

1 Influence of oyster reefs on infauna and sediment spatial distributions within intertidal mudflats

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13 **Abstract**

14 Oysters are described as estuarine ecosystem engineers because their reef structures
15 provide habitat for a variety of flora and fauna, alter hydrodynamics, and affect sediment
16 composition. To what spatial extent oyster reefs influence surrounding infauna and sediment
17 composition remains uncertain. We sampled sediment and infauna across eight intertidal
18 mudflats at distances up to 100 m from oyster reefs within coastal bays of Virginia, USA, to
19 determine if distance from reefs and physical site characteristics (reef elevation, local
20 hydrodynamics, and oyster cover) explain the spatial distributions of infauna and sediment.
21 Total infauna density increased with distance away from reefs, however, the opposite was
22 observed for predatory crustaceans (primarily crabs). Our results indicate a halo surrounding the
23 reefs of approximately 40 m (using an increase in ~25% of observance as the halo criterion). At
24 90 m from reefs, bivalves and gastropods were 70 % more likely to be found (probability of
25 observance), while there was an approximate 4-fold decrease for large crustaceans compared to
26 locations adjacent to reefs. Increases in percent oyster reef cover and/or mean reef area did not
27 statistically alter infauna densities but showed a statistical correlation with smaller sediment
28 grain size, increased organic matter, and reduced flow rates. Weaker flow conditions within the
29 surrounding mudflats were also associated with smaller grain sizes and higher organic matter
30 content, suggesting multiple drivers on the spatial distribution of sediment composition. This
31 study emphasizes the complexity of bio-physical couplings and the considerable spatial extent
32 over which oyster reefs engineer intertidal communities.

33 Key words: ecosystem engineers, oyster reefs, infauna, sediment, kriging, intertidal ecology,

34 community ecology

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1 1. INTRODUCTION

2 Ecosystem engineers are organisms that affect communities directly and indirectly by
3 influencing resource availability via the creation or modification of physical structures (Jones et
4 al. 1994, Angelini et al. 2011). Common examples of ecosystem engineers include beavers that
5 change hydrologic conditions by constructing dams (Jones et al. 1994, Wright & Jones 2002)
6 and trees whose tissues physically alter flows of nutrients, chemical cycling, and habitat
7 provisioning (Jones et al. 1997). However, the spatial footprint over which ecosystem engineers
8 affect communities and ecosystems is often difficult to define and is largely dependent on the
9 particular engineering process examined (Wright & Jones 2004, Hastings et al. 2007). Large
10 physical habitat modifications, such as beaver dams and tree canopies are easily observable,
11 while smaller scale processes such as changes to soil biogeochemistry require more careful
12 analysis over specified spatial and temporal scales (Jones et al. 1997, Wright & Jones 2004,
13 Hastings et al. 2007). Hence, small-scale effects may go undocumented because they are more
14 difficult to detect or measure. Therefore, careful consideration for the engineering species and
15 processes quantified are necessary in determining scales of influence.

16 Given their abilities to strongly impact environments, ecosystem engineers are often
17 incorporated into landscape restoration (Byers et al. 2006). Thus, to help guide the siting and
18 design of restoration projects, determining the spatial extent over which ecosystem engineers
19 impact their environment is important. Managers of estuarine ecosystems often incorporate
20 ecosystem engineers as a part of nature-based solutions to improve ecosystem functions such as
21 coastal protection, biodiversity, and water quality (Davis et al. 2006, Currin et al. 2010). Among
22 the most important ecosystem engineers for the restoration of coastal environments are reef-
23 building oysters (family Ostreidae), which build solid, fixed structures in otherwise unstable soft-

1 sediment systems and alter the abiotic environment in three major ways. First, physical reef
2 structures provide habitat and refuge to fauna including polychaetes, crustaceans, and fish (Posey
3 et al. 1999, Lenihan et al. 2001, Grabowski et al. 2005). Second, they change hydrodynamic
4 patterns by virtue of this physical structure. The rough surface of oyster reefs increases drag and
5 turbulence, altering flow patterns and locally increasing sediment resuspension and transport
6 from the reef crest, while also trapping fine sediments adjacent to the reef (Lenihan 1999,
7 Whitman & Reidenbach 2012, Reidenbach et al. 2013, Colden et al. 2016). Oyster reefs can also
8 attenuate wave energy and in some cases reduce shoreline erosion (Piazza et al. 2005, Wiberg et
9 al. 2019). Third, oysters can change sediment composition by altering grain size, organic matter
10 content, and sediment biogeochemistry through direct inputs of pseudofeces deposited from filter
11 feeding and the indirect facilitation of benthic microalgae productivity (Newell et al. 2002,
12 Kellogg et al. 2013, Southwell et al. 2017). The fine particles, which are likely to be trapped,
13 also hold nutrients in organic rich sediments more readily (Nedwell 1999).

14 Burrowing organisms (infauna) dominate muddy intertidal habitats, often impacting these
15 systems through bioturbation (Aller 1993, Meysman et al. 2006) which oxygenates sediment and
16 increases available habitat for themselves and other infauna (Solan et al. 2004, Byers &
17 Grabowski 2014, Murphy & Reidenbach 2016). Infauna community structure is dependent on
18 many factors, including sediment and water characteristics such as grain size, temperature, pH,
19 and oxygenation (Paterson et al. 2009, Widdicombe et al. 2009, Dauvin et al. 2017, Veiga et al.
20 2017). Sediment grain size, which is influenced by oyster reefs, can affect infauna's ability to
21 burrow, consume oxygen, and feed (Wilson 1990, Janssen et al. 2005, Dorgan et al. 2016). A
22 shift to finer sediments, which compact more easily, can limit the advection and diffusion of
23 water and dissolved gases through interstitial porewaters resulting in thinner oxic layers and

1 flatter topography relative to areas with coarser grained sediments and less compaction (Byers &
2 Grabowski 2014, Nybakken & Bertness 2005). Therefore, oyster mediated changes to sediments
3 and hydrodynamics may have cascading effects on estuarine ecosystem function, affecting
4 biodiversity, sediment stability (Dashtgard et al. 2008), and biogeochemical processes.

5 Relevant to restoration efforts, burrowers help prevent negative impacts of disturbances
6 by serving as a conduit between the sediment and water column, and increased biodiversity of
7 infauna may lead to greater overall stability in a coastal system(Snelgrove et al. 2000, Austen et
8 al. 2002). Maintaining diverse infauna populations is important for coastal ecosystems, because
9 different trophic levels above, below, and at the sediment-water interface benefit from increased
10 nutrient transfers. Additionally, increased diversity lessens the impact of species loss which can
11 stabilize trophic interactions (Austen et al. 2002). Benthic diversity can also have positive effects
12 on the overall health of estuarine environments by increasing water column nutrient availability
13 (Ieno et al. 2006) and nutrient cycling (Covich et al. 2004). Infauna are also important prey for
14 mobile invertebrates, birds, and fish, helping to shape community structure (Van der Zee et al.
15 2012). Therefore, changes to infauna, such as those facilitated by the engineering effects of
16 oysters, can have cascading effects on reef communities. However, the spatial footprint of this
17 effect is largely unknown.

