Biodiversity of oyster reef benthic macrofauna at the Virginia Coast Reserve

Sophia M. Rosenberg
Chesapeake, Virginia

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Max C.N. Castorani,
Thesis Advisor

Thomas M. Smith,
Director of Distinguished Majors Program

ABSTRACT

Within coastal lagoon ecosystems, oyster reefs create structurally-complex intertidal and subtidal habitats that influences the survival, growth, and reproduction of a diverse assemblage of organisms. Species assemblages within these environments may be mediated by a combination of abiotic and biotic factors across spatial scales. Local abiotic factors such as water salinity, and proximity to aquatic vegetation and ocean inlets can determine the type of species present due to species' tolerances and life history traits. Biotic factors such as predator-prey interactions and competition further influence species abundances. In this study, I characterized the biodiversity surrounding restored oyster reefs in the intertidal and subtidal at two locations (an exposed site and a sheltered site) within the seaside bays of Virginia's Eastern Shore, USA. To sample fauna, I used artificial benthic habitat units ("habitat trays") consisting of oyster shell hash within open mesh trays of varying mesh size (coarse vs. fine mesh).

I found that mesh size did not affect total fauna counts (no. of individuals per tray), but did alter relative species abundances (though this may have been due to slight seasonal changes that were conflated with trials of different mesh sizes). Additionally, the finer-mesh size increased the proportion of smaller crabs collected. I found that in both mesh sizes, bay locations shared a majority of the same common species of crabs, gastropods, shrimps, and fishes. Species diversity, richness, and evenness were comparable between sites, but we found differences in relative species abundances. Similarities in biodiversity between sites may be explained by similarities in spatial proximity and water quality. When looking across tidal zones, species richness was consistently greater in the subtidal, mainly due to a greater diversity of gastropods and shrimps. We also found differences in species composition between tidal zones, most likely due to a combination of biotic and abiotic factors.

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INTRODUCTION

Oysters are foundation species that create novel structural complexity and habitat heterogeneity in their immediate surroundings (Jones et al., 1994; Lehnert & Allen, 2002; Smyth & Roberts, 2010). The complex three-dimensional structure of oyster reefs facilitates biological community structure by providing critical space for foraging, reproduction, refuge from physical stress (Bruno et al., 2003; Lejart & Hily, 2011; Zwerschke et al., 2016), as well as nursery habitat (Coen & Luckenbach, 2000, Harding & Mann, 2001; Lehnert & Allen, 2002; Humphries et al., 2011). The interstitial spaces formed between oyster shells provide essential refuge from predation (Menge et al., 1985; Glancy et al., 2003), especially for species of decapod crustaceans (Fernandez et al., 1993b; Eggleston & Armstrong, 1995). The complex structure provided by oysters has been shown to enhance associated species abundance and diversity (MacArthur & MacArthur, 1961; Posey et al., 1999; Cordell et al., 2007; Humphries et al., 2011; Kon et al., 2015). Common species of benthic macrofauna documented on U.S. East Coast oyster reefs include grass shrimp (*Palaemonetes* spp.), penaeid shrimp, panopeid crabs, blue crabs (*Callinectes* spp.), gastropods, bivalves, and fishes, including oyster toadfish (*Opsanus tau*) and gobies (family Gobiidae) (Wells, 1961; Lehnert & Allen, 2002; Humphries et al., 2011; Paterno, 2015).

In addition to oyster reef structure, the benthic macrofaunal community is influenced by a suite of factors that vary from local to regional scales. At a local scale (e.g., meters to tens of meters) macrofaunal abundance and diversity can depend on whether an oyster reef is intertidal or subtidal. Above the mean low water level (MLW), the substrate exposed at low tide is considered intertidal habitat, and everything below the water line (submerged) is classified as subtidal habitat. As a result, intertidal organisms must be able to withstand desiccation conditions and temperature extremes during exposure between high and low tide (Peterson, 1991; Paganini et al., 2014).

Importantly, variation in mobile benthic faunal abundances between intertidal and subtidal habitat may reflect differences in behavioral responses between predators and prey, and interspecific competitive interactions. We might infer predator behavior will contribute to variation in prey abundance either directly through predation (Paine, 1966;

Connell, 1972; Grabowski, 2004), or indirectly through predator avoidance (Paine, 1966; Hughes, 1994; Grabowski, 2004). Similarly, prey abundance may determine predator behavior (Underwood & Chapman, 1996). For example, oyster toadfish mediate mud crab abundances either directly through consumption, or indirectly by initiating predator avoidance behavior in mud crabs (Grabowski, 2004; Ricci et al., 2017). This interaction also creates a tri-trophic interaction by mediating oyster predation by mud crabs. Top-down interactions such as these have the potential to initiate trophic cascades within oyster reef ecosystems (Gibbons & Castagna, 1985; Grabowski, 2004; Hughes et al., 2012). Interspecific competition within groups such as grass shrimp and mud crabs may also influence relative densities of different species due to better competitive ability of one species over another. For example, larger, more aggressive mud crabs (Beattie et al., 2012) and shrimp (Knowlton et al., 1994) have been found to have a competitive advantage over smaller, less competitive individuals within the same genus. Additionally, there may also be differences in predation pressure and food availability, and differences in faunal communities may reflect tradeoffs between the two (Werner et al., 1983; Beck & Watts, 1997; Cowlishaw, 1997; Heithaus & Dill, 2002; Grabowski et al., 2005).

At regional scales (e.g., kilometers to hundreds of kilometers), habitat characteristics can influence the composition of oyster reef communities (Menge & Olson, 1990; Denny et al., 2004; Fraschetti et al., 2005; Burrows et al., 2009). Species abundances can vary due to physical parameters such as water quality (e.g., salinity, water temperature, dissolved oxygen) and proximity to vegetated habitat or ocean inlets. Salinity can affect the type of species to colonize an area, depending on species tolerances and optimal habitat conditions (Wells, 1961; Menge & Olson, 1990; Liu et al., 2018). For example, differences in the abundance of certain grass shrimp species has been found according to species-specific salinity tolerances (Knowlton et al., 1994). Additionally, past studies have found increases in species richness and diversity on a gradient of increasing salinity (Wells, 1961; Liu et al., 2018). Salinity levels may also impact predation pressure due to a greater number of species and associated predators with increasing salinity (Wells, 1961; Kimbro et al., 2017).

The proximity to vegetated habitat types, such as seagrass meadows, can also influence species composition within an oyster reef. Seagrasses are known to enhance biodiversity in the areas they inhabit (Eggleston et al., 1998; McGlathery et al., 2012), especially blue crab densities, a notorious predator of oyster reefs and other invertebrates (Micheli & Peterson, 1999). Previous studies have postulated that seagrass communities may provide a corridor for which blue crabs can approach and prey on oyster reefs and their inhabitants (Moody, 1994; Micheli, 1997a; Grabowski et al., 2005). Additionally, a study by Gain et al. (2017) found that the spatial arrangement of habitat types in proximity to oyster reefs, such as seagrass, did not have an effect on species richness, but did have an effect on species density among sites. Another study by Grabowski et al. (2005) found intertidal reefs bordering mudflat doubled resident decapod densities relative to reefs that bordered seagrass communities.

The drivers of oyster reef macroinvertebrate community structure have been well studied. Past studies have examined the effects of reef size (Eggleston et al., 1998, 1999), new and old reef substrate (Brown et al., 2014), restored oyster reefs (Paterno, 2015), and shell-laden versus bare substrate (Lehnert & Allen, 2002). While diverse macroinvertebrate assemblages among both intertidal and subtidal oyster reefs have been documented in numerous parts of the U.S. Atlantic and Gulf Coasts (Bahr, 1981; Zimmerman et al., 1989; Lehnert & Allen, 2002; Rodney & Paynter, 2006; Brown et al., 2014), studies conducted along the seaside bays of coastal Virginia are lacking. The Nature Conservancy’s (TNC) Virginia Coast Reserve (VCR) Chapter, Virginia Marine Resources Commission (VMRC), and others have worked to restore oyster reef communities along the Eastern Shore of Virginia (ESVA) and elsewhere, but information regarding species diversity and their relative abundance in these areas since their restoration is not well explored. Additionally, previous studies have documented a predominance of intertidal oyster reefs along much of the U.S. Northeast and Mid-Atlantic (Bahr & Lanier, 1981; Paterno, 2015), despite a preference for Eastern oysters (*Crassostrea virginica*) to settle in the subtidal zone (Barnes et al., 2010). This difference is most likely due to several factors, with sedimentation and predation serving as dominant explanations (Wells, 1961; Giotta, 1999; Lenihan, 1999). Along the Atlantic

Coast of the ESVA, there is a similar occurrence of natural intertidal oyster reefs and lack of subtidal reefs. Documenting common epifaunal predators (e.g., crabs) present in these areas would give insight into the influence of predation on reef distributions.

In this study, I compared differences in the abundance and diversity of benthic macrofauna on restored *C. virginica* oyster reefs across two spatial scales: between outer bay and inner bay sites (< 11 km), and between intertidal and subtidal habitats (< 25 m). I predicted that species assemblages would differ according to local abiotic factors, such as water salinity and proximity to seagrass habitat and ocean inlets, as well as biotic factors such as predator-prey interactions and interspecific competition.

MATERIALS AND METHODS

Study site

I carried out my study at the Virginia Coast Reserve (VCR), located along the Virginia portion of the Delmarva Peninsula. The site consists of expansive coastal lagoons formed between the mainland and 14 undeveloped barrier islands. Remnant natural and restored intertidal oyster reefs are located throughout these lagoons (Luckenbach et al., 2008; Hogan & Reidenbach, 2019). The shallow bays are characterized by semidiurnal tide regimes with a tidal range of 1.2–1.3 m (McGlathery et al., 2012; Safak et al., 2015). Long-term data (>20 years) shows water quality in the area is high due to low nutrient inputs (Orth & McGlathery, 2012). Due to a limited mainland watershed, the bays composing the VCR do not have a significant freshwater source, and salinity conditions are consistently polyhaline (28–32 PSU; Woo et al., 1998). Oyster reefs are often fringed by bare mudflats and low marshes (cordgrass *Spartina alterniflora*). Oyster reefs towards the middle and outer parts of VCR are commonly adjacent to subtidal seagrass meadows (eelgrass *Zostera marina*).

