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RESEARCH ARTICLE

Evaluating biodegradable alternatives to plastic mesh for small-scale oyster reef restoration

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Polyethylene plastic mesh is commonly used for containing oyster shells in small-scale oyster reef restoration, but environmental and public health concerns have prompted investigations of biodegradable alternatives. Shallow (<0.5 m) and deep (approximately 1 m) oyster reefs (approximately 6 m^2) were constructed in the Mission-Aransas Estuary, Texas, U.S.A., in March 2020 using recycled oyster shells placed into four different replicated mesh bag types: polyethylene (plastic) and three biodegradable alternatives (cellulose, cotton, and jute). Biodegradable alternatives (cellulose, cotton, and jute) all completely degraded within 2 months of deployment, leaving piles of loose shell, while polyethylene bags remained intact. Despite rapid degradation, the biodegradable/loose shell successfully recruited and developed larger oysters (mean of 46 mm) than on the polyethylene-bagged shell (mean of 40 mm) after 7 months, although at less than half the density. Associated motile fauna density in the bagged shell was 2.4 times higher than in the loose shell after 7 months at both the deep and shallow locations. Faunal community composition and diversity varied more with reef depth than by bag type. The total cost of using polyethylene bags was lower than for biodegradable alternatives (22–45% the cost of cellulose, 35–72% the cost of jute, 49–99% the cost of cotton). However, because our estimate of the environmental cost of polyethylene plastic mesh only included impacts on marine natural capital, the true cost is likely much higher. Despite higher costs, biodegradable alternatives can still be successful for use in small-scale oyster restoration events without introducing plastics into the marine environment.

Key words: *Crassostrea virginica*, fauna, Gulf of Mexico, habitat restoration, plastic pollution

Implications for Practice

- Using biodegradable mesh materials to contain oyster shells in small-scale reef restoration can facilitate oyster and faunal recruitment and eliminate the introduction of plastics to the ocean.
- The direct costs of biodegradable bags are currently more expensive than polyethylene bags but using biodegradable bags avoids unquantified environmental costs.
- Restoring oyster reef using biodegradable oyster bags still facilitates oyster populations and associated epifaunal communities despite the bags rapid degradation in a subtropical, low-energy environment.

Introduction

Unsustainable harvest combined with pollution, disease, and other environmental changes have led to severe declines of native oyster populations (Kirby 2004; Beck et al. 2011; zu Ermgassen et al. 2016). In areas where reef habitat has been degraded or destroyed, one approach to combat the decline in shell resources involves placement of suitable substrate to facilitate recruitment and growth of larval oysters. At larger scales (approximately >0.4 ha), recycled oyster shells or other suitable substrates (e.g. river rock, limestone, clean concrete) are often transported by barge to a selected restoration site and deployed on the estuary bottom (Powers et al. 2009; Schulte et al. 2009; George et al. 2015; Graham et al. 2017). An alternative restoration method that can be used at smaller-scales (<0.4 ha) is to manually fill mesh bags with oyster shell and form a reef comprising these bags. Using mesh bags can minimize loss of loose shells due to waves and currents (e.g. Grizzle et al. 2002; Wall et al. 2005; Stiner & Walters 2008) and can create structural complexity similar to natural reefs (Ertel & McCall 2005; Kennedy et al. 2011). Shell bagging can be completed as a

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public event, which provides the additive benefits of connecting community volunteers with their environment and providing support for future restoration investments (Leigh 2005; DeAngelis et al. 2019).

Polyethylene plastic mesh is a commonly used material for containing (bagging) shells or other substrates in small-scale and volunteer-based restoration efforts (Brumbaugh & Coen 2009; Hadley et al. 2010) because of its affordability, durability, and versatility (Law 2017). However, plastic pollution has become a major environmental and public health concern (Beaumont et al. 2019), and has a great potential to harm the marine environment because it accumulates along coastlines, the open ocean, and within marine organisms (Thompson et al. 2004; Barnes et al. 2009; MacLeod et al. 2021). An ideal replacement for plastic mesh would be made of natural, biodegradable fibers that maintain substrate stability long enough for oysters and fauna to recruit, grow, and stabilize the reef structure. It is also important to balance ecological benefits with material costs because oyster reefs are one of the most costly marine and coastal habitats to restore (Bayraktarov et al. 2016), and limited availability of funds can have a considerable influence on restoration decisions (Miller & Hobbs 2007).

The goal of this study was to evaluate the efficacy of using biodegradable alternatives (cellulose, jute, and cotton) to polyethylene mesh in small-scale oyster reef restoration. The objectives were to compare oyster populations, faunal communities, and total cost [material + shipping + labor + (reduced marine natural capital from plastic pollution)] of using three biodegradable and one plastic mesh bags to create restored oyster reefs.

Methods

Site Description

St. Charles Bay is a shallow (mean approximately 1 m, Orlando et al. 1993) secondary bay in the Mission-Aransas Estuary, a microtidal, bar-built estuary in South Texas, U.S.A. (Fig. 1). The estuary receives freshwater inflow primarily from the Mission and Aransas Rivers, and exchange with the Gulf of Mexico occurs at Aransas Pass inlet (Orlando et al. 1993). While most of the estuary is open to oyster harvest, St. Charles Bay is closed to commercial oyster harvest to promote recovery of existing populations.

