



Alternative substrate types promote eastern oyster recruitment and benthic community productivity

Jainita Patel^{1,2,*}, Kathleen E. Knick¹, Gabrielle G. Saluta¹, Romuald N. Lipcius¹, Rochelle D. Seitz¹

¹Virginia Institute of Marine Science, William & Mary, PO Box 1346, Gloucester Point, VA 23062, USA

²Present address: Atlantic States Marine Fisheries Commission, 1050 N Highland St #200, Arlington, VA 22201, USA

ABSTRACT: Restoration of eastern oyster *Crassostrea virginica* reefs in Chesapeake Bay (USA) can provide habitat for estuarine communities. Oyster shell, a preferred settlement substrate, has become a limited resource. Thus, alternatives like concrete structures need to be evaluated in their performance relative to oyster shell substrate. Our goals were to (1) compare oyster recruitment among natural (shell and granite) and concrete-mix (castle, diamond, c-dome, and x-reef) reef types, and (2) determine how reef type influences macrofaunal community productivity. To address these goals, 2 replicates of each of the 6 reef types were deployed in a randomized-block experimental design at 3 sites. One year after deployment, oysters and the macrofaunal community associated with the reefs were sampled to determine density, biomass, and productivity. Oyster density (9853 ind. m⁻²) and biomass (744 g ash-free dry weight [AFDW] m⁻²) were highest on the natural shell reef type followed by the x-reef (3817 ind. m⁻²; 532 g AFDW m⁻²), and all reef types had density and biomass that far exceeded the target for successful restoration in Chesapeake Bay (50 ind. m⁻² and 50 g dry weight). All reef structures also had high oyster productivity. Notably, macrofaunal secondary productivity was highest on granite reefs (800 g C m⁻² yr⁻¹), and productivity of all concrete-mix structures ranged from 97 to 800 g C m⁻² yr⁻¹, with some substrates rivaling that of the natural shell substrate (644 g C m⁻² yr⁻¹). Hence, concrete-mix substrates are a viable alternative to using natural oyster shell for restoration.

KEY WORDS: Oyster reef · *Crassostrea virginica* · Chesapeake Bay · Restoration · Secondary production · Artificial substrates · Macrofauna

1. INTRODUCTION

Oyster populations in coastal habitats around the world have been declining rapidly in the last century. It is estimated that there has been an 85% loss of total oyster reef ecosystems around the world (Beck et al. 2011). This loss includes reefs in Chesapeake Bay (USA), where oyster populations have declined dramatically over the last century (Newell 1988, Héral et al. 1990, Rothschild et al. 1994, Schulte 2017). Since the peak of the oyster fishery in the late 1800s, overfishing and habitat degradation (Heinle et al. 1980, Rothschild et al. 1994), decreased water quality (Coen & Luckenbach 2000, Wilberg et al. 2011), and disease

(Mackin et al. 1950, Wood & Andrews 1962) led to this drastic decrease. Given that oysters play important economic and ecological roles, oyster reef restoration is a major focus in Chesapeake Bay and elsewhere (Beck et al. 2011, Baggett et al. 2015).

Constructing oyster reefs with shell bags and loose shell as substrate has yielded promising results for enhancing oyster populations, macrofaunal community density, and diversity (Wall et al. 2005, Taylor & Bushek 2008, Brumbaugh & Coen 2009, Schulte et al. 2009, Lipcius et al. 2015, Colden et al. 2017), but sourcing oyster shells for restoration can be difficult and expensive (George et al. 2015, Graham et al. 2017, Goelz et al. 2020). Therefore, the creation of oyster

*Corresponding author: jpatel@asmfc.org

reefs using artificial substrates is a potentially valuable tool in oyster restoration and may promote development of rich and diverse benthic macrofaunal communities similar to those of natural reefs (Theuerkauf et al. 2015, George et al. 2015, Lipcius & Burke 2018).

Artificial reef structure and composition influence the effectiveness of the reef (Burke 2010, George et al. 2015, Hogan & Reidenbach 2022). While oyster larvae prefer settling on calcium carbonate (CaCO_3), this chemical structure is more susceptible to dissolution in seawater and bioerosion compared to non- CaCO_3 -based substrates, such as concrete or riprap (Dunn et al. 2014). Riprap is composed of granite and thus mimics natural hard-bottom habitats, leading to high benthic production and vertical distribution of macrofauna similar to natural rocky intertidal habitats (Seitz et al. 2019, Sedano et al. 2020). In contrast to other materials, concrete independently or mixed with oyster shell is a cost-effective reef material that encourages oyster larval settlement (Theuerkauf et al. 2015, Berzoza Hernández et al. 2018) and can be molded to create high-rugosity environments that are architecturally complex (Soniata & Burton 2005, Margiotta et al. 2016, Lipcius & Burke 2018, Goelz et al. 2020).

Using alternative substrates in Chesapeake Bay and its tributaries has been successful in the past. In the Rappahannock River on modular concrete reefs, oyster recruitment densities were 1085 oysters m^{-2} of river bottom (Lipcius & Burke 2018). In the York River,

intertidal oyster castles (a concrete and oyster shell mixed structure) successfully recruited and retained oysters at ~ 440 oysters m^{-2} (Theuerkauf et al. 2015).

In this study, the goal was to use 5 different alternative substrate types (granite and 4 concrete plus oyster shell mixed substrates: oyster castles, diamonds, c-domes, and x-reefs) and compare them to natural oyster shell (6 treatments total) to determine which is the most effective alternative substrate to shell reefs to promote oyster recruitment, oyster biomass, benthic macrofaunal community density, and secondary productivity. Oyster recruitment and biomass are often treated as primary goals for restoration (Sustainable Fisheries GIT 2011), but benthic macrofaunal community density and secondary productivity can be used as alternative measures of success based on long-term restoration goals and overall ecosystem benefits (Wong et al. 2011, Kellogg et al. 2016, Searles et al. 2022).

2. MATERIALS AND METHODS

To determine the impact of substrate type on oyster recruitment and the macrofaunal community, field experiments were conducted at 3 shallow subtidal sites (~ 0.45 – 0.75 m below mean low water) in the polyhaline region of the York River, a tributary of lower Chesapeake Bay. The reefs were deployed at



Fig. 1. Overhead image of sites located at the Virginia Institute of Marine Science (VIMS) Beach with (A) exposed and protected sites and (B) Andrews. Open square: shell baskets; filled circle: granite reefs; filled square: oyster castles; diamond: diamond reefs; open circle: c-domes; x: x-reefs (illustrated in Fig. 2)

3 locations offshore from the campus of the Virginia Institute of Marine Science (VIMS) in Gloucester Point, Virginia, USA (Fig. 1). Site 1, hereafter 'protected', was on the west side of the Point and located inside of breakwaters, which protected the reef structures from wave energy. Site 2, hereafter 'exposed,' was also on the west side of the Point, but was located outside of breakwaters, such that the structures were exposed to wave energy. Site 3, hereafter 'Andrews,' was on the east side of the Point with intermediate exposure to wave energy.

At the protected and exposed sites, 12 reef structures (2 of each type) were placed in the shallow subtidal zone in 2 rows (6 reef structures per row), with each row 25 m long, parallel to shore, across from each other, and separated by a breakwater (protected sites) or a small cove entrance (exposed sites) (see Fig. 1A). At the Andrews site, the reefs were placed in 2 rows, each 25 m long and parallel to the shore; the 2 rows (6 reef structures per row) were next to each other and 5 m apart (see Fig. 1B). For all sites, the reefs were placed 5 m apart along the rows in a randomized block design using a random number generator in R (R Core Team 2022).