All field work was completed at two sites within the seaside bays of the VCR: Hillcrest Shellfish Sanctuary (37°16’46.639” N, 75°55’20.593” W) and Wreck Island (37°16’37.279” N, 75°48’3.106” W) (Fig. 1). Hillcrest Shellfish Sanctuary is located in Mockhorn Bay, immediately offshore from Oyster Harbor in Oyster, Virginia. The Sanctuary was built by TNC and VMRC in late 2017 (Creed et al., 2017). Wreck Island is a 1380-acre barrier island located in South Bay, approximately seven miles off the peninsular mainland. Wreck Island is situated directly adjacent to Sand Shoal Inlet off the Atlantic Ocean, and as a result, oyster reefs there are exposed to high-energy ocean waves and tidal forces. Both Hillcrest and Wreck reefs are relatively isolated from salt marsh habitat (>100 m), however, Wreck reefs are adjacent to a successful eelgrass restoration project (Orth & McGlathery, 2012). Both sites were previously restored using loose cultch oyster shell and have expanded over the course of subsequent years.

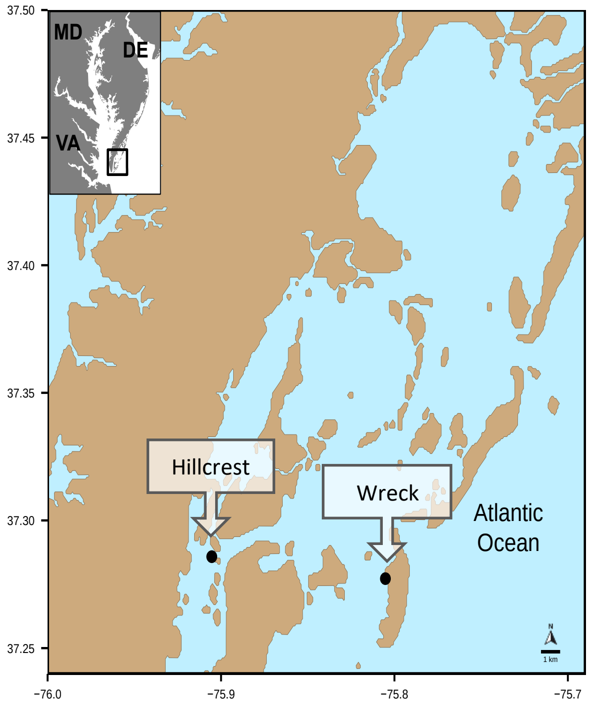

Fig. 1. Map showing Hillcrest and Wreck sites in VCR (credit: Kinsey N. Tedford).

Epibenthic macrofauna assemblage sampling

I used artificial benthic habitat units (“habitat trays”) consisting of loose oyster shell within open mesh trays to sample macroinvertebrate and fish communities at intertidal and subtidal heights at both sites. Habitat trays are used extensively to quantify estuarine macrofauna species diversity (Snelgrove et al., 1992; Eggleston et al., 1998, 1999; Rodney & Paynter, 2006; Paterno, 2015). The design used in this study was similar to past experiments, but with modifications to tray complexity and size due to constraints on feasibility and time. I used two mesh sizes to test for differences in sample collections between a coarse-mesh (6 mm; Fig. 2) and fine-mesh (1 mm; Fig. 3) tray design. I wanted to test if coarse-mesh trays "lost" a greater number of small species, particularly crabs (<5 mm carapace width, CW). All trays were constructed using a base wire mesh of ¼-in (6 mm) on all sides (41 cm × 13 cm deep), with an open top. Fine-mesh trays were then lined with an additional fiberglass mesh. Plastic kitchen trays (25 cm × 36 cm) were fitted within the interior of all trays, placed on top of two steel rebar weights for support. Trays were filled with approximately 1 L of loose, single-valve oyster shell because dead oyster shell attract similar faunal communities as live oyster shell (Tolley & Volety, 2005). Trays were positioned on the surface of the sediment. Trays do not accurately sample all species of demersal or water column fishes (Lehnert & Allen, 2002), but do sample many common benthic fishes living and foraging amongst oyster shell rubble (e.g., oyster toadfish, gobies).

Fig. 2. Coarse-mesh benthic habitat trays (0.09 m_2) deployed in July/August 2019.

Fig. 3. Fine-mesh benthic habitat trays (0.09 m^2) deployed in September/October 2019.

I deployed twelve trays at each site on two sample dates (12 trays × 2 sites × 2 sample dates = 48 samples), with half along existing intertidal reefs and half in areas representative of potential subtidal oyster habitats (6 replicates per treatment). At both sites, trays were placed in transects running parallel to shore, in order to minimize differences between trays in factors such as slope, wave action, and tidal height. Sample points were chosen relatively equidistant within intertidal and subtidal zones, and between intertidal and subtidal zones. At all sites, trays were placed at least 12 m between replicates at the same tidal height and at least 24 m between intertidal and subtidal habitat. Trays were deployed in two trials separated by approximately 1.5 months, due to constraints on materials, boat availability, and weather. Trays were placed in the field during low tide, and subsequently retrieved 17 and 15 days later during low tide in the first and second trials, respectively.

Field sampling

Field collections occurred towards the end of the warm season, in late August and September. This time was chosen due to high mobility of common epifauna and reef predators, which are more mobile and active during warmer months (Hines et al., 1987b, 1990; Ruiz et al., 1993). Measurements of bottom water temperature (°C), salinity (ppt), conductivity (mS), and D.O. (mgL^{-1}) were measured during both trials and retrievals using a YSI® multi-probe meter. Upon retrieval, trays were removed from the water and carried to a nearby anchored boat, where all contents were rinsed through a ca. 500-micron mesh bag. Oyster shells were rinsed thoroughly and removed from mesh bags. Individuals retained in the mesh bag were frozen until further identification.

Lab processing

All viable species were identified to the lowest practical taxon and counted. Crabs greater than 5 mm CW were measured to the nearest 0.01 mm and those smaller than 5 mm were all marked as “5.0 mm.” All fish were measured to the nearest 0.01 mm based on total length (TL).

STATISTICAL ANALYSIS

A three-way analysis of variance (ANOVA) was used to test for differences in abundance with three fixed factors: mesh size (coarse-mesh vs. fine-mesh), site (Hillcrest vs. Wreck), and tidal zone (intertidal vs. subtidal). A separate ANOVA was run for total counts of all individuals for each taxon group (gastropods, shrimp, fish, and crabs), and for each species (with sufficient data for testing). Tukey post-hoc comparison tests were used to compare pairwise differences if a significant interaction ($p < 0.05$) was found between mesh size × site or mesh size × tidal zone.

To examine diversity, I calculated Simpson’s Index of Diversity (SID) with the following equation:

$$D = 1 - \sum\left(\frac{n}{N}\right)^2 \tag{1}$$

Where n represents the number of organisms of a particular species and N is the total number of organisms of all species. Equitability was calculated by first calculating Shannon’s diversity index using the following equation:

$$H = -\sum_{i=1}^{R} p_i \ln p_i \tag{2}$$

Where p_i is the proportion of a species out of the total number of individuals collected. Equitability was then calculated by dividing the Shannon diversity index value by the natural log of species richness (S).

$$E = H/\ln(S) \tag{3}$$

I plotted species diversity on a diversity dominance curve, and compared both mesh size differences at a site and differences between sites. Diversity dominance curves provide a visual of species richness and evenness between sites. All crabs were grouped into size classes to assess crab size distributions and modality between mesh sizes. The first size class includes crabs less than or equal to 5 mm CW, and every consecutive size class after increases by 1 mm (Table 3).

I used the *lme4* and *vegan* packages (Bates et al., 2015; Oksanen et al., 2019) for these analyses and *ggplot2* (Wickham, 2016) for visualizations in R version 3. 5. 2 (R Core Team, 2018).

RESULTS

I collected a total of 4,157 individuals comprised of 36 species across all samples. Of the total number of individuals collected, 60.4% were gastropods, 25.6% shrimp, 11.5% crabs, 1.6% fish, and 0.9% bivalves. Of all individuals collected, 263 (6.3%) were designated as “unidentifiable” due to missing or damaged body parts and were not identified to species. These individuals were not included in analysis of species richness, evenness, or Simpson’s Diversity Index, but were included in analysis involving broad taxon groups (e.g. shrimp, crabs).

Crab and fish sizes varied by species (Table 1). Since all crabs less than 5 mm were listed as 5 mm, average crab sizes may be inflated. Only mud crabs were found with eggs, and the proportion of mud crabs with eggs differed by mud crab species (Table 2) with *Eurypanopeus depressus* and *Dyspanopeus sayi* having a much higher proportion with eggs than all other species. Overall, Xanthid crabs made up the majority of all crabs collected (446 individuals, 93%).

Table 1. Average sizes of crabs (carapace width) and fishes (total length) by species collected in coarse-mesh and fine-mesh trays. NA standard error values are indicated where only one count was recorded.

Species	Total count	Size range (mm)	Average size (mm)	Standard Error
CRABS				
Callinectes spp.	18	<5–25	11.3	1.56
Panopeus herbstii	162	<5–31.4	10.0	0.46
Eurypanopeus depressus	50	<5–12.2	9.9	0.24
Dyspanopeus sayi	120	<5–18.1	7.4	0.24
Hexapanopeus angustifrons	9	5.2–12.9	7.6	0.95
Hemigrapsus sanguineus	4	5.8–18.1	13.2	2.65
Unidentified Portunidae crab	3	<5	5	0
Libinia dubia	1	43.7	43.7	NA
FISHES				
Archosargus probatocephalus	1	135	135	NA
Centropristis striata	2	38–48	43	4.95
Fundulus heteroclitis	1	65	65	NA
Gobiosoma bosc	47	20–89	35	2.13
Opsanus tau	9	27–114	76	12.42
Tautoga onitis	10	38–87	61	5.68

Table 2. Total number and percentage of mud crab species with eggs in coarse- and fine-mesh trays.

Species	No. with eggs	Total abundance	% with eggs
Panopeus herbstii	5	162	3.1
Eurypanopeus depressus	23	50	46.0
Dyspanopeus sayi	26	120	21.7
Hexapanopeus angustifrons	0	9	0

Table 3. Proportion of crabs in each size class (based on carapace width) in coarse-mesh and fine-mesh trays. Grand total is the total number of crabs collected in each mesh size and is the denominator for proportion calculations.