Bag Material Description

Bags for containing oyster shells were created using three biodegradable (cellulose, cotton, jute fiber), or polyethylene plastic

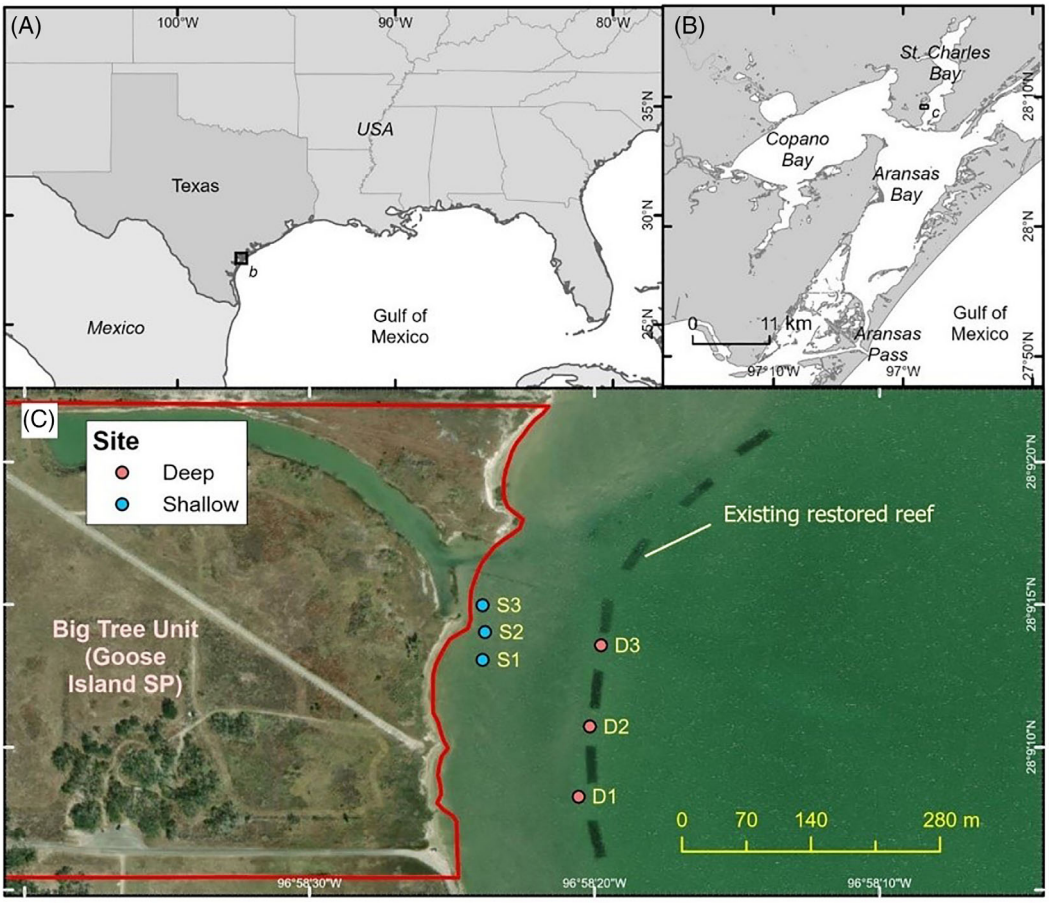

Figure 1. Map of the study area, including (A) Texas coastline and Gulf of Mexico, (B) the Mission-Aransas Estuary and St. Charles Bay, and (C) deep (D1, D2, D3; 1 m depth) and shallow (S1, S2, S3; < 0.5 m depth) experimental reef sites in St. Charles Bay.

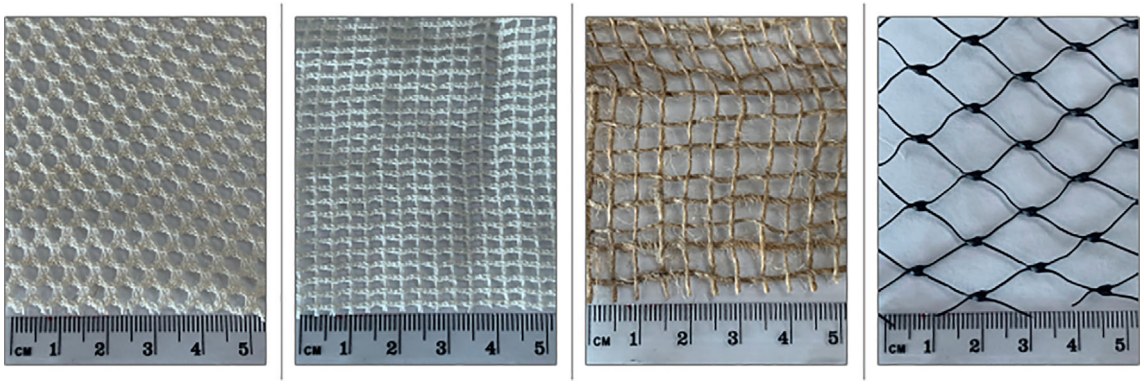

Figure 2. Images of mesh bag materials. From left to right: Cellulose, cotton, jute fiber, and polyethylene mesh.

(nonbiodegradable) materials (Fig. 2). The biodegradable bags came pre-assembled from their respective suppliers. Cellulose bags (derived from beech wood) were 70 × 30 cm with 0.3 cm mesh size (BESE Ecosystem Restoration Products, Netherlands). Cotton bags were 55 × 30 cm with 0.5 cm mesh size (Alibaba, China). Jute fiber bags were 50 × 30 cm with 0.7 cm mesh size (Tissus Papi, France). Polyethylene plastic mesh bags of approximately 50 × 20 cm with 2 cm mesh size were created by cutting 1-m sections from a 550-m long roll of tubular mesh and tying a knot at one end. All bags were filled with 11.5 L of sun-cured (>6 months) recycled whole oyster shells and tied shut.