2.1. Reef materials

The 6 substrate treatments for this experiment consisted of oyster shell, granite stones, oyster castles, oyster diamonds, c-domes, and x-reefs with varying dimensions (Table 1). For the oyster shell treatment, a plastic-coated metal wire basket (0.3 m long \times 0.3 m wide \times 0.3 m high) with a square mesh size of \sim 1 cm was filled to the top with loose oyster shells (Fig. 2A). The shell basket had more oyster shell, surface area, and interstitial space compared to the other treatments, to encourage oyster settlement (Table 2). Similarly, for the granite stone treatment, an identical basket was filled to the top with granite stones (purchased from Luck Stone Quarry, VA) with a median diameter of 10–35 cm (Fig. 2B). This treatment also had high surface area compared to the other treatments (Table 2). Oyster castles (Fig. 2C), manufactured by Allied Concrete, a family-owned business that operates throughout central Virginia, and composed of concrete mixed with crushed shell, were stacked with 4 modules on the bottom and 1 on top to create vertical space for settlement. The remaining structures, i.e. oyster diamonds (Fig. 2D), c-domes (Fig. 2E), and x-reefs (Fig. 2F), were made of concrete embedded with whole oyster shell. The c-domes and x-reefs had internal as well as external space for

Table 1. Dimensions of the reef types used for this study. Footprint references the true footprint of the structures without accounting for the sediment around the structure. Note that surface area for the shell structure and the granite basket were not calculated (NC) because each of the structures had shells and boulders of varying shapes and sizes, leading to inaccurate estimates of surface area. Qualitatively, the shell had the highest surface area and the granite had the second highest

Reef type	Reef height (m)	Reef width (m)	Reef length (m)	Footprint (m ²)	Surface area (m ²)
Oyster shell	0.30	0.30	0.30	0.09	NC
Granite	0.30	0.30	0.30	0.09	NC
Oyster castle	0.40	0.61	0.61	0.37	2.25
Oyster diamond	0.30	0.61	0.91	0.28	0.46
C-dome	0.46	0.48	0.48	0.18	1.38
X-reef	0.36	0.74	0.74	0.24	1.47

recruitment, and the diamonds had a 45° angle to promote settlement (Table 2). All structures were at least 0.3 m high, as is recommended for successful oyster restoration (Colden et al. 2017).

2.2. Measured variables

2.2.1. Oyster density and biomass

The reefs were deployed on 15 June 2021, prior to seasonal oyster settlement, which typically occurs in the summer and early fall in the York River. The reefs were sampled 1 yr after deployment (June 2022) to quantify density, biomass, and secondary production of oysters and of the reef-associated macrofauna. Each reef was removed from the water and immediately placed in a floating tray. A subsample was determined by placing a quadrat on the structure and a random number generator was used to select which quarter of the reef to sample. Oysters and macrofauna were removed with a chisel, bagged, and stored on ice.

In the laboratory, oysters were rinsed in freshwater to remove macrofaunal organisms and the remaining sample contents were frozen for subsequent macrofaunal processing. All oysters were enumerated and shell height (distance from the umbo to the farthest point of the shell) was measured to the nearest 0.1 mm using calipers.

To obtain biomass for individual reef structures, subsamples of 30 oysters across varying size classes from each reef structure were ordered by size, measured, and weighed to create a length–weight relationship.

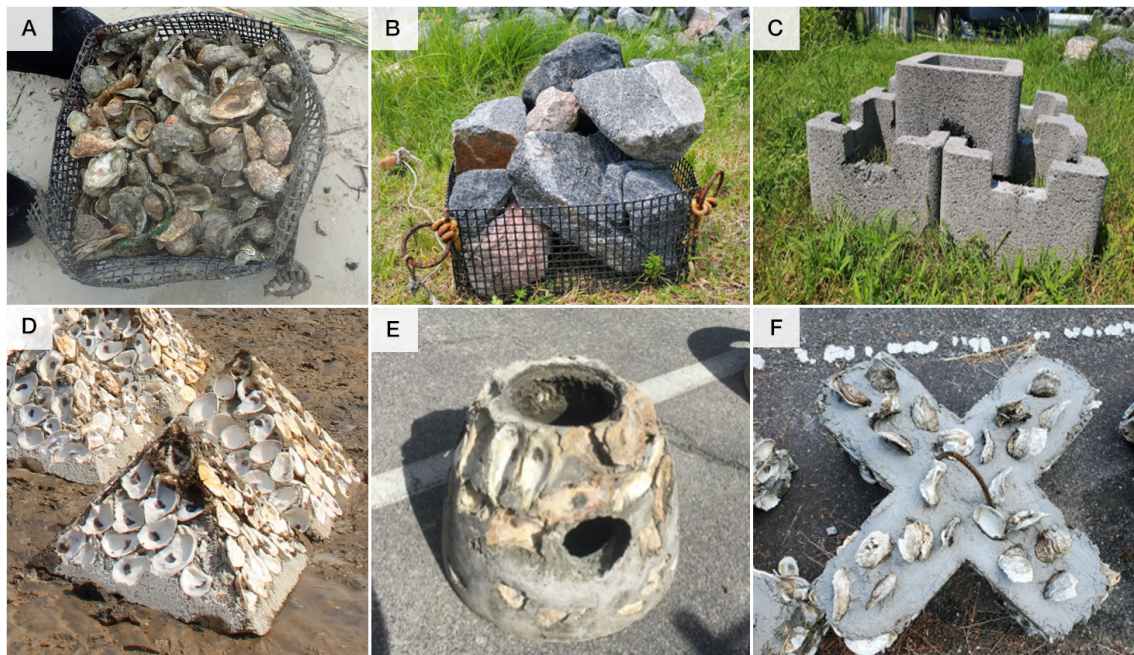


Fig. 2. Reef types used in this study: (A) loose oyster shell in a mesh basket made of plastic-covered metal wire, (B) loose granite in a mesh basket made of plastic-covered metal wire, (C) concrete and crushed shell oyster castles stacked 1 on top and 4 on the bottom, (D) oyster diamond composed of concrete embedded with oyster shell, (E) c-dome composed of concrete embedded with oyster shell, (F) top view of an x-reef, a table-like structure composed of concrete embedded with oyster shell

The oysters were shucked and flesh was dried for 48 h at 70°C to obtain dry weight. The oyster flesh was then combusted in a muffle furnace for 4 h at 550°C to obtain ash weight (e.g. ingested sediment, shell fragments), which was subtracted from dry weight to obtain ash-free dry weight (AFDW). Using the resultant lengths and corresponding weights (length as 'height' and weight as 'AFDW'), oyster biomass was calculated for each reef type (or individual reef) using a power regression (Luckenbach & Ross, 2003): $\ln(\text{AFDW}) = \beta_0 + \beta_1 \ln(\text{height})$ and then standardized to oyster biomass m^{-2} . Secondary productivity ($\text{g C m}^{-2} \text{yr}^{-1}$) for the

standardized oyster biomass was calculated using a P:B ratio of 2.9 (Diaz & Schaffner 1990).

Oyster density and biomass (AFDW) were modeled as a function of site and reef type. All analyses were conducted in R (version 4.1.3) (R Core Team 2022). Based on the distribution of the data, a negative binomial generalized linear model from the 'MASS' package in R was fit for the density data. To standardize density to 1 m^2 of river bottom, the models were run on the non-standardized raw oyster counts and offset with the footprint (bottom area) of each reef (Table 1). For oyster biomass, a linear model was used based on

Table 2. Comparison of the features of each reef type. Internal space: large pockets of space inside of the structure that offer room for recruitment; interstitial space: small spaces between specific discrete particles; 45° angle: availability of substrate that sits at a 45° angle; oyster shell: availability of natural oyster shell on the structure

Reef type	Surface area	Height	Internal space	Interstitial space	45° angle	Oyster shell
Oyster shell	High	Low	Medium	High	Medium	High
Granite	High	Low	Medium	Medium	Low	Low
Oyster castle	Medium	Medium	Medium	Low	Low	Low
Oyster diamond	Low	Low	Low	Low	High	Medium
C-dome	Medium	High	High	Low	Low	Medium
X-reef	Medium	High	High	Low	Low	Medium

the distribution, and the response variable was standardized to 1 m^2 of river bottom before running the models. For all response variables, the model with the lowest corrected Akaike's information criterion (AICc) was further examined to determine the magnitude of the model parameters. The estimated marginal means (least-squares means) were calculated using the 'emmeans' package in R (Lenth 2022), and pairwise comparisons were run to determine significance between means of models with the best fit.

