



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

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**ABSTRACT:** Oysters are described as estuarine ecosystem engineers because their reef structures provide habitat for a variety of flora and fauna, alter hydrodynamics, and affect sediment composition. To what spatial extent oyster reefs influence surrounding infauna and sediment composition remains uncertain. We sampled sediment and infauna across 8 intertidal mudflats at distances up to 100 m from oyster reefs within coastal bays of Virginia, USA, to determine if distance from reefs and physical site characteristics (reef elevation, local hydrodynamics, and oyster cover) explain the spatial distributions of infauna and sediment. Total infauna density increased with distance away from reefs; however, the opposite was observed for predatory crustaceans (primarily crabs). Our results indicate a halo surrounding the reefs of approximately 40 m (using an increase in ~25% of observance as the halo criterion). At 90 m from reefs, bivalves and gastropods were 70% more likely to be found (probability of observance), while there was an approximate 4-fold decrease for large crustaceans compared to locations adjacent to reefs. Increases in percent oyster reef cover and/or mean reef area did not statistically alter infauna densities but showed a statistical correlation with smaller sediment grain size, increased organic matter, and reduced flow rates. Weaker flow conditions within the surrounding mudflats were also associated with smaller grain sizes and higher organic matter content, suggesting multiple drivers on the spatial distribution of sediment composition. This study emphasizes the complexity of bio-physical couplings and the considerable spatial extent over which oyster reefs engineer intertidal communities.

**KEY WORDS:** Ecosystem engineers · Oyster reefs · Infauna · Sediment · Kriging · Intertidal ecology · Community ecology

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## 1. INTRODUCTION

Ecosystem engineers are organisms that affect communities directly and indirectly by influencing resource availability via the creation or modification of physical structures (Jones et al. 1994, Angelini et al. 2011). Common examples of ecosystem engineers include beavers, that change hydrologic conditions by constructing dams (Jones et al. 1994, Wright & Jones 2002), and trees, whose tissues physically alter flows of nutrients, chemical cycling, and habitat provisioning (Jones et al. 1997). However, the spatial

footprint over which ecosystem engineers affect communities and ecosystems is often difficult to define and is largely dependent on the particular engineering process examined (Wright & Jones 2004, Hastings et al. 2007). Large physical habitat modifications, such as beaver dams and tree canopies, are easily observable, while smaller-scale processes such as changes to soil biogeochemistry require more careful analysis over specified spatial and temporal scales (Jones et al. 1997, Wright & Jones 2004, Hastings et al. 2007). Hence, small-scale effects may go undocumented because they are more difficult to

detect or measure. Therefore, careful consideration for the engineering species and processes quantified are necessary in determining scales of influence.

Given their abilities to strongly impact environments, ecosystem engineers are often incorporated into landscape restoration (Byers et al. 2006). Thus, to help guide the siting and design of restoration projects, determining the spatial extent over which ecosystem engineers impact their environment is important. Managers of estuarine ecosystems often incorporate ecosystem engineers as a part of nature-based solutions to improve ecosystem functions such as coastal protection, biodiversity, and water quality (Davis et al. 2006, Currin et al. 2010). Among the most important ecosystem engineers for the restoration of coastal environments are reef-building oysters (family Ostreidae), which build solid, fixed structures in otherwise unstable soft-sediment systems and alter the abiotic environment in 3 major ways. (1) Physical reef structures provide habitat and refuge to fauna, including polychaetes, crustaceans, and fish (Posey et al. 1999, Lenihan et al. 2001, Grabowski et al. 2005). (2) These reef structures change hydrodynamic patterns by virtue of their physical structure. The rough surface of oyster reefs increases drag and turbulence, altering flow patterns and locally increasing sediment resuspension and transport from the reef crest, while also trapping fine sediments adjacent to the reef (Lenihan 1999, Whitman & Reidenbach 2012, Reidenbach et al. 2013, Colden et al. 2016). Oyster reefs can also attenuate wave energy and in some cases reduce shoreline erosion (Piazza et al. 2005, Wiberg et al. 2019). (3) Oysters can change sediment composition by altering grain size, organic matter content, and sediment biogeochemistry through direct inputs of pseudofeces deposited from filter feeding and the indirect facilitation of benthic microalgae productivity (Newell et al. 2002, Kellogg et al. 2013, Southwell et al. 2017). The fine particles, which are likely to be trapped, also hold nutrients in organic-rich sediments more readily (Nedwell et al. 1999).