Size class	**Size range (mm)**	**Coarse-mesh**		**Fine-mesh**	
		Count	**Proportion**	**Count**	**Proportion**
1	0-5	113	0.34	75	0.51
2	5-6	12	0.036	6	0.041
3	6-7	29	0.087	11	0.075
4	7-8	43	0.13	9	0.061
5	8-9	30	0.090	7	0.048
6	9-10	17	0.051	7	0.048
7	10-11	10	0.030	3	0.020
8	11-12	16	0.048	5	0.034
9	12-13	12	0.036	5	0.034
10	13-14	6	0.018	6	0.041
11	14-15	8	0.024	2	0.013
12	15-16	6	0.018	0	0
13	16-17	3	0.0090	0	0
14	17-18	6	0.018	4	0.027
15	18-19	5	0.015	2	0.014
16	19-20	0	0	0	0
17	>20	16	0.048	5	0.034
Grand total		**332**		**147**	

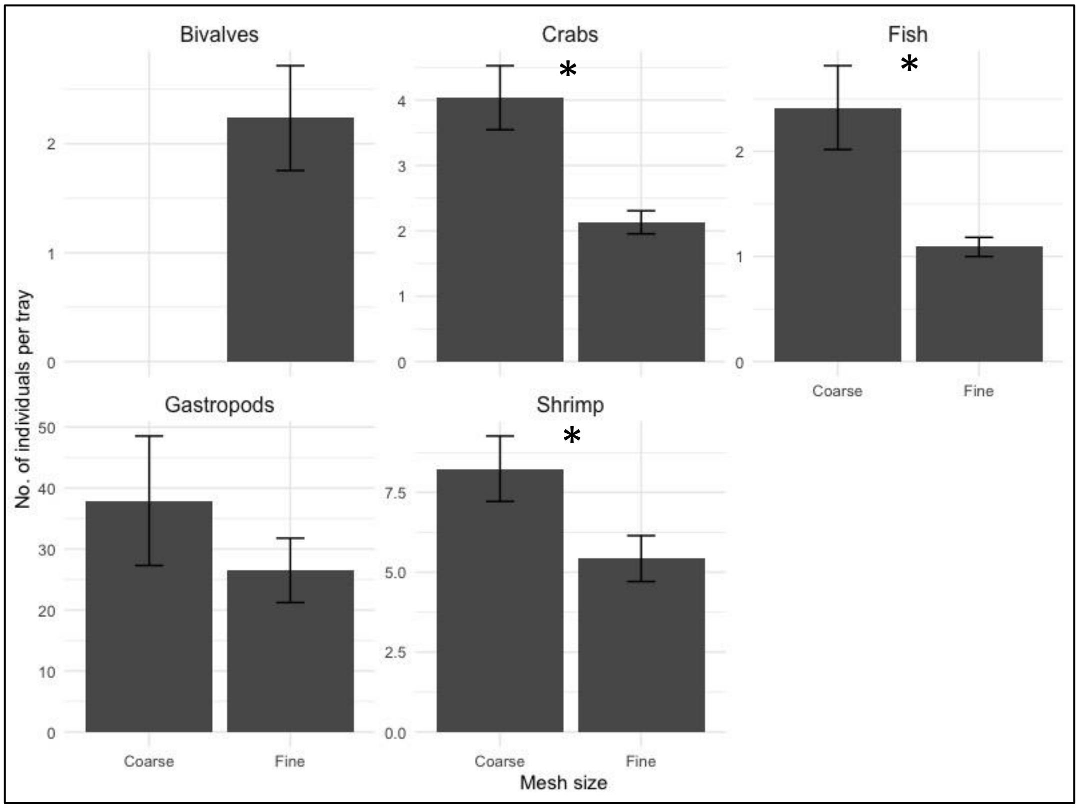

Fig. 4. Mean of number of individuals collected per tray by taxon group, separated by coarse-mesh and fine-mesh trays. Asterisks indicate significant differences between mesh sizes ($p < 0.05$). Error bars denote ± 1 standard error.

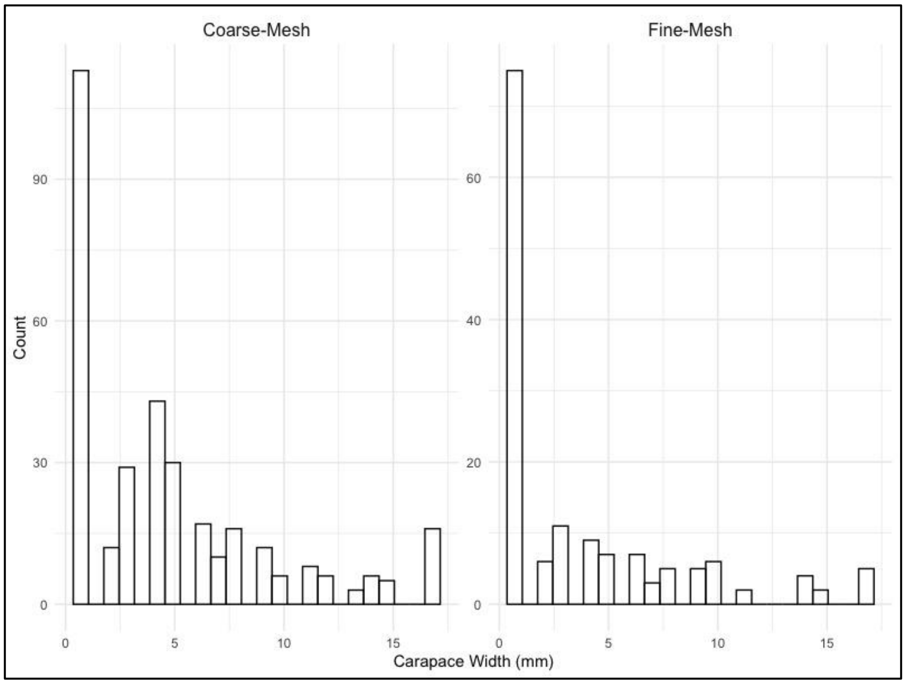

Fig. 5. Histograms showing the distributions of crab sizes in coarse-mesh and fine-mesh trays.

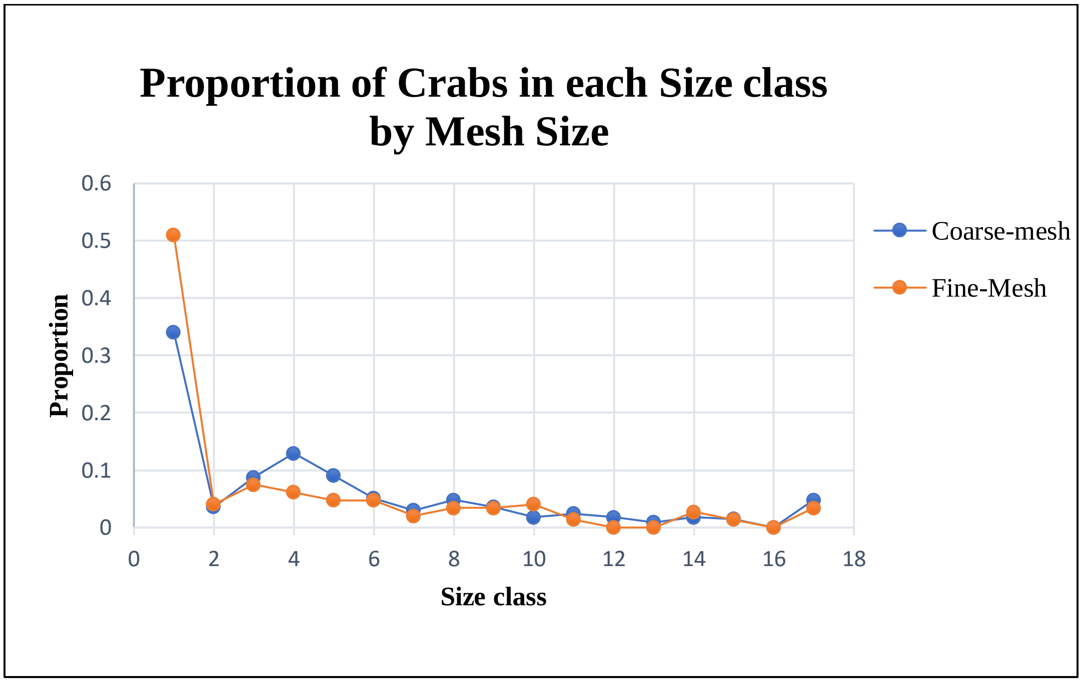

Fig. 6. Proportion of crabs within each size class in coarse-mesh and fine-mesh trays.

Species Diversity

Simpson's Diversity Index values were comparable between sites for both mesh sizes. Values ranged from 0.668 to 0.714 (Table 4), which indicates that one would have approximately a 70% chance of randomly picking two individuals of different species from all individuals collected in trays in each trial. Species richness did not differ between sites ($F_{1,40} = 1.68$, $p = 0.2$), regardless of mesh size (mesh size × site interaction: $F_{1,40} = 0.945$, $p = 0.3$). Species richness was greater in the subtidal zone overall ($F_{1,40} = 104.173$, $p < 0.001$), and though the three-way ANOVA did not indicate a significant mesh size × tidal zone interaction ($F_{1,40} = 0.026$, $p = 0.9$), a Tukey post-hoc test revealed species richness was significantly higher in the subtidal zone in both the coarse-mesh ($p_{adj} < 0.001$) and fine-mesh trays ($p_{adj} < 0.001$) (Table 5). Species evenness was similar across sites with values ranging from 0.484 to 0.587. Species diversity dominance curves show that species richness and evenness at each site were similar between mesh sizes (Fig. 7, Fig. 8) and between sites within a certain mesh size (Fig. 9, Fig. 10).

Table 4. Simpson's Diversity Index values at each site for each mesh size.

	Hillcrest	Wreck
Coarse-mesh	0.696	0.714
Fine-mesh	0.687	0.668

Table 5. Average species richness per tray by site and tidal zone for each mesh size.

	Hillcrest	Wreck	Intertidal	Subtidal
Coarse-mesh	7.33	6.17	4.17	9.33
Fine-mesh	7.25	7.08	4.50	9.83

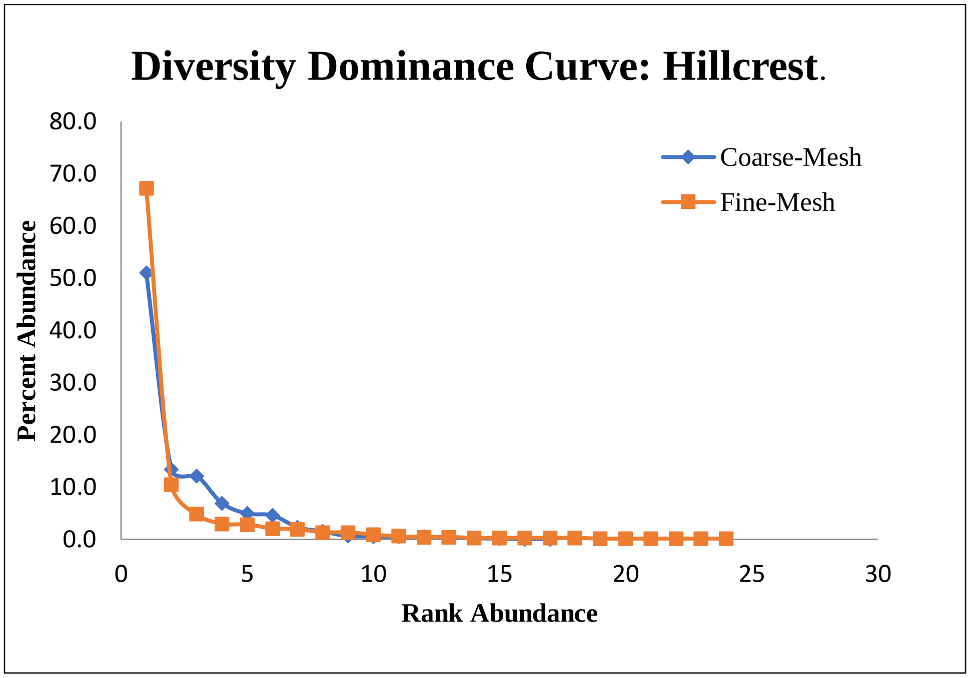

Fig. 7. Diversity dominance curve of macrofauna species collected at Hillcrest in coarse-mesh (blue) and fine-mesh (orange) trays.