Field Experiment

Three shallow (<0.5 m) and three deep (approximately 1 m) approximately 6 m^2 artificial oyster reefs were created within St. Charles Bay on 25 March 2020, adjacent to Goose Island State Park. Each reef contained four rows of bagged oyster shells (10 bags per row) with each row comprising bags made from a different material (cellulose, cotton, jute fiber, polyethylene; Fig. 2). Five bags in each row were placed directly on the sea floor and remained in place for the entire experiment. The other five bags in each row were placed in individual 0.45 × 0.30 m HDPE soda stacking trays (Piper Industries, Dallas, TX, U.S.A.; Model 16/20 OZ-1HD-24, 11.5-cm high) anchored with steel reinforcing bar (rebar) to be used for sampling. Five additional control trays with no bag or oysters were placed at each site to account for potential tray artifacts in statistical analyses. Sampling of the bags in trays was conducted monthly for the first 3 months after deployment (April, May, and June 2020), and every 2 months thereafter (August and October 2020). On each sampling date, one tray of each bag type and one control from each of the three shallow and three deep sites were sampled without replacement.

Oyster size and abundance, material degradation, and motile fauna community abundance were quantified for each sampled tray. Shell heights of up to 20 randomly selected nonspat live oysters (>25 mm) were measured, and all additional live oysters (>25 mm) were counted from each sampling tray. Spat (≤25 mm) densities were quantified on five randomly selected live oysters and dead shells (five of each). Material degradation was recorded using a qualitative scale (intact, small holes [<30 mm], large holes [>30 mm], disintegrated [>90% of bag has degraded]).

Motile epifauna were removed from each tray and fixed in buffered formalin for community composition analysis in the laboratory. Epifaunal taxa were identified to the lowest possible taxon (usually species) and enumerated. Dry weight biomass for each taxon was measured after drying organisms for 48 hours at 60°C. Mollusk shells were dissolved using 2 N HCl and rinsed with fresh water before drying.

Water quality parameters, including water temperature, salinity, dissolved oxygen concentration and saturation, pH, and turbidity, were measured at each site on each sampling date using a YSI ProDSS multiparameter water quality meter (YSI, Inc., OH, U.S.A.).

Data Analysis

Oyster density, epifauna density and biomass in control treatments were subtracted from those in each treatment for each date-site combination to account for tray effects. Oyster and epifauna metrics were reported per unit of volume (m^{-3}) because the bags were filled with a known volume of shell. Faunal diversity analyses excluded control treatments. Analysis of variance (ANOVA, $\alpha = 0.05$) tests were used to test the effects of date, depth (shallow or deep), and treatment (biodegradable-bagged shell or polyethylene-bagged shell) using station as a random effect, on motile macrofauna and encrusting fauna densities, biomass, and Hill's N1 diversity, as well as oyster density and shell height. The biodegradable-bagged treatments were combined into a single biodegradable-bagged treatment because of rapid disintegration of the biodegradable bags, and are hereafter referred to as a "loose shell" treatment, which contrasts with the continuously "plastic-bagged shell" polyethylene-bag treatment. The normality of residuals was assessed using the Shapiro–Wilk test. All data were either $\log_e$ or fourth-root transformed to meet ANOVA normality assumptions. All univariate analyses and data management were performed using the lme4 package in RStudio version 1.2.1335 (RStudio Team 2018).

Nonmetric multidimensional scaling (nMDS) and similarity profile (SIMPROF) cluster analyses (group average method;

Clarke & Ainsworth 1993) were used to determine faunal community composition among treatments over time. The similarity percentages (SIMPER) routine was used to determine the taxa that were characteristic of, and different among treatments. Multivariate analyses were performed on a Bray–Curtis similarity matrix on square-root transformed data using PRIMER 7 software (Clarke et al. 2014).

Cost Comparisons

Cost comparisons of each bag type were calculated by adding the 2020 purchase and shipping cost for 1,000 bags plus the cost of labor to fill 1,000 bags with shell. To determine the cost of labor, the time taken to fill each bag type, and a wage (cost/time) are both needed. The mean time to fill 1,000 bags of each bag type was calculated after timing how long it took two people to fill at least five bags of each type. The 2021 national estimate of the hourly value of volunteer time, $28.54 USD (Independent Sector 2021), was then multiplied by the fill rate to estimate the labor cost for each bag type. The annual cost of reduced marine natural capital from marine plastic pollution was calculated by converting the estimated cost per metric ton in 2011 USD ($3,300–$33,000; Beaumont et al. 2019) to 2021 USD ($3,975–$39,753), and adjusting by the weight of 1,000 polyethylene bags (35 kg = 0.035 metric ton).

