

Article

Utilizing Complex Pervious Oyster Shell Habitats for Oyster Reef Habitat Provision in Northeast Florida

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Abstract

Oyster reef restoration projects have been developed to provide habitat for fish and crustaceans. Some novel restoration structures employ greater complexity in attempts to better restore oyster reef habitat along degraded shorelines. The Pervious Oyster Shell Habitat (POSH) was created with greater structural complexity and strength to enhance oyster reef habitat for fish and crustaceans in energetic systems. The purpose of this study was to assess the POSH's short-term ability to provide oyster reef habitat by measuring utilization of the POSH by fish and decapod crustaceans. Nekton abundances, diversity indices, and community similarity were compared between POSH structures, Reef Innovations' "Oyster Ball", and a natural oyster reef control. Artificial reef modules were sampled using 2 m² bottomless lift nets, over one year, along two energetic shorelines in northeast Florida. Fish abundances were low and variable among treatments, with no significant differences detected. Crustacean abundances were greater on the POSH than the Oyster Ball, aside from winter at one site, with significant differences detected for all but two measurements. Nekton community analyses were similar among all treatments and sites. The POSH's design provided more interstitial space for utilization by common benthic crustaceans. Stakeholders attempting to restore degraded shorelines should consider employing the method.

Keywords: oyster; habitat; restoration; living shoreline; alternative substrates; POSH; Reef Ball



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1. Introduction

1.1. The Role of Oyster Reef Habitat

The Eastern Oyster (*Crassostrea virginica*, hereafter oyster) has been described as an ecosystem engineer for the numerous ecological benefits populations provide by the presence of their reefs [1,2]. In addition to water filtration, denitrification, and protection of salt marsh habitat via shoreline stabilization [3–5], oyster reefs provide important habitat in estuaries. As larval oysters settle and grow on established oysters, they form a complex three-dimensional reef that serves as habitat for many fish, crustaceans, and macroinvertebrates [6–12].

Oyster reefs benefit many resident and transient species that differ in their dependence on, and use of, the reef. Residents, such as gobies (*Gobiidae* spp.), blennies (*Blenniidae* spp.), toadfish (*Opsanus tau*), and mud crabs (*Xanthidae* spp., *Panopeidae* spp.), use oyster

reefs for reproduction and refuge throughout most of their lives. Transients like porgies (*Sparidae* spp.), snappers (*Lutjanidae* spp.), drum (*Sciaenidae* spp.), penaeid shrimp (*Penaeidae* spp.), and blue crabs (*Callinectes sapidus*) use structures, including oyster reefs, for feeding and refuge throughout periods of the year as they move between coastal waters and estuaries [7,9,10]. This connection results in benthic–pelagic coupling, or the transfer of energy from benthic reefs throughout coastal waters [13–18].

The acknowledged importance of the oyster reef in facilitating fish growth, survival, and reproduction has led to its designation as an “essential fish habitat” under the 1996 reauthorization of the Magnuson–Stevens Fisheries Conservation and Management Act, which prioritizes protection and restoration of those ecosystems deemed essential fish habitats [10,19–21]. Oyster reef restoration projects have been implemented to restore or enhance lost oyster reef habitat to benefit oyster populations and organisms that use their reefs. Many studies of these projects have shown to enhance fish production and provide habitat for oysters, fish, and crustaceans [4,16,18,22–25].

1.2. Habitat Complexity and the POSH

Habitat complexity has been identified as a key factor in promoting the diversity and abundance of organisms that utilize structured habitats like oyster reefs [26,27]. Fish and crustacean communities benefit from habitat complexity in many marine ecosystems, including saltmarsh, seagrasses, coral reefs, and oyster reefs [9,28–34]. In oyster reefs particularly, increases in interstitial space, or the number of unique spaces within a structure, can provide more areas for refuge from predation, reproduction, and feeding for larval, juvenile, and small-bodied organisms [34–38].

Oyster reefs are particularly complex habitats with interstitial space between attached oysters and vertical relief through the water column. The oyster reef matrix provides habitat for many small fish and crustaceans, allowing for protection from predation and facilitating reproduction. Increases in complexity of oyster reef habitat has been shown to increase prey survival and mediate trophic cascades among common prey species, Atlantic mud crabs (*Panopeus herbstii*) and predators, blue crab and oyster toadfish [34–38]. These studies measured complexity by the volume of loose shell placed in mesocosms, though field studies have supported the importance of structural complexity and integrity for habitat provision, especially in increasingly energetic systems, where a cement-bound structure can provide more stability than loose or bagged shell [39].

The Pervious Oyster Shell Habitat (POSH) is a novel living shoreline structure composed of recycled oyster shells bound by a thin layer of Portland cement (Figure 1a) [40]. By incorporating recycled oyster shells, a reduced amount of cement, and no plastic, the POSH is an attempt at a sustainable restoration method that improves ecological function. The method was developed in an attempt to provide a suitable substrate for oyster colonization, nekton utilization, and wave attenuation for use in restoration projects along eroding shorelines. A commonly used method for similar function in living shorelines is the aquaculture mesh oyster shell-bags. Compared to this method, the POSH does not incorporate degradable plastic, and cement stabilizes the shell, which can be displaced by boat- and storm-driven waves. Larger concrete structures like oyster castles, reef makers, and rip rap are commonly used for projects where shoreline stabilization is a high priority but which do not contain the same degree of complexity per unit, such as the POSH.



Figure 1. Typical POSH module (a) prior to deployment and (b) two years post-deployment at Kingsley Plantation along the Fort George River.

The POSH almost mimics the three-dimensional structure and relief of an oyster reef, measuring ~18 inches tall and containing a large amount of small interstitial spaces, ranging from around 1–4 cm in size. The many interstitial spaces built within the structure should provide refuge habitat for many benthic crustaceans and demersal fish that commonly use oyster reefs. Additionally, the cementitious and porous composition of the structure facilitates oyster recruitment, while it can maintain its strength and positioning along energetic shorelines [41]. Rapid colonization by oysters, other bio-fouling species, and epiphytes should further enhance provision of foraging habitat for larger nekton (Figure 1b) [24,42]. The structure's ability to reduce erosion has been measured in several computational and in situ studies [43–48].

1.3. Objectives

This is the first study that attempts to measure habitat provision by the POSH or, more broadly, restoration structures with cement-coated oyster shell engineered in a fashion similar to the POSH. The objective of this study was to measure the abundance and diversity of fish and decapod crustaceans utilizing the POSH for the purpose of oyster reef habitat restoration. More broadly, this study tests the potential benefits of engineering interstitial space into artificial oyster reef structures to enhance habitat provision. To address this, abundances and diversity of fish and decapod crustaceans were compared between the POSH, Reef Innovation's Oyster Ball, and a natural oyster reef as a positive control (Figure 2a,b). The living shoreline modules were assessed along two degraded, high-energy shorelines in northeast Florida. Kingsley Plantation (KP) along the Fort George River in the Timucuan Ecological and Historical Preserve and Wrights Landing (WL) along the Tolomato River in the Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR) (see Appendix A) were assessed. These sites were selected for their accessibility and suitability. These sites are similar and provide appropriate representations of degraded shorelines where the POSH may be deployed for oyster restoration and shoreline stabilization. They both lack any healthy oyster reefs or saltmarsh in the immediate area and experience regular wave energy from recreational boats. At KP, as many as 100 boats per hour have been measured passing the shoreline, generating up to 10 cm wave heights [43]. Along the ICW around WL, approximately 70 hectares of shoreline habitat (oyster reefs, saltmarsh, and some uplands) was lost from 1970 to 2002 due to erosion [49]. Similar erosion rates have been recorded more recently [50], with boat wakes likely being a major contributor. It should be noted that energetics were not measured for comparison between the sites for the purposes of this study. For further site description and information on saltmarsh loss along the Fort George River, see Mathews et al., 2023 [41].



Figure 2. Oyster Ball (a) and (b) lift nets deployed at the natural reef control at KP.

Due to its increased complexity, we hypothesized that the (H_1) density of fish and (H_2) decapod crustaceans would be greater on the natural oyster reef compared to the artificial reefs and that densities would be greater on the POSH compared to the Oyster Ball. Then, we hypothesized that (H_3) the diversity of fish and (H_4) decapod crustaceans would also be greater on the natural oyster reef compared to the artificial reefs and greater on the POSH compared to the Oyster Ball. The increased structural complexity may allow for utilization of the structure by a greater abundance of small-bodied fish and crustaceans, and greater oyster recruitment to the POSH may provide more habitat and resources for reef-dwellers. Nekton community similarity was also tested, and we predicted that (H_5) the POSH and oyster reef would have similar nekton communities and be different from the communities on the Oyster Ball. With greater oyster recruitment and smaller void spaces, the POSH may support a nekton community closely resembling that of a natural oyster reef. The results from this study will inform stakeholders on the POSH's short-term ability to create oyster reef habitat and the potential implications of engineering greater complexity into living shoreline structures.