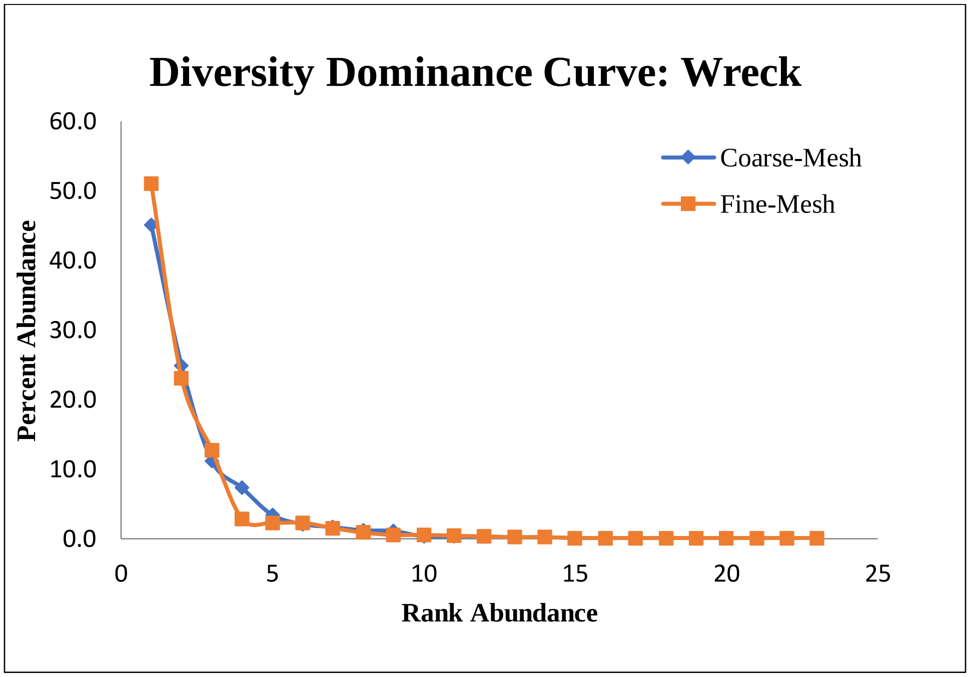

Fig. 8. Diversity dominance curve of macrofauna species collected at Wreck in coarse-mesh (blue) and fine-mesh (orange) trays.

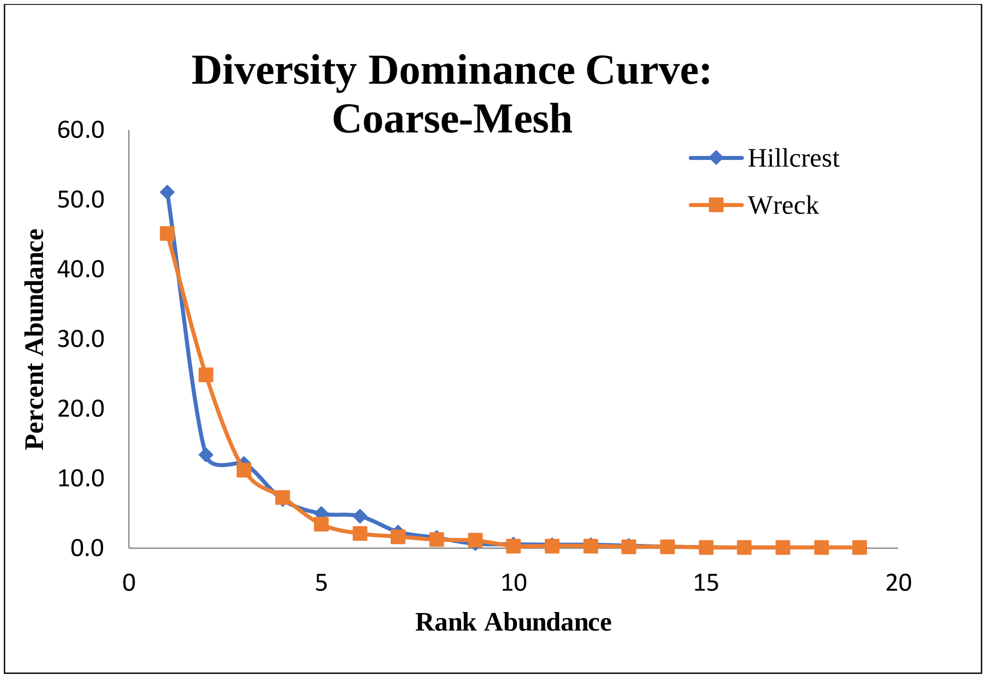

Fig. 9. Diversity dominance curve of macrofauna species collected in coarse-mesh trays collected at Hillcrest (blue) and Wreck (orange).

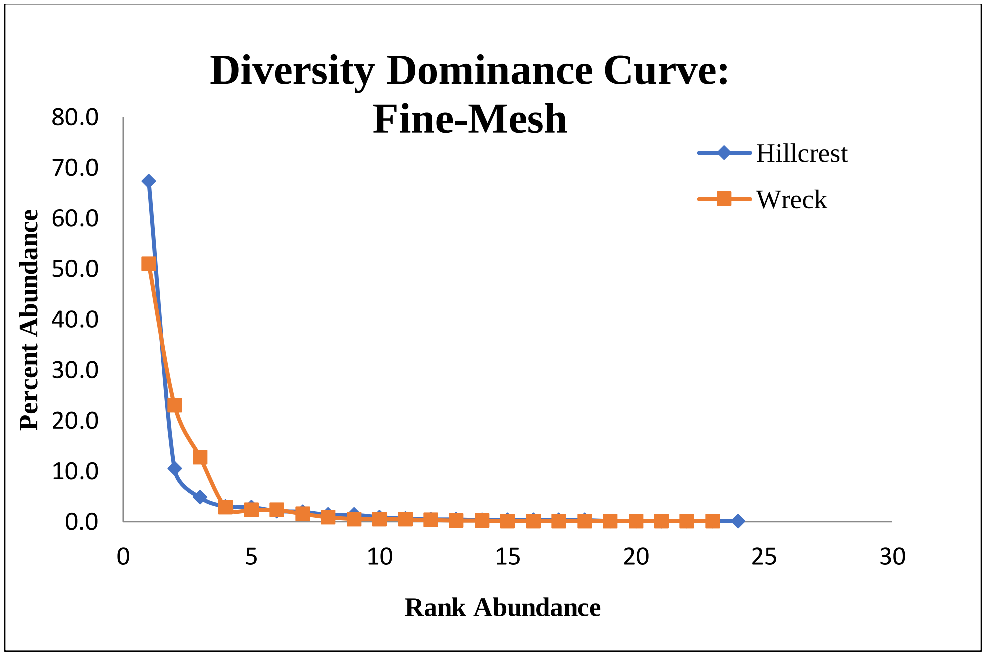

Fig. 10. Diversity dominance curve of macrofauna species in fine-mesh trays collected at Hillcrest (Blue) and Wreck (orange).

Site Comparison

At Hillcrest, a total of 1,514 individuals were collected using coarse-mesh trays, and 741 individuals were collected using fine-mesh trays. At Wreck, a total of 941 individuals were collected using coarse-mesh trays and 961 individuals were collected fine-mesh trays. Overall, there was no difference in the number of individuals per tray between sites ($F_{1,432} = 0.03$, $p = 0.9$). Water quality characteristics were measured in both mesh size trials, but measurements taken in the coarse-mesh trial at Hillcrest were taken outside the trial period. In the fine-mesh trial, water quality measurements were similar between Hillcrest and Wreck (Table 6).

Table 6. Bottom water quality measurements at Hillcrest and Wreck.

Date	Site	Salinity (PSU)	D.O. (mg/L)	Temperature (°C)	Conductivity (mS)
22-Jun-19	Hillcrest	28.2	6.24	25.9	43.8
30-Jun-19	Hillcrest	31.0	10.9	30.1	52.3
8-Aug-19	Wreck	34.3	4.58	26.1	53.0
23-Sep-19	Hillcrest	31.2	7.43	22.1	45.12
23-Sep-19	Wreck	30	7.14	23.1	45.12
10-Oct-19	Hillcrest	30.9	7.3	21.6	44.2
10-Oct-19	Wreck	30.4	6.5	21.5	43.51

The three-way ANOVA showed a significant interaction between mesh size × site ($F_{1,432} = 5.031$, $p = 0.03$), however a Tukey post-hoc test revealed counts per tray between sites were not significantly different, either in coarse-mesh ($p_{adj} = 0.3$) or fine-mesh trays ($p_{adj} = 0.5$). There were, however, differences in abundance between sites by taxon group (Fig. 11). In coarse-mesh trays, crabs per tray were significantly greater at Hillcrest than Wreck ($p_{adj} = 0.003$), but in fine-mesh trays there was no difference in crabs between sites ($p_{adj} = 0.9$). This may be explained by abundances of *Panopeus herbstii* and *Dyspanopeus sayi*, two of the most abundant crab species (Table 7, Table 8). A Tukey post-hoc test revealed both *P. herbstii* ($p_{adj} < 0.001$) and *D. sayi* ($p_{adj} = 0.01$) were significantly greater in the coarse-mesh trays than in the fine-mesh trays at Hillcrest. Additionally, the three-way ANOVA revealed *Eurypanopeus depressus* crabs carrying eggs were significantly higher at Hillcrest overall ($p < 0.001$; Table 10), but did not have a significant mesh × site interaction ($p = 0.4$; Table 10).