Results

Field Experiment

Temperatures followed seasonal trends and were similar between depths, ranging from 20.6°C (mean) in October 2020 to 30.3°C in August 2020 (Fig. S1a). Salinity was similar between depths and ranged from 22.8 in June 2020 to 29.8 in August 2020 (Fig. S1b). Shallow sites generally had higher DO concentrations than deep sites, although DO concentrations were high across all sampling dates, ranging from 5.45 mg/L at

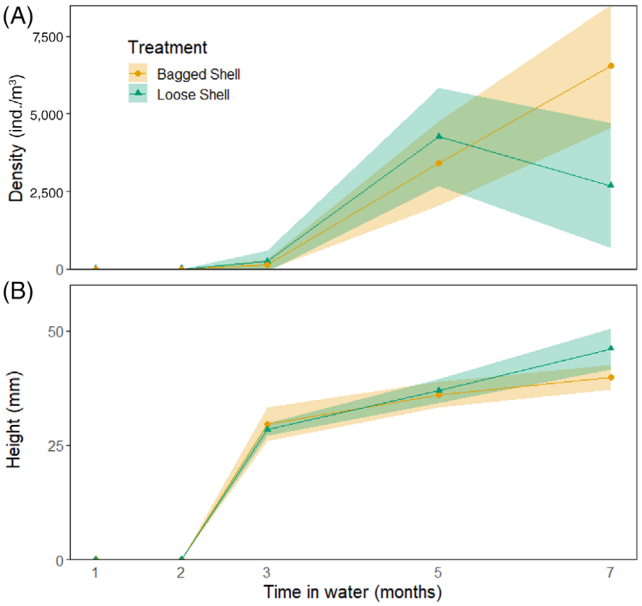

Figure 4. (A) Mean oyster density of plastic-bagged and loose shell treatments over time after subtracting respective control values. (B) Mean nonspat oyster height of plastic-bagged and loose shell treatments over time. Data were pooled for deep (approximately 1 m) and shallow (<0.5 m) sites. The shading indicates ±1 SD about the mean.

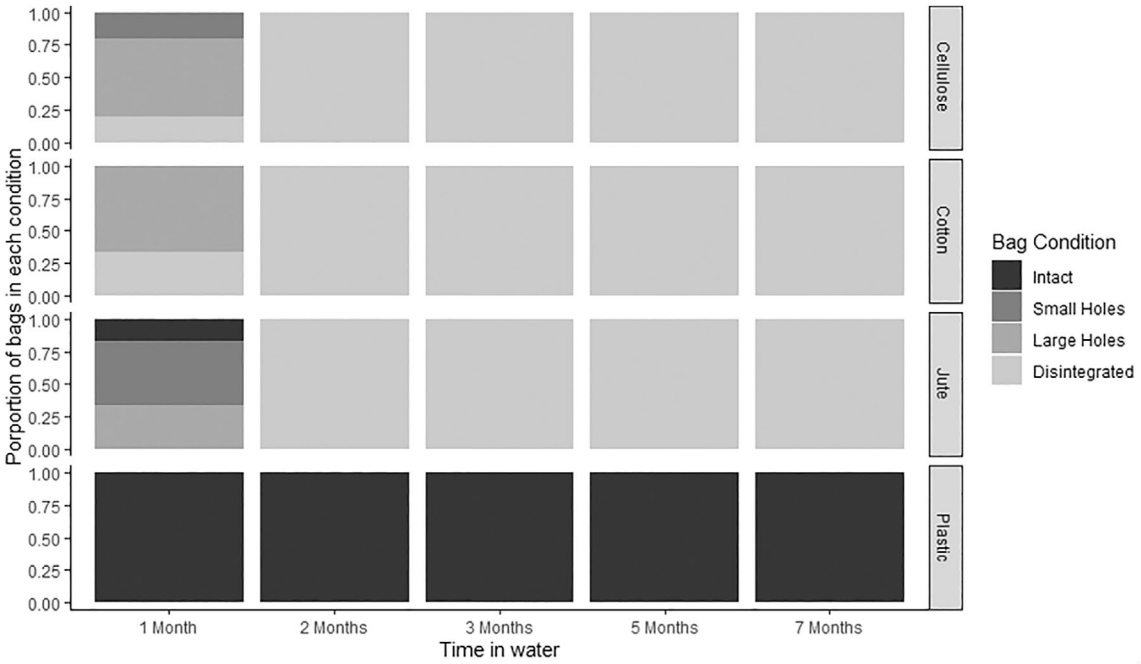

Figure 3. Proportion of each bag treatment in various levels of degradation over time (intact, small holes [<30 mm], large holes [>30 mm], disintegrated [>90% of bag has degraded]). All bags were intact when deployed.

deep sites in August 2020 to 7.37 mg/L at deep sites in October 2020 (Fig. S1c). pH levels were similar between depths and fluctuated between 7.93 at deep sites in June 2020 to 8.18 at deep sites in October 2020 and (Fig. S1d).

Twenty percent of cellulose and 33% of cotton bags were fully disintegrated and 25% of jute bags had large (>30 mm) holes after 1 month (30 days) in the water (Fig. 3). All biodegradable bag treatments were fully disintegrated within 2 months of deployment (56 days). Polyethylene plastic bags remained fully intact throughout the duration of the study. The oyster and fauna metrics of biodegradable bag treatments were combined into a single "loose shell" treatment and compared with the metrics of the continuously "plastic-bagged shell" polyethylene-bag treatment because of the rapid disintegration of all biodegradable materials (unbagging of shell).