2. Materials and Methods

2.1. Experimental Design

Sampling of artificial reef structures at KP and WL began in July of 2022, one year after the structures were initially deployed. Structures were sampled with 2 m² bottomless lift nets over the course of one year to assess utilization throughout seasonal changes in nekton abundance and community composition. Seasons are defined as summer, June–September; fall, October–December; winter, January–March; and spring, April–May, based on dates of the equinox and solstice. Each three-structure reef for both the POSH and Oyster Ball was to be sampled twice each season. A nearby natural oyster reef at KP was sampled simultaneously as a positive control. The natural reef was not sampled in the fall of 2022 due to the elevations of the tides at the time and feasibility of setting nets. At WL, there were no natural reefs adjacent which could be feasibly sampled, so only the POSH and Oyster Ball reefs were compared. A bare-substrate control was not sampled due to limitations of manpower and gear for the study. The oyster reef control was prioritized over a bare substrate control to more effectively assess the POSH in comparison to the desired habitat of restoration. Additionally, the presence of the lift nets overnight on the bare substrate would likely create unintended habitat by providing bunched netting for refuge. This lack of a bare-substrate control does not allow for an effective comparison between artificial reef structures and a negative control, nor does it allow us to understand the potential effects of sitting, bunched nets on nekton densities. Structures were initially deployed separated by structure type to allow for sampling of organisms with a seine or trawl in front of the structures (see Appendix B). This design does not allow for effective random sampling

and is subject to spatial bias and potential pseudo-replication from structures deployed in relatively close proximity.

2.2. Gear Selection

Bottomless lift nets measuring 2 m² (2 × 1 × 2 m) were used to assess the utilization of artificial reef structures and the natural oyster reef control. Lift nets were custom-made by Eagar Inc. (Randolph, UT, USA) from black nylon with a 3 mm mesh. Nets were pulled up using polypropylene braided rope that ran through key rings hooked to the top of the net and screw eyes that were attached to the top of galvanized steel rods that supported the corners of the net. The bottom ends of the nets were buried into small trenches dug in the sediment and secured with metal tent stakes. Nets were lifted by simultaneously pulling all four sides of the net up until the top end was above the water surface, completely enclosing the reefs. Using lift nets allowed us to collect a “snapshot” sample by quickly and completely enclosing each reef area simultaneously within the small spatial scale of the shorelines. By pulling the nets from the shore, we were able to minimize disturbance and escape of organisms.

Rozas found varying catch efficiencies for bottomless lift nets in intertidal salt marshes [51]. Efficiencies ranged from 93% for striped mullet (*Mugil cephalus*) to 32% for daggerblade grass shrimp (*Palaemonetes pugio*). Additionally, an 81% catch efficiency was found for gulf killifish (*Fundulus grandis*), 73% for white shrimp (*Litopenaeus setiferus*), and 58% for sheepshead minnow (*Cyprinodon variegatus*). To assess the catch efficiency of the 2 m² bottomless lift nets, daggerblade grass shrimp (*Palaemonetes* spp.) were used for mark–recapture from the lift nets. Grass shrimp was selected as the study organism to assess catch efficiency due to feasibility of collection and the low efficiency rates found by Rozas to provide an extreme reference point for comparison.

2.3. Catch Efficiency of 2 m² Bottomless Lift Nets

The catch efficiency of the bottomless lift nets was assessed at the WL site in the summer and fall of 2022 over two days for each season. *Palaemonetes* spp. were collected along the shore of the adjacent Guana Lake, an impounded estuary just east of the study site. Specimens were collected 24–48 h prior to sampling, placed into aerated holding tanks in the lab, and gradually acclimated to the temperature and salinity conditions near WL using real-time data collected by the GTMNERR’s System-Wide Monitoring Program (SWMP) YSI EXO2 data sonde at Pine Island, approximately 6 km northwest of WL [52]. During the holding period, specimens were examined for parasites and any other factors that could affect survival during sampling events.

Methylene-blue dye was chosen as the marker since it does not add additional weight like nail polish, the dye lasts for long periods, and it appears to cause minimal stress to organisms. The day before sampling, shrimp were dyed for 12 h in 0.06 g/L of methylene-blue dye. This dyeing time and concentration were chosen based on methods from Etherington et al. (2003) and preliminary concentration tests looking at 6 and 12 h dyeing periods with 0.06 g/L and 0.08 g/L [53]. This concentration minimized stress while keeping shrimp dyed for at least 12 h, long enough to ensure no loss of dye during sampling. The tank filter was removed during the 12 h dyeing period to keep the concentration in the tank at 0.06 g/L. This did not affect shrimp mortality.

After dyeing for 12 h, twenty grass shrimp were placed into one bucket for each lift net ($n = 120$ /sampling event). Just after each lift net was lifted, all shrimp were recounted to ensure no loss from escape or mortality and dumped into the center of each lift net, and buckets were inspected to make sure all shrimp were released and settled into the water column. Marked shrimp were collected from the lift nets with other sampled organisms,

confirmed for dye, counted, and released. All other grass shrimp were euthanized with an ice slurry and returned to the lab for confirmation of dye under a dissection scope.

2.4. Density of Fish and Crustaceans

Lift nets were placed around each reef at low tide (see Appendix C). At the natural oyster reef at KP, oyster clusters near the perimeter of the sample area were moved so the net could be buried and secured. It should be noted that moving the oyster clusters introduced alterations to the habitat which may have influenced crustacean behavior, potentially affecting nekton densities and communities. Percentage cover of live oysters within the sampled area was then confirmed to be ~70% by visual estimation to ensure that an adequate volume of live oyster was present for habitat. Nets were lifted the following day at slack high tide. If there were not enough field personnel to sample all reefs simultaneously, a random number generator or coin was used to select which treatment would be enclosed first, and then after about 5 min, the other treatment was enclosed. After lifting the nets, water depth (m) was measured in the landward right corner of each net with a weighted measuring tape. Water temperature (°C), salinity (ppt), and dissolved oxygen (mg/L) were measured with a YSI Pro Plus and chlorophyll-a (µg/L) with a Turner handheld fluorometer at the center net for each treatment.

As the tide dropped, 25 × 18 cm (0.8 mm mesh) Eager dipnets were swept throughout the entire enclosed area until several sweeps came up with no organisms. Lift nets were continuously cleared as the tide dropped until all visible organisms were removed. Organisms were immediately placed into aerated holding bins and covered to reduce heat stress and escape. When structures were exposed, each structure was carefully examined on the exterior surface and interstices, and then structures were lifted to examine organisms on the underside and those burrowed under structures. For the natural oyster reef, all oyster clusters and the sediment surface were carefully examined throughout the sample area. Specimens were recovered from structures when possible, identified, and measured to the nearest millimeter with calipers, a ruler, or a fish viewer. All fish were measured using standard length (SL), all crabs with carapace width (CW), and all shrimp with rostral length (RL). Subsamples of specimens were collected if they were not identifiable in the field or by photo. All larval fish were subsampled and identified in the lab. Larval fish were not quantified for density or community analysis since many were small enough to swim through the 3 mm mesh and therefore could not be reliably quantified. Presence/absence of larval fish were recorded for each season and all treatments.

2.5. Data Analysis

Catch efficiency raw observations, or the number of shrimp recovered per lift net pull, were compared between the POSH and Oyster Ball using Pearson's chi-squared test in the R version 4.5.2 statistical software. Efficiency percentages for each treatment and sampling event will also be discussed in comparison to Rozas' (1992) [51] results.

Fish and crustacean density analysis was performed through R version 4.5.2. Schooling pelagic species (herring and anchovies) were removed from all quantitative assessments due to their constant movement through the water and the likelihood of capturing large passing schools in the limited project area. All larval fish were excluded from statistical tests since they were likely to move into and out of the nets during sampling. Larval fish that were excluded ranged from 2.5–7.7 mm (SL) and had a body diameter smaller than 3 mm. All data were tested for normality using the Shapiro–Wilk test and for homogeneity of variance using Bartlett's test. Data that did not meet the assumptions of parametric tests after transformation were compared using the nonparametric equivalents. The nonparametric two-way crossed Analysis of Variance (ANOVA) and Scheirer–Ray–Hare tests were used

to detect differences in fish and crustacean densities between seasons and treatments and any potential interactions between the two factors. Dunn's test was used to detect pairwise differences among seasons and treatments. Fish and crustacean densities between treatments were compared for each season using one-way ANOVAs and the nonparametric Kruskal–Wallis test when necessary. Tukey's Honestly Significant Difference (HSD) test was used to detect pairwise differences between the three treatments at KP when necessary.

