerken et al. 2008).

Coastal ecosystems are also threatened by the construction of artificial structures, which in most cases replace natural shoreline, and can have local and regional ecological consequences. Artificial structures are implemented to harden coastal areas for protection of property against erosion, storms, flooding, sea-level rise, or for recreation, and are rarely built using ecological engineering which could reduce adverse impacts to the environment (Dafforn et al. 2015). The inclusion of artificial structures in the marine environment is a global problem and is only expected to increase. In the US alone, over 14% of the shoreline has been modified to some degree, with the majority occurring in sheltered lagoons and estuaries (Gittman et al. 2015). Because of the ubiquity of artificial structures throughout the world, there has been a recent interest in how these hard structures function as habitat for marine species. These additions provide a novel substrate in systems that are typically dominated by soft sediments. Natural hard surfaces such as rocky or coral reefs, oysters, and mangrove prop roots are the primary habitat for a highly diverse suite of encrusting and mobile invertebrates and algae. In areas where both natural and artificial habitat are present, comparisons between habitats are critical to better understand the potential negative effects of habitat displacement. This is important in predicting how continued shoreline hardening and the loss of natural habitat will affect the biodiversity and function of estuaries and coastal shores.

Comparisons of marine communities in natural and artificial habitats have shown that they are strongly dissimilar and vary in their species abundance and composition (Connell & Glasby 1999, Connell 2001, Smith & Rule 2002). Communities on artificial structures tend to be less diverse than those of natural hard substrates (Bacchiocchi & Airoidi 2003, Chapman 2003, Moschella et al. 2005). Differences in community composition between substrate types can be due to differing ecological processes. For example, artificial structures are found at different heights within the water column (Connell 2001), have a unique orientation, and are typically constructed of

novel materials, all of which can influence recruiting species and community composition (Glasby & Connell 2001, Bulleri & Chapman 2010). Artificial structures tend to favor large populations of non-native species (Lambert & Lambert 2003, Glasby et al. 2007, Tyrrell & Byers 2007, Airoidi et al. 2015) that are often well adapted to exploit open space (Simkanin et al. 2012). These structures can also enhance dispersal abilities, acting as a stepping stone for non-natives to increase their spread (Bulleri & Airoidi 2005). This, along with a general reduction in native predators associated with artificial structures, can have strong impacts on community development and overall community composition (Oricchio et al. 2016, Rogers et al. 2016).

In the Caribbean, southern Florida, and throughout the Gulf Coast, mangroves are a common component of the shoreline and provide a unique, critical habitat for many marine species. Throughout this region, *Rhizophora mangle* is the dominant mangrove species with prop roots that extend into the subtidal, providing refuge for fish and substrate for a diverse suite of invertebrates. Epifaunal communities on *R. mangle* have been well-studied in the Caribbean and shown to positively affect tree growth (Ellison et al. 1996), provide protection from infesting species (Ellison & Farnsworth 1990), and enhance overall ecosystem productivity (Nagelkerken et al. 2008). The northern range of this species is limited by thermal tolerance to freezing and extends to the northern border of Florida (Cavanaugh et al. 2014). Within the Indian River Lagoon (IRL), a subtropical estuary along the eastern shore of central Florida, mangrove forests are a significant component of the coast; however, as of 2007, 39% of the shoreline has been urbanized (Bricker et al. 2007). The IRL has also been subjected to a variety of other human-induced stressors, including water quality reduction, significant loss of seagrass beds, and continued algal blooms (Fletcher & Fletcher 1995, Nixon 1995, Lapointe et al. 2015), all of which have had lasting effects on the ecosystem. The IRL is one of the most species-rich estuaries in North America (Swain et al. 1995); however, there exists very little data on the epifaunal communities associated with *R. mangle* roots. There is also a general lack of data on established communities of marine species associated with artificial habitats in most parts of the world, including the IRL. The objectives of the study were to (1) examine and compare the spatio-temporal trends of community composition and percent cover of different species in mangrove and artificial habitats within the IRL, (2) examine and compare the seasonal colonization of

epifaunal species in the 2 different habitat types using recruitment panels, and (3) identify and compare native and non-native species presence within each of the habitats.

MATERIALS AND METHODS

Study region

The IRL is a shallow, narrow lagoon along the central eastern coast of Florida, USA, and serves as a transitional area between temperate and subtropical zones (Fig. 1). It is comprised of 3 connected main water basins, the Mosquito Lagoon, the Indian River, and the Banana River, which together span a distance of 251 km from Ponce de Leon Inlet south to Jupiter Inlet. The width of the lagoon varies from 2 to 4 km, and it has a depth range of approximately 1–3 m

(Woodward-Clyde Consultants 1994). The IRL has 5 inlets that allow estuarine/oceanic mixing to occur, while a 6th, located at a study site in Port Canaveral (Site B_03, see Fig. 1), is isolated from the lagoon by an on-demand lock system. Besides B_03, all other sites are estuarine and located relatively far from inlets (Fig. 1). Tides are semi-diurnal and the tidal amplitude is approximately 10–30 cm, with larger tides occurring closer in proximity to the inlets. Where the shoreline has not been modified, mangrove forests tend to dominate throughout the Indian and Banana Rivers, becoming less abundant in the Mosquito Lagoon. There is no strong salinity gradient throughout the IRL, but salinity is variable in certain regions resulting from proximity to oceanic and freshwater inputs and seasonality. Environmental data including water temperature, salinity, and relative chlorophyll concentrations, gathered from the St. Johns Water Management District (<http://webapub.sjrwmd.com/agws10/hdswq/>), were monitored continuously from 3 sites (close proximity to Sites M_06, IRL_02, and B_02) during the project within the study region (Fig. 2).

Seasonal sampling of epifaunal communities

Sampling was conducted on a quarterly schedule from October 2014 to July 2016 (8 sampling events). Each sampling event occurred during a particular season: October (fall), January (winter), April (spring), and July (summer). Twenty-nine sites spanning 150 km of the central and northern portions of the IRL were haphazardly chosen based on substrate type (either mangrove prop roots or artificial structures) and to account for a balanced coverage within the study region. Eighteen sites, found in all 3 water basins, consisted of artificial habitat, and the other 11 sites, found in 2 of 3 water basins, consisted of dense *Rhizophora mangle* stands (Fig. 1). All sites chosen had epifaunal communities that were subtidal and only exposed during the lowest tides of the year. There were no mangrove sites in the Mosquito Lagoon, as *R. mangle* stands are infrequent in this area, and those that are present lack dense subtidal roots. Artificial structures consisted of either wood pilings or seawalls constructed of concrete. Seawalls were either the bridge abutments (roughly 200 m in length) or supporting bridge pilings (<50 m in length). The timing of construction for artificial structures could not be estimated, although all sites chosen appeared to have well-established epifaunal communities. Despite differences in construction materials, the same methodology was used for data collection in this habi-