18 Studies of the effects of bivalves and structured reefs on adjacent infauna communities
19 are mixed and have largely focused on subtidal environments (Table A1). Researchers have
20 found, depending upon the composition of infauna, benthic communities in proximity to reefs
21 can either be enhanced (Ambrose and Anderson 1990, Dahlgren et al. 1999, Barros et al. 2001,
22 Barros et al. 2004, Langlois et al. 2005, Zalmon et al. 2014), or diminished (Posey & Ambrose
23 1994, Ambrose & Anderson 1990, Barros et al. 2001, Langlois et al. 2005, Reeds et a. 2018)

1 with respect to abundance, density, and/or richness. Reeds et al. (2018) identified that the
2 ecological footprint of a single constructed reef may be up to 15 times the area of the reef.
3 However, most studies found that patterns varied among species and with organism size (Davis
4 et al. 1982, Ambrose & Anderson 1990, Fabi et al. 2002, Langlois et al. 2006), demonstrating
5 that taxa-specific behaviors and tolerances are important to consider in understanding reef-
6 infauna relationships.

7 To determine how oysters' impact the spatial distribution of infauna and sediment
8 composition through ecosystem engineering, we sampled eight intertidal mudflats adjacent to
9 oyster reefs in coastal Virginia, USA. This work describes how local site characteristics,
10 including distance to oysters, elevation, and hydrodynamics, influence infaunal community
11 structure and sediment composition.

12 2. MATERIALS & METHODS

13 2.1 Study Site

14 We studied intertidal mudflats located within the Virginia Coast Reserve (VCR). The
15 VCR is a system of barrier islands, coastal bays, and upland marshes extending across more than
16 100 km of coastline along the Atlantic Ocean of the Delmarva Peninsula in Virginia, USA (Fig.
17 1). The VCR is also a National Science Foundation funded Long-term Ecological Research
18 (LTER) site. The tidal range is approximately 1.2 m (Hansen & Reidenbach 2013) and within the
19 intertidal mudflats, numerous oyster reefs exist primarily as patch reefs of the Eastern oyster,
20 *Crassostrea virginica*. Most oyster reefs in this area have been heavily influenced by human
21 activity and have largely undergone some form of restoration starting in the mid to late 1900s
22 (Luckenbach et al. 2005, Kennedy et al. 2011). The oysters are predominately intertidal and

1 restoration has relied on providing hard substrate suitable for larval settlement and growth
2 (Whitman & Reidenbach 2012). Previous work in the VCR has shown that oysters affect
3 resident flora and fauna, including effects on algal growth and snail densities (Thomsen &
4 McGlathery 2006), and alter benthic metabolism (Volaric et al. 2018).

5 2.2 Data Collection

6 We sampled eight intertidal mudflat sites in proximity to oyster reefs (Figs. 1 and 2)
7 during the summers of 2016 and 2019. In 2016, we collected infauna and sediment samples at 4
8 sites (sites 1-4, Table 1) along 100 m transects (2-4 transects per site) starting from oyster reefs.
9 Site 2 was largely a control with oyster patches interspersed and transects did not start at a
10 particular reef. Infauna cores (25 cm diameter, 10 cm deep) were collected at 0, 28, 56, and 98
11 m along each transect and sediment cores (3 cm diameter, 5 cm deep) were taken every 14 m
12 along each transect (n = 4 samples per transect for infauna, n = 8 samples per transect for
13 sediment), except for one transect where infauna samples were taken at 0, 12.5, 50, and 87.5 m
14 and sediment cores taken every 12.5 m. In 2019, we sampled infauna and sediment at 4
15 additional sites (sites 5-8, Table 1), using a gridded sampling design to ensure varied distances
16 from reefs. At each site, we sampled along four, 75 m transects spaced 25 m apart and arranged
17 parallel to reefs where they were continuous or the edge of the mudflat where reefs were patchy
18 (Fig. 2). At each transect, we collected infauna cores (15 cm diameter, 15 cm deep) every 25 m
19 (n = 4 per transect, 16 per site) and sediment cores (3 cm diameter, 5 cm deep) every 12.5 m (n =
20 7 per transect, n = 28 per site). Sediment samples for organic matter and grain size analysis were
21 kept frozen and refrigerated, respectively, until processed. Infauna samples were processed
22 immediately following collection.

1 Infauna cores were wet sieved (1mm mesh) and living fauna were identified to five broad
2 taxonomic levels: worms, bivalves, gastropods (dominated by snails), small crustaceans
3 (amphipods, isopods, shrimp), and large crustaceans (crabs). Though dominated by burrowers,
4 epifaunal gastropods were also included in the benthic infauna analysis. In 2016, polychaetes
5 were identified to the family level to determine the diversity of polychaetes, with a list of taxa
6 and total counts given in Table A2. Rarely, nemertean and acorn worms (*Enteropneusta*) were
7 identified. Hence, we termed this broad category ‘worms’. Abundance of each of the five taxa
8 and total biomass for each sample (ash free dry weight, AFDW) were recorded. Infauna were
9 dried for 48 h at 60 °C to measure dry weight and combusted for 6 h at 500 °C for AFDW.
10 Sediment organic matter was estimated using the same procedure for AFDW. In 2016, sediment
11 grain size was estimated using a Beckman Coulter LS I3 320 laser diffraction particle size
12 analyzer, following treatment with hydrogen peroxide to remove organic matter. Porosity was
13 also measured in 2016, but data was found to be highly correlated to grain size and was not
14 included as a separate parameter in the analysis. While sampling along transects guaranteed
15 various distances from oyster reefs, we estimated linear distance to the nearest oyster reef greater
16 than 5 m² using GIS software (ArcMap 10.5) with an existing oyster reef location dataset derived
17 from LiDAR elevation data and aerial imagery (Hogan & Reidenbach 2020). Reefs missing
18 from that dataset were added using the methods described in (Hogan & Reidenbach 2019). We
19 also generated a minimum circular boundary around sampling locations and extended a buffer 40
20 m around the boundaries at each location. We used the area of the boundary and the area of reefs
21 intersecting the boundary to calculate percent oyster cover at each mudflat. We then calculated
22 the mean oyster reef size, in terms of area, for reefs intersecting each buffered mudflat.