In coarse-mesh trays, shrimp were higher at Hillcrest than Wreck ($p_{adj} = 0.01$), but in fine-mesh trays, shrimp were not significant by site ($p_{adj} = 0.1$). This may be explained by abundances of *Alpheus* spp. and *Palaemonetes vulgaris*, two of the most abundant shrimp species (Table 7, Table 8). A three-way ANOVA revealed both *Alpheus* spp. ($p < 0.001$) and *P. vulgaris* ($p < 0.001$) had a significant mesh × site interaction (Table 10). A Tukey post-hoc test revealed *Alpheus* spp. ($p_{adj} < 0.001$) and *P. vulgaris* ($p_{adj} = 0.02$) were greater at Hillcrest in coarse-mesh trays, and *P. vulgaris* was greater at Wreck in the fine-mesh trays ($p_{adj} = 0.03$).

Gastropods showed a significant mesh × site interaction ($p = 0.03$; Table 9), but a Tukey-post hoc revealed gastropods did not differ between sites in either coarse-mesh trays ($p_{adj} = 0.2$) or fine-mesh trays ($p_{adj} = 0.6$) (Figure 11). There were, however, species differences between sites. The three-way ANOVA showed *Astyris lunata* had a significant mesh × site interaction ($p = 0.002$; Table 10). A Tukey post-hoc test revealed *A. lunata* were greater at Hillcrest than Wreck in coarse-mesh trays ($p_{adj} = 0.008$), but did not differ by site in the fine-mesh trays ($p_{adj} = 0.8$). Bivalves were only collected in fine-mesh trays, and were too rare to be analyzed.

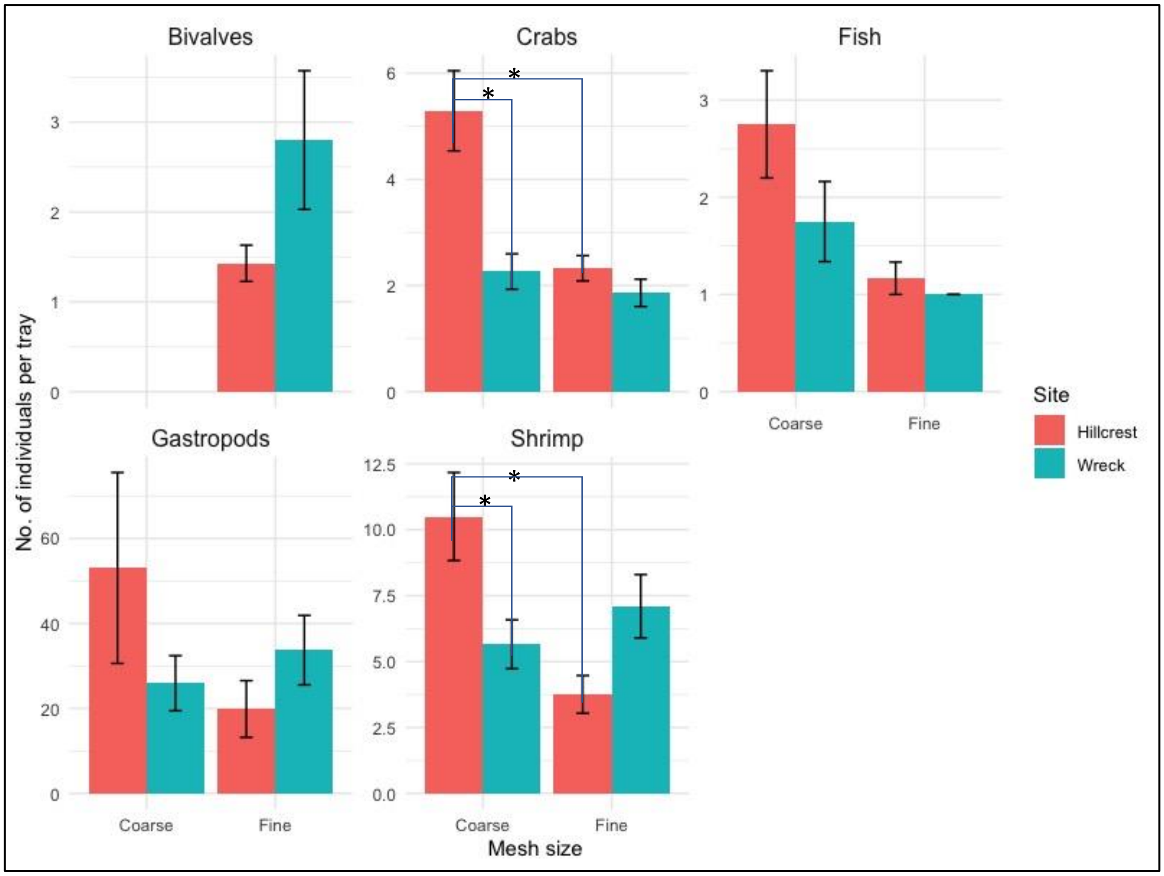

Fig. 11. Mean number of individuals collected per tray by taxon group, separated by mesh size and site. Asterisks indicate mean abundance was significant between groups ($p < 0.05$). Error bars denote ± 1 standard error.

Table 7. Species abundances for all species by site and tidal height collected in coarse-mesh trays (24 trays total, 12 at each sites). % indicates percentage caught per species out of total catch (including unidentifiable catch not presented here).

		Count	**Wreck**		**Hillcrest**		**Intertidal**		**Subtidal**	
Species	**Common name**		**Total**	**%**	**Total**	**%**	**Total**	**%**	**Total**	**%**
SHRIMP										
Alpheus spp.	big-clawed snapping shrimp	255	66	26	189	74	3	1	252	99
Palaemonetes intermedius	brackish grass shrimp	1	1	100	0	0	0	0	1	100
Palaemonetes vulgaris	marsh grass shrimp	273	101	37	172	63	56	21	217	79
Unidentified shrimp #1	-	10	3	30	7	70	0	0	10	100
Mysidae	Family of opossum shrimp	0	0	0	0	0	0	0	0	0
Unidentified shrimp #2	-	0	0	0	0	0	0	0	0	0
Unidentified *Palaemonetes* sp.	grass shrimp	1	1	100	0	0	0	0	1	100
Thalassinoidea	Superfamily of mud shrimp	0	0	0	0	0	0	0	0	0
CRABS										
Callinectes spp.	blue crab	9	1	11	8	89	3	33	6	67
Dyspanopeus sayi	Say's mud crab	85	15	18	70	82	12	14	73	86
Eurypanopeus depressus	flat back mud crab	40	19	48	21	53	39	98	1	3
Hemigrapsus sanguineus	Asian shore crab	3	3	100	0	0	3	100	0	0
Hexapanopeus angustifrons	smooth mud crab	7	0	0	7	100	2	29	5	71
Libinia dubia	longnose spider crab	0	0	0	0	0	0	0	0	0
Panopeus herbstii	Atlantic mud crab	129	31	24	98	76	96	74	33	26
Unidentified Portunidae sp.	Family of swimming crabs	0	0	0	0	0	0	0	0	0
FISH										
Archosargus probatocephalus	sheepshead	0	0	0	0	0	0	0	0	0
Centropristis striata	black sea bass	2	0	0	2	100	0	0	2	100
Fundulus heteroclitus	mummichog	1	0	0	1	100	1	100	0	0
Gobiosoma bosc	naked goby	44	11	25	33	75	5	11	39	89
Opsanus tau	oyster toadfish	6	1	17	5	83	0	0	6	100
Tautoga onitis	tautog	3	0	0	3	100	0	0	3	100
BIVALVES								0		
Anadara transversa	transverse ark	0	0	0	0	0	0	0	0	0
Abra aequalis	common Atlantic abra	0	0	0	0	0	0	0	0	0
Tagelus divisus	purplish tagelus	0	0	0	0	0	0	0	0	0
GASTROPODS								0		
Anachis sertulariarum	-	0	0		0	0	0	0	0	0
Aparvanachis obesa	fat dove snail	10	10	100	0	0	0	0	10	100
Astyris lunata	lunar dove snail	1129	408	36	721	64	18	2	1111	98
Bittiolum varium	grass cerith	1	1	100	0	0	0	0	1	100
Boonea impressa	impressed odostome	2	2	100	0	0	0	0	2	100
Costoanachis avara	greedy dove snail	290	225	78	65	22	8	3	282	97
Seila adamsii	Adams miniature cerith	0	0	0	0	0	0	0	0	0
Unidentified *Boonea* sp.	-	0	0	0	0	0	0	0	0	0
Unidentified *Anachis* sp.	-	2	2	100	0	0	0	0	2	100
Pyrgocythara sp.	-	1	0	0	1	100	0	0	1	100
Unidentified *Mitrella* sp.	-	0	0	0	0	0	0	0	0	0
Urosalpinx cincerea	Atlantic oyster drill	12	3	25	9	75	0	0	12	100

Table 8. Species abundances for all species by site and tidal height collected in fine-mesh trays (24 trays total, 12 at each sites). % indicates percentage caught per species out of total catch (including unidentifiable catch not presented here).

		Count	**Wreck**		**Hillcrest**		**Intertidal**		**Subtidal**	
Species	**Common name**		**Total**	**%**	**Total**	**%**	**Total**	**%**	**Total**	**%**
SHRIMP										
Alpheus spp.	big-clawed snapping shrimp	40	8	20	32	80	2	5	38	95
Palaemonetes intermedius	brackish grass shrimp	4	2	50	2	50	1	25	3	75
Palaemonetes vulgaris	marsh grass shrimp	280	210	75	70	25	110	39	170	61
Unidentified shrimp #1	-	18	5	28	13	72	0	0	18	100
Mysidae	Family of opossum shrimp	23	21	91	2	9	0	0	23	100
Unidentified shrimp #2	-	1	1	100	0	0	0	0	1	100
Unidentified *Palaemonetes* sp.	grass shrimp	5	5	100	0	0	0	0	5	100
Thalassinoidea	Superfamily of mud shrimp	1	1	100	0	0	0	0	1	100
CRABS										
Callinectes spp.	blue crab	9	0	0	9	100	3	33	6	67
Dyspanopeus sayi	Say's mud crab	35	21	60	14	40	6	17	29	83
Eurypanopeus depressus	flat back mud crab	10	4	40	6	60	10	100	0	0
Hemigrapsus sanguineus	Asian shore crab	1	1	100	0	0	1	100	0	0
Hexapanopeus angustifrons	smooth mud crab	2	0	0	2	100	0	0	2	100
Libinia dubia	longnose spider crab	1	1	100	0	0	0	0	1	100
Panopeus herbstii	Atlantic mud crab	33	14	42	19	58	30	91	3	9
Unidentified Portunidae sp.	Family of swimming crabs	3	0	0	3	100	1	33	2	67
FISH										
Archosargus probatocephalus	sheepshead	1	0	0	1	100	0	0	1	100
Centropristis striata	black sea bass	0	0	0	0	0	0	0	0	0
Fundulus heteroclitus	mummichog	0	0	0	0	0	0	0	0	0
Gobiosoma bosc	naked goby	3	1	33	2	67	1	33	2	67
Opsanus tau	oyster toadfish	1	1	100	0	0	1	100	0	0
Tautoga onitis	tautog	7	3	43	4	57	0	0	7	100
BIVALVES										
Anadara transversa	transverse ark	1	0	0	1	100	0	0	1	100
Abra aequalis	common Atlantic abra	35	26	74	9	26	4	11	31	89
Tagelus divisus	purplish tagelus	2	2	100	0	0	0	0	2	100
GASTROPODS										
Anachis sertulariarum	-	1	0	0	1	100	0	0	1	100
Aparvanachis obesa	fat dove snail	4	1	25	3	75	0	0	4	100
Astyris lunata	lunar dove snail	912	464	51	448	49	13	1	899	99
Bittiolum varium	grass cerith	1	0	0	1	100	1	100		0
Boonea impressa	impressed odostome	1	1	100	0	0	1	100	0	0
Costoanachis avara	greedy dove snail	136	116	85	20	15	4	3	132	97
Seila adamsii	Adams miniature cerith	2	0	0	2	100	0	0	2	100
Unidentified *Boonea* sp.	-	1	0	0	1	100	1	100	0	0
Unidentified *Anachis* sp.	-	0	0	0	0	0	0	0	0	0
Pyrgocythara sp.	-	0	0	0	0	0	0	0	0	0
Unidentified *Mitrella* sp.	-	1	1	100	0	0	0	0	1	100
Urosalpinx cincerea	Atlantic oyster drill	1	0	0	1	100	0	0	1	100