Burrowing organisms (infauna) dominate muddy intertidal habitats, often impacting these systems through bioturbation (Aller 1994, Meysman et al. 2006), which oxygenates sediment and increases available habitat for themselves and other infauna (Solan et al. 2004, Byers & Grabowski 2014, Murphy & Reidenbach 2016). Infauna community structure is dependent on many factors, including sediment and water characteristics such as grain size, temperature, pH, and oxygenation (Paterson et al. 2009, Widdicombe et al. 2009, Dauvin et al. 2017, Veiga et al. 2017). Sediment grain size, which is influenced by

oyster reefs, can affect infauna's ability to burrow, consume oxygen, and feed (Wilson 1990, Janssen et al. 2005, Dorgan et al. 2016). A shift to finer sediments, which compact more easily, can limit the advection and diffusion of water and dissolved gases through interstitial porewaters, resulting in thinner oxic layers and flatter topography relative to areas with coarser-grained sediments and less compaction (Nybakken & Bertness 2005, Byers & Grabowski 2014). Therefore, oyster-mediated changes to sediments and hydrodynamics may have cascading effects on estuarine ecosystem function, affecting biodiversity, sediment stability (Dashtgard et al. 2008), and biogeochemical processes.

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

Studies of the effects of bivalves and structured reefs on adjacent infauna communities are mixed and have largely focused on subtidal environments (Table A1 in the Appendix). Researchers have found, depending upon the composition of infauna, that benthic communities in proximity to reefs can either be enhanced (Ambrose & Anderson 1990, Dahlgren et al. 1999, Barros et al. 2001, 2004, Langlois et al. 2005, Zalmon et al. 2014), or diminished (Ambrose & Anderson 1990, Posey & Ambrose 1994, Barros et al. 2001, Langlois et al. 2005, Reeds et al. 2018) with respect to abundance, density, and/or richness. Reeds et al. (2018) identified that the ecological footprint of a single constructed reef may be up to 15 times the area of the reef. However, most studies found that patterns varied among species and with organism

size (Davis et al. 1982, Ambrose & Anderson 1990, Fabi et al. 2002, Langlois et al. 2006), demonstrating that taxa-specific behaviors and tolerances are important to consider in understanding reef–infauna relationships.

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

## 2. MATERIALS AND METHODS

### 2.1. Study site

We studied intertidal mudflats located within the Virginia Coast Reserve (VCR). The VCR is a system of barrier islands, coastal bays, and upland marshes extending across >100 km of coastline along the Atlantic Ocean of the Delmarva Peninsula in Virginia, USA (Fig. 1). The VCR is also a National Science Foundation-funded Long-Term Ecological Research (LTER) site. The tidal range is approximately 1.2 m (Hansen & Reidenbach 2013), and within the intertidal mudflats, numerous oyster reefs exist, primarily as patch reefs of the eastern oyster *Crassostrea virginica*. Most oyster reefs in this area have been heavily influenced by human activity and have largely undergone some form of restoration starting in the mid to late 1900s (Luckenbach et al. 2005, Kennedy et al. 2011). The oysters are predominately intertidal, and restoration has relied on providing hard substrate suitable for larval settlement and growth (Whitman & Reidenbach 2012). Previous work in the VCR has shown that oysters affect resident flora and fauna, including effects on algal growth and snail densities (Thomsen & McGlathery 2006), and alter benthic metabolism (Volaric et al. 2018).