23 2.3 Data Analysis

1 2.3.1 Interpolated surfaces

2 To determine how infauna communities and sediment composition change with distance
3 to oyster reefs, geospatially-interpolated prediction surfaces for total infauna, sediment organic
4 matter, and sediment grain size distributions at each sampling site were created using the
5 Geostatistical Analyst extension in ArcMap (10.5). Geostatistical interpolation has the
6 advantage of modeling data between known data points. We used Empirical Bayesian Kriging
7 (EBK) to create a distribution of prediction surface responses based on spatial autocorrelation,
8 semivariogram estimation, and associated errors. EBK predictions are ideal for non-stationary
9 and less spatially dense data because predictions are based on the probability of likelihoods from
10 many semivariogram parameters estimated using restricted maximum likelihood compared to
11 other kriging methods that use only one semivariogram with estimation using weighted least
12 squares (Krivoruchko 2012, ESRI 2016). The Exploratory Spatial Data Analysis (ESDA)
13 package was used to help examine distributions and normality to meet modeling assumptions
14 and determine if transformations would likely lead to the best fitting semivariograms.
15 Semivariogram model, transformation type, and search neighborhood type (standard circular or
16 smoothed circular with minimum 10 neighbors) were chosen from all possible combinations with
17 the lowest root-mean-square-error (RMSE; Gunarathna et al. 2016, Gupta et al. 2017).

18 Geostatistical layers for total infauna specimen were created for 6 of the 8 sites (sites 1, 2,
19 and 5-8). We were unable to create interpolated rasters for two of the sites (sites 3 and 4)
20 because we collected only 8 infauna cores from these sites. Sediment organic matter was
21 modeled for all 8 sites and grain size for the 4 sites from 2016 (sites 1-4).

22 2.3.2 Statistical Analyses

1 To determine the spatial extent to which oyster reefs affect the composition of infauna
2 and sediment surrounding the reefs, we examined sediment organic matter and infauna variables
3 (biomass, density, and presence/absence for taxon groups and the total community) as a function
4 of distance to the reef, elevation, water residence time (as a proxy for flow speed), percent
5 oyster cover, and mean reef area. A low water residence time (WRT) suggests active flushing of
6 water masses, typically associated with higher mean flow rates. Elevation relative to NAVD88
7 (North American Vertical Datum of 1988) was determined at each sample location using a 2015
8 USGS LiDAR elevation raster layer with a vertical accuracy for non-vegetated terrain of 12.5 cm
9 (Dewberry 2016). WRT was estimated using an empirically validated regional hydrodynamic
10 model (Safak et al. 2015). Safak et al. (2015) used the Delft 3D numerical model with a 3D
11 unstructured grid finite-volume coastal ocean model to estimate WRT and particle exchange
12 using Lagrangian particle tracking. The model consisted of approximately 42,000 nodes and
13 80,000 elements with 200 m horizontal resolution and was forced with wind and water-level
14 data. Modeled data were validated to field observations of water-levels and velocities using
15 local tide gauges and acoustic Doppler current meters deployed within the surrounding coastal
16 bays and inlets.

17 2.3.3. Correlation analysis

18 Data analysis showed highly non-normal distributions. Therefore, we used non-
19 parametric Spearman's rank correlation (Hauke & Kossowski 2011, Zar 2014), to quantify
20 pairwise associations between infauna variables (total faunal AFDW and density of each the
21 broad taxon group) and site characteristics (distance from reef, elevation, WRT, percent oyster
22 cover, and mean reef area). Because sampling cores for infauna differed in size between the two
23 sampling years, we converted the abundances and AFDW measurements in 2016 and 2019 to

1 volumetric density (m^{-3}). We removed three observations where AFDW estimates were less than
2 0, likely due to minimal AFDW that were below the accuracy of our measurements.

3 For sediment characteristics, we fit Spearman's rank correlations between percent
4 organic matter with distance, elevation, WRT, percent oyster cover, and mean reef area. Grain
5 size was only sampled for 2016 (samples $n = 88$, sites = 4). For grain size, the same variables of
6 distance, elevation, WRT, percent oyster cover, and mean reef area were used in correlations.
7 We also examined the correlation between organic matter and grain size.

8 We used the `rcorr` function in the "Hmisc" package (Harrell 2021) in R 4.0.3 (R Core
9 Team 2020) to obtain correlation coefficients and p-values.

10 2.3.4. Multiple Regression Analysis

11 Because infauna density was largely driven by worms (present in all but 2 samples), we
12 used binomial multiple regression analyses to explain variation in the presence or absence of
13 bivalves, gastropods, small crustaceans, and large crustaceans (one model per faunal group).
14 Specifically, we used generalized linear mixed models (GLMM) to model the presence or
15 absence of individual taxa (with logit link function, i.e., mixed effects logistic regression) as a
16 function of elevation and distance. We also analyzed the total number of taxa (including worms)
17 present -our metric for taxonomic richness- as a continuous independent variable. Taxa richness
18 was modeled using a Poisson GLMM (log link function). We fit a linear mixed-model to predict
19 sediment grain size as a function of distance, elevation, and WRT with a random intercept for
20 site. To control for heterogeneity among sites and collection dates, we specified site and year as
21 random intercept terms for all GLMMs.

22

1 Mixed models were fit in R using ‘lme4’ 1.1.25 (Bates et al. 2015) and were validated by
2 examining simulated residuals using ‘DHARMA’ package in R (Hartig 2020). The effects of
3 distance on probability of infauna occurrence were examined using the ‘effects’ package in R
4 (Fox & Weisberg 2019). Data for sediment organic matter did not meet the assumptions from
5 DHARMA; thus, we analyzed these data using Spearman’s rank correlations only. We did not
6 include WRT in the multiple regression analyses for infauna because with this additional
7 variable, the models failed to converge.

8 3. Results

9 3.1 Mudflat Site Characteristics

10 Utilizing the existing oyster reef location dataset derived from LiDAR elevation data and
11 aerial imagery (Hogan & Reidenbach 2020), we derived general trends regarding oyster cover
12 and the physical characteristics of the surrounding mudflat for the 8 mudflat locations where
13 infauna sampling occurred. We observed that distance from oyster reefs was not correlated with
14 elevation, suggesting no statistical trend of either increasing or decreasing elevation of the
15 mudflat where infauna were collected with distance from the reefs. The elevation from which
16 infauna were sampled ranged from -0.7 to -0.06 m NAVD88. As expected, distance from reefs
17 was negatively correlated with percent oyster cover, and positively correlated with mean oyster
18 reef size. As mudflat elevation increased (estimated at each sampling location), percent oyster
19 cover and mean oyster area decreased. Mean reef size was also positively related to water
20 residence time, suggesting that larger reefs in general experienced reduced local velocities (Table
21 2).