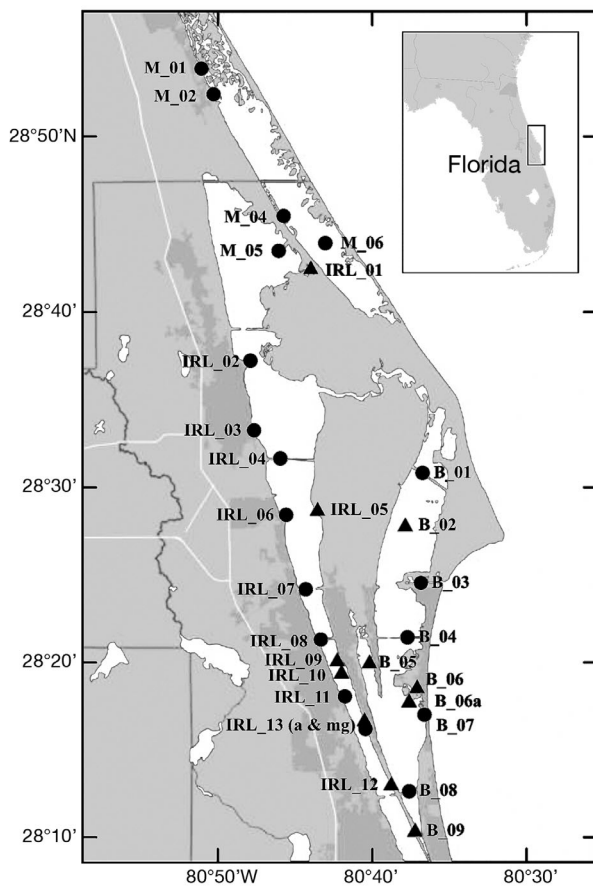


Fig. 1. Study region within the Indian River Lagoon (inset: Florida). Letters for each site indicate the corresponding water body (M = Mosquito Lagoon, IRL = Indian River, B = Banana River). Symbols designate habitat type (circle = artificial habitat site, triangle = mangrove site). Environmental data were collected in close proximity to Sites M_06, IRL_02, and B_02

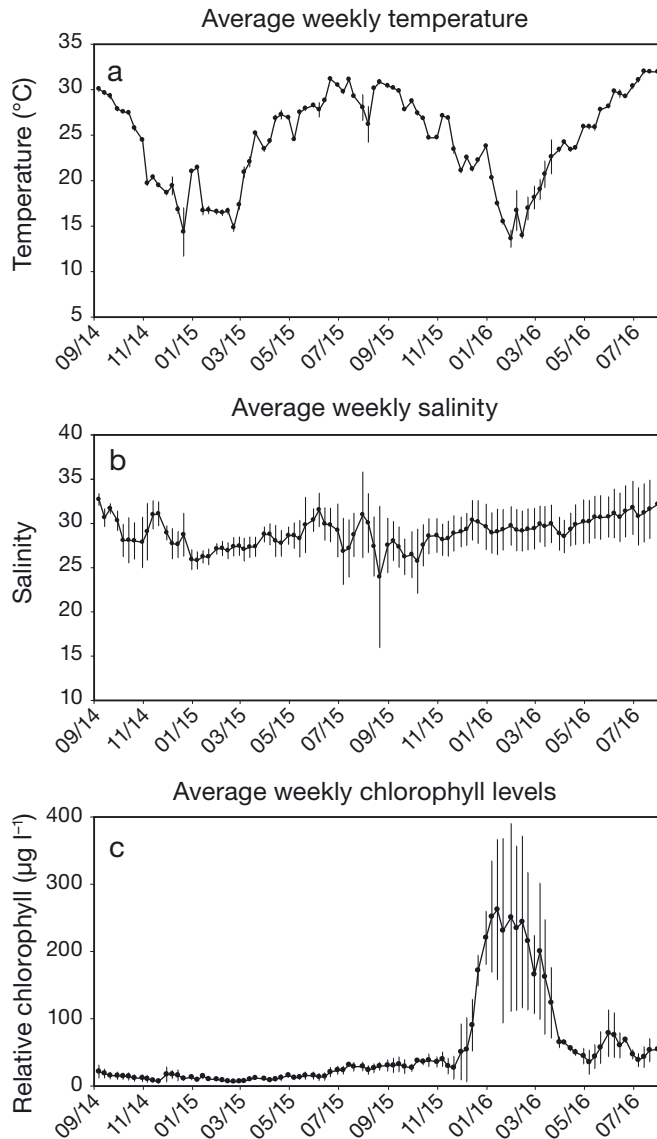


Fig. 2. Environmental measurements for (a) temperature, (b) salinity, and (c) chlorophyll levels taken daily and then averaged by week and averaged from 3 stations within the range of the study region. Error bars indicate ± 1 SE. Dates are mo/yr

tat type. At each of the artificial structure sites, a Go-Pro video camera (1080p resolution [1920 \times 1080 pixels], 60 frames s^{-1} [fps]) was used to record vertical video transects of sessile epifaunal communities. The camera was attached to an L-shaped PVC frame and set at a fixed distance (25 cm) away from the substrate such that the same amount of area was recorded each time. The shaft of the frame was 2 m long, and when handled from a boat, could record communities approximately 1.5 m below the water level, which corresponds to mean depth of the IRL.

Transects approximately 1 m in length were taken vertically to the sediment surface along 3 separate

pilings at each site during each sampling event. At sites with a seawall, triplicate transects were taken vertically to mimic video taken of pilings and were separated from each other by at least 1 m. Epifaunal collections were also taken within each transect using a standard garden hoe and communities of approximately 200–300 cm^2 were scraped off the surface. Detached communities were collected into a 5 mm mesh net held below the scraped area. Samples were not rinsed or sieved and were immediately placed in separate bags, put on ice, and brought back to the laboratory for species identification and to account for rare or small species not visible in the video. There was no visible species loss resulting from the mesh size used. From the video, a single screen capture was taken from each transect that was both of high resolution and representative of the surrounding community. A 250 cm^2 frame was placed around each screen capture, and percent cover was estimated using 100 randomly assigned points using the point-count software CPCe 4.1 (Kohler & Gill 2006). At mangrove sites, the ends of 3 subtidal prop roots with epifauna were cut at a standard size (25 cm in length, roughly an area of 250 cm^2) and brought back to the laboratory, where each root was photographed for a permanent record and examined under a dissecting microscope. All invertebrates present were identified and a visual estimate of percent cover (0–100) was made.