### 2.2. Data collection

We sampled 8 intertidal mudflat sites in proximity to oyster reefs (Figs. 1 & 2) during the summers of 2016 and 2019. In 2016, we collected infauna and sediment samples at 4 sites (sites 1–4, Table 1) along 100 m transects (2–4 transects per site) starting from oyster reefs. Site 2 was largely a control with oyster patches interspersed and transects did not start at a

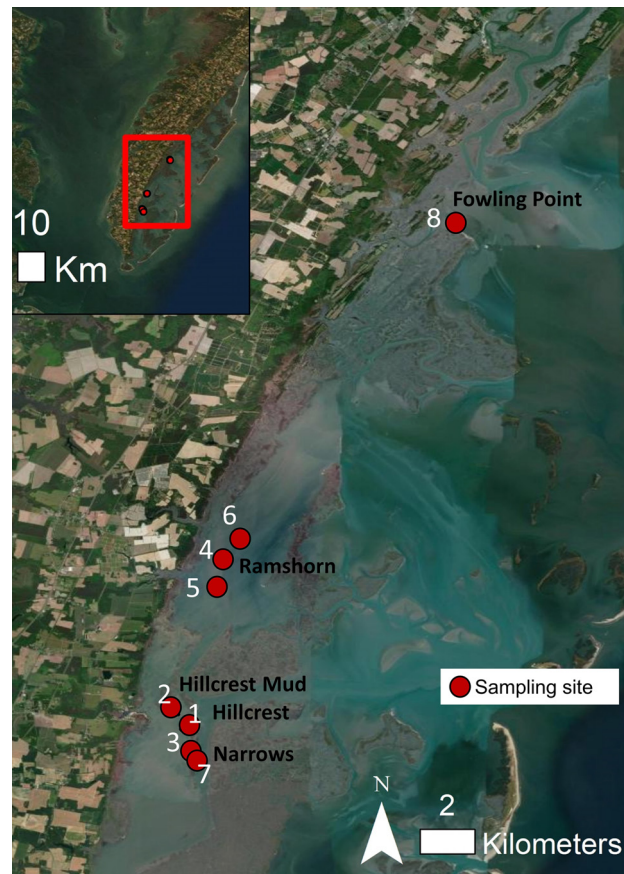


Fig. 1. The 8 intertidal mudflats situated near oyster reefs that were sampled, labeled according to sites in Table 1. Inset: the extent of the Virginia Coast Reserve, found on the eastern side of the Delmarva Peninsula

particular reef. Infauna cores (25 cm diameter, 10 cm deep) were collected at 0, 28, 56, and 98 m along each transect, and sediment cores (3 cm diameter, 5 cm deep) were taken every 14 m along each transect ( $n = 4$  samples per transect for infauna,  $n = 8$  samples per transect for sediment), except for 1 transect where infauna samples were taken at 0, 12.5, 50, and 87.5 m and sediment cores taken every 12.5 m. In 2019, we sampled infauna and sediment at 4 additional sites (sites 5–8, Table 1), using a gridded sampling design to ensure varied distances from reefs. At each site, we sampled along four 75 m transects spaced 25 m apart and arranged parallel to reefs where they were continuous or the edge of the mudflat where reefs were patchy (Fig. 2). At each transect, we collected infauna cores (15 cm diameter, 15 cm deep) every 25 m ( $n = 4$  per transect, 16 per site) and sediment cores (3 cm diameter, 5 cm deep) every 12.5 m ( $n = 7$  per transect,  $n = 28$  per site). Sediment samples for organic matter and grain size