22 3.2 Infauna

1 There was a trend of increasing total infauna abundance away from oyster patches, as
2 evidenced from kriging analysis (Fig. 3A, S1). Ranked correlation analysis showed that total
3 infauna abundance increased further from reefs and at lower elevations, while total biomass
4 increased with lower WRT (See Table 2 for test statistics). We found that the observed patterns
5 of infauna abundance increasing at further distances from reefs was driven by bivalves,
6 gastropods, and worms, whose abundances increased at further distances (Fig 4. C-E). Bivalve,
7 gastropod, and worm abundances also increased at lower elevations, and with lower WRT (faster
8 flows). By contrast, large crustaceans (i.e., crabs) were found in greater abundance closer to
9 reefs and at higher elevations (Fig. 4A and 5A - B). Small crustacean abundances did not vary
10 significantly with distance from reefs or elevation but were more abundant with lower WRT
11 (Fig. 5C). Neither infauna abundances nor AFDW for each sample varied with oyster percent
12 cover or mean oyster reef area (Table 2). However, sites with patchier oyster reefs exhibited
13 weaker spatial patterns in infauna abundance as a function of distance from the reefs, as well as
14 lower variability in infauna abundance (S1).

15 Predicted values from the regression models showed bivalves (Fig. 6A) and gastropods
16 (Fig. 6B) had similar distributions out to 90 m from reefs and were on average 70% more likely
17 to be found 90 m from a reef than immediately adjacent to a reef. Contrary to other infauna,
18 there was a predicted general decrease in probability of observing large crustaceans away from
19 reefs, decreasing from 48% adjacent to a reef to 7% at a distance of 90 m (Fig. 6D). Small
20 crustacean presence was highly variable and there was no measurable trend in their occurrence
21 (Fig. 6C). The richness (number of broad taxa represented) was not measurably affected by
22 distance ($p = 0.27$) from the reef or local elevation of the mudflat at the location infauna were
23 collected ($p = 0.67$).

1 3.3. Sediment

2 Utilizing the interpolated surfaces from sediment distributions, visual patterns suggested
3 that sediment organic matter tended to be higher closer to reefs (Fig. 3B, S2). Sites with patchier
4 oyster reefs showed less variability. These patterns were supported statistically by Spearman's
5 rank correlations, which showed that organic matter decreased further from oyster reefs at higher
6 elevations, and with lower WRT (i.e., faster flows; Table 3, Fig. 5 and 7). Kriging analysis
7 suggested a trend for smaller sediment grain size nearer to the reef (Fig. 3C, S3), but this was not
8 borne out by the regression analysis, which showed no trend with distance ($t = 2.3$, $p = 0.13$) or
9 other site characteristics [elevation ($t = 1.6$, $p = 0.21$), or WRT ($t = 1.9$, $p = 0.26$)]. Kriging also
10 showed that for one of the eight sites (site 4) this spatial pattern reversed. However, Spearman's
11 rank correlations found grain size decreased with increasing WRT and sediment organic matter
12 (Table 3, Fig. 5), suggesting that finer sediment particles are associated with high organic matter
13 and slower moving flows. These findings for organic matter and grain size are congruent because
14 organic matter is negatively related to grain size (Southwell et al. 2017), and with slower flows
15 that retain smaller sediment grain sizes. Greater mean oyster reef size was positively correlated
16 with sediment organic matter and negatively with grain size. Organic matter was also positively
17 correlated with percent oyster cover.

18 4. DISCUSSION

19 4.1 Site Characteristics and Physical Variables

20 Oysters have been previously found to alter mudflats by modifying fauna communities
21 and sediment composition (Lenihan 1999, Grabowski et al. 2005, Colden et al. 2016). We found
22 that distance, elevation, and local flow are important variables in determining infauna and
23 sediment distributions. Our analysis utilizing interpolated surfaces demonstrated that gradients in

1 infauna and sediment distributions are less distinct when oysters are patchy throughout the
2 region, compared to regions composed of a few large intact oyster reefs (Fig. 2). This result
3 supports the idea that distance from a reef, along with flow, may indeed alter the distributions of
4 sediment and infauna because oyster cover and size can influence site characteristics, including
5 flow and consequent sediment composition. Larger reefs were also associated with reduced
6 flows. Although our work cannot determine the extent to which oysters form within reduced
7 flow regions, or oysters reduce the flow directly, previous work has shown that oyster reefs can
8 significantly reduce local flow rates due to the drag imposed by their rough topography (Lenihan
9 1999, Whitman & Reidenbach 2012, Reidenbach et al. 2013, Colden et al. 2016). This
10 reinforces the role that oysters may play in engineering their physical environment and helps
11 explain our findings that reefs alter sediment composition and the infaunal community. It also
12 builds upon previous findings within our study region showing that water residence time and
13 sediment characteristics are strongly linked (Wiberg et al. 2015).

14 4.2 Sediment Analyses

15 While studies have documented that oyster reefs can trap fine sediment (Colden et al.
16 2016) and promote increased sediment organic matter (Southwell et al. 2017), other
17 environmental factors such as wave and/or tidally-driven current velocities may be the dominant
18 drivers of sediment distribution (Wiberg et al. 2015), especially in high energy environments
19 (Reidenbach et al. 2013, Byers & Grabowski 2014). Our results show that sediment organic
20 matter decreased with distance from oyster reefs, but also with decreased water residence time
21 and elevation, suggesting that a combination of variables is responsible for its distribution.
22 Additionally, while the regression analyses suggest none of the site variables significantly
23 explain grain size distribution, there were significant negative correlations found with water

1 residence time and organic matter, emphasizing the importance of the local flow in altering
2 sediment characteristics and agreeing with studies suggesting that finer sediments hold more
3 nutrients (Nedwell 1999).

4 These findings are supported by our interpolated surfaces that indicate higher organic
5 matter closer to oyster reefs (Fig. 3). However, while spatial patterns were evident for sediment
6 with respect to distance from the reef, the range of grain size and organic matter content for
7 many sites was very narrow, showing that variables other than distance from oyster reefs such as
8 the local flow environment likely impact sediment distributions. Grain size for all samples
9 across the 8 sites ranged from 40 to 127 μm , while at the individual site level the range was
10 typically much smaller (for example, grain size ranged from 40 to 61 μm at site 4).
11 Nevertheless, sediment organic matter increased with greater oyster cover and mean reef area,
12 while sediment grain size was reduced with greater percent oyster cover, showing that oyster
13 abundance at a reef scale is likely to influence sediment and flow.

14 4.3 Infauna Communities

15 Bivalves and gastropods were more common and abundant further from reefs. This result
16 agrees with previous findings of ‘halos’ of low faunal density around oyster reefs (Posey &
17 Ambrose 1994, Reeds et al. 2018). Reeds et al. (2018) found an infauna abundance halo 30m
18 around an artificial reef outside Sydney Harbour, Australia. Our results build upon this earlier
19 finding by characterizing infauna communities around multiple, patchier oyster reefs over two
20 years. Our results indicate a halo of approximately 40 m for bivalves and gastropods (using an
21 increase in ~25% of observance as the halo criterion), a similar distance observed by Reeds et al.
22 (2018). Reeds et al. (2018) determined a footprint of 15x reef area, which is similar for oyster
23 reefs in our study.