Table 3. Models and parameters for linear models and generalized linear negative binomial models compared with corrected values of Akaike's information criterion (AICc) for univariate data across reef types and experimental sites for 2022. β represents inclusion of the parameter in the model; k : number of parameters; β_0 : intercept of the model which is the mean of the shell reef at the Andrews site. Note that community density data used negative binomial models that are offset by the footprint of each reef type (Table 1). R: reef; S: site

Model	k	Intercept	R	S
u_1 (null)	2	β_0		
u_2	7	β_0	β_{1-5}	
u_3	4	β_0		β_{6-7}
u_4	9	β_0	β_{1-5}	β_{6-7}

2.2.2. Macrofaunal production

The macrofaunal samples (organisms removed from the oysters and scraped off the reefs) were rinsed in cool water over a 1 mm sieve, stored in 70% ethanol, and identified to the lowest possible taxonomic group. To obtain density counts, organisms were sorted twice without a microscope. Clams, decapods, polychaetes, mollusks, and tunicates were identified to species. Anemones were identified to the order Actiniaria, and nemerteans were identified to phylum. Amphipods were grouped by family (Gammariidae, Corophiidae, and Caprellidae). Sponges and fish were noted, but not included in the analysis. To calculate biomass (species, family, order, or phylum), each sample was dried for 48 h at 70°C and combusted in a muffle furnace for 4 h at 550°C to obtain AFDW to the nearest 0.0001 g.

Secondary productivity ($\text{g C m}^{-2} \text{yr}^{-1}$) was calculated by species (clams, decapods, polychaetes, snails, tunicates), family (amphipods), or phylum (nemerteans) using P:B ratios from Diaz & Schaffner (1990): crustaceans (decapods and amphipods), 5.7; polychaetes, 4.9; nemerteans, 4.3; mollusks (bivalves and snails), 2.9; and chordates (tunicates), 2.3. Sponges and anemones made up a small part of the macrofauna and were not included in secondary productivity. Analyses were run on secondary productivity both with and without oysters.

2.3. Analyses

To test for differences among treatments (reef types and sites) using the community and univariate data, several models were fit in R (version 4.1.3; R Core Team 2022) with reef and site as fixed factors

(Table 3). The model with the lowest AICc and highest weighted probability was tested against the second-best model using a likelihood-ratio χ^2 test.

For the response variable 'density,' a generalized linear negative binomial model was used with an offset of reef footprint (bottom area; Table 1) to standardize density by 1 m² of river bottom (the accepted metric for oyster restoration success in Chesapeake Bay; Allen et al. 2011). For linear models, the appropriate transformations (i.e. square-root or log) were applied to normalize the data. For biomass and secondary productivity, the response variable was standardized by 1 m² of river bottom before running the models on macrofaunal biomass and secondary production alone and on macrofaunal and oyster secondary production together. 'Emmeans' and pairwise comparisons were run to determine differences between the means of the models with the best fit.

A LOESS curve was fit in R (version 4.3.2; R Core Team 2024) to determine if oyster density was correlated with macrofaunal secondary production without oysters. Due to low sample size, the treatment-specific data are not presented.

To test differences in macrofaunal assemblages by reef and site variables, a Type III distance-based permutational multivariate analysis of variance (PERMANOVA) was run for both density and biomass (Anderson 2001, McArdle & Anderson 2001). Note that for multivariate analyses, mobile fauna including fish and crabs were included in the analyses. Macroalgae were also included in the multivariate biomass analysis because they provide habitat for organisms including amphipods (Fredette & Diaz 1986) and can inform differences between community assemblages between the structures.

3. RESULTS

3.1. Oyster density, biomass, and shell height

The model that included reef type and site best fit the oyster density data (model m_d4 in Table S1 in the Supplement at www.int-res.com/articles/suppl/m754p051_supp.pdf). Based on the parameter estimates, all alternative reef types had significantly lower ($p < 0.01$) oyster densities than shell reefs (Fig. 3A; Table S2). Oyster densities ranged from 716 to 9853 oysters m⁻², with the shell reef at the highest of that range and diamond reef the lowest (Table S3). After the shell reef, the c-dome and x-reef structures had the next highest densities and had, on average,

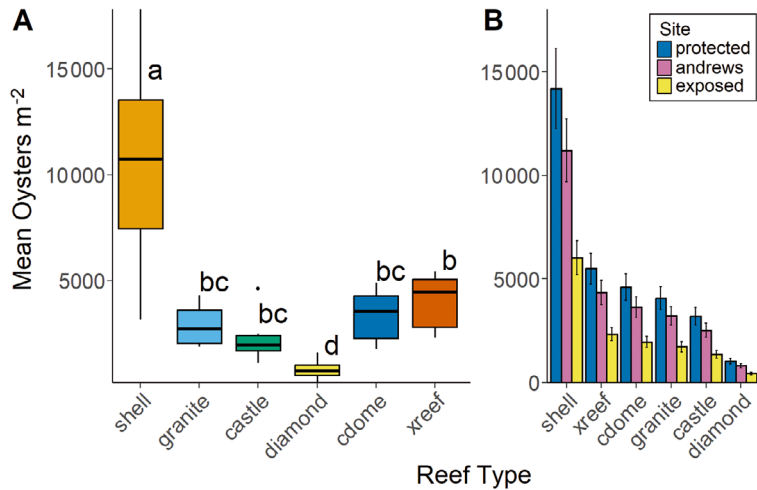


Fig. 3. (A) Oyster density per m² river bottom by reef type in summer of 2022 based on generalized linear model m_{44} (see Table S1 for model parameters). Densities were standardized to 1 m² of river bottom using an offset of the area of river bottom covered by each structure. The boxes represent the first and third quartile of the data while the central lines represent the median. Whiskers represent the full range of the data without outliers while dots represent the outliers. Different letters represent significant differences between corresponding treatments as seen through a pairwise test. (B) Model-estimated means (\pm SE) for model m_{44} across sites and reef types

oyster densities similar to each other after 1 yr, with means of 3202.3 and 3816.7 oysters m⁻², respectively. Among sites, model-estimated means ranged between 1743.8 and 4110.4 oysters m⁻², with the protected site having the highest density and the exposed site having the lowest (Fig. 3B).

All reef types had high oyster biomass. As with oyster density, the model that included both reef type and site best fit the oyster biomass data (model ' m_{b4} ' in Table S4). Based on parameter estimates for this model, all alternative reef types had significantly lower ($p < 0.01$) oyster biomass than shell reefs (Fig. 4A; Table S5). Model-estimated means of oyster biomass ranged between 117.5 and 743.9 g AFDW m⁻² (Table S6). The castle, c-dome, and x-reef structures had mean oyster biomass greater than the granite and diamond structures. Comparing by site, the protected site had the highest biomass and the exposed site had the lowest (Fig. 4B).

Oyster shell heights across sites ranged from 2 to 115 mm with means of 25.4 mm for shell substrate, 26.3 mm for granite, 32.2 mm for oyster castles, 28.7 mm for diamonds, 28.3 mm for c-domes, and 29.7 mm for x-reefs.

3.2. Macrofaunal density, biomass, and production

Without including oysters, a total of 55 036 individual organisms were sampled from the reef structures. These macrofauna included bivalves, polychaetes, nemertean, decapods, amphipods, gastropods, tunicates, sponges, and anemones (Table 4). Amphipods and tube-building polychaetes had high densities across reef types, with caprellid amphipods reaching raw counts of 6480 on a quarter of 1 oyster castle reef structure at the Andrews site and the nereid polychaete *Alitta succinea* reaching raw counts of 687 on 1 oyster castle reef module at the exposed site. Large amounts of *Ulva lactuca* and *Gracilaria* sp. grew on top of all reef structures.