Oyster recruitment was first observed on the experimental reefs 3 months after deployment (after all biodegradable bags were disintegrated). Oyster density was similar between depths ($p \leq 0.624$) but varied over time depending on the bag type ($p \leq 0.005$; Tables S1 & S2). Oyster densities increased in a similar manner at both bag treatments from 3 to 5 months (mean ± standard deviation of 214 ± 314 and 4,051 ± 1,546 ind./m^3; Fig. 4A). However, oyster density increased in the plastic-bagged shell treatment (6,551 ± 1,982 ind./m^3) but decreased in the loose shell treatment after 7 months (2,686 ± 2,000 ind./m^3).

Mean oyster height was similar between depths ($p \leq 0.838$) and increased throughout the study period in all treatments (Fig. 4B; Tables S1 & S2). Shell height was similar in plastic-bagged and loose shell treatments until 5 months. However, at 7 months, shell height on loose shell (46.1 ± 4.4 mm) was greater than that on plastic-bagged shell (40.0 ± 2.7 mm, $p < 0.001$).

Thirty-two motile epifauna taxa were collected throughout the field experiments (Table 1). Faunal density was variable throughout the study period and, within treatments, was generally greater in deeper sites (Fig. 5A). Faunal density on loose shell ranged from 4,772 ± 1,764 ind./m^3 after 1 month to

Table 1. Mean total (± SD) taxa densities across the study period for each treatment and depth.

	Treatment			*Depth*	
Taxa	*Loose Shell*	*Plastic-Bagged Shell*	*Control*	*Deep*	*Shallow*
Crustaceans					
Petrolisthes armatus	49.55 ± 40.98	78.88 ± 75.07	10.20 ± 8.26	67.02 ± 63.50	29.70 ± 21.01
Panopeidae	38.21 ± 39.30	56.07 ± 56.13	12.33 ± 12.18	28.71 ± 25.72	47.66 ± 52.83
Eurypanopeus turgidus	14.86 ± 10.19	19.44 ± 12.67	12.41 ± 13.09	13.43 ± 11.33	17.50 ± 11.10
Eurypanopeus depressus	8.23 ± 10.89	10.44 ± 20.42	6.62 ± 11.07	11.98 ± 15.81	3.39 ± 5.02
Alpheus heterochaelis	6.27 ± 4.19	7.11 ± 5.27	1.40 ± 0.55	5.07 ± 3.46	7.40 ± 5.06
Palaemonetes vulgaris	3.82 ± 3.40	6.17 ± 10.28	3.25 ± 2.76	4.86 ± 3.39	3.94 ± 6.22
Callinectes sapidus	0.00 ± 0.00	2.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	1.50 ± 0.71
Menippe adina	1.14 ± 0.38	1.33 ± 0.58	1.00 ± 0.00	1.17 ± 0.39	0.00 ± 0.00
Farfantepenaeus aztecus	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00
Panopeus herbstii	1.75 ± 1.50	1.00 ± 0.00	0.00 ± 0.00	1.60 ± 1.34	1.00 ± 0.00
Clibanarius vittatus	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00
Fish					
Gobiosoma bosc	4.77 ± 3.42	6.46 ± 3.19	2.55 ± 1.92	5.52 ± 3.68	4.44 ± 3.05
Opsanus beta	6.99 ± 25.63	3.47 ± 2.05	1.00 ± 0.00	4.88 ± 12.13	6.74 ± 27.69
Chasmodes longimaxilla	1.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00
Gobiesox strumosus	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00
Lagodon rhomboides	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00
Microphis brachyurus	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
Myrophis punctatus	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
Sygnathidae	0.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00
Larval fish	2.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.00 ± 0.00
Gastropods					
Marshallora nigrocincta	8.45 ± 8.10	30.42 ± 37.22	3.27 ± 3.41	12.88 ± 23.04	10.47 ± 14.67
Boonea impressa	29.38 ± 27.14	24.92 ± 28.43	8.62 ± 7.71	28.41 ± 30.18	21.00 ± 19.35
Parvanachis ostreicola	13.67 ± 12.16	12.69 ± 13.39	7.75 ± 6.44	17.24 ± 13.17	6.72 ± 6.21
Pyrgocythara plicosa	7.59 ± 7.24	19.32 ± 25.20	2.78 ± 1.72	13.15 ± 16.03	5.98 ± 10.65
Costoanachis avara	14.40 ± 12.93	14.81 ± 12.85	13.67 ± 12.89	20.73 ± 14.10	7.27 ± 5.36
Bittiolum varium	4.88 ± 6.07	5.00 ± 6.52	9.80 ± 9.34	2.52 ± 2.06	6.85 ± 7.63
Astyris lunata	5.30 ± 9.21	4.20 ± 5.16	10.00 ± 12.92	3.92 ± 4.34	8.38 ± 12.89
Boonea seminuda	2.40 ± 3.13	1.50 ± 0.71	1.00 ± 0.00	2.00 ± 2.45	0.00 ± 0.00
Eulimastoma canaliculatum	2.50 ± 0.71	1.00 ± 0.00	18.00 ± 0.00	3.00 ± 0.00	7.00 ± 9.54
Nassarius vibex	2.33 ± 1.53	1.00 ± 0.00	2.00 ± 1.41	2.00 ± 1.26	0.00 ± 0.00
Parvanachis obesa	5.25 ± 2.50	1.00 ± 0.00	0.00 ± 0.00	6.00 ± 0.00	4.00 ± 3.16
Flatworms					
Turbellaria	2.77 ± 2.00	4.58 ± 2.87	1.33 ± 0.58	2.87 ± 2.33	3.50 ± 2.52

13,227 ± 4,120 ind./m^3 after 5 months in deep sites, and from 4,812 ± 5,226 ind./m^3 after 7 months to 11,198 ± 7,844 ind./m^3 after 2 months in shallow sites. Faunal density in plastic-bagged shell ranged from 8,783 ± 3,197 ind./m^3 after 1 month to 29,391 ± 8,711 ind./m^3 after 5 months in deep sites, and from 8,899 ± 2,924 ind./m^3 after 3 months to 15,101 ± 2,255 ind./m^3 after 1 month in shallow sites. Faunal density differed by treatment ($p < 0.001$) and varied over time depending on depth ($p < 0.001$; Tables S1 & S2); faunal density in bagged shell was higher than in loose shell, and was higher in deep areas than in shallow areas after 2 months.