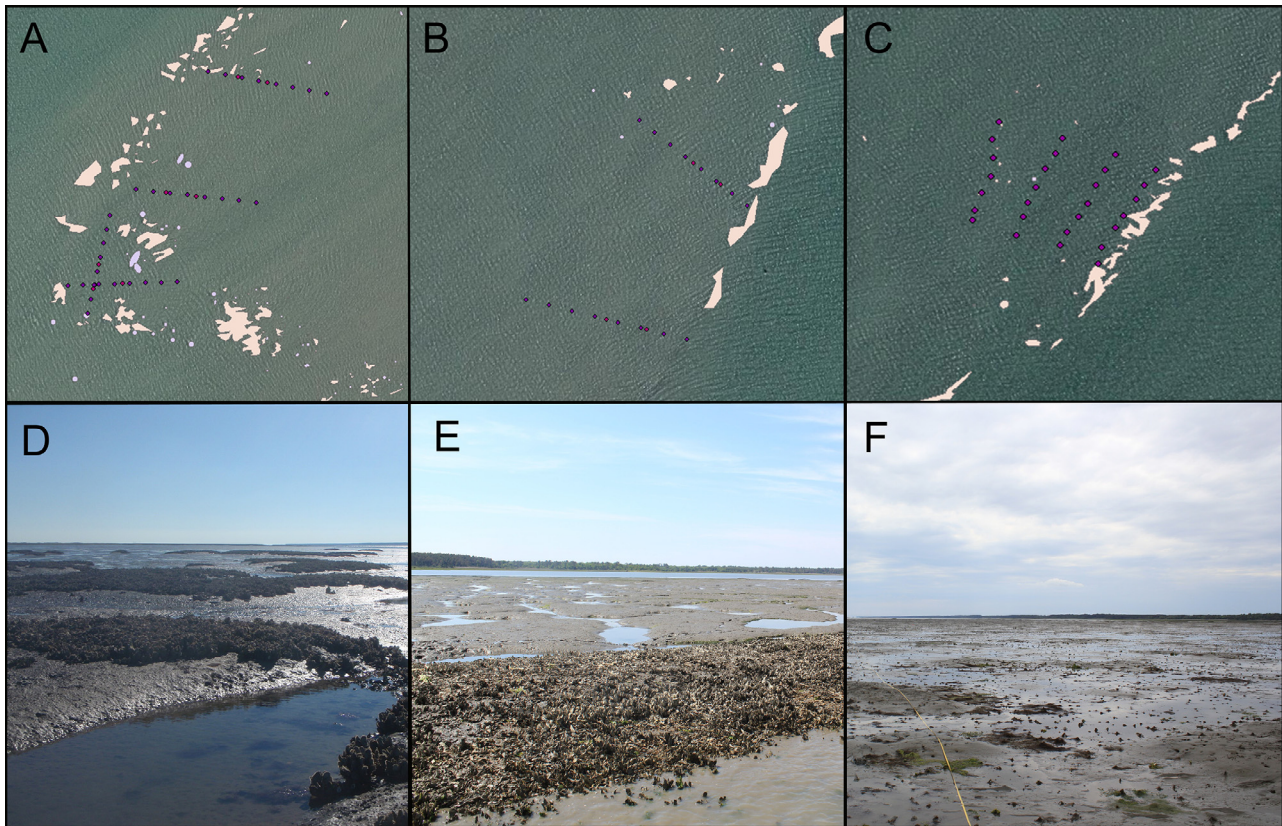


Fig. 2. Infauna and sediment sampling locations along transects at (A) site 1, (B) site 4, and (C) site 6, and ground views of the oyster reefs at (D) site 1 and (E) site 4 (see Fig. 1 for site locations). (A,D) Site 1 illustrates a patchy oyster reef complex, while (B,E) site 4 illustrates a more continuous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

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

Site no.	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

analysis were kept frozen and refrigerated, respectively, until processed. Infauna samples were processed immediately following collection.

Infauna cores were wet-sieved (1 mm mesh), and living fauna were identified to 5 broad taxonomic levels: worms, bivalves, gastropods (dominated by snails), small crustaceans (amphipods, isopods, shrimp), and large crustaceans (crabs). Though dominated by burrowers, epifaunal gastropods were also

included in the benthic infauna analysis. In 2016, polychaetes were identified to the family level to determine the diversity of polychaetes, with a list of taxa and total counts given in Table A2. Rarely, nemertean and acorn worms (Enteropneusta) were identified. Hence, we termed this broad category 'worms'. Abundance of each of the 5 taxa and total biomass for each sample (ash-free dry weight, AFDW) were recorded. Infauna were dried for 48 h at 60°C to measure dry weight and combusted for 6 h at 500°C for AFDW. Sediment organic matter was estimated using the same procedure for AFDW. In 2016, sediment grain size was estimated using a Beckman Coulter LS I3 320 laser diffraction particle size analyzer, following treatment with hydrogen peroxide to remove organic matter. Porosity was also measured in 2016, but data was found to be highly correlated to grain size and was not included as a separate parameter in the analysis. While sampling along transects guaranteed various distances from oyster reefs, we estimated linear distance to the nearest oyster reef >5 m<sup>2</sup> using GIS software (ArcMap 10.5) with an existing oyster reef location dataset derived from