1 Crabs, birds, and fish utilize bivalve reefs for habitat and to feed upon infauna (Lenihan
2 et al. 2001, Kulp et al. 2011, Van der Zee 2012). These trophic interactions may explain why
3 large crustaceans (i.e., crabs) were more abundant closer to reefs and at higher elevations
4 (contrary to other taxonomic groups). Crabs are important mesopredators that also serve as prey
5 for larger predators (Van der Zee 2012, Hill & Weissburg 2013). Hence crabs may be sheltering
6 near reefs to take advantage of reef interstices.

7 Predation by crabs and other predators may have reduced mollusk and worm densities
8 closer to reefs or caused them to move farther from reefs through a ‘landscape of fear’ behavioral
9 response observed in coastal environments (Langlois et al. 2005, Madin et al. 2011, Bilodeau et
10 al. 2021). Reefs are generally higher in elevation compared to their surrounding mudflat (Hogan
11 & Reidenbach 2019), therefore if infauna predators are more likely found on reefs, they will also
12 be found at higher elevations. Large crustaceans also represented the only taxonomic grouping
13 where WRT data was not significantly correlated to density. This could be because crabs are
14 more transient and mobile than worms and mollusks, spending less time in and dependent upon
15 sediment and more tolerant to environmental disturbances (Davis et al. 1982, Langlois et al.
16 2006).

17 All infauna correlation coefficients with WRT were negative, indicating faster flows
18 increased infauna abundances, richness, and biomass. This suggests that water residence time
19 represents an important variable in species distributions. In fact, WRT was the only variable
20 tested that explained small crustacean abundance. WRT is highly correlated with flow and tidal
21 currents, with decreases in the residence time of water correlating strongly with high mean water
22 velocities (Safak et al. 2015), which have been shown to impact small crustacean distributions
23 and possibly limit their abundance at other locations (Grant 1980). Local hydrodynamics can

1 also create microtopographic features (such as sediment ripples) that affect distributions of
2 infauna (Barros et al. 2004, Besterman et al. 2021).

3 Higher flow rates can also indirectly affect infauna abundance by increasing predation
4 and disturbance by increasing larval and infaunal transport (Palmer 1988) and dictating the
5 success of passive and choice settlement (Butman et al. 1988, Snelgrove et al. 1998).

6

7 4.4 Study Limitations

8 Future efforts to understand how infauna and sediment are affected by oyster reefs would
9 benefit from repeated measurements at these mudflats to see if the spatial distributions we found
10 are representative, and possibly to identify longer-term, seasonal, and year-to-year variations.
11 While each of the sampling events in 2016 and 2019 were completed during the summer months,
12 there is likely variation within and among seasons (Zajac & Whitlatch 1982, Harwell et al.
13 2011). The 10 - 15 cm depth to which cores were sampled may affect taxa presence, abundance,
14 and biomass in samples. However, it has been found in our region that estuarine macrofauna are
15 relatively rare below 15 cm (Hines & Comtois 1985), resulting in the recommended depth range
16 of 10 - 15 cm (Raz-Guzman & Grizzle 2001). We were also unable to address the size and age
17 of oysters needed to affect communities due to patchy areas with multiple reefs of unknown age
18 in proximity to sampling locations. The nearness of reefs to one another could explain some of
19 the effects we observed, as other studies have found that isolation from reefs alter infauna
20 abundances and sediment characteristics (Zalmon et al. 2014). Knowing how these variables
21 affect infauna and sediment distributions could be informative in designing future oyster
22 restoration projects to maximize biodiversity and overall ecosystem function.

23 4.5 Conclusions

1 This study shows that oyster reefs affect their surroundings by significantly altering
2 distributions of infauna and sediment adjacent to oyster reefs on intertidal mudflats. Oyster reefs
3 also likely provide habitat to large crustaceans and increase sediment organic matter, while
4 decreasing median grain size. We found that oyster reefs impact both sediment and infauna
5 characteristics up to 100 m away from the reefs with changes in occurrence of 2.5 times for most
6 taxa within 40 m. Our findings also highlight the importance of local variation in the physical
7 characteristics of mudflats, such as site elevation and water residence time, in altering infauna
8 and sediment characteristics. As large-scale oyster restoration projects continue to address a
9 wider range of ecosystem services consideration should be made to the spatial extent of reef
10 effects on infauna and sediment. The management of intertidal mudflat communities will
11 become increasingly challenging with sea-level rise and damaging storms under climate change,
12 and benthic communities will be directly challenged with changing time of submergence, tide
13 levels, temperature, and salinity, all of which will alter suitable habitat and community structures
14 (Fujii 2012). Therefore, understanding how systems are connected, such as interactions between
15 oyster reefs, infauna and sediment, can help create management strategies in a changing world.

16

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19 7. TABLES

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21 Table 1. Sampling site metadata including mudflat local name, year sampled, and the number of
22 cores collected.

Site number	Local name	Year	Infauna cores	Sediment cores
1	Hillcrest	2016	16	32
2	Hillcrest Mud	2016	12	24
3	Narrows	2016	8	16
4	Ramshorn C	2016	8	16
5	Ramshorn A	2019	16	28
6	Ramshorn B	2019	16	28
7	Narrows A	2019	16	28
8	Fowling Point	2019	16	28

23

24 Table 2. Spearman's rank correlation coefficients (ρ) and p-values (ρ /p-value) for taxa density
25 (count m⁻³), biomass (AFDW m⁻³), and site variables (distance, elevation, WRT, percent oyster
26 cover, and mean oyster reef size (m²). Red text indicates significant correlations.

DISTANCE ELEVATION WRT PERCENT MEAN SIZE

	COVER				
DISTANCE	1/--	-0.05 /0.63	-0.02/0.87	-0.34/0.00	0.30/0.00
PERCENT COVER	-0.34/0.00	-0.37/0.00	0.04/0.65	1/--	-0.01/0.89
MEAN SIZE	0.30/0.00	-0.20/0.04	0.45/0.00	-0.01/0.89	1/--
TOTAL INFAUNA	0.26/0.01	-0.29/0.00	-0.38/0.00	-0.12/0.23	-0.11/0.27
TOTAL AFDW	-0.02/0.87	0.02/0.81	-0.22/0.02	-0.03/0.76	-0.07/0.46
WORMS	0.24/0.02	-0.43/0.00	-0.32/0.00	-0.01/0.91	-0.06/0.51
BIVALVES	0.25/0.01	-0.22/0.03	-0.39/0.00	-0.00/0.97	0.01/0.96
GASTROPODS	0.39/0.00	-0.22/0.02	-0.43/0.00	-0.17/0.08	-0.06/0.52
SMALL CRUSTACEANS	0.16/0.10	-0.17/0.08	-0.24/0.01	-0.00/0.96	-0.13/0.19
LARGE CRUSTACEANS	-0.27/0.00	0.30/0.00	-0.06/0.55	-0.09/0.37	-0.18/0.06

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2 Table 3. Spearman's rank correlation coefficients (ρ) and p-values for sediment grain size and
 3 percent organic matter with site variables (distance, elevation, WRT, percent oyster cover, mean
 4 reef area (m^2), and each other).