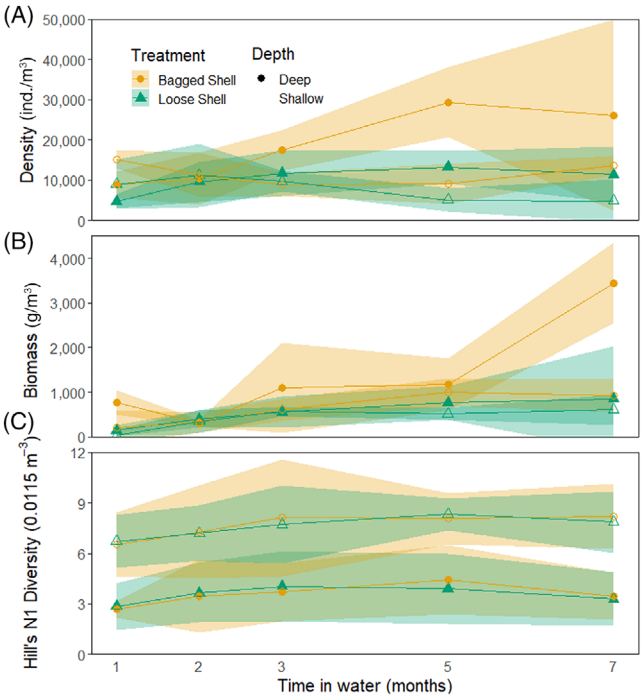

Figure 5. Mean motile epifauna (A) density, (B) biomass, and (C) diversity of plastic-bagged and loose shell treatments after subtracting respective control treatments at deep (approximately 1 m) and shallow (<0.5 m) sites over time. Shading indicates ±1 SD about the mean.

Epifaunal biomass generally increased throughout the study period (Fig. 5B). Faunal biomass on loose shell ranged from 145 ± 128 g/m^3 after 1 month to 852 ± 1,174 g/m^3 after 7 months in deep sites, and from 28 ± 136 g/m^3 after 1 month to 606 ± 344 g/m^3 after 7 months in shallow sites. The widest range of faunal biomass was observed on plastic-bagged shell in deep sites, ranging from 306 ± 75 g/m^3 after 3 months to 3,448 ± 900 g/m^3 after 7 months, and from 212 ± 389 g/m^3 after 1 month to 1,004 ± 314 g/m^3 after 5 months in shallow sites. There were significant interactions between treatment and depth ($p \leq 0.037$), and treatment and date on faunal biomass ($p \leq 0.009$; Tables S1 & S2); faunal biomass was higher in bagged shell and deep areas but only after 5 months.

Hill's N1 diversity of motile epifauna generally increased throughout spring and summer, with a slight decline in fall (Fig. 5C). Faunal diversity on loose shell ranged from 2.8 ± 1.4 after 1 month to 4.0 ± 2.1 after 5 months in deep sites, and from 6.7 ± 1.6 after 1 month to 8.3 ± 1.0 after 5 months in shallow sites. Faunal diversity on plastic-bagged shell ranged from 2.7 ± 0.5 after 1 month to 4.5 ± 1.1 after 5 months in deep sites, and from 6.6 ± 1.9 after 1 month to 8.2 ± 1.9 after 7 months in shallow sites. Combining both treatments, diversity was greater in shallow sites, ranging from 6.7 ± 1.6 after 1 month to 8.3 ± 1.0 after 5 months, than deep sites, ranging from 2.8 ± 1.2 after 1 month to 4.0 ± 2.0 after 5 months (Fig. S3). Faunal diversity was similar among treatments but differed by depth ($p \leq 0.032$; Tables S1 & S2).

Faunal community composition clustered into deep and shallow treatments with samples in each cluster being at least 68% similar to each other as determined by nMDS and SIMPROF cluster analysis (Figs. 6 & S2). Differences in community composition between depths were driven primarily by higher