Quarterly sampling of colonizing species

Colonization panels were deployed during the same intervals as seasonal sampling to measure seasonality of recruiting epifaunal species over time and between habitats. When samples were first collected (October 2014), a set of colonization panels (100 cm^2 , PVC) were deployed in triplicate at 24 of the 29 sites. Five sites were not used because of a lack of usable structure from which to deploy panels. Because of the variation of habitat structure and construction at each of the sites, colonization panels were hung in a variety of configurations to optimize retrieval and stability. At artificial structure sites, panels were either hung from a dock, with the colonization surface facing downward, or wrapped around a piling, with the colonization surface facing outward. At mangrove sites, individual panels were attached to subtidal prop roots with the colonization surface facing outwards. Regardless of habitat type or orientation, all panels were hung at the same distance from the bottom where seasonal samples were taken for

each of the sites. At each quarterly sampling event, panels were collected, placed into bags, and put on ice with new panels being simultaneously deployed. Panels were brought back to the laboratory, photographed, and examined under a dissecting microscope for species identification. Diversity, community composition, and percent cover of epifaunal species was estimated from photographs as described above (see previous subsection) and used as a proxy for colonization.

Statistical analysis

Similar statistical methods were used for video transect and colonization panels to examine differences in communities. For all analyses, sites for each particular habitat type were used as replicates for each season to get a robust estimate of community composition. Included in all community analyses was the response variable open space, an important limiting factor in sessile benthic communities and a useful measure of seasonality. Differences between the 2 types of habitat (artificial and mangrove) as well as how those differences varied over time were then compared. To visually examine similarity of community composition over time and between the 2 habitat types, non-parametric multi-dimensional scaling (nMDS) was used. An nMDS analysis was also conducted for each individual sampling event to examine specific site differences over time. To examine differences in the abundances of percent cover in community composition, a non-parametric multivariate analysis of variance (PERMANOVA) was used to test the factors habitat and season. When the interaction between habitat and season was significant, an analysis of similarity (SIMPER) was used to examine what particular species contributed the most dissimilarity between the 2 habitat types for each season (i.e. seasonal differences in species). For those species that were found to be important or dominant within the overall study, a separate 2-way ANOVA was used to examine differences in percent cover for the factors habitat and season. To test for differences in richness and Shannon-Wiener diversity within communities, a 2-way ANOVA was used for the factors habitat and season. A 2-way ANOVA was also used to test for differences in habitat and season for richness and Shannon-Wiener diversity for colonizing species during each quarterly sampling event. When the interaction term was significant, a Student-Newman-Keuls pairwise comparison test was used to examine differences between habitat types for each season.

A separate analysis was conducted for 2 sites, IRL_13mg (mangrove) and IRL_13a (artificial) (see Fig. 1), which were within 10 m of each other, to examine communities between habitat types at a very small spatial scale. The artificial habitat was a small dock (5 m) with a few wooden pilings surrounded by mangrove forest. To visually examine similarities between communities and over time, an nMDS plot was constructed. To examine community composition in percent cover, a PERMANOVA analysis was conducted to test for differences in season and habitat. A SIMPER analysis was also conducted to examine which variables caused the most dissimilarity between habitat types.

Lastly, for all taxa identified to the species level from seasonal samples, a 2-way ANOVA was used to examine differences in native and non-native species richness within the 2 habitats over time. No analyses were done for colonizing species because artificial panels were being used as a substrate in both habitat types. Native/non-native status for each species was assessed using the WoRMS (WoRMS Editorial Board 2017), WRiMS (Pagad et al. 2017), and NEMESIS (Fofonoff et al. 2017) databases.

All non-parametric analyses were conducted using Primer-E. All parametric analyses were conducted using SigmaPlot v12.5. All data were visually checked for normality and equal variances, and when assumptions were not met for parametric tests, data were transformed using either an arcsine square root transformation for percent cover or log transformation for continuous data to correct the issues.

RESULTS

Seasonal sampling of epifaunal communities

A total of 175 morphospecies, from 11 phyla, were identified from both habitats during the study (Table 1). In artificial habitat, 164 taxa were found, while in mangroves, only 84 taxa were found. Out of all species found, 146 were identified to the species level (Table S1 in the Supplement at www.int-res.com/articles/suppl/m607p085_supp.pdf). The most speciose group was ascidians (37 taxa), although the majority of these were found at only 2 sites, one near Port Canaveral inlet (B_03) and the other being the northernmost site (M_01), near Ponce de Leon inlet. Both sites were artificial structures and atypical in community composition. Species richness was consistently greater in artificial habitats (habitat type: $df = 1$, $F = 9.973$, $p = 0.002$) and varied among seasons

Table 1. Number of species and origin of all species found throughout the study

Phylum	Native	Non-native	Unknown
Porifera	10	1	4
Platyhelminthes	2	0	0
Cnidaria	7	10	6
Mollusca	19	2	1
Sipuncula	1	0	0
Annelida	11	7	7
Arthropoda	13	9	1
Bryozoa	11	12	2
Entoprocta	0	0	1
Echinodermata	0	0	1
Chordata	23	7	7
Total	97	48	30

(df = 7, $F = 26.773$, $p < 0.001$), with a particularly strong decline in October 2015 (Fig. 3a). Shannon-Wiener diversity showed some seasonal variability (df = 7, $F = 13.108$, $p < 0.001$), but otherwise there were no statistically significant differences between the 2 habitat types (Fig. 3b). Community composition for each habitat type generally clustered together, although there was no strong similarity within both habitats among seasons (Fig. 4). Composition based on percent cover was statistically different for both habitat (df = 1, Pseudo- $F = 13.559$, $P(\text{perm}) < 0.001$) and season (df = 7, Pseudo- $F = 3.539$, $P(\text{perm}) < 0.001$), and the magnitude of these differences varied over time (Season \times Habitat, df = 7, Pseudo- $F = 1.802$, $P(\text{perm}) < 0.001$).

For each season, communities at the majority of sites clustered together, indicating that the same dominant species were present and in relatively similar abundances (Fig. S1 in the Supplement). Several sites were consistently dissimilar, including M_01, the most northern site in the Mosquito Lagoon near Ponce de Leon inlet, and B_03, a large marina in the Banana River located adjacent to the Port Canaveral inlet. Both sites were artificial habitats and in areas with strong water exchange and were composed of communities with higher diversity and low barnacle cover.