Tidal Zone Comparison

In the intertidal zone, a total of 299 individuals were collected using coarse-mesh trays, and 237 individuals were collected using fine-mesh trays. In the subtidal zone, a total of 2,156 individuals were collected in coarse-mesh trays and 1,465 individuals were collected fine-mesh trays. Including all counts (from both mesh trials) the subtidal zone had greater counts per tray than intertidal ($F_{1,432} = 11.541$, $p < 0.001$), however there was no interaction between mesh size and tidal zone ($F_{1,432} = 0.137$, $p = 0.7$). There were differences in abundance between tidal zones by taxon group (Fig. 12). Shrimp were significant by a mesh size × tidal zone interaction ($p = 0.003$; Table 9B), and a Tukey post-hoc test revealed in coarse-mesh trays, shrimp were greater in the subtidal zone ($p_{adj} = 0.01$). This may be explained by the abundance of *Alpheus* spp. ($p = 0.007$) and *Palaemonetes vulgaris* ($p = 0.05$), both of which showed a significant mesh × tidal zone interaction (Table 10). *Alpheus* spp. ($p_{adj} = 0.004$) and *P. vulgaris* ($p_{adj} = 0.005$) were significantly greater in the subtidal zone in coarse-mesh trays. In fine-mesh trays, shrimp were not significant by tidal zone ($p_{adj} = 0.6$). Crabs were not significant by a mesh size × tidal zone interaction ($p = 0.3$; Table 9A). In coarse-mesh trays, however, a Tukey post-hoc test revealed *Panopeus herbstii* was greater in the intertidal zone ($p_{adj} = 0.002$). This same relationship was not shown in fine-mesh trays ($p_{adj} = 0.9$). Overall, *Dyspanopeus sayi* was greater in the subtidal zone ($p = 0.01$; Table 10), but did not show a significant mesh × tidal zone interaction ($p = 0.08$; Table 10). Gastropods ($p = 0.8$; Table 9C) and fish ($p = 0.6$; Table 9D) were not significant by a mesh size × tidal zone interaction. Bivalves were only collected in fine-mesh trays, and were too rare to be analyzed.

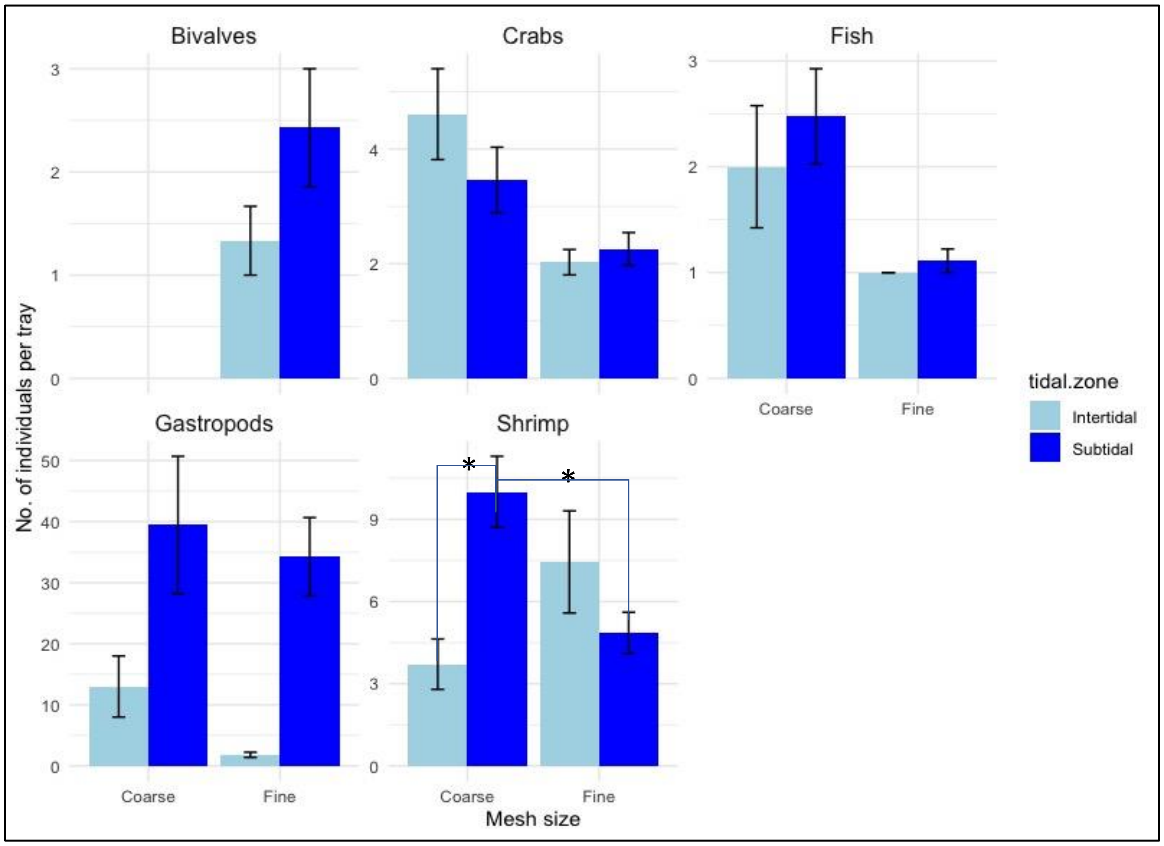

Fig. 12. Mean abundance per tray by taxon group between intertidal and subtidal tidal zones, separated by coarse-mesh and fine-mesh trays. Asterisks indicate mean abundance was significant between groups ($p < 0.05$). Error bars denote ± 1 standard error.

Mesh Size Comparison

There was no overall difference in total counts per tray between coarse-mesh and fine-mesh trays ($F_{1,432} = 1.165$, $p = 0.3$). There were, however, differences in abundances of taxon groups between mesh sizes (Fig. 4; Table 9). Crabs ($p < 0.001$; Table 9A), shrimp ($p = 0.02$; Table 9B), and fish ($p = 0.04$; Table 9D) collected per tray were greater in coarse-mesh trays than in fine-mesh trays. There were no differences in the relative abundance of gastropods between mesh sizes ($p = 0.3$; Table 9C), and bivalves were only found in fine-mesh trays. There were differences between mesh sizes found for some species. *Alpheus* spp. ($p < 0.001$), *Panopeus herbstii* ($p < 0.001$), *Dyspanopeus sayi* ($p = 0.02$), *Astyris lunata* ($p = 0.007$), and *Costoanachis avara* ($p = 0.02$) were greater in coarse-mesh trays than in fine-mesh trays (Table 10). *Palaemonetes vulgaris* did not differ between mesh sizes ($p = 0.5$; Table 10). There was greater richness of novel, smaller, shrimp species in the fine-mesh trays that were not found in coarse-mesh trays, possibly due to mesh size differences. Given that there were more crabs, shrimp, and fish in coarse-mesh trays, I speculate that mesh size did not have an effect on overall abundance of individuals, however, there could have been other confounding factors (e.g., month of collection).

The frequency of all crabs sampled, separated by size class, were right-skewed for both coarse-mesh and fine-mesh trays (Fig. 5). Both mesh sizes had a mode at size class one (0–5 mm CW), meaning the most frequent crab size collected in both trials was 5 mm or less. The fine-mesh did, however, catch a higher proportion of smaller crabs (0–5 mm CW) than coarse-mesh trays (Table 3; Fig. 6), indicating finer mesh was more effective at catching crabs smaller than the coarse-mesh size (less than 5 millimeters).

Site comparison

The three-way ANOVA showed a significant interaction between mesh size × site ($F_{1,432} = 5.031$, $p = 0.03$), however, a Tukey post-hoc test revealed there was no difference in the number of individuals per tray at Hillcrest between coarse-mesh and fine-mesh trays ($p_{adj} = 0.1$), or Wreck between coarse-mesh and fine-mesh trays ($p_{adj} = 0.8$). There were, however, differences in abundance by taxon group between mesh sizes at the two sites (Fig. 11). A Tukey post-hoc test revealed crabs ($p_{adj} < 0.001$) and shrimp ($p_{adj} < 0.001$) were significantly greater in coarse-mesh trays than in fine-mesh trays at Hillcrest. Gastropod ($p_{adj} = 0.1$) and fish ($p_{adj} = 0.2$) abundances did not differ at Hillcrest between coarse-mesh and fine-mesh. Crabs ($p_{adj} = 1.0$), shrimp ($p_{adj} = 0.7$), gastropods ($p_{adj} = 0.9$), and fish ($p_{adj} = 0.8$), did not differ between coarse-mesh and fine-mesh trays at Wreck (Fig. 11).

At both Hillcrest and Wreck, the most abundant species were the same using either coarse-mesh or fine-mesh trays. There were, however, differences in relative abundances of these species between mesh sizes at either site (Table 7, Table 8). At Hillcrest, the most abundant species were *Astyris lunata, Alpheus* spp., and *Palaemonetes vulgaris*. A three-way ANOVA showed all three species had a significant mesh × site interaction (Table 10), and a Tukey post-hoc test revealed all were greater in the coarse-mesh than the fine-mesh trays at Hillcrest (*Astyris lunata*: $p_{adj} = 0.001$, *Alpheus* spp.: $p_{adj} < 0.001$, and *Palaemonetes vulgaris*: $p_{adj} = 0.04$). At Wreck, the most abundant species were *Astyris lunata*, *Costoanachis avara*, and *Palaemonetes vulgaris*. Of those species, only *Palaemonetes vulgaris* was significantly greater in the fine-mesh trays than in the coarse-mesh trays at Wreck ($p_{adj} = 0.01$).