LiDAR elevation data and aerial imagery (Hogan & Reidenbach 2020). Reefs missing from that dataset were added using the methods described in Hogan & Reidenbach (2019). We also generated a minimum circular boundary around sampling locations and extended a buffer 40 m around the boundaries at each location. We used the area of the boundary and the area of reefs intersecting the boundary to calculate percent oyster cover at each mudflat. We then calculated the mean oyster reef size, in terms of area, for reefs intersecting each buffered mudflat.

### 2.3. Data analysis

#### 2.3.1. Interpolated surfaces

To determine how infauna communities and sediment composition change with distance to oyster reefs, geospatially interpolated prediction surfaces for total infauna, sediment organic matter, and sediment grain size distributions at each sampling site were created using the Geostatistical Analyst extension in ArcMap 10.5. Geostatistical interpolation has the advantage of modeling data between known data points. We used empirical Bayesian kriging (EBK) to create a distribution of prediction surface responses based on spatial autocorrelation, semivariogram estimation, and associated errors. EBK predictions are ideal for non-stationary and less spatially dense data because predictions are based on the probability of likelihoods from many semivariogram parameters estimated using restricted maximum likelihood compared to other kriging methods that use only 1 semivariogram with estimation using weighted least squares (Krivoruchko 2012, ESRI 2016). The Exploratory Spatial Data Analysis (ESDA) package was used to help examine distributions and normality to meet modeling assumptions and determine if transformations would likely lead to the best-fitting semivariograms. Semivariogram model, transformation type, and search neighborhood type (standard circular or smoothed circular with minimum 10 neighbors) were chosen from all possible combinations with the lowest root mean square error (RMSE; Gunarathna et al. 2016, Gupta et al. 2017).

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

#### 2.3.2. Statistical analyses

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

#### 2.3.3. Correlation analysis

Data analysis showed highly non-normal distributions. Therefore, we used non-parametric Spearman's rank correlation (Hauke & Kossowski 2011, Zar 2014) to quantify pairwise associations between infauna variables (total faunal AFDW and density of each the broad taxon group) and site characteristics (distance from reef, elevation, WRT, percent oyster cover, and mean reef area). Because sampling cores for infauna differed in size between the 2 sampling years, we converted the abundances and AFDW measurements in 2016 and 2019 to volumetric density ( $\text{m}^{-3}$ ). We removed 3 observations where AFDW estimates were  $<0$ , likely due to minimal AFDW that were below the accuracy of our measurements.

For sediment characteristics, we fit Spearman's rank correlations between percent organic matter with distance, elevation, WRT, percent oyster cover, and mean reef area. Grain size was only sampled for 2016 (samples:  $n = 88$ , sites = 4). For grain size, the

same variables of distance, elevation, WRT, percent oyster cover, and mean reef area were used in correlations. We also examined the correlation between organic matter and grain size.

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

#### 2.3.4. Multiple regression analysis

Because infauna density was largely driven by worms (present in all but 2 samples), we used binomial multiple regression analyses to explain variation in the presence or absence of bivalves, gastropods, small crustaceans, and large crustaceans (1 model per faunal group). Specifically, we used generalized linear mixed models (GLMM) to model the presence or absence of individual taxa (with logit link function, i.e. mixed-effects logistic regression) as a function of elevation and distance. We also analyzed the total number of taxa (including worms) present—our metric for taxonomic richness—as a continuous independent variable. Taxa richness was modeled using a Poisson GLMM (log link function). We fit a linear mixed model to predict sediment grain size as a function of distance, elevation, and WRT with a random intercept for site. To control for heterogeneity among sites and collection dates, we specified site and year as random intercept terms for all GLMMs.

Mixed models were fit in R using `lme4` v.1.1.25 (Bates et al. 2015) and were validated by examining simulated residuals using the `DHARMA` package in R (Hartig 2020). The effects of distance on probability of infauna occurrence were examined using the ‘effects’ package in R (Fox & Weisberg 2019). Data for sediment organic matter did not meet the assump-

tions from `DHARMA`; thus, we analyzed these data using Spearman's rank correlations only. We did not include WRT in the multiple regression analyses for infauna because with this additional variable, the models failed to converge.