A SIMPER analysis was used to examine which species for each season were most important in the dissimilarity between habitat types (Table S2 in the Supplement). For most seasons, the barnacle *Amphibalanus eburneus* was the highest contributor to the dissimilarity of habitats, with abundances typically higher in artificial habitat. Throughout the entire study, *A. eburneus* was also the most dominant species found in both habitat types. Barnacle percent

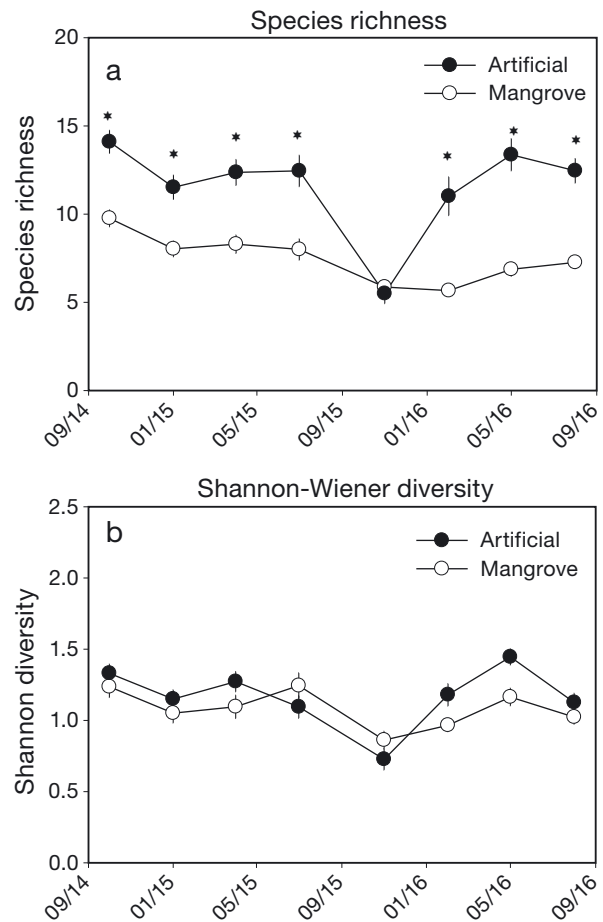


Fig. 3. (a) Species richness and (b) Shannon-Wiener diversity for established communities. *: Significant Student-Newman-Keuls pairwise comparisons tests for each season. Error bars indicate ± 1 SE. Dates are mo/yr

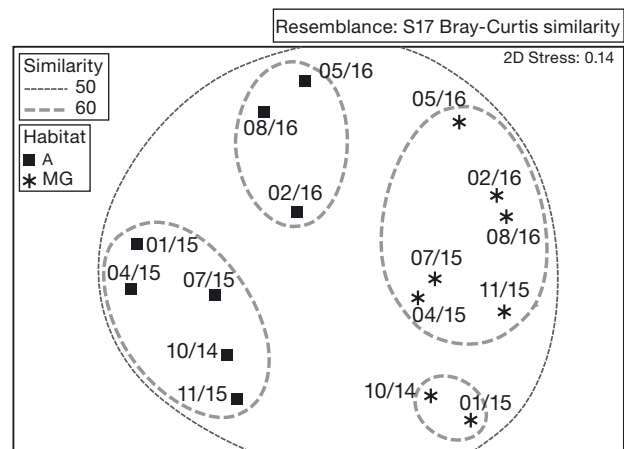


Fig. 4. nMDS plot for established communities. Data were log (x + 1)-transformed and averaged by site. Enclosures indicate the percent similarity among clusters and labels indicate sampling events (dates are mo/yr). A = artificial habitat, MG = mangrove habitat

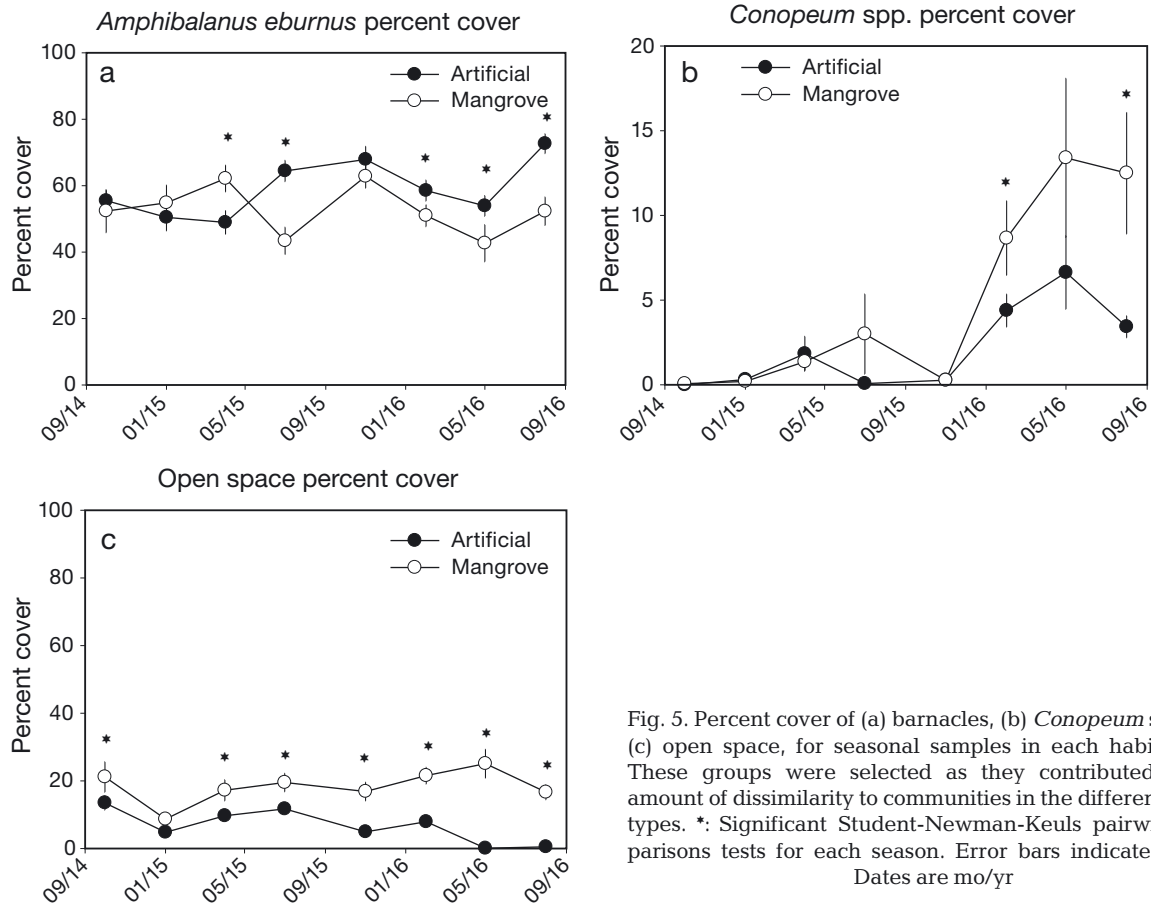


Fig. 5. Percent cover of (a) barnacles, (b) *Conopeum* spp., and (c) open space, for seasonal samples in each habitat type. These groups were selected as they contributed a high amount of dissimilarity to communities in the different habitat types. *: Significant Student-Newman-Keuls pairwise comparisons tests for each season. Error bars indicate ± 1 SE. Dates are mo/yr