Community analysis was performed through the vegan package in R version 4.5.1. Species richness, evenness, Shannon's diversity index, and Simpson's diversity index were calculated for each treatment during all seasons at both sites. Both Shannon's and Simpson's indices were used as Shannon's equation puts more weight on richness and Simpson's puts more weight on abundance [54,55]. Analysis of similarity (ANOSIM) tests and non-metric multidimensional scaling (nMDS) plots were performed in Past4. ANOSIMs were run to assess overall community similarity among treatments and seasons and similarity between treatments for each season. Specimens that were not identified to species were omitted from analysis of similarity tests and nMDS plots. Non-metric multidimensional scaling plots were created for visualization of similarity among nekton communities. Complete nekton communities sampled on each treatment are presented in nMDS plots.

3. Results

3.1. Catch Efficiency of 2 m² Bottomless Lift Nets

Catch efficiencies of the 2 m² bottomless lift nets were highly variable and similar among treatments (Figure 3). Efficiencies on the POSH reefs measured: August: $x = 41\%$, 42% and October: $x = 37\%$, 80% . Efficiencies on the Oyster Ball reefs measured: August: $x = 51\%$, 25% and October: $x = 50\%$, 83% . Pearson's chi-squared test resulted in no significant difference in the proportions of grass shrimp recovered between the two structures ($p = .098$) (see Appendix D).

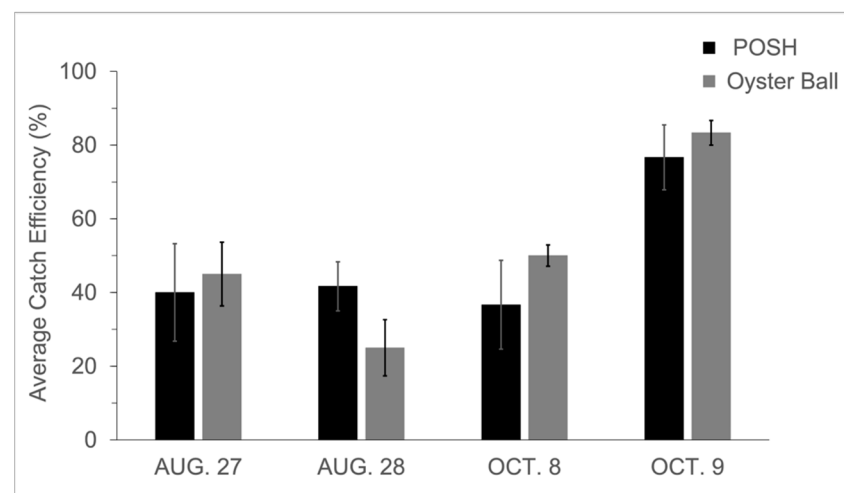


Figure 3. Catch efficiencies of *Palaemonetes* spp. in 2 m² bottomless lift nets at WL. Error bars represent ± 1 SE.

3.2. Density of Fish and Crustaceans

Fish densities were low and variable due to the small sample sizes and selectivity of the gear (Tables 1 and 2). Fish densities among both treatments varied by season, with the greatest densities at both sites measured in the fall (Figure 4). Seasonal densities were significantly greater in the fall over winter ($p = .003$) and spring over winter ($p = .002$) at KP. Fish densities at WL were significantly greater in the fall over summer ($p < .001$), spring ($p < .001$) and winter ($p = .013$). Fish densities did not differ among treatments during any

season at either site, and no interactions between season and treatment were detected (see Appendix D for test statistics).

Table 1. Fish density summary and diversity metrics at KP.

Season	Treatment	<i>n</i>	#/m ²	SE	<i>p</i>	S	J	H'	D
Summer 2022	POSH	9	0.72	0.24	.604	5	0.82	1.33	0.69
	OB	9	0.39	0.14		7	0.98	1.91	0.84
Fall 2022	Oyster Reef	6	0.50	0.26	.874	4	0.73	1.01	0.53
	POSH	6	1.09	0.42		5	0.96	1.55	0.78
	OB	6	1.42	0.44		5	0.62	1	0.48
Winter 2023	POSH	6	0.17	0.17	.391	1	NA	NA	NA
	OB	6	0.09	0.09		1	NA	NA	NA
	Oyster Reef	6	0	0		0	NA	NA	NA
Spring 2023	POSH	6	0.92	0.24	.986	3	0.78	0.86	0.51
	OB	6	0.84	0.38		3	0.94	1.03	0.62
	Oyster Reef	6	1.00	0.29		3	0.98	1.07	0.65

Sample size (*n*) is the total number of lift nets sampled per treatment per season. Densities are represented as the number (#) of individuals per m². *p*-value (*p*) represents overall difference among treatments. Species richness (S), evenness (J), Shannon's index (H'), and Simpson's index (D). Oyster Ball is denoted as "OB" in figures and tables. Pairwise *p*-values are given in the text. Not applicable due to insufficient data (NA). Test statistics are reported in Appendix D.

Table 2. Fish density summary and diversity metrics at WL.

Season	Treatment	<i>n</i>	#/m ²	SE	<i>p</i>	S	J	H'	D
Summer 2022	POSH	6	0.09	0.09	.341	1	NA	NA	NA
	OB	6	0.34	0.17		3	0.94	1.04	0.63
Fall 2022	POSH	6	1.34	0.25	.456	8	0.38	0.78	0.32
	OB	6	1.92	0.46		9	0.50	1.10	0.48
Winter 2023	POSH	3	1.00	0.77	.374	1	NA	NA	NA
	OB	3	0.34	0.17		2	1.00	0.69	0.50
Spring 2023	POSH	6	0.33	0.17	.341	3	0.86	0.95	0.56
	OB	6	0	0		0	NA	NA	NA

Sample size (*n*) is the total number of lift nets sampled per treatment per season. Densities are represented as the number (#) of individuals per m². *p*-value (*p*) represents overall difference among treatments. Species richness (S), evenness (J), Shannon's index (H'), and Simpson's index (D). Oyster Ball is denoted as "OB" in figures and tables. Pairwise *p*-values are given in the text. Not applicable due to insufficient data (NA). Test statistics are reported in Appendix D.

Crustacean abundances for all treatments were much greater than fish abundances (Tables 3 and 4). Densities at KP were significantly greater in fall and winter over spring (fall: *p* = .042; winter: *p* = .021) and summer (fall: *p* = .025; winter: *p* = .012) (Figure 5). Crustacean densities were significantly greater on the POSH than the Oyster Ball during summer (*p* < .001), fall (*p* < .001), and spring (*p* < .001). Densities were significantly greater on the Oyster Ball in winter (*p* = .013). The natural oyster reef control had significantly greater crustacean densities than both experimental groups in summer (Reef/POSH: *p* = .009; Reef/OB: *p* < .001) and spring (Reef/POSH: *p* = .016; Reef/OB: *p* < .001) with the exception of the Oyster Ball in winter (Reef/OB: *p* = .263; Reef/POSH: *p* < .001). A significant interaction between treatment and season was detected at KP (*p* = .006). There were no significant differences in seasonal crustacean densities at WL (*p* = .521). Crustacean densities were significantly greater on the POSH than the Oyster Ball during summer (*p* < .001) and spring (*p* = .046).