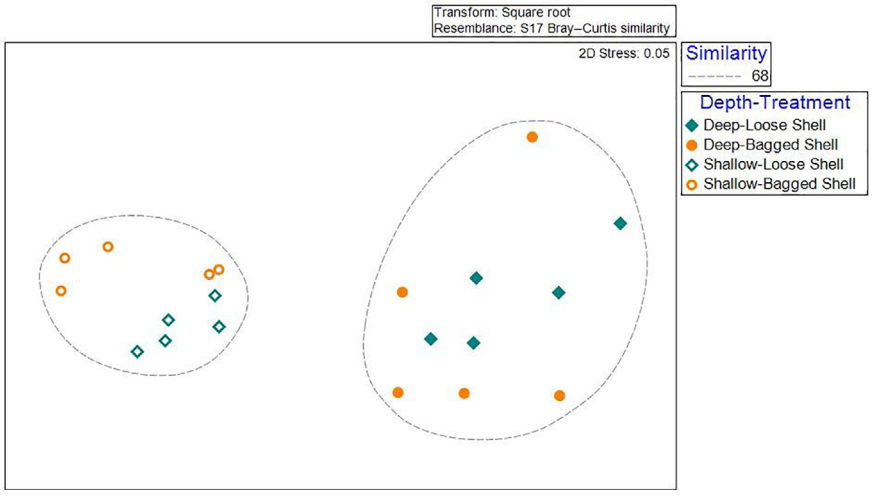

Figure 6. Nonmetric multidimensional scaling plot of density-based faunal community composition among treatments and depths. Each point represents one sampling date of the respective depth-treatment. Samples in each cluster are at least 68% similar to each other as determined by SIMPROF cluster analysis.

Table 2. Cost comparison of bag materials for purchasing, shipping, and filling 1,000 units. Labor cost is calculated as \$28.54 × time (hours).

	Material Cost	*Shipping Cost*	*Time (hours)*	*Labor Cost*	*Environmental Cost*	*Total Cost*
Cellulose	\$4,400	\$660	11.9	\$339	\$0	\$5,411
Jute	\$2,200	\$550	22.2	\$633	\$0	\$3,405
Cotton	\$1,500	\$520	14.9	\$426	\$0	\$2,460
Plastic	\$127	\$188	25.1	\$717	\$139–\$1,391	\$1,196–\$2,448

densities of the porcelain crab *Petrolisthes* sp. and several gastropods including *Costoanachis avara*, *Boonea impressa*, *Parvanachis ostricola*, and *Marshallora nigrocincta* at the shallow reefs, and higher densities of mud crabs (Panopeidae) at the deep reefs (Table S3).

Cost Comparisons

Total costs for each material were calculated per 1,000 units and included material and shipping costs, volunteer labor costs (\$28.54 per hour; Independent Sector 2021) required for conducting restoration using each bag type, and the estimated cost of reduced marine natural capital from plastic pollution (Table 2). Polyethylene plastic bags had the lowest material and shipping costs (\$127 and \$188), and cellulose bags had the highest (\$4,400 and \$660). However, plastic bags took the longest time to fill and had the highest labor costs (approximately 25 hours and \$717) compared to cellulose, which had the lowest (approximately 12 hours and \$339). The estimated annual cost of reduced marine natural capital from plastic pollution was \$0 for cellulose, jute, and cotton mesh bags and ranged from \$139–\$1,391 for polyethylene plastic mesh bags. Total costs of using 1,000 units for conducting oyster reef restoration were lowest for polyethylene plastic (\$1,196–2,448) and cotton (\$2,460) mesh bags, followed by jute (\$3,405) and cellulose (\$5,411) mesh bags.

Discussion

One of the most common approaches for small-scale, community-based oyster reef restoration is to construct reefs using polyethylene plastic mesh bags filled with reclaimed shells (Brumbaugh & Coen 2009; Hadley et al. 2010). However, in part due to its durability, plastic has become a persistent pollutant, with dramatic increases in the marine environment over the past 50 years (Thompson et al. 2004; Barnes et al. 2009), necessitating use of plastic-free materials for habitat restoration. The ideal mesh material for containing oyster shell would be biodegradable yet maintain stable, three-dimensional substrate long enough for spat to recruit and grow into adult oysters to stabilize the reef structure.

Although the biodegradable materials in this study were anticipated to eventually break down, the speed of disintegration (<2 months) was remarkable. The cellulose mesh bags are specifically marketed for use in oyster reef restoration, and are touted to last 1 year in the water (BESE Ecosystem Restoration Products 2020). However, these bags are manufactured in the Netherlands and estimates of degradation are based on rates observed in the Baltic Sea, an ecosystem with lower temperatures, salinities and faunal abundance (Elmgren 1984; Ojaveer et al. 2010) than Gulf of Mexico estuaries (Ward & Tunnell 2017). The jute mesh bags and cotton mesh bags are not specifically marketed for restoration purposes, but were selected based on dimensions, practicality for use in community-based restoration events, and plausibility of being an alternative to plastic mesh. Regardless of material, all biodegradable bags rapidly disintegrated, leaving behind piles of loose, unconsolidated shell. Oyster shells are relatively flat and tend to settle into even layers, reducing the three-dimensional complexity that normally promotes prey survivorship and oyster recruitment success (Humphries et al. 2011*a*; Graham et al. 2017; De Santiago et al. 2019). However, the presence of oyster shells alone (relative to unstructured soft sediments) can be more than important than the degree of structural habitat complexity for producing enhanced habitat value (Lehnert & Allen 2002; Shervette & Gelwick 2008; Humphries et al. 2011*b*; Zacherl et al. 2015), and loose shell deployments have been shown to successfully support oysters along low-energy, low-slope shorelines (Thayer et al. 2005; Wall et al. 2005; Keller et al. 2019).