cover was significantly different for season ($df = 7$, $F = 4.069$, $p < 0.001$) and habitat type ($df = 1$, $F = 37.946$, $p < 0.001$) as well as for the interaction between the two ($df = 7$, $F = 5.733$, $p < 0.001$). Pairwise comparison tests indicated that for the majority of seasons, barnacle cover was significantly higher on artificial structures (Fig. 5a). The bryozoans *Conopeum chesapeakeensis* and *C. tenuissimum* (pooled as *Conopeum* spp.) comprised a significant proportion of the community throughout the study region. *Conopeum* spp. were present in greater abundances in mangroves (Fig. 5b, $df = 2$, $F = 10.331$, $p = 0.001$). These differences were not consistent though time (season, $df = 7$, $F = 15.757$, $p < 0.001$), with increased abundances found towards the end of the study (Fig. 5b). Other less-significant contributing species were tube-building amphipods (*Erichthonius brasiliensis* and *Monocorophium insidiosum*), more abundant in mangroves, and hydroids (mostly *Obelia* spp.), more abundant in artificial habitat. Other bryozoans, including *Schizoporella pungens* and *Victorella pavid*a, were also abundant, though differed between habitats. In artificial habitats, *S. pungens*

was found in greater amounts, while *V. pavid*a was found in greater amounts on mangrove prop roots (Table S2). The amount of open space found between the 2 habitat types was an important factor in the dissimilarity when community composition was compared (Table S2). Throughout the study, open space was consistently greater on mangrove prop roots (Fig. 5c, habitat type: $df = 1$, $F = 116.767$, $p < 0.001$) and varied significantly by season ($df = 7$, $F = 6.353$, $p < 0.001$).

A separate comparison for Sites IRL_13mg and IRL_13a showed that replicates clustered together according to habitat type, although this varied seasonally (Fig. 6). Overall, communities significantly differed between the 2 habitat types ($df = 1$, Pseudo- $F = 11.444$, $P(\text{perm}) = 0.001$) as well as during the different seasons ($df = 7$, Pseudo- $F = 11.129$, $P(\text{perm}) = 0.001$), despite being in close proximity to each other. For some seasons, the communities in the 2 habitats were similar (Oct 2014, Jan 2015, and Jul 2015), and for others, they were quite different (May 2016 and Aug 2016), indicating that the magnitude of difference was strongly dependent on season ($df = 7$, Pseudo- $F =$

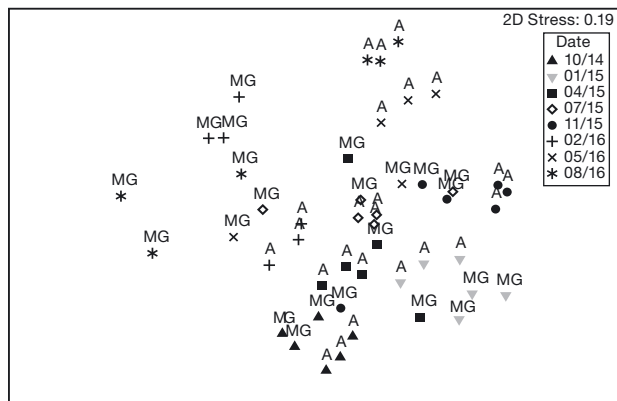


Fig. 6. nMDS plot for established communities from Sites IRL_13mg (MG = mangrove habitat) and IRL_13a (A = artificial habitat) for each sampling event. Both sites were in close proximity (<10 m) and data were selected to show differences in community composition at a relatively small spatial scale. Dates are mo/yr

5.846, $P(\text{perm}) = 0.001$). SIMPER comparison of the sites indicated that the barnacle *A. eburneus*, open space, and *Conopeum* spp. were the most abundant species/variables at the sites and caused the largest dissimilarity between the habitats (Table 2).

Table 2. SIMPER analysis for Sites IRL_13mg and IRL_13a for all variables that accounted for 75% of dissimilarity between habitats. All sampling events were pooled together for analysis. SD = standard deviation

Average dissimilarity = 39.48 ^a Species or variable	Average abundance Mangrove	Average abundance Artificial	Average dissimilarity	SD of dissimilarity	Contribution %	Cumulative %
<i>Amphibalanus eburneus</i>	48.75	68.28	13.19	1.11	33.42	33.42
Open space	18.13	16.42	7.06	1.27	17.89	51.31
<i>Conopeum</i> spp.	9.96	1.88	4.07	0.52	10.3	61.61
<i>Amphibalanus reticulatus</i>	4.75	3.56	3.11	0.62	7.88	69.49
Hydroids	4.92	4.96	2.37	1.09	6	75.49

^aA global comparison between habitat types

Quarterly sampling of colonizing species

Community composition measured as percent cover on recruitment panels was significantly different for season ($df = 6$, Pseudo- $F = 3.995$, $P(\text{perm}) = 0.001$) as well as for habitat type ($df = 2$, Pseudo- $F = 3.406$, $P(\text{perm}) = 0.006$), and the difference between habitats was consistent through time (Season \times Habitat type, $P(\text{perm}) = 0.759$). Richness for colonizing species varied by season ($df = 6$, $F = 19.912$, $p < 0.001$) and was generally greater in artificial habitats ($df = 1$, $F = 18.413$, $p < 0.001$), and these differences were consistent over time (Season \times Habitat type, $p = 0.681$, Fig. 7a). There was an overall difference in Shannon-Wiener diversity for season ($df = 6$, $F = 7.737$, $p < 0.001$) and habitat type ($df = 7$, $F = 7.034$, $p = 0.008$), although the difference between habitat types for each season was negligible (Fig. 7b) and no significance was found for pairwise comparisons.