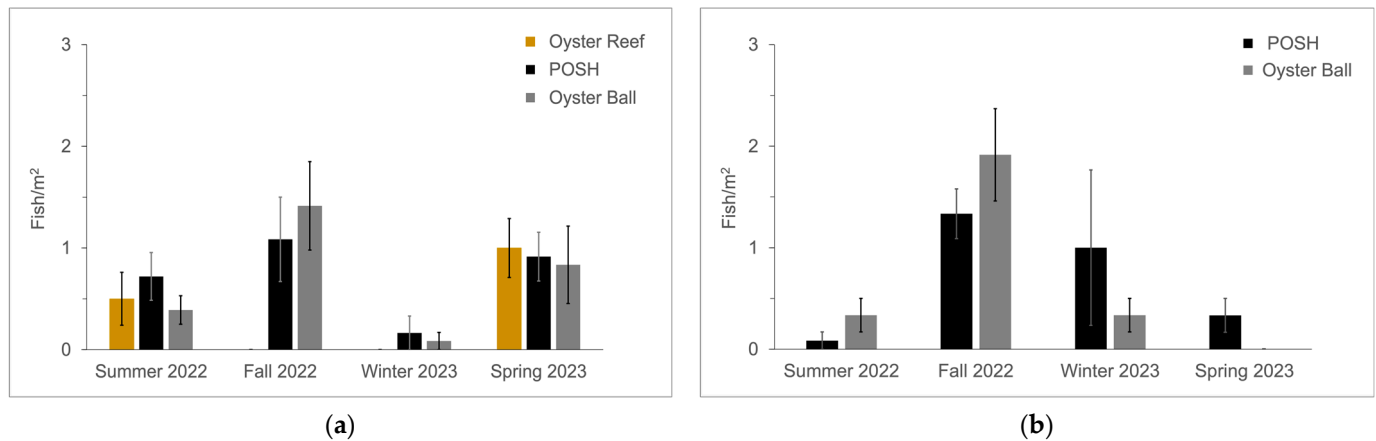


Figure 4. Seasonal fish densities at (a) KP and (b) WL. Error bars represent ± 1 SE. No significant differences were found (one-way ANOVA). Note: the oyster reef control at KP was not sampled in fall, and in winter, 0 fish were caught. The data presented are raw averages, not transformed.

Table 3. Crustacean density summary and diversity metrics at KP.

Season	Treatment	<i>n</i>	#/m ²	SE	<i>p</i>	S	J	H'	D
Summer 2022	POSH	9	10.17	1.72	<.001 *	8	0.61	1.28	0.64
	OB	9	2.28	0.45		7	0.73	1.42	0.67
	Reef	6	28.84	5.45		7	0.44	0.86	0.44
Fall 2022	POSH	6	44.59	3.75	<.001 *	9	0.38	0.87	0.39
	OB	6	10.84	2.34		7	0.81	1.68	0.76
	Reef	6	72.84	20.66		6	0.30	0.54	0.25
Winter 2023	POSH	6	9.09	3.14	<.001 *	5	0.70	1.13	0.64
	OB	6	29.42	4.95		5	0.30	0.75	0.41
	Reef	6	72.84	20.66		6	0.30	0.54	0.25
Spring 2023	POSH	6	11.17	1.30	<.001 *	6	0.72	1.29	0.68
	OB	6	2.84	0.59		8	0.83	1.73	0.78
	Reef	6	21.34	2.42		7	0.50	0.97	0.51

Sample size (*n*) is the total number of lift nets sampled per treatment per season. Densities are represented as the number (#) of individuals per m². *p*-value (*p*) represents overall difference among treatments with significant differences denoted (*). Species richness (S), evenness (J), Shannon's index (H'), and Simpson's index (D). Oyster Ball is denoted as "OB" in figures and tables. Pairwise *p*-values are given in the text. Not applicable due to insufficient data (NA). Test statistics are reported in Appendix D.

Table 4. Crustacean density summary and diversity metrics at WL.

Season	Treatment	<i>n</i>	#/m ²	SE	<i>p</i>	S	J	H'	D
Summer 2022	POSH	6	14.17	1.18	<.001 *	6	0.46	0.83	0.51
	OB	6	4.00	0.55		7	0.75	1.46	0.72
Fall 2022	POSH	6	11.75	1.61	.075	6	0.78	1.39	0.71
	OB	6	7.25	1.63		6	0.88	1.57	0.77
Winter 2023	POSH	3	20.17	4.48	.207	6	0.71	1.27	0.63
	OB	3	10.84	6.60		6	0.74	1.32	0.69
Spring 2023	POSH	6	12.17	0.71	.046 *	7	0.65	1.26	0.66
	OB	6	7.83	2.47		6	0.62	1.12	0.60

Sample size (*n*) is the total number of lift nets sampled per treatment per season. Densities are represented as the number (#) of individuals per m². *p*-value (*p*) represents overall difference among treatments with significant differences denoted (*). Species richness (S), evenness (J), Shannon's index (H'), and Simpson's index (D). Oyster Ball is denoted as "OB" in figures and tables. Pairwise *p*-values are given in the text. Not applicable due to insufficient data (NA). Test statistics are reported in Appendix D.

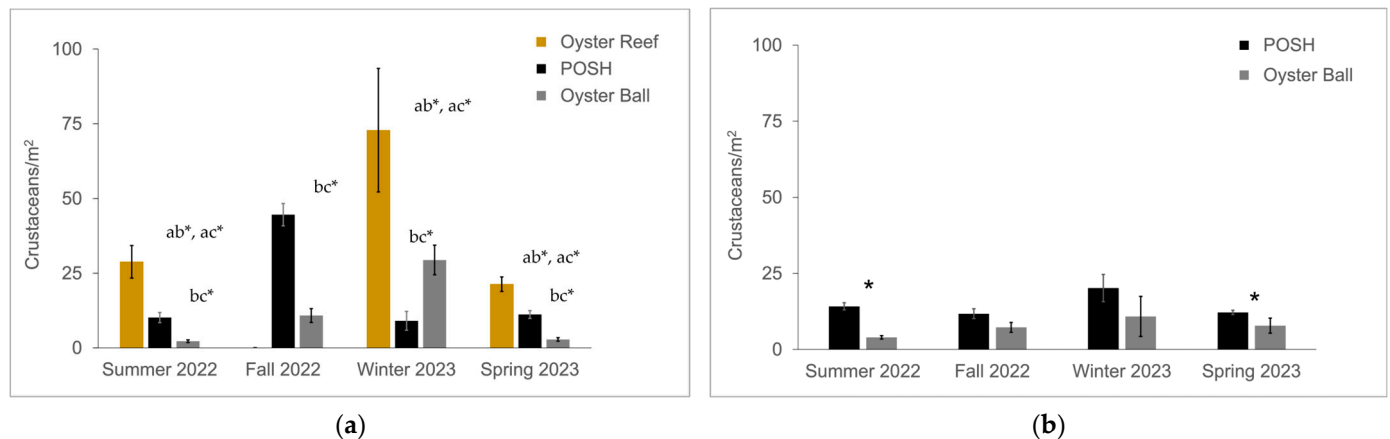


Figure 5. Seasonal crustacean densities at (a) KP and (b) WL. Error bars represent ± 1 SE. Significant differences (one-way ANOVA) are denoted (*). For pairwise differences between treatments at KP, groups are denoted as (a) oyster reef, (b) POSH, and (c) Oyster Ball (Tukey's HSD test). Note: the oyster reef was not sampled in fall. The data presented are raw averages, not transformed.

3.3. Community Diversity and Similarity

Species richness, evenness, and Shannon's and Simpson's diversity indices were similar between all treatments for both metrics and sites. Crustacean diversity metrics were greater than those measured on the fish communities at both sites, with some variation between seasons.

Species richness of fish at KP was low, with the fewest species collected in winter ($S = 0$) and the greatest in summer ($S = 7$) (Table 1). Species evenness at KP was high and consistent (J : 0.62–0.98). Coinciding with the low richness and high evenness, Shannon's and Simpson's diversity indices were low across all measures (H' : 0.86–1.91, D : 0.48–0.84). Species richness of fish at WL was generally lower than at KP, excluding fall, when richness was greatest throughout the study ($S = 9$) (Table 2). All diversity metrics were slightly lower than at KP (J : 0.38–1.0, H' : 0.69–1.10, D : 0.32–0.63).

Species richness of crustaceans at KP was high throughout the year, peaking in the fall ($S = 9$) (Table 3). The evenness of crustacean communities was more variable than the fish communities (J : 0.30–0.83). Shannon's and Simpson's index were both relatively low. Crustacean richness at WL was similar to KP, though it was more consistent throughout the year ($S = 6$ –7) (Table 4). Evenness and Shannon's and Simpson's indices at Wrights Landing were also low and more similar between treatments throughout the year, with the exception of summer (J : 0.46–0.88, H' : 0.83–1.57, D : 0.51–0.77).

The results of the ANOSIMs generally showed similar communities between treatments and seasons, which was inconsistent with our hypothesis that nekton communities on the Oyster Ball would be different from the POSH and the natural oyster reef. The overall nekton community on the natural oyster reef was slightly significantly different compared to that on the Oyster Ball ($p = .044$). All other nekton communities among seasons and treatments were similar (see Appendix D). nMDS plots support the ANOSIM results by showing a significant overlap of the POSH, Oyster Ball, and oyster reef communities (Figure 6). Almost complete overlap in both plots shows similarity among treatments. The narrow ellipse for the Oyster Ball at Kinsley Plantation shows a more transient-dominated community, with greater weight coming from transient fish and crustaceans such as lane snapper, planehead filefish (*Stephanolepis hispidus*), blackcheek tonguefish (*Symphurus plagiusa*), and Indonesian swimming crab (*Charybdis hellerii*) (Figure 6a).