For macrofaunal density, the model that included both reef and site best fit the data (Table S7). Granite reefs had significantly higher ($p < 0.01$) and diamond reefs had significantly lower community density ($p < 0.01$) than the shell reefs (Fig. 5A; Table S8). Model means were the lowest for the diamond structure, at 10 168 ind. m⁻², and highest for the granite structure, at 51 696 ind. m⁻² (Table S9).

For macrofaunal community biomass, the model with the best fit included both reef type and site (Table S7). Granite reefs had significantly higher bio-

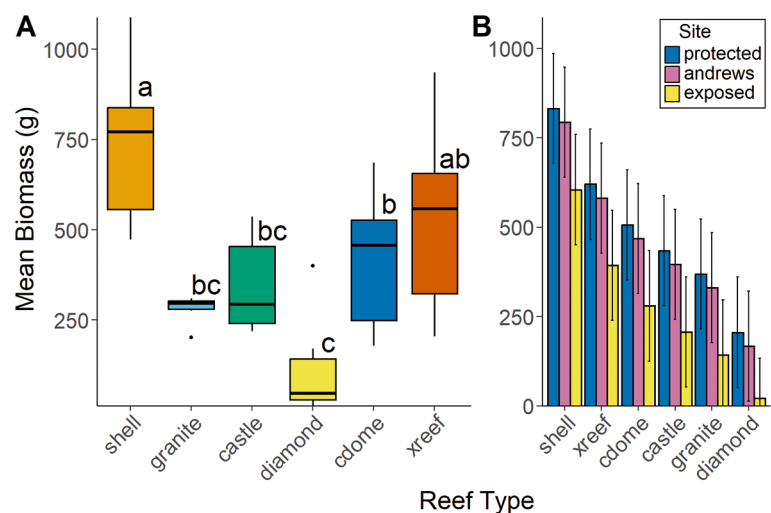


Fig. 4. (A) Mean oyster ash-free dry weight (biomass) by reef type in summer of 2022 based on linear model m_{b4} (see Table S4) standardized to 1 m² of river bottom. Box plot parameters and letters as in Fig. 3. (B) Model-estimated means (\pm SE) for m_{b4} across sites and reef types

Table 4. Mean species densities on substrate treatments (shell, granite, diamond, castle, c-dome, and x-reef) pooled across sites and standardized to 1 m² of river bottom

Species	Shell	Granite	Castle	Diamond	C-dome	X-reef
<i>Ameritella mitchelli</i>	0.00	0.00	0.00	0.00	0.00	2.69
<i>Macoma balthica</i>	0.00	0.00	0.00	2.39	0.00	2.69
<i>Mya arenaria</i>	100.46	193.75	5.38	9.57	10.93	8.07
<i>Geukensia demissa</i>	114.82	337.27	127.37	90.90	145.78	314.84
<i>Ischadium recurvum</i>	107.64	86.11	105.85	33.49	145.78	201.82
<i>Anadara transversa</i>	0.00	28.70	1.79	0.00	0.00	2.69
<i>Glycera dibranchiata</i>	0.00	0.00	0.00	2.39	0.00	0.00
<i>Alitta succinea</i>	3516.21	7864.83	3738.67	1956.64	6877.27	4897.58
<i>Potamilla neglecta</i>	236.81	5015.98	3464.19	650.62	4683.25	3460.60
<i>Parasabella microphthalma</i>	143.52	2734.03	719.39	196.14	794.51	823.44
<i>Loimia medusa</i>	7.18	7.18	3.59	0.00	0.00	5.38
<i>Hydroides protulicola</i>	0.00	0.00	21.53	0.00	10.93	18.84
Capitellidae	0.00	0.00	0.00	11.96	0.00	0.00
<i>Molgula manhattensis</i>	2913.43	4915.52	3074.89	442.52	3957.98	2109.73
<i>Callinectes sapidus</i>	14.35	0.00	0.00	0.00	0.00	0.00
<i>Hexapanopeus angustifrons</i>	222.45	301.39	60.55	9.57	87.47	48.44
<i>Panopeus herbstii</i>	566.90	574.08	173.12	126.77	612.28	411.72
<i>Eurypanopeus depressus</i>	1356.25	1994.91	705.93	145.91	736.20	444.01
<i>Dyspanopeus sayi</i>	1262.97	825.23	281.21	236.81	1013.19	753.47
<i>Penaeus setiferus</i>	78.94	71.76	0.00	2.39	3.64	2.69
<i>Alpheus heterochelis</i>	14.35	0.00	0.00	0.00	0.00	0.00
<i>Rhithropanopeus harrisi</i>	7.18	0.00	8.97	0.00	0.00	0.00
<i>Crepidula plana</i>	1779.63	896.99	575.87	420.99	798.16	939.15
<i>Boonea impressa</i>	1018.98	35.88	138.14	28.70	105.69	45.75
<i>Astyris lunata</i>	143.52	222.45	217.07	35.88	131.20	131.86
<i>Triphora nigrocincta</i>	71.76	14.35	120.42	0.00	7.29	80.73
<i>Costoanachis avara</i>	0.00	21.53	3.59	0.00	3.64	0.00
<i>Littoraria irrorata</i>	0.00	0.00	0.00	2.39	0.00	0.00
<i>Pyrgocythara plicosa</i>	21.53	0.00	0.00	0.00	0.00	0.00
Gammaridae	4908.35	2396.77	758.41	279.86	994.96	984.90
Corophiidae	129.17	839.59	1296.15	583.64	1698.36	780.38
Caprellidae	5991.91	43.06	15331.40	10153.96	6028.09	11191.78
Actiniaria	0.00	14.35	1.79	19.14	0.00	40.36
<i>Zaops ostreum</i>	93.29	21.53	33.19	0.00	25.51	78.04
<i>Libinia dubia</i>	0.00	0.00	0.00	0.00	0.00	5.38
Total	24821.6	29457.24	30968.46	15442.63	28872.11	27787.03

mass than shell reefs ($p < 0.01$) and greater biomass than most of the concrete structures (Fig. 5B; Table S8). Model means were the lowest for the diamond structure at 43.0 g AFDW m⁻² and highest for the granite structure at 333.3 g AFDW m⁻² (Table S9).

For macrofaunal secondary productivity without oysters, the model with the best fit included only reef type (Table S7). All of the concrete structures had significantly lower secondary productivity than the shell structure (Table S8), but the granite reef did not differ from the shell reef (Fig. 5C; Table S8). The diamond reef had the lowest estimated model mean at 97.16 g C m⁻² yr⁻¹ and granite had the highest at 800.3 g C m⁻² yr⁻¹ (Table S9). Macrofaunal secondary production was positively related to oyster density (Fig. S1) with combined treatment types. The relationship between oyster density and secondary production was gen-

erally linear below ~5000 oysters m⁻², regardless of treatment type, but it tended to level-off at densities >5000 oysters m⁻².

For secondary productivity of the macrofaunal community combined with oysters, the model with the best fit had both reef type and site as factors (Table S7). All structures had significantly lower secondary productivity than the shell structure, and structures aside from the shell and diamond had similar secondary productivity (Fig. 5D; Table S8). The diamond reef had the lowest model-estimated mean at 362.78 g C m⁻² yr⁻¹ and shell had the highest at 2768.19 g C m⁻² yr⁻¹ (Table S9). The x-reef had the second highest model-estimated mean at 1797.29 g C m⁻² yr⁻¹. Amphipods, polychaetes, and mud crabs had higher densities and biomass than other taxa (Table 4). Amphipod families had the highest den-

sities across all reef types, with model estimates of more than 120 000 ind. m^{-2} of river bottom on granite structures. Polychaetes such as *Alitta succinea*, *Potamilla neglecta*, and *Parasabella microphthalma* also attained high densities. Mud crabs, which included species such as *Panopeus herbstii*, *Eurypanopeus depressus*, and *Dyspanopeus sayi*, had high biomass. Mud crab biomass on the granite structures reached over 150 g AFDW m^{-2} (Table 5).