A SIMPER analysis for communities revealed that *A. eburneus*, tube-building amphipods, *Conopeum* spp., and open space were the most common variables measured within communities that caused dissimilarity among habitat types (Table S3 in the Supplement), similar to what was found for epifaunal

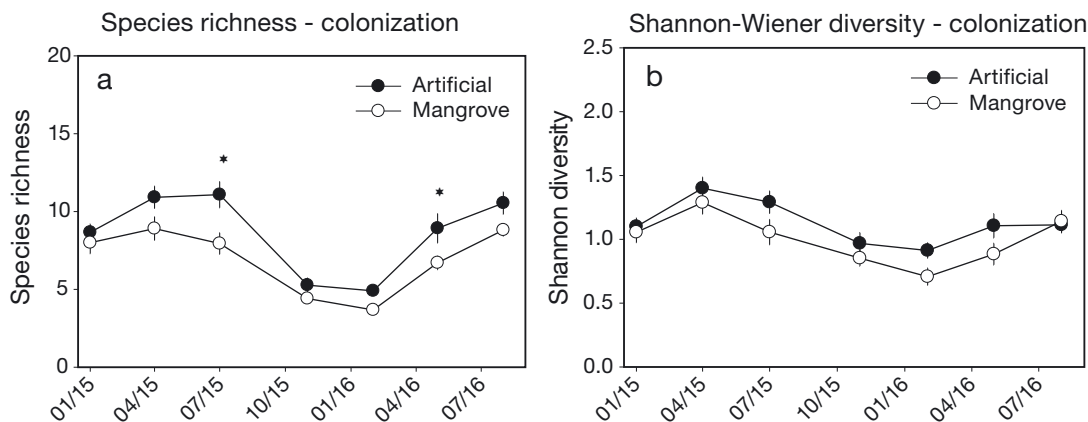


Fig. 7. (a) Species richness and (b) Shannon-Wiener diversity for colonization panels. *: Significant Student-Newman-Keuls pairwise comparisons tests for each season. Error bars indicate ± 1 SE. Dates are mo/yr

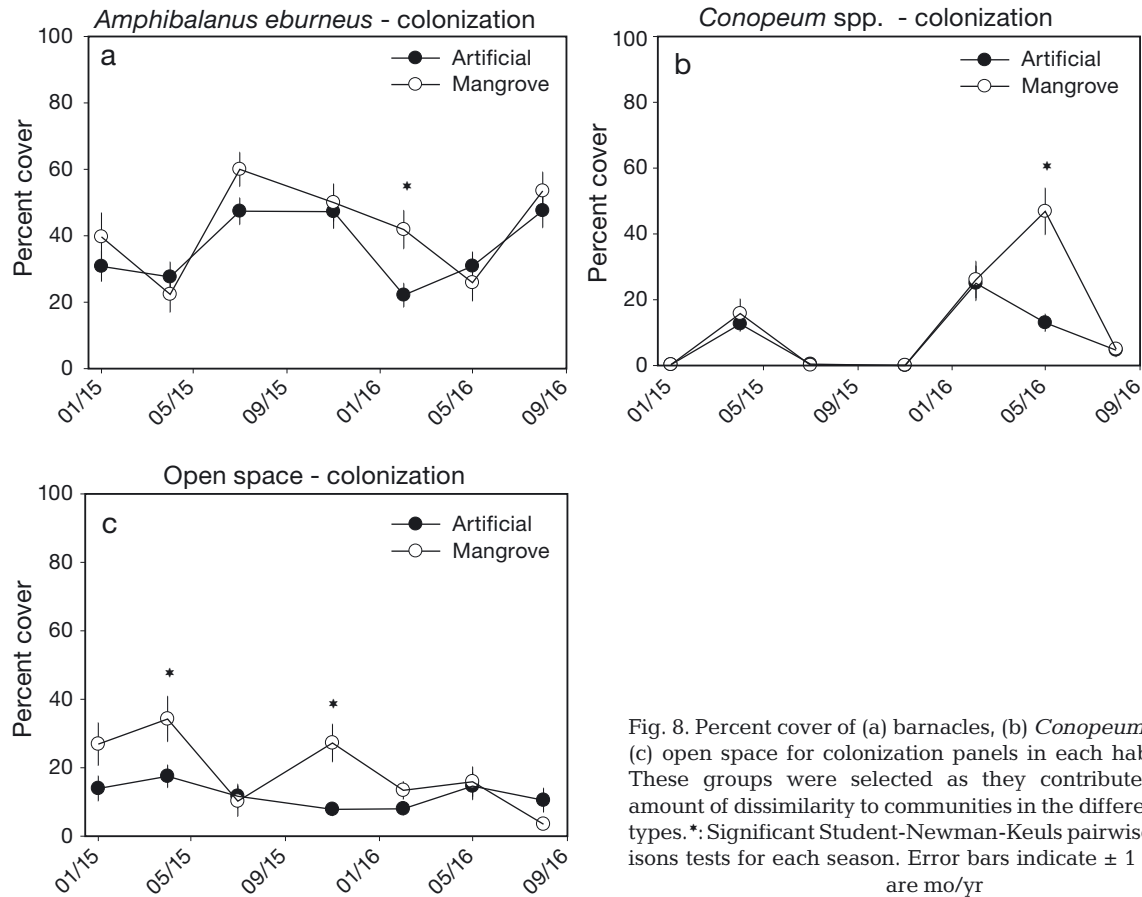


Fig. 8. Percent cover of (a) barnacles, (b) *Conopeum* spp., and (c) open space for colonization panels in each habitat type. These groups were selected as they contributed a high amount of dissimilarity to communities in the different habitat types. *: Significant Student-Newman-Keuls pairwise comparisons tests for each season. Error bars indicate ± 1 SE. Dates are mo/yr

communities. *A. eburneus* recruited in large numbers throughout the entire study, and abundances were significantly different for season ($df = 6$, $F = 8.299$, $p < 0.001$) but not for habitat type ($p = 0.056$) or the interaction between the two ($p = 0.191$). Barnacles showed some seasonality, with increased rates of colonization in the summer and decreases in the winter (Fig. 8a); however, colonization was continuous throughout the duration of the study. The bryozoans *Conopeum* spp. recruited in large abundances in the late winter/early spring (January–April) and in particularly high amounts in 2016 following a brown tide (Figs. 2c & 8b), consistent with what was found for the established epifaunal samples. *Conopeum* spp. colonization was significantly different for season ($df = 6$, $F = 30.047$, $p < 0.001$), habitat type ($df = 1$, $F = 10.095$, $p = 0.002$), and their interaction ($df = 6$, $F = 8.565$, $p < 0.001$), indicating a seasonal trend for which the magnitude varied by habitat type. Open space, or the seasonal rate of colonization, was different for season ($df = 6$, $F = 4.496$, $p < 0.001$), habitat type ($df = 1$, $F = 6.257$, $p = 0.013$), as well as the interaction between the two ($df = 6$, $F = 2.49$, $p = 0.022$). Open space tended to be relatively consistent on

panels in artificial habitats, while more variable on mangrove prop roots (Fig. 8c).