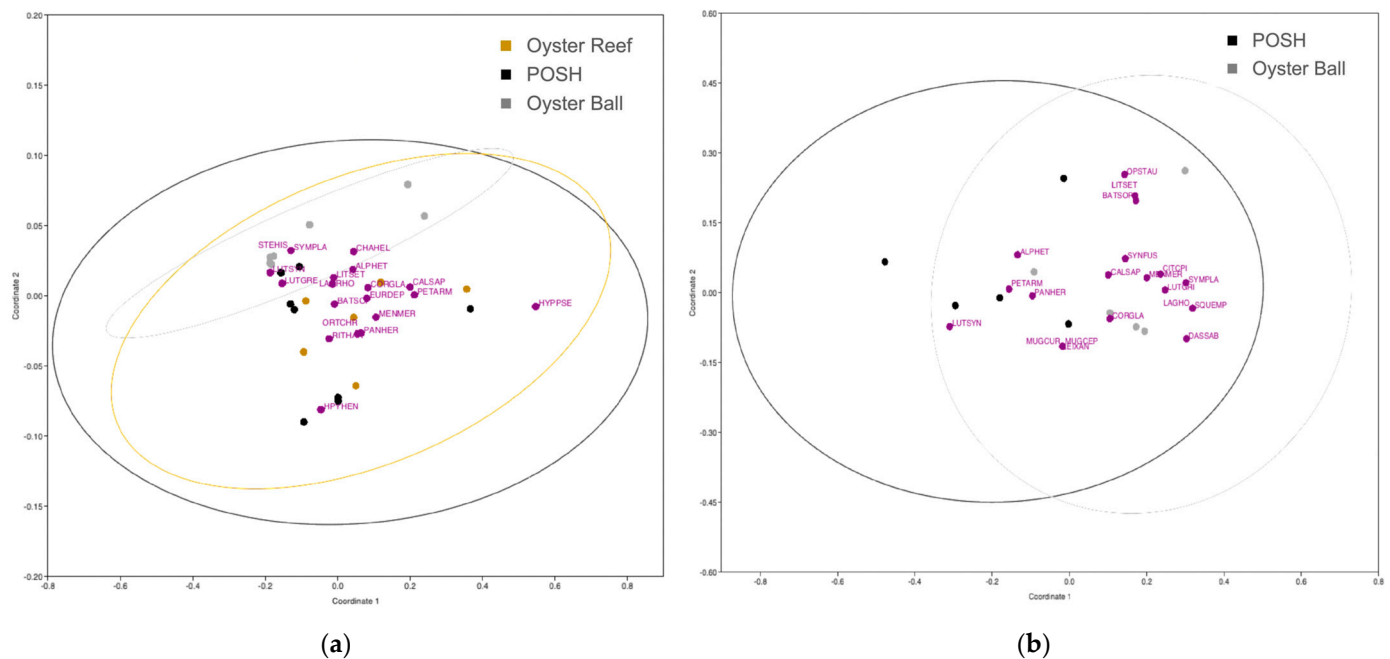


Figure 6. Nekton community nMDS plot for (a) KP and (b) Wrights Landing. Ordination of species observations is depicted by pink dots. The corresponding species codes are the first three letters of the species and genus name for a given species; 95% confidence ellipses are shown for each treatment.

Fish catch at both sites was composed of a mix of oyster reef residents, structure-oriented transients, and pelagic fish. Excluding schooling pelagics, fish catch at both sites was dominated by demersal residents, like gobies and blennies. The majority of fish captured by the lift nets were small-bodied, juvenile, and larval fish (KP: $\bar{x}$ = 46.7 mm, WL: $\bar{x}$ = 36.2 mm). Only a few outlier samples exceeded 100 mm, including the striped mullet (*Mugil cephalus*) (n = 2), Atlantic stingray (*Dasyatis sabina*) (n = 1), and oyster toadfish (n = 1). Proportions of reef residents and transients utilizing the two structures were similar between sites, with the POSH having a greater proportion of residents (74%, both sites) and the Oyster Ball having a more even split (KP: 66%; WL: 58%). The oyster reef control unexpectedly had a greater proportion of transient species, resulting from greater abundances of juvenile pinfish and pigfish. The dominant species at KP was the frillfin goby (*Bathygobius soporator*), followed by the bridled goby (*Coryphopterus glaucofraenum*), pigfish (*Orthopristis chrysoptera*), and pinfish (*Lagodon rhomboides*) (Table 5). Most species were relatively evenly distributed among the POSH and Oyster Ball, with the oyster reef having the lowest overall richness. Larval Atlantic menhaden (*Brevoortia smithi*), mojarra (*Gerreidae* spp.), mangrove snapper (*Lutjanus griseus*), spot (*Leiostomus xanthurus*), and other drum (*Sciaenidae* spp.) were observed on the POSH treatment throughout the year. Of the larval fish, only mojarra was seen on the Oyster Ball and spot on the oyster reef. Species composition observed at WL was similar to that at KP (Table 6). The dominant species at WL was also the frillfin goby, followed by the mangrove snapper, and all other species had three or fewer total samples. There were three more mangrove snapper observed on the Oyster Balls, as well as three blackcheek tonguefish (*Symphurus plagusia*), two bay whiff (*Citharichthys spilopterus*), and one Atlantic stingray (*Dasyatis sabina*), which were not observed among the POSH reefs. Larval bay anchovy (*Anchoa mitchilli*), striped anchovy (*Anchoa hepsetus*), herring (*Brevoortia* spp.), mojarra (*Gerreidae* spp.), pinfish (*Lagodon rhomboides*), spot (*Leiostomus xanthurus*), and Atlantic croaker (*Micropogonias undulatus*) were observed among the POSH reefs. Larval herring, pinfish, and croaker were not collected from the Oyster Ball reefs.

Table 5. Fish and crustacean species list with total abundances at KP. Presence/absence of schooling pelagic species and larval fish (✓). Residents (^R) and transients (^T) according to Coen et al. 1999 [10].

Species	Common	POSH	OB	Oyster Reef
Fish				
<i>Anchoa hepsetus</i>	Striped Anchovy ^T	✓	✓	✓
<i>Anchoa mitchilli</i>	Bay Anchovy ^T	✓	✓	✓
<i>Bathygobius soporator</i>	Frillfin Goby ^R	11	7	3
<i>Blenniidae</i> spp.	Blenny ^R	4	1	-
<i>Brevoortia smithi</i>	Yellowfin Menhaden ^T	✓	✓	✓
<i>Coryphopterus glaucofraenum</i>	Bridled Goby ^R	8	3	1
<i>Gobiidae</i> spp.	Goby ^R	3	12	-
<i>Hypleurochilus pseudoaequipinnis</i>	Oyster Blenny ^R	1	-	-
<i>Hypsoblennius hentz</i>	Feather Blenny ^R	2	-	-
<i>Lagodon rhomboides</i>	Pinfish ^T	2	5	7
<i>Lutjanus griseus</i>	Mangrove Snapper ^T	1	1	-
<i>Lutjanus synagris</i>	Lane Snapper ^T	-	1	-
<i>Orthopristis chrysoptera</i>	Pigfish ^T	7	3	7
<i>Stephanolepis hispidus</i>	Planehead Filefish ^T	-	1	-
<i>Symphurus plagiusa</i>	Blackcheek Tonguefish ^T	-	1	-
Crustaceans				
<i>Alpheus heterochaelis</i>	Big-Clawed Snapping Shrimp ^R	18	27	1
<i>Callinectes sapidus</i>	Greater Blue Crab ^T	2	2	10
<i>Charybdis hellerii</i>	Indonesian Swimming Crab ^T	4	16	-
<i>Eurypanopeus depressus</i>	Flatback Mud Crab ^R	3	-	11
<i>Farfantepanaeus aztecus</i>	Brown Shrimp ^T	2	2	2
<i>Menippe mercenaria</i>	Stone Crab ^T	40	16	8
<i>Palaemonetes</i> spp.	Grass Shrimp ^T	74	88	788
<i>Panopeus herbstii</i>	Atlantic Mud Crab ^R	222	62	170
<i>Penaeidae</i> spp.	Penaeid Shrimp ^T	13	9	-
<i>Petrolisthes armatus</i>	Green Porcelain Crab ^R	575	323	479
<i>Rithropanopeus harrisi</i>	Estuarine Mud Crab ^R	2	-	-
Larval Fish				
<i>Brevoortia smithi</i>	Atlantic Menhaden	✓	-	-
<i>Gerreidae</i> spp.	Mojarra	✓	✓	-
<i>Leiostomus xanthurus</i>	Spot	✓	-	✓
<i>Lutjanus griseus</i>	Mangrove Snapper	✓	-	-
<i>Sciaenidae</i> spp.	Drum	✓	-	-
	Total	994	580	1487