### 3. RESULTS

#### 3.1. Mudflat site characteristics

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

#### 3.2. Infauna

There was a trend of increasing total infauna abundance away from oyster patches, as evidenced from

Table 2. Spearman's rank correlation coefficients/p-values for taxa density (count  $m^{-3}$ ), biomass (ash-free dry weight [AFDW],  $m^{-3}$ ), and site variables (distance, elevation, water residence time [WRT], percent oyster cover, and mean oyster reef size in  $m^2$ ).

**Bold:** significant correlations

	Distance	Elevation	WRT	Percent cover	Mean size
Distance	1/–	–0.05/0.63	–0.02/0.87	<b>–0.34/0.00</b>	<b>0.30/0.00</b>
Percent cover	<b>–0.34/0.00</b>	<b>–0.37/0.00</b>	0.04/0.65	1/–	–0.01/0.89
Mean size	<b>0.30/0.00</b>	<b>–0.20/0.04</b>	<b>0.45/0.00</b>	–0.01/0.89	1/–
Total infauna	<b>0.26/0.01</b>	<b>–0.29/0.00</b>	<b>–0.38/0.00</b>	–0.12/0.23	–0.11/0.27
Total AFDW	–0.02/0.87	0.02/0.81	<b>–0.22/0.02</b>	–0.03/0.76	–0.07/0.46
Worms	<b>0.24/0.02</b>	<b>–0.43/0.00</b>	<b>–0.32/0.00</b>	–0.01/0.91	–0.06/0.51
Bivalves	<b>0.25/0.01</b>	<b>–0.22/0.03</b>	<b>–0.39/0.00</b>	–0.00/0.97	0.01/0.96
Gastropods	<b>0.39/0.00</b>	<b>–0.22/0.02</b>	<b>–0.43/0.00</b>	–0.17/0.08	–0.06/0.52
Small crustaceans	0.16/0.10	–0.17/0.08	<b>–0.24/0.01</b>	–0.00/0.96	–0.13/0.19
Large crustaceans	<b>–0.27/0.00</b>	<b>0.30/0.00</b>	–0.06/0.55	–0.09/0.37	–0.18/0.06