Tidal zone comparison

The three-way ANOVA examining total number of individuals per tray showed there was not a significant mesh size × tidal zone interaction ($F_{1,432} = 0.137$, $p = 0.7$). Among taxon groups, crabs ($p = 0.3$; Table 9A), gastropods ($p = 0.8$; Table 9C), and fish ($p = 0.6$; Table 9D) abundances did not differ between mesh sizes in the intertidal or the subtidal zone (Fig. 12). Shrimp abundances were significant by a mesh × tidal zone interaction ($p = 0.003$; Table 9B); a Tukey post-hoc test revealed abundances did not differ in the intertidal zone between mesh sizes ($p_{adj} = 0.5$), but were greater in the subtidal zone in coarse-mesh trays over fine-mesh trays ($p_{adj} = 0.002$; Fig. 12).

In both the intertidal and subtidal zone, the most abundant species were the same between coarse-mesh and fine-mesh trays. There were, however, differences in relative abundances of these species between mesh sizes at either site (Table 7, Table 8). In the intertidal zone, the most abundant species were *Panopeus herbstii* and *Palaemonetes vulgaris.* A Tukey post-hoc test revealed *P. herbstii* was significantly higher in the coarse-mesh trays over fine-mesh trays in the intertidal zone ($p_{adj} < 0.001$). In the subtidal zone, the most abundant species were *Astyris lunata*, *Costoanachis avara*, *Alpheus* spp. and *Palaemonetes vulgaris* (Table 1, Table 2). Of those species, only *Alpheus* spp. was greater in coarse-mesh trays over fine-mesh trays in the subtidal zone ($p_{adj} < 0.001$).

Table 9. Three-way ANOVA showing effects of mesh size (coarse-mesh or fine-mesh), tidal zone (intertidal or subtidal) and site (Hillcrest or Wreck) for abundance of individuals in each taxon group per tray. Significant effects ($p < 0.05$) are shown in bold.

Effect	Df	Sum Sq	F	p
A. Crabs				
Mesh Size	1	136.1	12.761	**0.000483**
Site	1	126	11.814	**0.00077**
Tidal Zone	1	4	0.375	0.541
Mesh Size: Site	1	18.5	1.737	0.19
Mesh Size: Tidal Zone	1	53.78	5.041	**0.0263**
Site: Tidal Zone	1	7.3	0.688	0.408
Mesh Size: Site: Tidal Zone	1	3.4	0.314	0.576
Residuals	143	10.67		
B. Shrimp				
Mesh Size	1	310	5.996	**0.0155**
Site	1	12	0.237	0.627
Tidal Zone	1	112	2.169	0.143
Mesh Size: Site	1	746	14.425	**0.000212**
Mesh Size: Tidal Zone	1	485	9.376	**0.00261**
Site: Tidal Zone	1	157	3.029	0.0838
Mesh Size: Site: Tidal Zone	1	10	0.201	0.655
Residuals	149	7704		
C. Gastropods				
Mesh Size	1	2546	1.151	0.2869
Site	1	235	0.106	0.7454
Tidal Zone	1	10160	4.592	**0.0355**
Mesh Size: Site	1	10995	4.969	**0.0289**
Mesh Size: Tidal Zone	1	220	0.099	0.7536
Site: Tidal Zone	1	960	0.434	0.5122
Mesh Size: Site: Tidal Zone	NA	NA	NA	NA
Residuals	73	161518		
D. Fish				
Mesh Size	1	13.26	4.57	**0.0414**
Site	1	4.16	1.433	0.2414
Tidal Zone	1	1.04	0.36	0.5532
Mesh Size: Site	1	1.64	0.566	0.458
Mesh Size: Tidal Zone	1	0.66	0.227	0.6373
Site: Tidal Zone	1	0.02	0.006	0.9407
Mesh Size: Site: Tidal Zone	NA	NA	NA	NA
Residuals	28	81.22		

Table 10. Three-way ANOVA showing effects of mesh size (coarse-mesh or fine-mesh), tidal zone (intertidal or subtidal) and site (Hillcrest or Wreck) for species abundance per tray. Significant effects ($p < 0.05$) are shown in bold.

Effect	Df	Sum Sq	F	p
Palaemonetes vulgaris				
Mesh Size	1	26.5	0.552	0.462739
Site	1	3.4	0.071	0.791718
Tidal Zone	1	479.3	9.972	**0.003325**
Mesh Size: Site	1	885.9	18.433	**0.000139**
Mesh Size: Tidal Zone	1	196.4	4.086	**0.051178**
Site: Tidal Zone	1	72.4	1.507	0.22804
Mesh Size: Site: Tidal Zone	1	39.7	0.826	0.369937
Residuals	34	1634.2		
***Alpheus* spp.**				
Mesh Size	1	643.7	23.106	**3.73e-05**
Site	1	552.2	19.823	**0.000102**
Tidal Zone	1	193.6	6.949	**0.012986**
Mesh Size: Site	1	411.3	14.762	**0.000565**
Mesh Size: Tidal Zone	1	234.2	8.408	**0.006808**
Site: Tidal Zone	1	0.2	0.006	0.936552
Mesh Size: Site: Tidal Zone	NA	NA	NA	NA
Residuals	31	863.6		
Panopeus herbstii				
Mesh Size	1	105.19	14.681	**0.000631**
Site	1	164.78	22.997	**4.48e-05**
Tidal Zone	1	103.79	14.484	**0.000676**
Mesh Size: Site	1	70.98	9.906	**0.003794**
Mesh Size: Tidal Zone	1	22.51	3.142	0.086820
Site: Tidal Zone	1	219.94	30.694	**5.66e-06**
Mesh Size: Site: Tidal Zone	NA	NA	NA	NA
Residuals	29	207.8		
Dyspanopeus sayi				
Mesh Size	1	68.71	6.607	**0.0171**
Site	1	19.92	1.915	0.1797
Tidal Zone	1	72.09	6.932	**0.0149**
Mesh Size: Site	1	61.94	5.956	**0.0228**
Mesh Size: Tidal Zone	1	35.53	3.416	0.0775
Site: Tidal Zone	1	3.23	0.31	0.5828

Table 10 (*continued*)

Mesh Size: Site: Tidal Zone	1	16.88	1.624	0.2153
Residuals	23	239.18		
Costoanachis avara				
Mesh Size	1	893.6	6.307	**0.02073**
Site	1	1747.2	12.332	**0.00219**
Tidal Zone	1	1009.5	7.125	**0.01473**
Mesh Size: Site	1	0.7	0.005	0.94445
Mesh Size: Tidal Zone	1	145.4	1.027	0.32307
Site: Tidal Zone	NA	NA	NA	NA
Mesh Size: Site: Tidal Zone	NA	NA	NA	NA
Residuals	20	2833.7		
Astyris lunata				
Mesh Size	1	13361	8.919	**0.00703**
Site	1	3150	2.103	0.16177
Tidal Zone	1	32273	21.545	**0.00014**
Mesh Size: Site	1	17874	11.933	**0.00237**
Mesh Size: Tidal Zone	1	4577	3.056	0.09506
Site: Tidal Zone	1	52	0.035	0.85433
Mesh Size: Site: Tidal Zone	NA	NA	NA	NA
Residuals	21	31457		
***Eurypanopeus depressus* with eggs**				
Mesh Size	1	2.027	3.764	0.0744
Site	1	17.611	32.706	**7.07e-05**
Tidal Zone	1	0.475	0.883	0.3646
Mesh Size: Site	1	0.498	0.925	0.3536
Mesh Size: Tidal Zone	NA	NA	NA	NA
Site: Tidal Zone	NA	NA	NA	NA
Mesh Size: Site: Tidal Zone	NA	NA	NA	NA
Residuals	13	7		

DISCUSSION

Oyster reefs provide an opportunity to study potential differences in community assemblage among a diverse suite of factors. Their complex three-dimensional structure attracts a wide variety of species that utilize the reef for protection, foraging, or reproduction, and these benthic macrofaunal communities can vary depending on local environmental factors present in a particular area. Abiotic factors such as water salinity and adjacent habitat structure can determine the type of species present due to species-specific tolerances and life history traits, and biotic factors such as predation and competition can influence relative abundances of species in relation to each other.

Site Comparison

Across both mesh sizes, species diversity, species richness, and species evenness were similar between Hillcrest and Wreck, indicating sites were relatively identical in biodiversity. Both sites shared a majority of the most common species of crabs, shrimp, gastropods, and fish. Notably, sites were dominated by the same few species, primarily shrimp and gastropods. Similarities in species assemblages and species richness between sites may be explained by both the relative proximity of the sites to each other (< 11 kilometers), and the similarity in salinity between sites. Similarities in species composition between sites may also be indicative of similar levels of species recruitment. Differences in species composition were mainly found in rare species that made up very small percentages of total abundance in samples. There were no differences in overall abundances between sites, however, there were differences in abundance in individual species. This difference may be explained by spatial differences in reef location.

However, in coarse-mesh trays, all crabs were significantly more abundant at Hillcrest than Wreck. We did not see this same relationship in fine-mesh trays. Of the crab species collected, *P. herbstii* and *D. sayi* were primarily driving crab abundance, due to their high abundance in the area. These results may be due to the close proximity of Hillcrest to mudflat habitat. A study by Grabowski et al. (2005), found mudflat-fringing (isolated from vegetation) oyster reefs housed higher densities of resident decapods (primarily Xanthid crabs) than seagrass-fringing reefs. Though results were not consistent between mesh sizes, a higher abundance of Xanthid crab mesopredators may indicate higher predation pressure on oysters at Hillcrest, especially juvenile oysters (Rindone & Eggelston, 2011; Carroll et al., 2015). It was also found that *E. depressus* females carrying eggs were more abundant at Hillcrest than Wreck. There was some occurrence of *D. sayi* with eggs, but only in coarse-mesh. In general, mud crabs have been found carrying eggs from spring to early fall (McDonald, 1982; Micu et al., 2010). Both greater abundances of *P. herbstii* in general and the greater number of females carrying eggs from *E. depressus* than any other crab species can be explained by associated life histories. *P. herbstii*, due to its larger body size, have been found to have 5 times greater egg production per year than *E. depressus* (McDonald, 1982), and may explain why *P. herbstii* is more abundant compared to *E. depressus*. Additionally, *E. depressus* females are known to have short generation times (0.5 per year) and produce a large number of broods in their lifetime (McDonald, 1982), which may explain why it had a much higher proportion of individuals bearing eggs than any other species.