Most crustaceans captured by the lift nets were small, benthic crustaceans (crabs; KP: $\bar{x}$ = 18.0 mm, WL: $\bar{x}$ = 17.4 mm, shrimp; KP: $\bar{x}$ = 8.1 mm, WL: $\bar{x}$ = 6.5 mm). Crustaceans observed at both sites were dominated by the green porcelain crab (*Petrolisthes armatus*), mud crabs, and shrimp. The Atlantic mud crab and daggerblade grass shrimp (*Palaemonetes* spp.) were the most abundant species following *P. armatus* (Tables 5 and 6). At KP, these species were followed by the stone crab (*Menippe mercenaria*) and big-clawed snapping shrimp (*Alpheus heterochaelis*). Most species were relatively well distributed among the three treatments, with the exception of the estuarine mud crab (*Rithropanopeus harrisi*), which was only observed on the POSH reefs. The flatback mud crab (*Eurypanopeus depressus*) was not seen on the Oyster Balls, and the invasive Indonesian swimming crab (*Charybdis hellerii*), which was observed in the fall, was not found on the oyster reef. Penaeid shrimp (*Penaeidae* spp.) were also not sampled on the oyster reef. WL had many big-clawed snapping shrimp, greater blue crabs, and penaeid shrimp. All species were distributed

among both treatments except for one mantis shrimp (*Squilla empusa*), which was observed on the Oyster Balls.

Table 6. Fish and crustacean species list with total abundances at WL. Presence/absence of schooling pelagic species and larval fish (✓). Residents (^R) and transients (^T) according to Coen et al. 1999 [10].

Species	Common	POSH	OB
Fish			
<i>Anchoa mitchilli</i>	Bay Anchovy ^T	✓	✓
<i>Bathygobius soporator</i>	Frillfin Goby ^R	7	10
<i>Blenniidae</i> spp.	Blenny ^R	1	-
<i>Citharichthys spilopterus</i>	Bay Whiff ^T	-	2
<i>Coryphopterus glaucofraenum</i>	Bridled Goby ^R	2	1
<i>Dasyatis sabina</i>	Atlantic Stingray ^T	-	1
<i>Gobiidae</i> spp.	Goby ^R	8	5
<i>Lagodon rhomboides</i>	Pinfish ^T	-	1
<i>Leiostomus xanthurus</i>	Spot ^T	1	-
<i>Lutjanus griseus</i>	Mangrove Snapper ^T	1	4
<i>Lutjanus synagris</i>	Lane Snapper ^T	1	-
<i>Mugil cephalus</i>	Striped Mullet ^T	2	-
<i>Mugil curema</i>	White Mullet ^T	1	-
<i>Opsanus tau</i>	Oyster Toadfish ^R	2	1
<i>Syngnathus fuscus</i>	Northern Pipefish ^T	1	1
<i>Symphurus plagiatus</i>	Blackcheek Tonguefish ^T	-	3
Crustaceans			
<i>Alpheus heterochaelis</i>	Big-Clawed Snapping Shrimp ^R	30	9
<i>Callinectes sapidus</i>	Greater Blue Crab ^T	14	19
<i>Menippe mercenaria</i>	Stone Crab ^T	1	2
<i>Palaemonetes</i> spp.	Daggerblade Grass Shrimp ^T	29	43
<i>Panopeus herbstii</i>	Atlantic Mud Crab ^R	182	76
<i>Petrolisthes armatus</i>	Green Porcelain Crab ^R	291	101
<i>Squilla empusa</i>	Mantis Shrimp ^T	-	1
Larval Fish			
<i>Anchoa mitchilli</i>	Bay Anchovy	✓	✓
<i>Anchoa hepsetus</i>	Striped Anchovy	✓	✓
<i>Brevoortia</i> spp.	Herring	✓	-
<i>Gerreidae</i> spp.	Mojarra	✓	✓
<i>Lagodon rhomboides</i>	Pinfish	✓	-
<i>Leiostomus xanthurus</i>	Spot	✓	✓
	Total	574	280

4. Discussion

The purpose of this study was to examine the POSH's ability to provide oyster reef habitat by measuring utilization of the structure through fish and crustacean abundances and community analyses. The POSH hosted a variety of fish and crustaceans throughout the year, and the complexity of the structure allowed for utilization by large abundances of crustaceans when compared to the Oyster Ball. The results of the study have shown that the POSH can be a suitable method for rapidly providing benthic oyster reef habitat in energetic systems. More broadly, the study has supported findings showing enhanced oyster reef habitat creation for benthic crustaceans with increased complexity [30,39]. These results support efforts to develop oyster reef restoration methods which are intentionally engineered with complexity to enhance benthic habitat functionality.

Fish densities were low and variable among all measurements. Low sample sizes and variable catch efficiencies limit the study's ability to make strong assumptions about fish

habitat provision. Abundances were greatest in the fall, with no other apparent seasonal trends or correlations with environmental variables, contradictory to other studies [56–59], which is likely due to infrequent sampling and small sample sizes, particularly at WL in winter (see Appendix E for environmental data). No significant differences were measured between treatments at either site, inconsistent with the hypothesis that fish densities would be greater on the oyster reef followed by the POSH (Figure 4). Karp et al. (2018) and Humphries et al. (2011) also found that fish densities do not increase with increasing structural complexity of oyster reefs, especially for larger transient fish that cannot access smaller void spaces for refuge [60,61]. In larger structured habitats like coral reefs, there can be a positive relationship between complexity and fish abundance and diversity [53]. These contradictions and results from other studies point out the importance of varying void space, vertical relief, and design on the different fish communities that utilize structured habitats [26,31,62–68]. This further supports suggestions that specific ecological goals and restoration methodologies should be defined for living shoreline projects aimed at fish habitat provision [68–70].

All fish community diversity indices were similar among treatments at both sites, inconsistent with our hypothesis that the POSH would support greater diversity. The overall fish communities at either site were dominated by small-bodied demersal resident fishes like blennies and gobies. These fish are common on oyster reefs throughout the year [10,67,69,71–73] and are selected for by gear like the bottomless lift nets used in this study [51,65–67,72,74]. The POSH had a slightly greater proportion of resident fish than the Oyster Ball at both sites, likely due to greater oyster recruitment and smaller void spaces on the structure. Observations from a small un-baited remote underwater video survey in spring of 2023 suggest that the Oyster Ball may be more readily utilized by larger transient fish, as the large hollow interior was commonly utilized by small pinfish, and sheepshead (*Archosargus probatocephalus*) often fed on the abundant barnacles [41]. Early successful recruitment of oysters, epiphytes, and common prey, such as the Atlantic mud crab, could increase the habitat value of the POSH for larger fish as feeding grounds. This behavior would likely be missed by the small spatial scale of the project and static nature of the lift nets.

Crustacean densities were much greater than fish densities among all treatments and sites. At KP, densities were greater in the colder months than in spring and summer. At WL, densities were greatest in the winter. Generally, the POSH had greater crustacean densities than the Oyster Ball, consistent with our second hypothesis (Figure 5). The exception was winter at KP, following a freeze and a dramatic drop in water temperature in the area (see Appendix E). Most crustaceans observed at KP during winter were green porcelain crabs on the underside of the Oyster Ball. The green porcelain crabs were likely seeking refuge from, or unaffected by, colder temperatures in flowing water at the structure–sediment interface, and therefore, the freeze is the most likely cause of the significantly greater crustacean abundances on the Oyster Ball in winter. The increase in interstitial spaces on the POSH provided more refuge space for a greater abundance and diversity of mud crabs and juvenile stone crabs, as they were mostly sampled within the structure’s many void spaces and newly recruited oysters. This is consistent with Karp et al. (2018) [60], who found a positive relationship between rugosity and mud crab density and diversity. The orientation of oyster shells to provide more vertical relief, as designed in the POSH, can be more effective for creating complex oyster reef habitat [68,69]. Additionally, greater oyster recruitment to the POSH provides more refuge, as oysters contribute to habitat complexity through reef formation [57,73,75,76]. High densities of crustacean prey species found on the POSH may result in a benefit to commercially valuable fish species by providing a rich food source [15], as long-term reef development could promote greater fish productivity [16,77].

This is outside of this study's scope due to the timescale sampled and selectivity of the methodology employed.