PERMANOVA revealed that both reef type and site had significant impacts on community assemblages for both density and biomass (Table S10). Looking closer at differences among community assemblages on reef types, shell had significantly different community density assemblages to all other reef types. Diamond also significantly differed in community density assemblages from other reef types. For community assemblage by biomass, the shell reef signifi-

cantly differed from all other structures except granite, and diamond differed significantly from all structures. For both density and biomass, the c-dome and x-reef structures did not differ with regard to community structure (Patel 2023).

4. DISCUSSION

Key findings include that (1) all reef types had high oyster density, biomass, and secondary production in the subtidal lower York River after 1 yr. Although shell reefs had the highest oyster density and biomass (9853 oysters m^{-2} and 744 g AFDW m^{-2} of river bottom) of all reef types, x-reefs also had high oyster densities of 3816 oysters m^{-2} river bottom. (2) Shell reefs had the highest oyster secondary productivity, while granite substrates had the highest community secondary productivity, which should be considered during future reef selection if secondary productivity is a key goal of restoration.

4.1. Oyster density and biomass

All of the reef structures sustained oyster density and biomass that were well above the Chesapeake Bay Sustainable Fisheries Goal Implementation Team targets for successful oyster reef restoration (50 oysters m^{-2} and 50 g dry weight m^{-2} , respectively, of river bottom; Allen et al. 2011). Oyster shell is the preferred settlement substrate for oyster larvae (Nestlerode et al. 2007, Brumbaugh & Coen 2009, Goelz et al. 2020), and post-settlement survival is enhanced by factors such as vertical relief (Soniati et al. 2004), interstitial space to facilitate protection from predation and reduce competition (Lavan 2019, Nestlerode et al. 2007), and the accessibility of oyster shell. Thus, it is unsurprising that the shell reefs supported higher densities and biomass than the granite and concrete-mix structures. The taller and architecturally complex concrete-mix structures (x-reefs, c-domes, and castles) also sustained high oyster densities and biomass, while the shorter and sloping diamond substrates had the lowest oyster densities and biomass. This was likely because the shape of the dia-

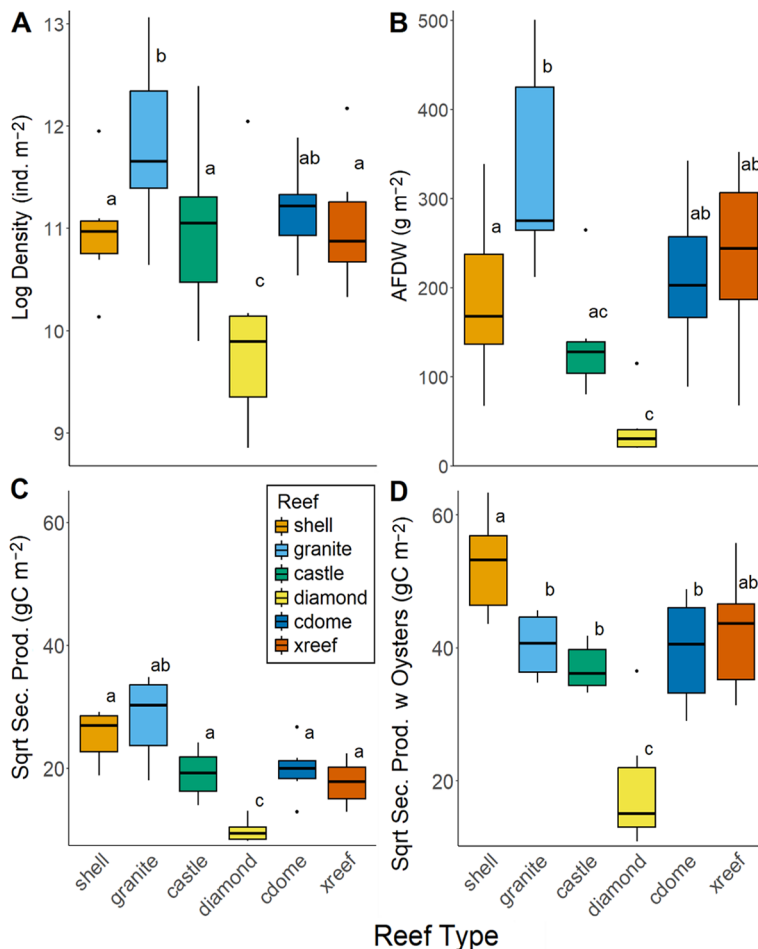


Fig. 5. (A) Log of macrofaunal community density, (B) biomass (ash-free dry weight, AFDW), (C) secondary productivity without oysters, and (D) secondary productivity with oysters by reef type at the sites in summer 2022. All numbers standardized to 1 m^2 of river bottom. Box plot parameters and letters as in Fig. 3

Table 5. Mean species biomass (g ash-free dry weight) on substrate treatments (as in Table 4) pooled across sites and standardized to 1 m² of river bottom

Species	Shell	Granite	Castle	Diamond	C-dome	X-reef
<i>Ameritella mitchelli</i>	0.00	0.00	0.00	0.00	0.00	0.01
<i>Macoma balthica</i>	0.00	0.24	0.00	0.02	0.00	0.01
<i>Mya arenaria</i>	7.95	24.16	0.40	0.14	0.31	0.15
<i>Geukensia demissa</i>	0.83	2.42	1.11	1.36	1.19	3.39
<i>Ischadium recurvum</i>	0.81	0.93	2.61	0.65	3.72	5.88
<i>Anadara tranversa</i>	0.00	0.46	0.06	0.00	0.00	0.09
Misc bivalve tissue	0.00	0.00	0.02	0.00	0.00	0.00
<i>Glycera dibranchiata</i>	0.00	0.00	0.00	0.16	0.00	0.00
<i>Alitta succinea</i>	7.45	7.75	4.42	3.30	8.46	5.91
<i>Potamilla neglecta</i>	0.54	11.21	8.23	1.58	13.03	7.41
<i>Parasabella microphthalmia</i>	0.47	10.96	17.83	0.93	15.25	7.40
Phyllodocid parts	0.10	0.13	0.02	0.04	0.01	0.03
<i>Loimia medusa</i>	0.05	0.37	0.04	0.00	0.00	0.12
<i>Hydroides protulicola</i>	0.00	0.08	0.03	0.00	0.02	0.02
<i>Sabellaria vulgaris</i>	0.00	0.02	0.00	0.00	0.00	0.00
Ophillidae parts	0.00	0.00	0.00	0.00	0.05	0.00
Capitellidae	0.00	0.00	0.00	0.01	0.00	0.00
<i>Molgula manhattensis</i>	20.36	44.77	38.64	2.26	50.74	27.60
<i>Callinectes sapidus</i>	6.83	0.00	0.00	0.00	0.00	0.00
<i>Hexapanopeus angustifrons</i>	13.23	11.91	4.07	0.31	3.29	2.25
<i>Panopeus herbstii</i>	15.00	8.63	6.44	3.10	13.49	8.95
<i>Eurypanopeus depressus</i>	26.83	43.75	14.51	2.28	14.08	13.50
<i>Dyspanopeus sayi</i>	14.36	16.46	3.61	1.36	10.07	3.83
<i>Penaeus setiferus</i>	1.72	1.42	0.00	0.30	0.19	0.04
<i>Alpheus heterochelis</i>	0.92	0.00	0.00	0.00	0.00	0.00
<i>Zaops ostreum</i>	1.42	0.18	0.12	0.00	0.06	0.96
<i>Libinia dubia</i>	0.00	0.00	0.00	0.00	0.00	0.65
<i>Rhithropanopeus harrisi</i>	0.04	0.00	0.20	0.00	0.00	0.00
<i>Crepidula plana</i>	7.29	4.37	2.27	1.46	3.19	4.49
<i>Boonea impressa</i>	2.67	0.15	0.13	0.04	0.10	0.09
<i>Astyris lunata</i>	0.16	0.42	0.29	0.04	0.16	0.14
<i>Triphora nigrocincta</i>	0.03	0.04	0.03	0.00	0.06	0.07
<i>Costoanachis avara</i>	0.00	0.05	0.00	0.00	0.01	0.00
<i>Littoraria irrorata</i>	0.00	0.00	0.00	0.01	0.00	0.00
<i>Pyrgocythara plicosa</i>	0.20	0.05	0.08	0.00	0.00	0.00
<i>Margarites</i> spp.	0.10	0.05	0.00	0.00	0.00	0.00
Gammaridae	0.96	0.64	0.20	0.07	0.29	0.24
Corophiidae	0.03	0.26	0.23	0.03	0.15	0.07
Caprellidae	0.57	2.94	1.41	0.94	0.68	1.00
<i>Actiniaria</i>	0.00	7.18	0.00	2.48	0.00	5.63
<i>Clathria prolifera</i>	0.00	1.36	8.01	0.00	0.00	25.74
Sponge A	0.71	0.89	3.52	0.20	18.99	12.66
Sponge B	0.02	0.00	0.24	0.00	0.63	0.00
Total	131.65	204.25	118.77	23.07	158.22	138.33