Oyster density and size were remarkably similar among treatments for 5 months after deployment, even though all biodegradable bags were reduced to piles of unconsolidated shells within 2 months. It is likely that multiple processes influenced recruitment and post-settlement faunal dynamics (Osman et al. 1989; Knights et al. 2012). Oyster recruitment and survival was similar between treatments for 5 months before declines were observed in the biodegradable/loose shell treatments. The intact polyethylene bags maintained structural complexity and may have excluded predators and differentially increased survival (and density) of oysters and fauna in that treatment beyond 5 months (Brown et al. 2008; Humphries et al. 2011*a*; Carroll et al. 2015; Temmink et al. 2021). Predator dynamics also likely changed with time after deployment, with predation by crabs possibly decreasing with increasing oyster size (Bisker & Castagna 1987), and predation by drills being greatest for medium sized (50–75 mm) oysters (Pusack et al. 2018). The biodegradable/loose shell treatment also likely experienced greater physical disturbance and movement of shells, which can also increase oyster mortality (McGuinness 1987; Wall et al. 2005). The persistent three-dimensional structure provided by the plastic-bagged shell treatment also maintained greater vertical relief, which has been positively correlated with oyster density (Taylor & Bushek 2008; Schulte et al. 2009; Lipcius et al. 2015).

In contrast to oysters, faunal community composition was influenced more by depth than by treatment, with higher densities of gastropods and porcelain crabs characterizing shallow

sites. This pattern likely reflects differences in adjacent habitat, with shallow sites near submerged aquatic vegetation (primarily *Halodule wrightii*) and deep sites near unvegetated soft bottom and oyster reef. Our results corroborate those from previous studies indicating the importance of the surrounding landscape and connectivity among habitats in predicting the response of associated fauna to restored oyster reefs (Geraldi et al. 2009; La Peyre et al. 2014). The presence of multiple structured habitats can enrich faunal communities unique to each habitat, increase mobility between habitat patches, and enhance overall restoration success (Kindlmann & Burel 2008; Gain et al. 2017; McAfee et al. 2021). However, in some cases, functional redundancy of structured habitats (e.g. for refuge, food) may mediate abundance enhancements for nekton (Grabowski et al. 2005; Geraldi et al. 2009). Patterns in faunal community composition were unaffected by the breakdown of biodegradable materials and the resulting loose shell, therefore, for restoration projects with the goal of faunal enhancement, material longevity and bag type may be less important than proximity to adjacent habitat. Indeed, mounded loose substrate can still greatly enhance oyster recruitment and faunal communities in areas with substrate limitation (Humphries et al. 2011*a*, 2011*b*; Graham et al. 2017; Blomberg et al. 2018). Longer-term studies are warranted to determine the longevity of observed patterns for both oysters and associated fauna.

Small-scale and community-based oyster reef restoration projects around the world use the shell bagging method to replace lost ecosystem services and enhance community participation (DeAngelis et al. 2019). Given the current awareness of widespread and persistent plastic pollution in marine environments globally (MacLeod et al. 2021), there is an urgent need to switch from plastic-based to natural fiber-based materials for oyster reef restoration; use of polyethylene plastic should no longer be acceptable. However, results from our study identify a number of barriers in several key areas. The total cost for using an oyster bag made of polyethylene is lower than for biodegradable mesh (22–45% the cost of cellulose, 35–72% the cost of jute, 49–99% the cost of cotton). However, because the environmental cost of polyethylene plastic mesh only considered impacts on marine natural capital, the true cost (including broader social and economic costs) is likely much higher (Beaumont et al. 2019) and warrants additional study. Continued introduction of plastic to the marine environment mean that total costs are liable to increase in the future, albeit at unknown rates (Jambeck et al. 2015; Law 2017). A final barrier to overcome to facilitate widespread adoption of biodegradable bags for restoration is durability. Whereas polyethylene plastic bags successfully contained shells for the duration of the study, cellulose, cotton, and jute were partially disintegrated after 1 month and fully disintegrated within 2 months of deployment. Additional research is warranted to elucidate what factors may have influenced the breakdown of biodegradable materials in the field, including breakdown by grazers and microorganisms, abrasion due to water flow or water-borne sediment, and photochemical or thermal degradation.

Replacement of plastic with biodegradable materials to contain oyster shells for habitat restoration is unlikely without substantial cost reductions, but widespread use cannot be based on direct monetary cost alone. Whole scale adoption will require coordinated, multidisciplinary research and development efforts to advance materials science and improve durability in support of habitat restoration agendas. In the meantime, we encourage practitioners to consider whether the affordability and persistence of plastic mesh outweighs the environmental benefits of using biodegradable alternatives, regardless of differences in oyster densities. Although relatively higher costs may limit the amount of reef that can be restored using biodegradable materials, it is offset by the benefits of teaching and modeling reductions in plastic pollution to coastal communities and garnering support for future restoration investments. Our results support the calls to action in the UN Decade on Ecosystem Restoration and the co-occurring UN Decade of Ocean Science for Sustainable Development by taking steps toward identifying best practices to restore habitats and biodiversity and reverse degradation of ocean ecosystems.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Mean temperature (a), salinity (b), dissolved oxygen (c), and pH (d) at deep (approximately 1 m) and shallow (<0.5 m) sites over time.
Figure S2. Cluster analysis (group average method) with similarity profile (SIMPROF) test of square root transformed fauna samples by depth and treatment.
Figure S3. Fauna diversity in combined treatments in deep (approximately 1 m) and shallow (<0.5 m) sites over time.
Table S1. *p* Values of main effects ANOVAs.
Table S2. ANOVA outputs for transformed oyster and fauna metrics.
Table S3. Similarity percentage (SIMPER) results comparing fauna communities of deep and shallow sites.
Table S4. Lab experiment statistical output from three-way repeated measures ANOVA (grazing experiment) and three-way main effects ANOVA (light and temperature experiment).

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