Native and non-native comparison

Of the 146 organisms identified to the species level, 97 were found to have a native range within the Florida/Caribbean region, while 48 were classified as non-native (Table S1). The remaining species were either not fully identified to the species level or had an unknown native range. Differences in non-native species richness were found for habitat type, with more non-natives found in artificial habitats ($df = 1$, $F = 60.218$, $p < 0.001$), and this varied by season ($df = 7$, $F = 24.022$, $p < 0.001$), indicating some seasonality in colonization patterns (Fig. 9). Non-native species made up roughly one-third to one-half of the total community richness in each of the habitats for each season. Non-natives that were relatively common and found in both habitats were the hydroid *O. geniculata*, the serpulid *Ficopomatus enigmaticus*, the barnacle *A. reticulatus*, and the bryozoans *S. pungens*, *Hippopodina indica*, *V. pavida*, and *Bugula neritina*.

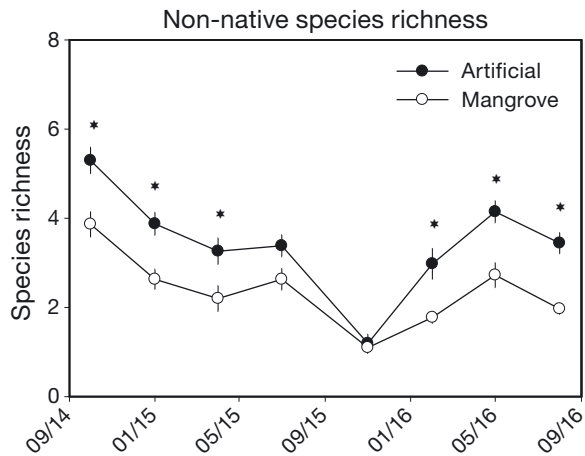


Fig. 9. Total count of non-native species identified from established communities in both habitat types throughout the study. *: Significant Student-Newman-Keuls pairwise comparisons tests for each season. Error bars indicate ± 1 SE. Dates are mo/yr

DISCUSSION

Seasonal sampling of epifaunal communities

Mangrove forests are being lost at an alarming rate while human-made structures are becoming fairly ubiquitous, providing a novel habitat for epifaunal communities. The goal of our study was to compare the epifaunal community structure on mangrove prop roots and artificial structures in the IRL. There were strong differences in community composition and percent cover of individual species between the 2 habitats, and these results are similar to previous studies that demonstrate differences in communities in artificial and natural habitats (Airoldi et al. 2015, Torre & Targett 2016). Artificial structures hosted a greater number of species, which generally covered a higher percentage of the substrate. This is in contrast to previous studies that have shown artificial structures have reduced species richness compared to natural substrates such as rocky shores (Connell & Glasby 1999, Chapman 2003, Bulleri & Chapman 2010). Mangroves roots are relatively small and discrete compared to rocky shores, and this may in part explain the differences in species richness.

Unlike mangrove root communities in the nearby Florida Keys that show large amounts of variation in the short term (Bingham & Young 1995), communities on mangroves in the IRL remained relatively similar through space and time. Communities were dominated by species that are generally thought of as

stress-tolerant, similar to what has been found on a global scale (Australia: Bishop et al. 2012, Kenya: Crona et al. 2006, Costa Rica: Perry 1988, Jamaica: Elliott et al. 2012, and Philippines: Salmo et al. 2017), and were mainly composed of barnacles, bryozoans, hydroids, and tube-dwelling amphipods. Similarly, the same dominant species were also found on artificial structures, though in larger percent cover. Strong seasonal differences were also found for the minor taxa (<10% of community), and unlike the dominant species, the composition of these species differed between the habitats. Overall, community composition varied in 2 ways: (1) the abundance of the dominant taxa differed, with percent cover being higher in artificial habitats, and (2) the composition of the less-abundant taxa differed by habitat as well as by season (see Table S2).

At a local scale, community differences between artificial structures and mangrove roots were also evident. One site in the central Indian River, IRL_13, a small 5 m long wooden dock with few pilings and surrounded by mangroves, contained both habitats. Despite their close proximity, communities still differed significantly over some seasons, though this was not consistent between years. Because of the spatial scale of the study, many artificial structures sampled were pilings and relatively small docks similar to IRL_13a that were distant from larger, more urbanized areas. It is common to study large-scale artificial habitats, which have a variety of intrinsic factors that make them more than likely to host unique communities, but our study highlights the unique role that even small artificial structures in remote areas play as substrate for invertebrate communities. A large number of artificial structures were only present at a single site in Port Canaveral (B_03), which contained communities that were the most diverse, most likely because of the proximity to the inlet and decreased environmental variability (Mook 1980, Attrill 2002). The majority of sites sampled were estuarine, which differs from previous research studies that have focused on communities on artificial structures that are more coastal or have a strong oceanic influence similar to the Port Canaveral site (Gittman et al. 2016).

Globally, gastropods and decapod crustaceans are the most common mobile groups found in mangroves, while sponges are typically the dominant sessile group (Cannicci et al. 2008). While these groups are relatively diverse in the IRL, in the present study they were relatively rare. The most dominant species found in communities in both habitats throughout the entire study region was the barnacle *Amphibalanus*

eburneus. The dominance of barnacles was consistent at both the habitat and site level and caused community composition to be somewhat similar through time. Unlike the positive effects of sponges in the Caribbean (e.g. Ellison et al. 1996), barnacle fouling has been shown to have negative effects on root growth (Perry 1988) and leaf and stem morphology, resulting in a reduction in gas exchange (Li & Chan 2008).

Open space was found in significantly greater amounts on mangrove prop roots with no evidence of seasonal changes. Besides barnacle abundances, the percent of open space found caused communities to be consistently dissimilar (see Table S2). Open space can be created or maintained by both abiotic and biotic means and can provide insight into why communities in contrasting habitat types can differ. Physical forces are particularly strong determinants of community structure in shallow mangrove communities (Bingham & Young 1995, Farnsworth & Ellison 1996), and this is presumably the case here as well. Many of the artificial structures sampled in this study were slightly deeper and generally off the shoreline. Pilings were situated several meters from the coast and seawalls extended deeper, which in both cases caused environmental stress to be reduced (e.g. increased flow, less wave action, and reduced sand scouring). Other potential differences that can influence the amount of open space are substrate availability and age. Prop roots are constantly adding substrate as they grow and can be of various ages, whereas artificial structures are a constant size, and at least locally at each site, were constructed at the same time.