mond structure encouraged sedimentation and sinking, decreasing the amount of substrate protruding into the water column and available for settlement, and suffocating young juveniles (Colden & Lipcius 2015, Colden et al. 2017). Oyster biomass was highest on both the shell substrate and the x-reef (744 and 531 g AFDW m⁻², respectively). The protected internal area of the x-reef likely allowed oysters to grow large without risk of mortality from predation, as occurred in previous studies that used artificial oyster

settlement substrates; intertidal castles accumulated up to 440 ind. m⁻² (Colden & Lipcius 2015, Theuerkauf et al. 2015). Like alternative-substrate reefs in previous studies, the x-reefs had greater vertical space than the other reefs tested herein, had a large surface area, were mostly elevated off the bottom, and offered complex habitats which aided in the protection of settled oysters.

The oyster density and biomass reported in this study were higher than those reported for similar res-

toration projects in Chesapeake Bay (Nestlerode et al. 2007, Lipcius & Burke 2018). Results were driven by high densities of small oysters, as few large (>50 mm shell height) oysters were present after 1 yr. Because of the short time frame of this experiment (1 yr), these reefs were still in the early stages of development, and densities may be reduced in the future, as the current oysters increase in size and mortality occurs. As habitat complexity increases through time, macrofaunal community metrics are also expected to increase (Grabowski 2004, Margiotta et al. 2016, Karp et al. 2018).

In addition, our experimental sites were located between or adjacent to breakwaters with productive oyster populations. The sites were also close to an oyster hatchery outflow pipe and the sites at the Andrews location had been used for previous oyster recruitment studies, which may have influenced oyster densities for this study. Additionally, Gloucester Point, the location of this study, is a constriction point for the York River, which may have increased recruitment from oyster populations elsewhere in the river.

Although high for the Chesapeake Bay, oyster densities reported here are similar to those occurring on reefs elsewhere along the eastern coast of the USA, particularly where exploitation is low. For example, about 14 600 and 4400 oysters m^{-2} were reported from unharvested sections of Georgia reefs (Bahr 1974) and South Carolina reefs (Dame 1976), respectively. More recently, densities of over 6000 oysters m^{-2} were reported in unharvested sections of Georgia reefs (Manley et al. 2010). The present study was conducted on shallow, subtidal reefs, whereas the previous studies with high densities focused on intertidal oyster populations. The subtidal structures may have benefited oyster survival by allowing more time for feeding and less stress from desiccation (Bodenstein et al. 2021).

4.2. Macrofaunal production

Reef structures provide the only hard substrates available in otherwise soft-sediment communities (Bertness et al. 2001, Seitz et al. 2019). Such structures, along with the additional structure provided by settled oysters, led to high density, biomass, and secondary productivity of benthic organisms across taxonomic groups.

Excluding oysters, secondary productivity was extremely high across all reef types, ranging from 345.85 to 654.46 $g C m^{-2} yr^{-1}$. Recruitment of second-

ary macrofauna was positively correlated with oyster density, suggesting that macrofaunal productivity is contingent upon natural oyster recruitment, to a point. This suggests that oyster restoration using the substrates in this experiment would substantially increase secondary productivity provided that reefs are placed in areas with low productivity of soft sediments they replace and sufficient natural oyster recruitment (Karp et al. 2018, Lipcius & Burke 2018, Pfirrmann & Seitz 2019).

The granite structure had the highest macrofaunal density of all reef types, possibly due to the interstitial space surrounding the granite rocks. Although interstitial space was not directly measured, from qualitative observations, the granite structure had larger spaces between the stones than the shell structure, which was tightly packed with shell, and also had smaller interstitial spaces than the concrete-mix structures. Although small interstitial spaces can provide early post-settlement refuge to oysters from small predators (Nestlerode et al. 2007, Callaway 2018), they can limit the quantity of other macrofauna since there is no room for larger organisms to settle, grow or move through the structure. In contrast, very large interstitial spaces (>5 cm) may not provide sufficient protection from predation. Except for the diamond structure, concrete-mix structures had similar macrofaunal community densities. Like the mechanisms suggested for the low oyster density on the diamond structures, the low macrofaunal density may have resulted from sedimentation and sinking of the diamond structures.

High biomass and secondary productivity on the granite reefs were possibly driven by abundant mud crab populations (>2000 ind. m^{-2}). These organisms have high biomass, and crustaceans have a high P:B ratio, both of which are used to derive secondary production. Although macrofaunal biomass on the shell reefs was similar to that of the c-dome and the x-reef, the large number of mud crabs on the shell reefs led to higher secondary productivity, approaching that of the granite structures. Fish were not included in the analysis since the methodology could not accurately sample quick-moving, transient organisms on the reef structure, but large oyster toadfish *Opsanus tau* were found in both of the basket structures (shell and granite) and may have influenced oyster recruitment and survival, as well as the mesopredator populations, through density- or trait-mediated effects (Grabowski 2004). Large fish may have consumed mud crabs and other bivalve-eating organisms, which could have increased juvenile oyster survival (Grabowski 2004).

4.3. Caveats and limitations

The data for this study were collected after just 1 yr, and the trends observed for both oyster recruitment and community secondary productivity in this study are likely to change over time. However, many other long-term restoration projects are only sampled one or a few years after the completion of the project, so this study is similarly representative of what 1 yr post-restoration in the York River could look like. Typically, oyster densities will decline over subsequent years, and the percentage of adult oysters will increase (e.g. La Peyre et al. 2014), but patterns among substrate configurations generally remain the same (e.g. Hogan & Reidenbach 2022). Additionally, this study shows that concrete-mix substrates are initially viable alternatives to other substrate types when other substrate types are scarce or at sites where other substrates can be difficult to deploy.

One important factor that could have driven community differences among structures was that a basket was used only for the shell and granite structures. These baskets were an additional form of protection for the macrofauna within and likely prevented predation of the macrofauna and oysters by higher trophic level organisms, such as fish and large blue crabs that were external to the reef structure. Additionally, the Andrews site collected large amounts of the branching alga *Gracilaria* sp., which may have provided structured habitat for amphipods. This may have led to 1 high-density outlier (Fig. 5A,B), which could have over-emphasized the success of granite in recruiting macrofauna. This study also used a methodology which required lifting reef structures out of the water, which may have resulted in the loss of some mobile species not contained in a basket. The small size of the reefs also likely impacted use by mobile species (i.e. these small reefs are more useful for small macrofauna, such as mud crabs), but sessile species were likely not affected, as seen by the high abundance of benthic macrofauna in residence on the structures.