All crustacean diversity indices were similar throughout the study period, inconsistent with our fourth hypothesis that the oyster reef and POSH would support greater crustacean diversity. Abundances were dominated by common oyster reef residents in the region like the green porcelain crab, Atlantic mud crab, and daggerblade grass shrimp. The POSH had a greater proportion of green porcelain crabs and mud crabs, coinciding with greater overall abundances at both sites. At KP, the POSH hosted a greater abundance of stone crabs and low abundances of flatback mud crabs and estuarine mud crabs, which were not observed utilizing the Oyster Ball. The Oyster Ball had greater proportions and abundances of Portunid swimming crabs and shrimp. The invasive Indonesian swimming crab has shown to feed on native crabs [78] and may have had an impact on crustacean densities by predating on, or affecting the behavior of, native mud crabs or porcelain crabs, especially on the Oyster Ball, where refuge space is limited. Lastly, the oyster reef's total catch was dominated by shrimp due to the high abundance of grass shrimp sampled.

Sampling artificial reefs can present challenges and require a combination of gear types to effectively sample a greater variety of fish [64,79]. Enclosure samplers like the bottomless lift nets used in this study effectively sample small-bodied fish and crustaceans in intertidal structured habitats but require much time and labor [51,64–66,72,73,79]. To sample crustaceans utilizing the POSH, the interstices were visually inspected on the exterior and underside, and this likely gave an underestimation of mud crab and green porcelain crab abundances. Structures have been subsampled and dissected in the lab to get a better understanding of crustacean utilization of the POSH, following two years of deployment, and early results seem to support this claim. Catch efficiencies of daggerblade grass shrimp in the lift nets were variable, ranging from 20–83% (Figure 3). Variable catch efficiencies were likely due to a combination of escape and issues with the nets addressed below. Based on preliminary testing, specimens stayed dyed by the methyl-blue for greater than 12 h and were easily observable in the lab under dissection scope and were therefore not likely missed if caught. Except for one sampling event, catch efficiencies of grass shrimp found in this study were greater than Rozas's rate of 32%. The particularly high catch efficiencies measured during the last sampling event are likely due to sweeping the nets sooner after releasing shrimp. This indicates that higher efficiencies may be achieved if organisms can be collected closer to the initial capture at high tide. KP is a highly energetic shoreline with a steep slope and great tidal range. At this site, the gear faced difficulties with water splashing over the top of the net and stakes occasionally coming loose on the bottom. Lining the bottom with chains, digging deeper trenches [80], and sampling on neap tides may minimize challenges. The presence of sampling materials (nets, rope, stakes) may have deterred some fish from utilizing the structures, and additionally, wave action interfering with the nets might have caused further disturbance. These challenges should be considered when sampling in high-energy systems. The gear proved to be time- and labor-intensive, limiting our ability to collect a larger sample size. Additionally, the active sampling method gave a "snapshot sample" for utilization at one point in time. The limited sample size and active nature of the method led to a lot of variation in large, motile fish.

The aim of this study was to provide an early understanding of the POSH's short-term ability to create oyster reef habitat for nekton to inform restoration stakeholders. It should be reiterated that certain design and procedural flaws, including nonrandom deployment of units, limited spatial scale, reduced sampling in winter, lack of a negative control, and catch variability, limit our ability to make strong inferences on short-term success, particularly

on fish utilization. It was outside the scope of this study to understand the long-term restoration success of the POSH. If possible, a larger shoreline would be studied for 5 or more years post-deployment to address changes in colonization and long-term community establishment [39,81,82]. The bottomless lift nets were successful in accurately sampling smaller and less motile fish and crustaceans, though they were not selective of larger motile fish. Utilizing a suite of methods to sample a greater variety of fish is necessary to understand the habitat value provided to larger transient fish.

This is the first assessment of the novel Pervious Oyster Shell Habitat's ability to provide oyster reef habitat for fish and decapod crustaceans. The POSH's increased complexity has been shown to provide space for high abundances of reef resident decapod crustaceans compared to a less structurally complex restoration method. The high vertical relief, increased complexity, and ability to rapidly recruit a healthy oyster population have made the POSH an effective method for restoring a benthic oyster reef community. Further, the structure provides a sustainable and cost-effective option for practitioners with access to oyster shell recycling programs. Any stakeholders who wish to restore oyster reef habitat for the purpose of rebuilding populations of oysters and associated fauna should consider using the method or engineering greater complexity into artificial reefs.

Author Contributions: Conceptualization, H.M. and K.J.S.; methodology, H.M., G.N. and K.J.S.; software, H.M.; validation, G.N. and K.J.S.; formal analysis, H.M.; resources, K.J.S.; data curation, H.M. and G.N.; writing—original draft preparation, H.M.; writing—review and editing, H.M., G.N. and K.J.S.; visualization, H.M.; supervision, K.J.S.; project administration, K.J.S.; funding acquisition, K.J.S. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: Author Hunter Mathews is employed by Jax Oyster Conservation, 501(c)3, Atlantic Beach, FL 32233. Author Gabrielle Nelson is employed by Gulf Shellfish Institute, Palmetto, FL 34221. The remaining author declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflict of interest.

Appendix A

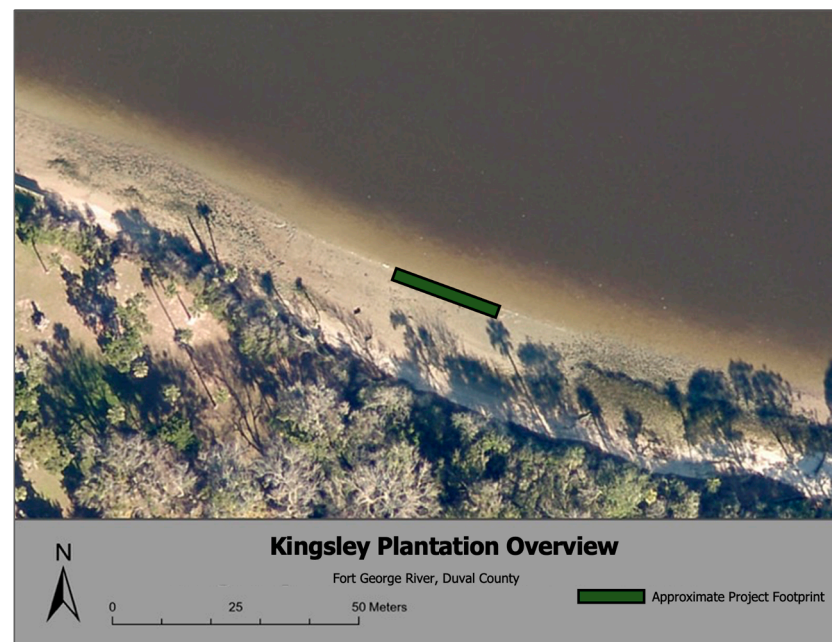


Figure A1. Kingsley Plantation overview map. The map depicts the footprint of the experimental living shoreline in relation to small fringe oyster reefs preceding patches of smooth cordgrass (*Spartina alterniflora*) to the east and west. No healthy oyster or smooth cordgrass populations exist in the area surrounding the project.



Figure A2. Wrights Landing overview map. The map depicts the footprint of the experimental living shoreline in relation to previously enhanced oyster reefs to the northwest. Smooth cordgrass, black mangrove (*Avicennia germinans*), saltwort (*Batis maritima*), and Virginia glasswort (*Salicornia ambigua*) are between the living shoreline and the Guana Peninsula uplands. No healthy oyster or smooth cordgrass populations exist in the immediate area surrounding the project.

Appendix B

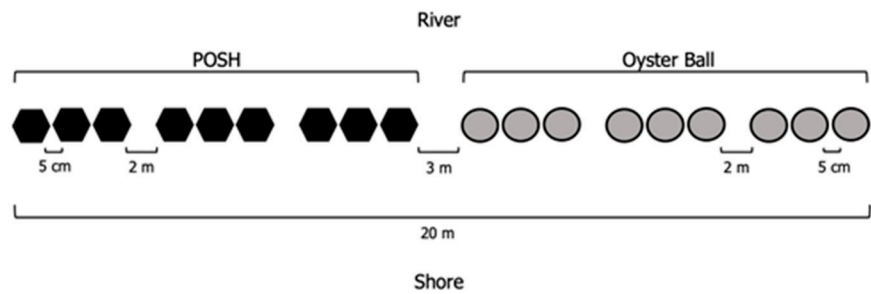


Figure A3. Living shoreline design schematic at KP and WL (Mathews et al. 2023) [41].

Appendix C



Figure A4. Lift nets set at WL, prior to lifting.



Figure A5. Lift nets pulled at WL.

Appendix D

Table A1. Number of marked *Palaemonetes* spp. recovered from 20 released per lift net.