Site Variable	Percent OM		Grain size	
	ρ	p-value	ρ	p-value
Distance	-0.25	0.001	-0.08	0.47
WRT	0.48	0.00	-0.27	0.01
elevation	-0.28	0.00	0.02	0.84
% Cover	0.34	0.00	0.12	0.27
Mean area	0.24	0.00	-0.33	0.00
OM	---	---	-0.87	0.00

5

6 Table 4. Results (estimated coefficients (β), standard errors (SE), z-values, and p-values) of the
 7 regression analyses predicting the presence of taxa and richness using distance and elevation.
 8 Number of observations = 108.

Taxa (P/A)	Distance				Elevation			
	β	SE	z-value	P-value	β	SE	z-value	P-value
Bivalves	0.04	0.01	2.74	0.01	-5.88	2.37	-2.48	0.01
Gastropods	0.04	0.014	3.07	0.002	-5.55	2.73	-2.04	0.04
Sm Crustaceans	0.01	0.01	0.98	0.33	-1.79	-1.83	-0.98	0.33
L Crustaceans	-0.03	0.01	-2.17	0.03	3.38	1.70	1.98	0.047
Richness	0.003	0.002	1.09	0.27	-0.16	0.38	-0.43	0.67

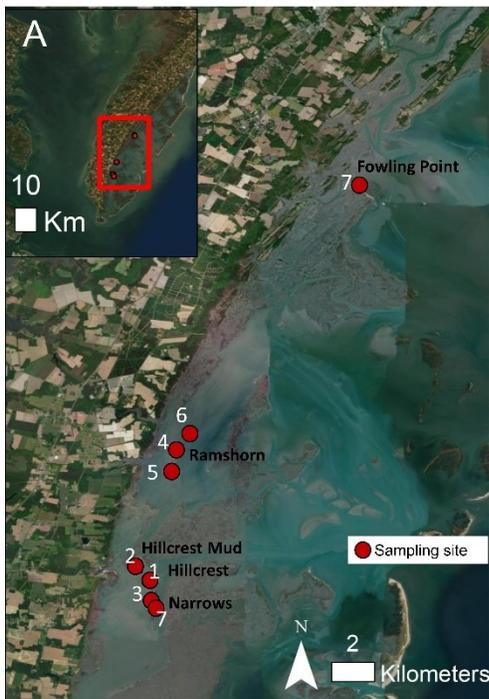
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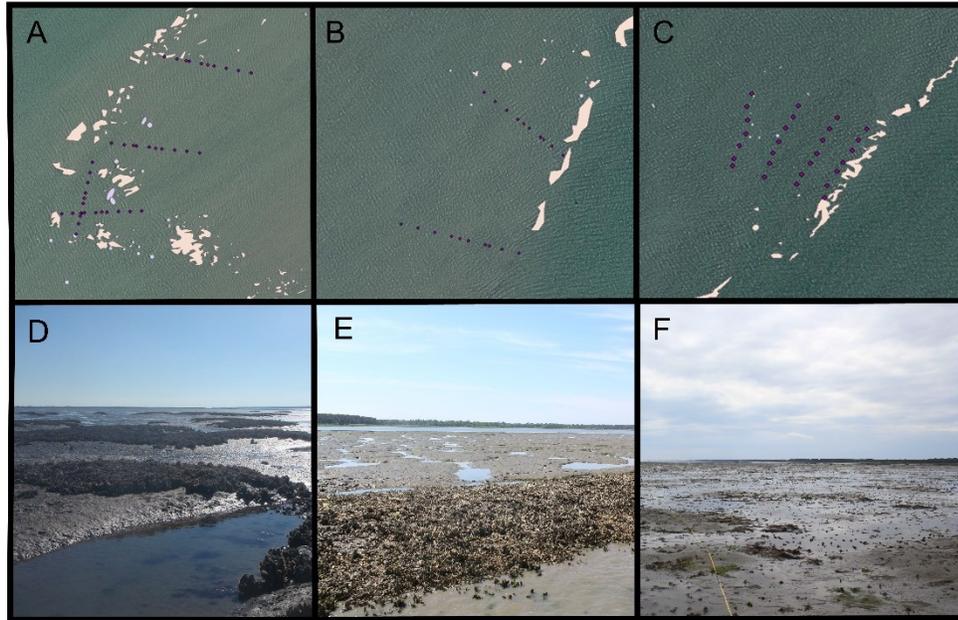
8. FIGURES



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Fig. 1. A) Locations of the 8 intertidal mudflats situated near oyster reefs that were sampled, labeled according to sites in Table 1. The inset shows the extent of the Virginia Coast Reserve (VCR), found on the eastern side of the Delmarva Peninsula.

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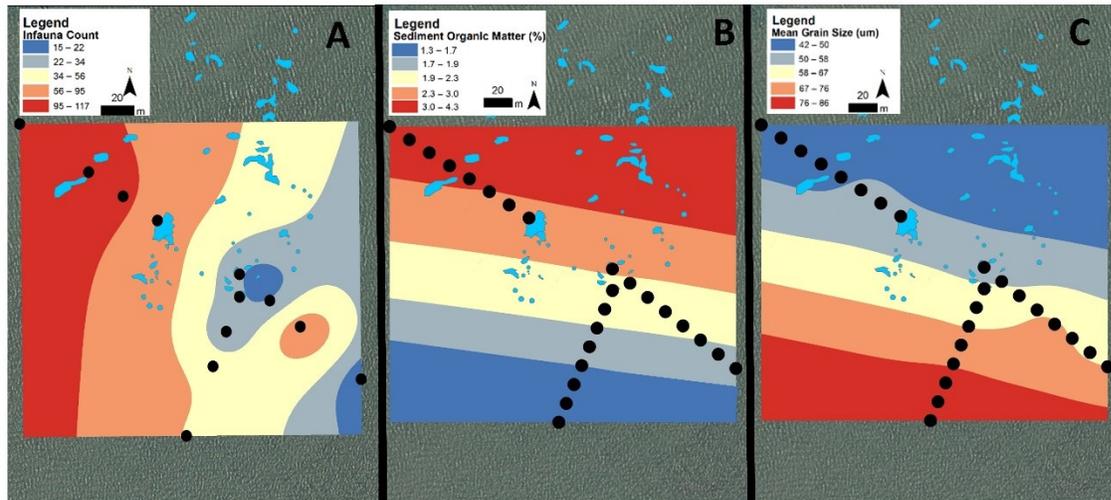
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3 Fig. 2. Infauna and sediment sampling locations along transects at site 1 (A), site 4 (B), and site 6
4 (C) and ground views of the oyster reefs at site 1 (D) and site 4 (E). Site 1 (A & D) illustrates a
5 patchy oyster reef complex, where site 4 (B & E) illustrates a more continuous reef. Panel F
6 shows a ground view of a sampling transect directed away from a reef.