4.4. Implications for restoration

As large-scale oyster restoration projects often occur over 10s to 100s of acres, the feasibility of using small structures like the reefs studied in this project should be considered with regard to logistics and cost. One estimate put the concrete structures as 5 times more expensive than shell (Bersoza Hernández et al. 2018), although costs likely have changed in more recent years. The granite structures are inexpensive and

easily accessible, although transport and deployment costs for large-scale granite reefs could prove similar compared to oyster shell reefs, as both substrates frequently require the use of barges and cranes to deploy. If macrofaunal density and biomass are used as measures of success for restoration, using granite in conjunction with other material may be beneficial. Despite their cost, concrete-mix structures have been used effectively in conjunction with other materials to address common issues such as shell scarcity, transport logistics, and poaching (Beck et al. 2009, Schulte & Burke 2014). The oyster castle structures are relatively economical and can be stacked to various desired heights. They can be labor-intensive to construct and difficult to transport depending on the scale of the project. Castles are often used intertidally for shoreline protection in living shorelines, as they can be arranged in long sill-like structures and act as barriers against erosion (Morris et al. 2021, Salatin et al. 2022). With the right equipment and for large-scale projects, c-domes and x-reefs are easy to deploy and transport as they require no on-site assembly. The c-dome and x-reef structures, although costly compared to shell reefs, provide structure with plenty of vertical space for settlement and space within the structure for water flow, which could encourage recruitment. Both granite and concrete-mix structures overall provide less interstitial space than oyster shell reefs, but they have the benefit of using much less oyster shell than traditional oyster shell reefs. This is beneficial in times of shell scarcity, especially in regions like the Chesapeake Bay, which is seeing an increase in the amount and scale of oyster reef restoration projects. Based on the goals of restoration for the area and the size of the project, a combination of structures can be used to increase oyster populations while utilizing some of the physical benefits of hard substrate such as erosion protection or barriers against poaching (Meyer et al. 1997, Wall et al. 2005). Overall, concrete-mix substrates for oyster reefs are a viable alternative to using natural oyster shell for restoration.

Acknowledgements. The present work was part of J.P.'s Master's thesis at the Virginia Institute of Marine Science, William & Mary. All parts of this project were conducted on the homelands and in the home waters of the Cheroenhaka (Nottoway), Chickahominy, Eastern Chickahominy, Mattaponi, Monacan, Nansemond, Nottoway, Pamunkey, Patowomeck, Upper Mattaponi, and Rappahannock tribes. These indigenous communities are the current and traditional caretakers of these lands and waters. We hope this project honors them and the work they have already placed into preserving the natural ecosystems of this area. Special thanks to the Marine Community Ecology and Marine Conservation Biology programs at the Virginia Institute of Marine Science

for their support of this research in both the field and the lab. The project was funded by the Department of Defense's Readiness and Environmental Protection Integration program, National Fish and Wildlife Foundation, Naval Weapons Station Yorktown, and Virginia Institute of Marine Science's Office of Academic Affairs.

LITERATURE CITED

- Allen S, Carpenter AC, Luckenbach MW, Paynter K and others (2011) Restoration goals, quantitative metrics and assessment protocols for evaluating success on restored oyster reef sanctuaries—report of the oyster metrics workgroup. Chesapeake Bay Program Sustainable Fisheries Goal Implementation Team, Annapolis, MD
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- ✦ Baggett LP, Powers SP, Brumbaugh RD, Coen LD and others (2015) Guidelines for evaluating performance of oyster habitat restoration. *Restor Ecol* 23:737–745
- Bahr LM (1974) Aspects of the structure and function of the intertidal oyster reef community in Georgia. PhD dissertation, University of Georgia, Athens, GA
- Beck MW, Brumbaugh RD, Airoidi L, Carranza A and others (2009) Shellfish reefs at risk. A global analysis of problems and solutions. The Nature Conservancy, Arlington, VA
- ✦ Beck MW, Brumbaugh RD, Airoidi L, Carranza A and others (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. *BioScience* 61: 107–116
- ✦ Bersozza Hernández A, Brumbaugh RD, Frederick P, Grizzle R, Luckenbach MW, Peterson CH, Angelini C (2018) Restoring the eastern oyster: How much progress has been made in 53 years? *Front Ecol Environ* 16:463–471
- Bertness MD, Gaines SD, Hay ME (2001) Marine community ecology. Sinauer Associates, Sunderland, MA
- ✦ Bodenstern S, Walton WC, Steury TD (2021) Effect of farming practices on growth and mortality rates in triploid and diploid eastern oysters *Crassostrea virginica*. *Aquacult Environ Interact* 13:33–40
- ✦ Brumbaugh RD, Coen LD (2009) Contemporary approaches for small-scale oyster reef restoration to address substrate versus recruitment limitation: a review and comments relevant for the Olympia oyster, *Ostrea lurida* Carpenter 1864. *J Shellfish Res* 28:147–161
- Burke RP (2010) Alternative substrates as a native oyster (*Crassostrea virginica*) reef restoration strategy in Chesapeake Bay. PhD dissertation, Virginia Institute of Marine Science, William & Mary, Gloucester Point, VA
- ✦ Callaway R (2018) Interstitial space and trapped sediment drive benthic communities in artificial shell and rock reefs. *Front Mar Sci* 5:288
- ✦ Coen LD, Luckenbach MW (2000) Developing success criteria and goals for evaluating oyster reef restoration: ecological function or resource exploitation? *Ecol Eng* 15: 323–343
- ✦ Colden AM, Lipcius RN (2015) Lethal and sublethal effects of sediment burial on the eastern oyster *Crassostrea virginica*. *Mar Ecol Prog Ser* 527:105–117
- ✦ Colden AM, Latour RJ, Lipcius RN (2017) Reef height drives threshold dynamics of restored oyster reefs. *Mar Ecol Prog Ser* 582:1–13
- ✦ Dame R (1976) Energy flow in an intertidal oyster population. *Estuar Coast Mar Sci* 4:243–253
- Diaz RJ, Schaffner LC (1990) The functional role of estuarine benthos. In: Haire M, Krome EC (eds) Perspectives on the Chesapeake Bay. Advances in Estuarine Science. Chesapeake Research Consortium Rep CBP/TRS-41/90. Chesapeake Bay Program, Annapolis, MD, p 25–56
- ✦ Dunn RP, Eggleston DB, Lindquist N (2014) Effects of substrate type on demographic rates of eastern oyster (*Crassostrea virginica*). *J Shellfish Res* 33:177–185
- ✦ Fredette TJ, Diaz RJ (1986) Life history of *Gammarus mucronatus* Say (Amphipoda: Gammaridae) in warm temperate estuarine habitats, York River, Virginia. *J Crustac Biol* 6: 57–78
- ✦ George LM, De Santiago K, Palmer TA, Beseres Pollack J (2015) Oyster reef restoration: effect of alternative substrates on oyster recruitment and nekton habitat use. *J Coast Conserv* 19:13–22
- ✦ Goelz T, Vogt B, Hartley T (2020) Alternative substrates used for oyster reef restoration: a review. *J Shellfish Res* 39: 1–12
- ✦ Grabowski JH (2004) Habitat complexity disrupts predator–prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85:995–1004
- ✦ Graham PM, Palmer TA, Beseres Pollack J (2017) Oyster reef restoration: substrate suitability may depend on specific restoration goals. *Restor Ecol* 25:459–470
- Heinle DR, D'Elia CF, Taft JL, Wilson JS, Cole-Jones M, Caplins AB, Cronin LE (1980) Historical review of water quality and climatic data from Chesapeake Bay with emphasis on effects of enrichment. Tech Rep EPA/600/3-82/083. Chesapeake Research Consortium Publication No. 84. Chesapeake Bay Program, Environmental Protection Agency, Annapolis, MD
- Héral M, Rothschild BJ, Gouletquer P (1990) Decline of oyster production in the Maryland portion of the Chesapeake Bay: causes and perspectives. ICES-CM-1990/K:20. ICES, Copenhagen
- ✦ Hogan S, Reidenbach MA (2022) Quantifying tradeoffs in ecosystem services under various oyster reef restoration designs. *Estuaries Coasts* 45:677–690
- ✦ Karp MA, Seitz RD, Fabrizio MC (2018) Faunal communities on restored oyster reefs: effects of habitat complexity and environmental conditions. *Mar Ecol Prog Ser* 590:35–51
- ✦ Kellogg ML, Paynter KT, Ross PG, Dreyer JC and others (2016) Integrated assessment of oyster reef ecosystem services: macrofauna utilization of restored oyster reefs. Final report to NOAA Chesapeake Bay Office. Virginia Institute of Marine Science, William & Mary, Gloucester Point, VA
- ✦ La Peyre MK, Humphries AT, Casas SM, La Peyre JF (2014) Temporal variation in development of ecosystem services from oyster reef restoration. *Ecol Eng* 63:34–44
- Lavan B (2019) Examining the effect of interstitial space on eastern oysters (*Crassostrea virginica*): applications of photogrammetry and three-dimensional modeling. MSc thesis, James Madison University, Harrisonburg, VA
- ✦ Lenth RV (2022) emmeans: estimated marginal means, aka least-squares means. R package version 1.7.3. <https://CRAN.R-project.org/package=emmeans>
- ✦ Lipcius RN, Burke RP (2018) Successful recruitment, survival and long-term persistence of eastern oyster and hooked mussel on a subtidal, artificial restoration reef system in Chesapeake Bay. *PLOS ONE* 13:e0204329
- ✦ Lipcius RN, Burke RP, McCulloch DN, Schreiber SJ, Schulte DM, Seitz RD, Shen J (2015) Overcoming restoration paradigms: value of the historical record and metapop-