	POSH 1	POSH 2	POSH 3	OB 1	OB 2	OB 3
8/27/22	3	12	9	12	6	9
8/28/22	11	7	7	6	7	2
10/8/22	6	12	4	11	9	10
10/9/22	18	12	16	16	18	16

Table A2. Test statistics of Pearson's chi-squared test for catch efficiency.

Chi ²	df	p
17.34	11	0.098

Tests were run on counts of shrimp received per net/event.

Table A3. Test statistics for the Scheirer–Ray–Hare two-way ANOVAs for fish densities at KP.

	Df	Sum Sq	H	p. Value
Treatment	2	275.6	0.8243	0.66222
Season	3	5698.9	17.0425	0.00069
Treatment–Season	5	246.6	0.7375	0.98085

Table A4. Test statistics for Dunn's post hoc test for fish densities by treatment and season at KP.

Comparison	Z	p. Unadj	p. Adj
Oyster Reef–POSH	−0.9518197	0.3411884	1.0000000
Oyster Reef–OB	−0.1397777	0.8888356	0.8888356
POSH–OB	0.9078905	0.3639361	0.5459041
Fall–Spring	0.4585501	0.6465572762	0.646557276
Fall–Summer	2.2169848	0.0266241292	0.053248258
Spring–Summer	1.9657523	0.0493272312	0.073990847
Fall–Winter	3.5114748	0.0004456277	0.002673766
Spring–Winter	3.4132736	0.0006418748	0.001925624
Summer–Winter	1.6831906	0.0923381954	0.110805834

Table A5. Test statistics for the Scheirer–Ray–Hare two-way ANOVAs for fish densities at WL.

	Df	Sum Sq	H	p. Value
Treatment	1	2.38	0.0237	0.87778
Season	3	2194.17	21.7955	0.00007
Treatment–Season	3	168.70	1.6758	0.64233

Table A6. Test statistics for Dunn’s post hoc test for fish densities by season at WL.

Comparison	Z	<i>p. Unadj</i>	<i>p. Adj</i>
Fall–Spring	4.0078272	6.127992×10^{-5}	0.0001838398
Fall–Summer	4.0078272	6.127992×10^{-5}	0.0003676795
Spring–Summer	0.0000000	1.000000×10^0	1.0000000000
Fall–Winter	2.7242125	6.445502×10^{-3}	0.0128910032
Spring–Winter	−0.5481647	5.835788×10^{-1}	0.7002945694
Summer–Winter	−0.5481647	5.835788×10^{-1}	0.8753682117

Table A7. Test statistics for the Scheirer–Ray–Hare two-way ANOVAs for crustacean densities at KP.

	Df	Sum Sq	H	<i>p. Value</i>
Treatment	2	12,093.9	27.628	0.0000010
Season	3	8355.9	19.089	0.0002621
Treatment–Season	5	7229.1	16.515	0.0055184

Table A8. Test statistics for Dunn’s post hoc test for crustacean densities by treatment and season at KP.

Comparison	Z	<i>p. Unadj</i>	<i>p. Adj</i>
Oyster Reef–POSH	2.991676	2.774504×10^{-3}	4.161757×10^{-3}
Oyster Reef–OB	4.792208	1.649554×10^{-6}	4.948661×10^{-6}
POSH–OB	2.013056	4.410870×10^{-2}	4.410870×10^{-2}
Fall–Spring	2.19628649	0.028071444	0.04210717
Fall–Summer	2.64179283	0.008246848	0.02474054
Spring–Summer	0.37044705	0.711049421	0.85325931
Fall–Winter	−0.08728146	0.930447792	0.93044779
Spring–Winter	−2.55310659	0.010676682	0.02135336
Summer–Winter	−3.09983280	0.001936299	0.01161779

Table A9. Test statistics for the Scheirer–Ray–Hare two-way ANOVAs for crustacean densities at WL.

	Df	Sum Sq	H	<i>p. Value</i>
Treatment	1	2545.93	16.9908	0.00004
Season	3	377.48	2.5192	0.47183
Treatment–Season	3	361.88	2.4151	0.49083

Table A10. Test statistics for the Scheirer–Ray–Hare two-way ANOVAs for crustacean densities by season at WL.

Comparison	Z	<i>p. Unadj</i>	<i>p. Adj</i>
Fall–Spring	−0.1250661	0.9004712	0.9004712
Fall–Summer	0.2834832	0.7768065	0.9321678
Spring–Summer	0.4085493	0.6828705	1.0000000
Fall–Winter	−1.3070854	0.1911837	0.5735511
Spring–Winter	−1.2049694	0.2282151	0.4564302
Summer–Winter	−1.5385485	0.1239146	0.7434874

Table A11. ANOSIM results for KP. Significant differences are denoted (*). Not applicable due to insufficient data (NA).

	Oyster Reef × POSH	Oyster Reef × OB	POSH × OB
Overall	0.511	0.043 *	0.0756
Summer 2022	0.103	0.099	0.104
Fall 2022	NA	NA	0.343
Winter 2023	0.337	0.332	0.333
Spring 2023	0.336	0.338	0.339

Table A12. ANOSIM results for WL.

	POSH × OB
Overall	0.155
Summer 2022	0.337
Fall 2022	0.661
Winter 2023	NA
Spring 2023	0.652

Appendix E

Table A13. Environmental measurements at KP. Water depth (m), water temperature (°C), salinity (ppt), dissolved oxygen (mg/L), and chlorophyll-a (µg/L) measured at the time of sampling.

Date	Treatment	Depth (m)	Temp (°C)	Salinity	DO (mg L ⁻¹)	Chla-a (µg L ⁻¹)
7/26/22	POSH	1.0	28.8	31.7	5.0	10.3
	OB	0.9	28.8	31.5	4.8	8.7
	Oyster Reef	0.7	29.0	27.2	4.8	10.7
7/27/22	POSH	0.9	29.1	28.2	5.0	8.3
	OB	0.8	29.2	27.9	5.1	7.7
	Oyster Reef	0.6	29.3	27.4	5.2	8.3
9/13/22	POSH	1.4	29.4	32.1	5.6	4.3
	OB	1.4	29.4	32.2	5.4	4.7
11/5/22	POSH	1.7	22.1	31.1	8.2	6.0
	OB	1.6	22.1	31.3	8.4	7.0
11/6/22	POSH	1.3	22.7	29.8	7.6	5.0
	OB	1.3	22.7	30.0	7.6	5.0
1/7/23	POSH	1.3	15.0	31.2	12.8	3.0
	OB	1.2	15.0	31.2	13.6	5.0
	Oyster Reef	1.1	14.7	31.2	12.7	3.0
1/8/23	POSH	1.4	15.5	30.3	12.9	4.0
	OB	1.3	15.5	30.9	14.6	6.0
	Oyster Reef	1.2	15.5	30.9	13.3	7.0
5/6/23	POSH	1.3	22.1	32.5	7.3	7.0
	OB	1.3	22.9	32.3	7.4	6.0
	Oyster Reef	1.2	22.9	32.3	7.3	6.0
5/7/23	POSH	1.2	23.4	31.9	6.3	3.0
	OB	1.2	23.3	32.2	6.2	3.0
	Oyster Reef	1.1	23.7	32.2	6.2	3.0

Table A14. Environmental measurements at WL (* data taken from the nearby SWMP station at Pine Island). Water depth (m), water temperature (°C), salinity (ppt), dissolved oxygen (mg/L), and chlorophyll-a (µg/L) measured at the time of sampling.

Date	Treatment	Depth (m)	Temp (°C)	Salinity	DO (mg L ⁻¹)	Chla-a (µg L ⁻¹)
8/27/22	POSH	0.9	30.0	30.3	4.4	9.0
	OB	1.0	30.0	30.3	4.5	7.0
8/28/22	POSH	1.1	29.7	31.0	4.6	6.3
	OB	1.1	29.7	31.0	4.6	6.7
10/8/22	POSH	1.2	23.8	28.4	5.4	9.0
	OB	1.3	23.8	28.3	5.3	8.0
10/9/22	POSH	1.3	24.2	29.1	5.7	8.7
	OB	1.3	24.3	29.6	5.7	8.0
2/4/23	POSH	1.1	17.1	29.0	6.8	6.6
	OB	1.2	17.1	29.6	6.5	10.0
4/1/23	POSH	0.7	22.7 *	28.5 *	6.1 *	2.7 *
	OB	0.8	22.7 *	28.5 *	6.1 *	2.7 *
4/2/23	POSH	0.7	22.9	28.8	6.4	9.0
	OB	0.7	23.0	29.4	6.4	6.0

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