In recent years, the northern IRL has been subjected to increased algal blooms that have had devastating effects on fisheries and seagrasses (Proffitt 2017 and references within). During our study, a brown tide occurred from December 2015 to May 2016 at the majority of sites, though it appeared to have no major effects on the majority of species. However, one particular bryozoan, *Conopeum* spp. (mostly *C. chesapeakeensis*), which was present in small amounts prior to the bloom, was found in large abundances at all sites and in both habitat types during and post-bloom, and this carried through until the end of the study. In the Chesapeake Bay, this species (reported as *C. seurati*) had its greatest growth rates when food availability was highest and nearing bloom conditions (O'Dea & Okamura 1999). Besides 2 barnacle species (*A. eburneus* and *A. reticulatus*), this was the only other species that occurred in relatively high abundances at the majority of sites, but

this was only the case when bloom conditions were present.

Quarterly sampling of colonizing species

Colonization panels were used in this study as a standardized way to examine seasonal changes in recruitment as well as to determine if the larval pool was capable of reaching both habitat types. Both artificial and mangrove habitats showed a similar seasonal trend in species richness on panels, with richness levels greater in the summer coinciding with warmer temperatures. Despite only 2 significantly different sampling events, the general trend was that richness was greater in artificial habitats, mainly resulting from rare or low-abundance species. Barnacle recruitment was consistent and ranged from 20–40% cover in the winter to 50–60% cover in the summer. Barnacles have a relatively long-lived pelagic larval phase and should have good dispersal capabilities, reaching both habitat types. Consistent recruitment of barnacles in high numbers is most likely the cause of its continued dominance in established communities. Other species present on panels at the majority of sites for both habitat types included bryozoans, tube-building amphipods, and hydroids, similar to what was found in sampled communities. *Conopeum* spp. were found more in mangrove sites, and unlike barnacles, have a shorter pelagic larval duration. On mangrove roots, *Conopeum* spp. were typically on the root itself, while in artificial habitats, colonies were growing on barnacles.

Open space was generally found in greater amounts on panels in mangrove habitats. Colonization rates of barnacles for each habitat were similar and it was expected that the available open space on mangrove roots would be filled by barnacles, but this was not the case. Open space in this case does not necessarily reflect a lack of recruitment, and this suggests that other mechanisms are limiting colonization on mangroves roots either resulting from predation or environmental stress. Mangroves are an important refuge for a variety of fish species, particularly in estuarine habitats (Faunce & Serafy 2006), and therefore epifauna on mangrove roots are presumably heavily consumed. Mangrove roots in the IRL may also be simply too shallow to support many species. The amount of open space found on mangrove roots was similar to that found on panels deployed in mangrove habitat, indicating that overall, mangrove habitat in the IRL might be more stressful for epifaunal communities.

Native and non-native comparison

The majority of non-natives within the marine environment are found in estuaries, where they are located on a variety of artificial structures (see review by Ruiz et al. 2009). In our study, non-native species richness was found to be higher in artificial habitats as well, and this pattern was consistent through space and time. The IRL is a biodiverse estuary and it is not surprising that non-natives were found; however, this group made up roughly one-third to one-half of the species richness at most sites. Surprisingly, the number of non-natives present was similar in both habitat types and not restricted to only artificial structures. The taxonomic group in which most non-natives occurred were the Bryozoa (12 out of 23 species), though in many studies, ascidians are the most common group of non-natives found (Gittenberger & van der Stelt 2011, Airoidi et al. 2015) because of their strong competitive abilities (Blum et al. 2007, Janiak et al. 2013). Unique to our study, the dominance of the native *A. eburneus* in artificial habitats greatly reduced the amount of suitable space for non-natives to utilize. In most cases, bryozoans were able to grow on top of barnacles, which likely contributed to their persistence in communities.

Specific non-natives were not persistently dominant in communities, though typically there was at least 1 species that contributed significantly to the community composition during each of the sampling events. Our sampling design utilized a variety of substrate types, including seawalls, individual pilings, as well as docks, and supports the generality that non-native species, at least in terms of richness, are more prevalent on artificial structures. Similar studies have also shown that artificial substrates favor non-natives (Glasby et al. 2007, Tyrrell & Byers 2007). The reasoning for this is still unclear, but it has been suggested that artificial structures are a unique form of substrate and favorable for non-natives (Simberloff 1997, Connell & Glasby 1999) because of a lack of use by natives, reducing competition. Our study suggests that when a dominant native species utilizes artificial structures, the potential for non-natives to dominate that space is reduced. In our study, this was primarily due to the continuous recruitment of barnacles throughout both years reducing any potential available space. Of particular importance, predation in artificial habitats has received little attention, though it has been shown that predators as well as overall consumption strength are generally reduced in artificial habitats (Able et al. 2013, Kornis et al. 2017, Rodemann & Brandl 2017), leading to a reduction in potential biotic control.

CONCLUSIONS

In general, the composition and percent cover of species on colonization panels was similar to that in the sampled communities and recruitment was not a limiting factor structuring these communities. However, there was strong evidence that either predation or environmental stress altered community composition and contributed to the differing amount of open space between the 2 habitats. If these trends were driven by predation, it would suggest that predators are less abundant in artificial habitats. Such shifts in trophic community structure could have consequences in urbanized estuaries at a larger scale. Examining higher trophic levels is therefore important and can improve our understanding of non-recruitment processes in shaping communities.

The IRL, like many other estuaries around the world, is in constant transition resulting from increased urbanization and decreased ecosystem health (Sime 2005). Mangroves along the Florida coastline are slowly extending their range northward into new areas (Cavanaugh et al. 2014); however, in most parts of the world, mangroves are on the decline. Mangrove roots provide an important hard surface for marine epifauna in an otherwise sedimentary system, and it is important to understand how artificial structures, now globally ubiquitous, can function as potential habitat in areas where natural habitat is being lost. Results from our study support the general trend that communities on artificial structures are distinct at both the local and regional scale from mangrove roots, but not necessarily in a negative way. Artificial structures had higher species richness and abundances of dominant species and could provide an important hard structure to help maintain biodiversity when natural structures are being lost. A caveat to this is that artificial structures may select for non-native species that could influence the community composition of dominant native species. Most importantly, when considering how to maintain biodiversity in systems that are losing important foundation species such as mangroves, it is critical to understand the role that artificial structures play in the preservation of biodiversity, as well as the spread of non-native species.

Acknowledgements. We thank Sherry Reed and Woody Lee for field assistance. Funding was provided by the St. Johns River Water Management District (Contract #27799). Permits for species collections were provided by the Florida Fish and Wildlife Conservation Commission (SAL-14-1567-SR). Comments and suggestions from 2 anonymous reviewers greatly improved the manuscript. This is contribution

#30 from the Smithsonian's MarineGEO network and contribution #1099 from the Smithsonian Marine Station.

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Editorial responsibility: Erik Kristensen,
Odense, Denmark

Submitted: January 3, 2018; Accepted: October 8, 2018
Proofs received from author(s): November 13, 2018