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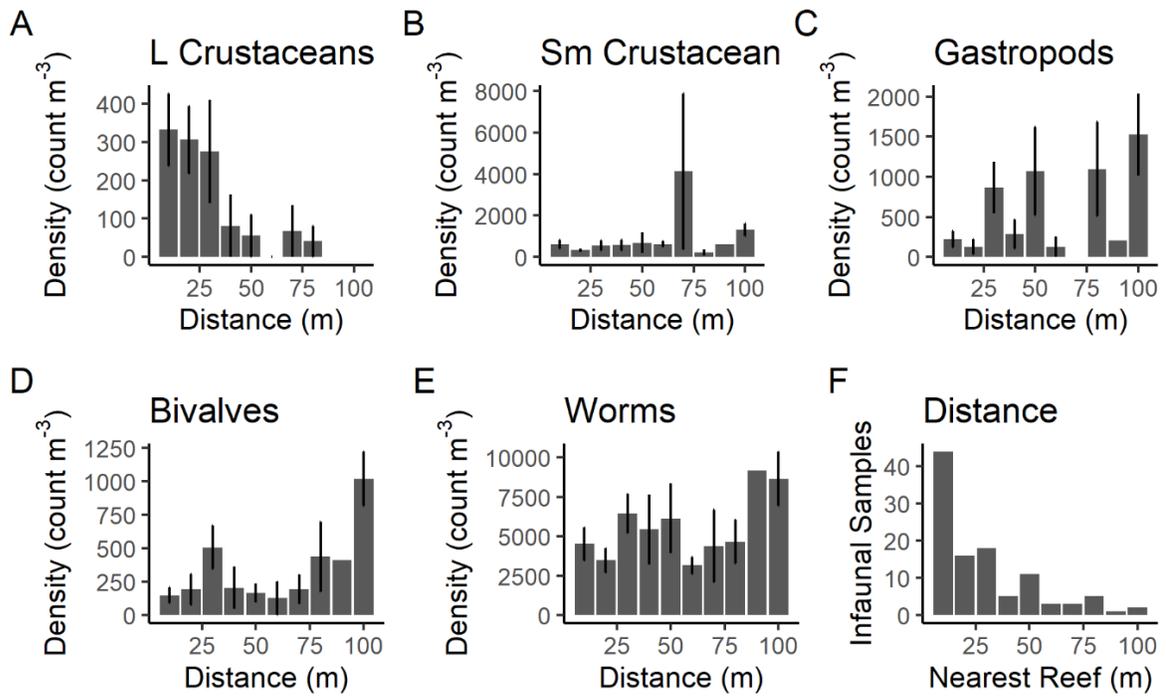


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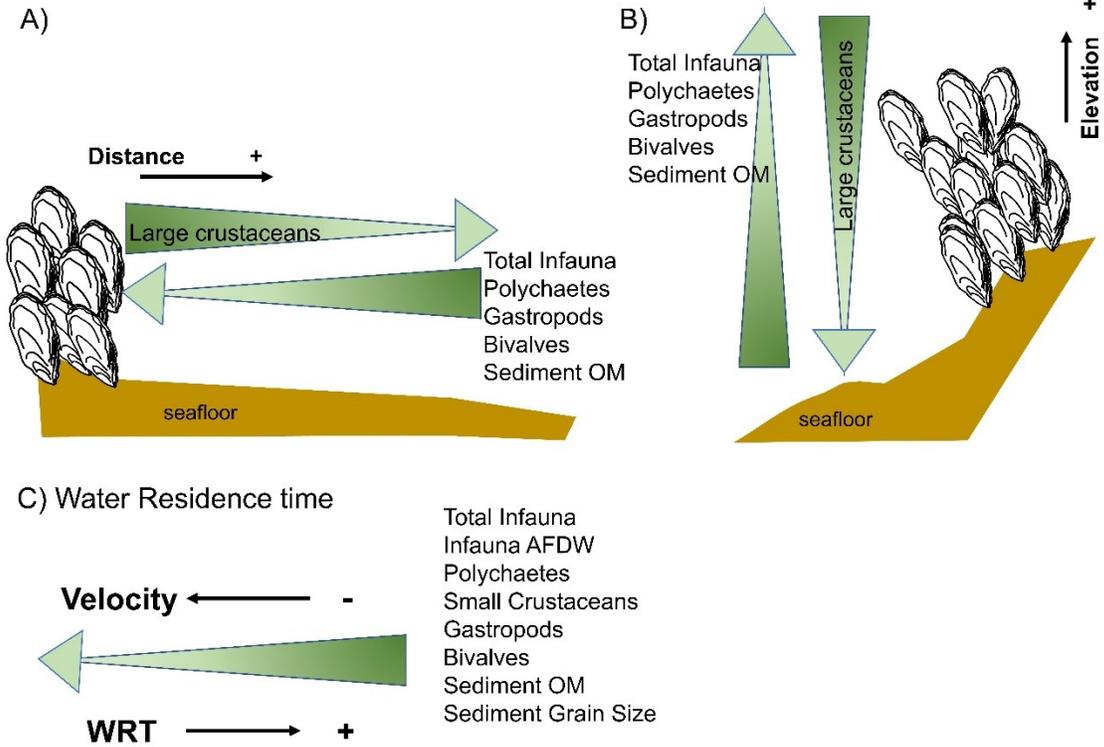
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3 Fig. 3. Interpolated surfaces for A) total infauna count B) sediment organic matter (%) and C)
4 mean sediment grain size(μm) for site 2. High to low values are colored along a red – blue
5 gradient, though the scale changes between site and for each variable. Digitized oyster reef
6 polygons are seen overlaid the surfaces in light blue. Black points indicate sampling locations.
7 There are channels on both sides of the mudflat.