- ulation dynamics in native oyster restoration. *Front Mar Sci* 2:65
- Luckenbach MW, Ross PG (2003) An experimental evaluation of the effects of scale on oyster reef restoration. Virginia Institute of Marine Science, William & Mary, Gloucester Point, VA
- Mackin JG, Owen HM, Collier A (1950) Preliminary note on the occurrence of a new protistan parasite, *Dermocystidium marinum* n. sp. in *Crassostrea virginica* (Gmelin). *Science* 111:328–329
- Manley J, Power A, Walker R, Hurley D, Belcher C, Richardson J (2010) Ecological succession on restored intertidal oyster habitat in the tidal creeks of coastal Georgia. *J Shellfish Res* 29:917–926
- Margiotta AM, Shervette VR, Hadley NH, Plante CJ, Wilber DH (2016) Species-specific responses of resident crabs to vertical habitat complexity on intertidal oyster reefs. *J Exp Mar Biol Ecol* 477:7–13
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290–297
- Meyer DL, Townsend EC, Thayer GW (1997) Stabilization and erosion control value of oyster cultch for intertidal marsh. *Restor Ecol* 5:93–99
- Morris RL, La Peyre MK, Webb BM, Marshall DA and others (2021) Large-scale variation in wave attenuation of oyster reef living shorelines and the influence of inundation duration. *Ecol Appl* 31:e02382
- Nestlerode JA, Luckenbach MW, O'Beirn FX (2007) Settlement and survival of the oyster *Crassostrea virginica* on created oyster reef habitats in Chesapeake Bay. *Restor Ecol* 15:273–283
- Newell RIE (1988) Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica*? In: Understanding the estuary: advances in Chesapeake Bay research. Proceedings of a Conference, 29–31 March 1988, Baltimore, MD. Chesapeake Bay Research Consortium Publication 129. CBP/TRS 24/88, p 536–546
- Patel J (2023) Impact of substrate type on eastern oyster (*Crassostrea virginica*) recruitment and benthic community structure and productivity in the York River. MSc thesis, The College of William & Mary, Gloucester Point, VA
- Pffirrmann BW, Seitz RD (2019) Ecosystem services of restored oyster reefs in a Chesapeake Bay tributary: abundance and foraging of estuarine fishes. *Mar Ecol Prog Ser* 628:155–169
- Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rothschild BJ, Ault JS, Gouletquer P, Héral M (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. *Mar Ecol Prog Ser* 111:29–39
- Salatin R, Wang H, Chen Q, Zhu L (2022) Assessing wave attenuation with rising sea levels for sustainable oyster reef-based living shorelines. *Front Built Environ* 8:884849
- Schulte DM (2017) History of the Virginia oyster fishery, Chesapeake Bay, USA. *Front Mar Sci* 4:127
- Schulte DM, Burke RP (2014) Recruitment enhancement as an indicator of oyster restoration success in Chesapeake Bay. *Ecol Restor* 32:434–440
- Schulte DM, Burke RP, Lipcius RN (2009) Unprecedented restoration of a native oyster metapopulation. *Science* 325:1124–1128
- Searles AR, Gipson EE, Walters LJ, Cook GS (2022) Oyster reef restoration facilitates the recovery of macroinvertebrate abundance, diversity, and composition in estuarine communities. *Sci Rep* 12:8163
- Sedano F, Navarro-Barranco C, Guerra-García J, Espinosa F (2020) Understanding the effects of coastal defence structures on marine biota: the role of substrate composition and roughness in structuring sessile, macro- and meio-faunal communities. *Mar Pollut Bull* 157:111334
- Seitz RD, Aguilera S, Wood MA, Lipcius RN (2019) Production and vertical distribution of invertebrates on rip rap shorelines in Chesapeake Bay: a novel rocky intertidal habitat. *Estuar Coast Shelf Sci* 228:106357
- Soniat TM, Burton GM (2005) A comparison of the effectiveness of sandstone and limestone as cultch for oysters, *Crassostrea virginica*. *J Shellfish Res* 24:483–485
- Soniat TM, Finelli CM, Ruiz JT (2004) Vertical structure and predator refuge mediate oyster reef development and community dynamics. *J Exp Mar Biol Ecol* 310:163–182
- Sustainable Fisheries GIT (Goal Implementation Team) (2011) Restoration goals, quantitative metrics, and assessment protocols for evaluating success on restored oyster reef sanctuaries. Tech Rep. Sustainable Fisheries Goal Implementation Team, Chesapeake Bay Program, Annapolis, MD
- Taylor J, Bushek D (2008) Intertidal oyster reefs can persist and function in a temperate North American Atlantic estuary. *Mar Ecol Prog Ser* 361:301–306
- Theuerkauf SJ, Burke RP, Lipcius RN (2015) Settlement, growth, and survival of eastern oysters on alternative reef substrates. *J Shellfish Res* 34:241–250
- Wall LM, Walters LJ, Grizzle RE, Sacks PE (2005) Recreational boating activity and its impact on the recruitment and survival of the oyster *Crassostrea virginica* on intertidal reefs in Mosquito Lagoon, Florida. *J Shellfish Res* 24:965–973
- Wilberg MJ, Livings ME, Barkman JS, Morris BT, Robinson JM (2011) Overfishing, disease, habitat loss, and potential extirpation of oysters in upper Chesapeake Bay. *Mar Ecol Prog Ser* 436:131–144
- Wong MC, Peterson CH, Piehler MF (2011) Evaluating estuarine habitats using secondary production as a proxy for food web support. *Mar Ecol Prog Ser* 440:11–25
- Wood JL, Andrews JD (1962) *Haplosporidium costale* (Sporozoa) associated with a disease of Virginia oysters. *Science* 136:710–711

Editorial responsibility: James McClintock,
Birmingham, Alabama, USA

Reviewed by: 2 anonymous referees

Submitted: June 2, 2024; Accepted: January 6, 2025

Proofs received from author(s): February 10, 2025

This article is Open Access under the Creative Commons by Attribution (CC-BY) 4.0 License, <https://creativecommons.org/licenses/by/4.0/deed.en>. Use, distribution and reproduction are unrestricted provided the authors and original publication are credited, and indicate if changes were made.