Notably, small juvenile blue crabs (*Callinectes* spp.) in this study were found almost exclusively at Hillcrest. These early juvenile blue crabs are known to inhabit seagrass habitat until they reach later stages of development, when they migrate out into less vegetated environments (Orth & van Montfrans, 1990; Heck & Coen, 1995; Pile et al., 1996; Eggleston et al., 1998). The maximum size blue crabs reach before migrating out of seagrass is approximately 20 mm (Orth & van Montfrans, 1990; Hines, 2007); I primarily collected crabs in the first-third instar (2.2-5.9 mm CW; classified according to Newcombe et al., 1994) and in the fifth-seventh instar stage (8-11 mm CW), stages prior to dispersal from seagrass meadows. It is possible the oyster reefs at Hillcrest were using oyster reef habitat in place of seagrass for refuge. This correlation may also be due to the lower wave energy environment at Hillcrest, where juvenile crabs may prefer to settle. Further study must be conducted to understand early juvenile blue crab utilization of oyster reefs in conjunction to seagrass meadows, and between wave energy environments.

Crabs as well as other fauna may also be influenced by the presence of the non-native plant species *Agarophyton vermiculophyllum (*previously *Gracilaria* *vermiculophylla*) (Besterman et al., 2020). *A. vermiculophyllum* is an introduced red algae found in U.S. estuaries from South Carolina to Massachusetts. It is prominent among bays in the Delmarva Peninsula (Nyberg et al., 2009), and has been documented in Elkin Marsh outside Oyster Harbor, Virginia (Thomsen et al., 2009). In general, drifting algae such as *A. vermiculophyllum* can act as habitat modifiers, altering surrounding physical and biological processes (Pihl et al., 1996; Wallentinus & Nyberg, 2007; Nyberg et al., 2009). Past studies have found increased biofaunal abundances associated with *A. vermiculophylla*, including *Callinectes* spp., *Astyris lunata*, and *Panopeus* spp. (Thomsen et al., 2009; Nyberg et al., 2009), species that were collected in the current study. A study by Johnston & Lipcius (2012) conducted in the York River estuary of the Chesapeake Bay found a positive relationship between *A. vermiculophylla* volume and *Callinectes* spp. density. Dense aggregations of *A. vermiculophyllum* were found almost exclusively in trays at Hillcrest in both trials (pers. obs.), and may explain higher crab and shrimp abundances in the area.

Shrimp were also more abundant at Hillcrest in coarse-mesh trays, but in fine-mesh trays were more abundant at Wreck. This pattern can primarily be explained by relative abundances of *P. vulgaris* and *Alpheus* spp., two of the most common shrimp species collected in the study. *P. vulgaris* abundances did not change between mesh sizes, but there was a change in their distribution across Hillcrest and Wreck. Further study should examine the possible drivers of variability in *P. vulgaris* across bay sites. Gastropods, bivalves, and fish abundances did not differ by site in either coarse- or fine-mesh trays, however, gastropod species (*Astyris lunata* and *Costoanachis avara*) varied depending on mesh size and site.

More broadly, differences in crab and shrimp species abundances between Hillcrest and Wreck may be due to spatial variation in larval recruitment. Reef proximity to ocean inlets may influence the species to colonize the reef by manipulating larval supply, food resources, or other environmental factors. This may be explained by differences in residence times between Hillcrest, a more sheltered bay, and Wreck, a more exposed bay. A study by Safak et al. (2015) examined residence times within the VCR. Shorter residence times of less than a week were found closer to ocean inlets, such as South Bay (bordering Wreck island), and were generally associated with higher turnover resulting in increased flux of suspended resources, such as phytoplankton. These bays were primarily tide-driven. Longer residence times on the magnitude of a week or more were found in more confined bays, including Mockhorn Bay (bordering Hillcrest), and were associated with lower turnover and decreased availability of allochthonous resources. These bays were primarily wind-driven whose effect decreased closer to more confined bays. Additionally, closer proximity to an ocean inlet may induce higher relative wave exposure on reef communities. Relative effects of wave exposure have been well documented for sessile invertebrates along rocky intertidal shorelines (Peterson, 1991; Silva et al., 2010). A study by Silva et al. (2010) conducted in sheltered and exposed rocky shores in southwest Britain found species-specific differences in crab abundances between sheltered and exposed sites. It is not well explored how wave exposure may influence intertidal and subtidal oyster reef communities between sheltered and exposed bay sites.

Additionally, the high prevalence of *P. vulgaris* and absence of *P. pugio*, a common grass shrimp species in areas nearby, may be explained by salinity tolerances and interspecific competition between the two species. A study by Knowlton et al. (1994) found that *P. vulgaris* has a preference for salinities in the upper range of 15–35 PSU, whereas *P. pugio* thrives in salinities <15 PSU. Both can coexist in ranges 15–35 PSU, and the authors theorized that *P. vulgaris* may be a better competitor and displace *P. pugio* when co-occurring in the same area due to its more aggressive behavior. We may be seeing a similar relationship here, given similarity in salinity between sites.

Tidal zone Comparison

Species richness did not change between mesh sizes, and was consistently greater in the subtidal zone regardless of mesh size. This was mainly driven by rarer species collected in subtidal trays, which were primarily gastropod and shrimp species. These species were most likely using the soft sediment that accumulated in the tray bottoms in the subtidal zone, which was less conspicuous in intertidal trays where tidal action continuously disturbed bottom tray sediment. Differences in total abundance per tray between tidal zones differed by mesh size; only coarse-mesh trays showed the subtidal zone with higher organismal abundances per tray.

In coarse-mesh trays, there were no differences in abundances among groups of crabs, gastropods, and fish. However, there were differences in species composition between intertidal and subtidal habitat. I found more of *P. herbstii* in the intertidal zone, and, though *Eurypanopeus depressus* was not abundant enough to statistically analyze, it was found exclusively in the intertidal zone. *Dyspanopeus sayi* was greater in abundance in the subtidal zone. Both *P. herbstii* and *E. depressus* have been well documented as common inhabitants in the intertidal zone on the East Coast (McDonald, 1982; Meyer, 1994; Meyer & Townsend, 2000), though in the past the has been some documentation of its occurrence in the subtidal zone within the Chesapeake Bay (Ryan, 1956). Interestingly, the co-occurrence of *P. herbstii* and *E. depressus* has been well-documented in the literature, and has been theorized to be due to differences in habitat partitioning (Meyer,1994) and feeding strategies (McDonald, 1977). Adult *P. herbstii* species are larger than adult *E. depressus* individuals, and therefore can consume larger prey species, such as oysters. *E. depressus'* diet primarily consists of algae and detritus found within small crevices in oyster reefs inaccessible to the larger *P. herbstii* species (Bahr, 1974; McDonald, 1977). *Dyspanopeus sayi* may prefer subtidal habitat due to the competitive pressure in the intertidal zone by *P. herbstii* and *E. depressus*. *D. sayi* has also been documented to hide among polychaete worm tubes to avoid predation by blue crabs (Heck & Hambrook, 1991). The presence/abundance of polychaete worm tubes or the abundance of adult blue crabs in the subtidal zone was not examined in this study, but would be interesting to explore in the future.

Additionally, though not abundant enough to analyze, the *Hemigrapsus sanguineus* (Asian shore crab) was found exclusively in the intertidal zone at Wreck. *H. sanguineus* is a nonnative, invasive crab in the Varunidae family that was introduced to the eastern U.S. around the late 20th century (O'Conner, 2018). It has been found primarily in the intertidal zone of oyster reefs, and as an "opportunistic omnivore" presents a source of competition for space and resources among native crab species. There have, however, been conflicting accounts of the effects of *H. sanguineus* abundances on native crab species, including Xanthidae crabs (Jensen et al., 2002; O'Conner, 2014; O'Conner, 2018). Low abundances collected in trays may indicate the species is not posing as a significant competitive predator, however, further study must be done to understand its co-existence with Xanthid crab species collected in the intertidal zone in this study.

Shrimps were the only group with greater abundances in the subtidal zone in coarse-mesh trays. This pattern may be explained by higher abundances of *Alpheus* spp. and *P. vulgaris* in the subtidal zone. Greater abundances of shrimp in general may be explained by greater food availability in the subtidal zone. A study by Rozas & Hackney (1984) concluded that the common daggerblade grass shrimp, *Palaemonetes pugio*, showed a greater selection of habitat that offered better food availability over differences in salinity.

Mesh Comparison

Overall, a finer mesh size did not increase the number of individuals collected in all taxon groups, and in fact the coarse-mesh trays had higher abundances of almost all taxon than fine-mesh trays (gastropod abundances were not significantly different). At either site or tidal zone, mesh size did not affect the most common species collected, but there were some differences in relative abundances of specific species between mesh sizes. The trays with finer mesh had a higher proportion of crabs in the range of 0–5 mm CW, which include individuals that would have likely washed out more easily in coarse-mesh trays. The most common size range collected in both mesh sizes was 0–5 mm CW, indicating smaller crabs in general were more commonly collected overall than any other size. The greater number of individuals among taxon groups, the high frequency of small crabs, as well as the higher abundance of crabs in the coarse-mesh, is most likely driven by seasonal differences in deployment time between the two mesh sizes, with higher abundances associated with late summer. Past studies have documented greater abundances of mud crabs in August than in September (Abbe & Breitburg, 1992; Luckenbach et al., 1999), and many studies have found drastic decreases in overall faunal abundance between summer and winter (Wells, 1961; Zimmerman et al., 1989); we may be seeing decreases in abundance as a result of the approaching winter season. Finally, by observation, the fine-mesh size collected additional small species of shrimp not found in the coarse-mesh trays, and this difference is primarily due to the finer mesh.

Future studies

This study documented common resident benthic macrofauna composing oyster reef communities but was not intended to survey transient reef epifauna, including prominent predators such as adult blue crabs and nektonic fishes. Future investigations should explore relative densities of transient fauna composing oyster reefs at the Virginia Coast Reserve, in order to cover the entire biological community among subtidal and intertidal oyster reefs. This would enable researchers to better understand predator-prey and interspecific interactions, and how these vary between tidal zones and across sheltered and exposed bay sites. Further research could also explore many of the questions brought up in this study, such as (1) the effects floating *A. vermiculophyllum* has on oyster reef communities in comparison to seagrass, (2) the presence and density of polychaete worm tubes, and how they affect *D. sayi* abundances and predation by blue crabs, and (3) potential factors driving the coexistence between Xanthid crab species and the invasive nonnative crab *Hemigrapsus sanguineus*.

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