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3 Fig. 4. Bar plots for taxa densities sampled at different distances from oyster reefs. Bars (\pm
4 standard error) represent the mean density (count m^{-3}) from binned data from every 10 m
5 from oyster reefs for A) large crustaceans, B) small crustaceans, C) gastropods, D) bivalves,
6 and E) worms, in addition to F) a histogram showing the number of infauna samples
7 collected at each binned distance.
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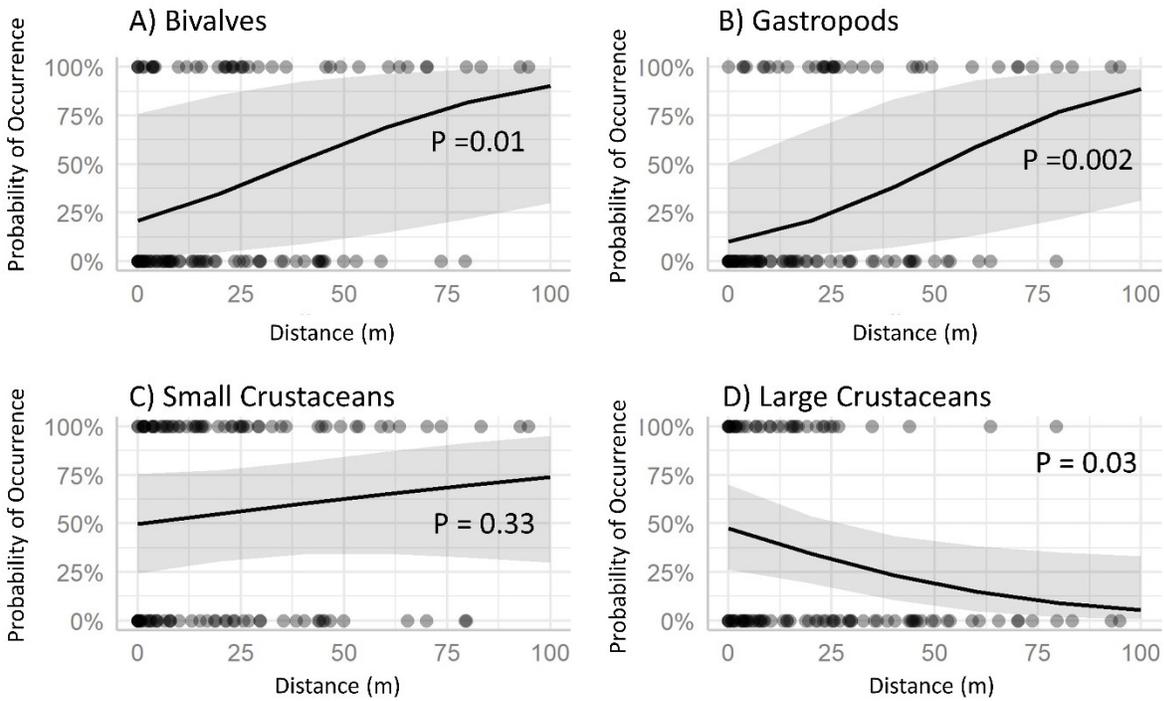
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Fig. 5. Conceptual diagrams for significant correlations for infauna and sediment variables with A) distance B) elevation, and C) WRT. For infauna and sediment variables the direction of the green arrow indicates a decreasing magnitude of the variable. The magnitude of the site variables is indicated by +/- signs.



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2 Fig. 6. Distance effects plots for A) bivalves, B) gastropods, C) small crustaceans, and D) large
3 crustaceans. The plots indicate that the probabilities of observing gastropods and large
4 crustaceans are strongly affected by distance from reefs, though in opposite directions, where
5 likelihood of observing gastropods increases further from reefs but decreases for crustaceans.
6 Distance does not strongly affect the likelihood of observing small crustaceans. The shaded area
7 shows the 95% confidence intervals using the “ggeffects” package (Lüdecke 2018) and raw data
8 is represented as filled circles.

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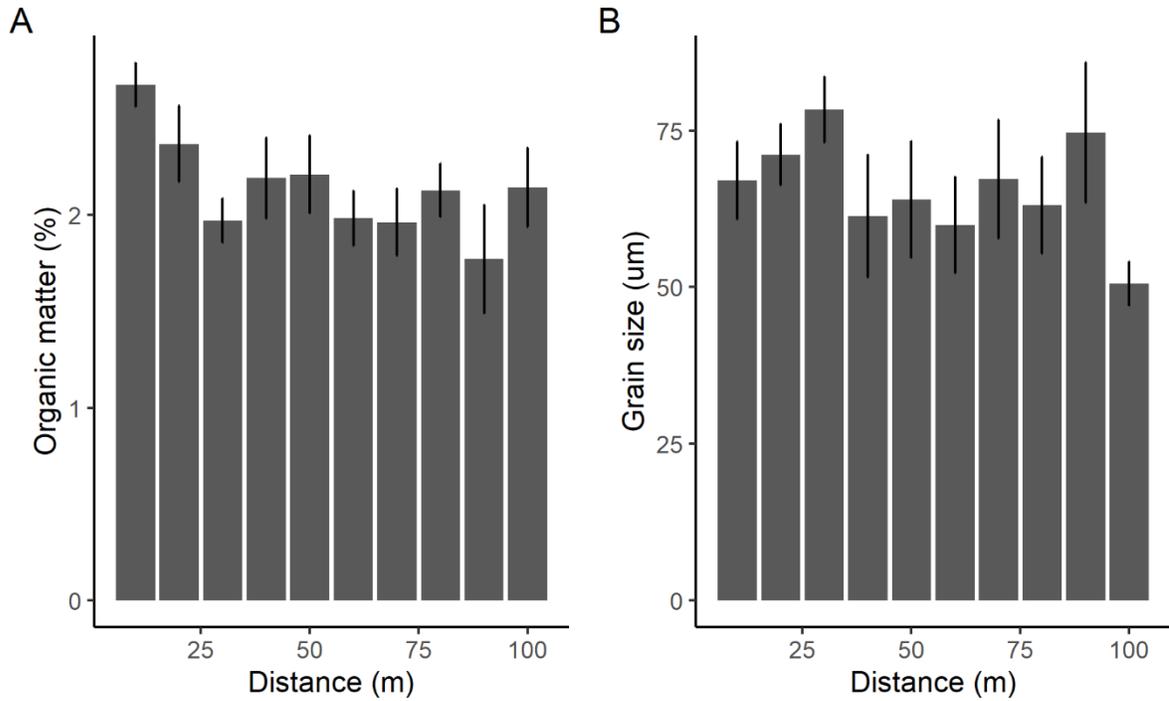


Fig. 7. Bar plots of A) organic matter (%) and B) grain size (µm) at varied distances from oyster reefs. Bars (\pm standard error) represent the mean from binned data every 10 m from oyster reefs.

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2 Table A2. Polychaete families collected during 2016 sampling, total number in each family over
 3 44 cores (25 cm diameter). Polychaete identifications were made using Polychaete Key for
 4 Chesapeake Bay and Coastal Virginia (Bartholomew 2001).

Polychaete family	Total from 2016
<i>Lumbrineridae</i>	422
<i>Capitellidae</i>	322
<i>Nereidae</i>	256
<i>Spionidae</i>	164
<i>Glyceridae</i>	128
<i>Maldanidae</i>	111
<i>Oeononidae</i>	63
<i>Eunicidae</i>	54
<i>Hesionidae</i>	42
<i>Cirratulidae</i>	40
<i>Orbiniidae</i>	38
<i>Paraonidae</i>	35
<i>Phyllodocidae</i>	18
<i>Ampharetidae</i>	11
<i>Arabellidae</i>	5
<i>Arenicolidae</i>	2
<i>Pectinariidae</i>	2
<i>Phyllodocidae</i>	2
<i>Terebellidae</i>	4
<i>Nephtyidae</i>	1

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