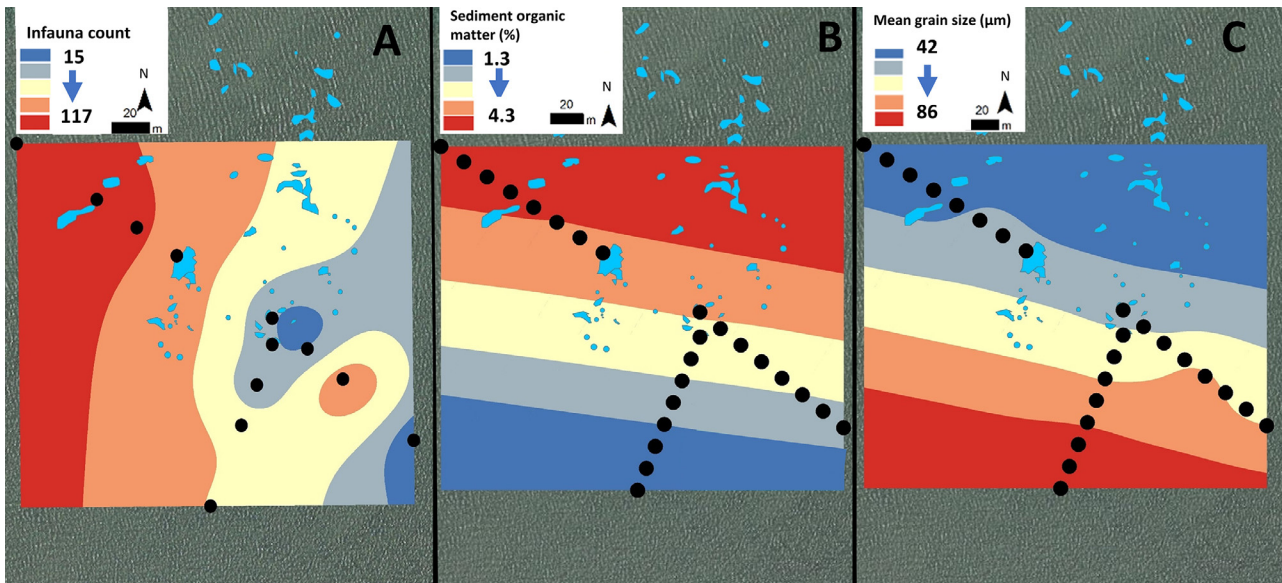


Fig. 3. Interpolated surfaces for (A) total infauna count, (B) sediment organic matter, and (C) mean sediment grain size for site 2. High to low values are colored along a red–blue gradient, though the scale changes between sites and for each variable. Digitized oyster reef polygons are seen overlaid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

kriging analysis, though more difficult to observe in patchier environments (Fig. 3A, Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m686p091\\_supp.pdf](http://www.int-res.com/articles/suppl/m686p091_supp.pdf)). Ranked correlation analysis showed that total infauna abundance increased further from reefs and at lower elevations, while total biomass

increased with lower WRT (see Table 2 for test statistics). We found that the observed patterns of infauna abundance increasing at further distances from reefs was driven by bivalves, gastropods, and worms, whose abundances increased at further distances (Fig. 4). Bivalve, gastropod, and worm abundances

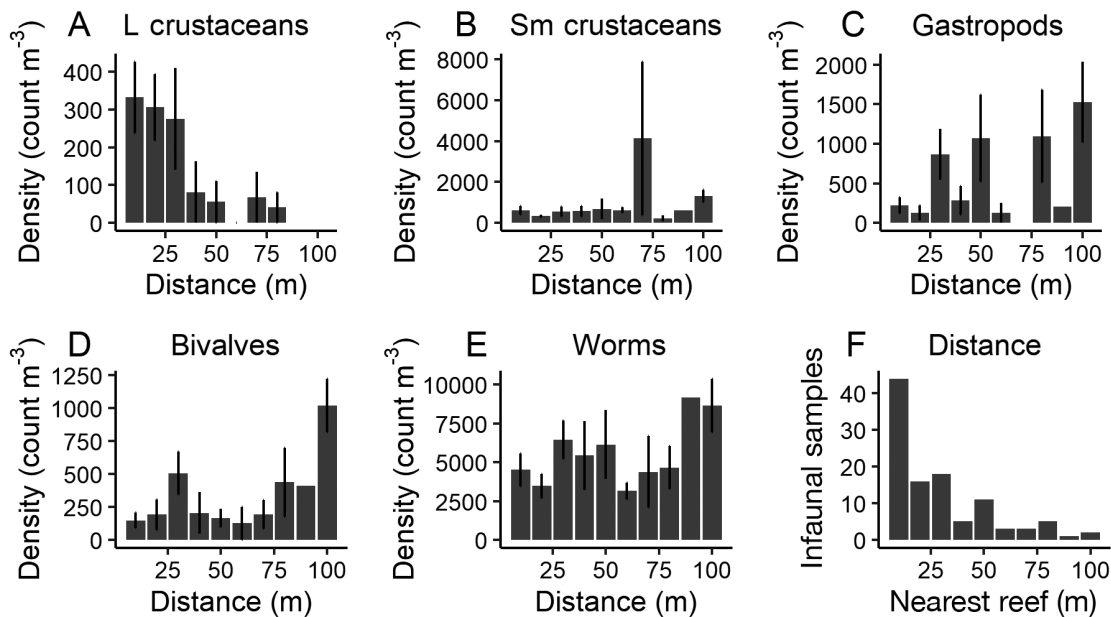


Fig. 4. Taxa densities sampled at different distances from oyster reefs. Bars: mean density ( $\pm$ SE) from binned data from every 10 m from oyster reefs for (A) large crustaceans, (B) small crustaceans, (C) gastropods, (D) bivalves, and (E) worms. (F) Number of infauna samples collected at each binned distance

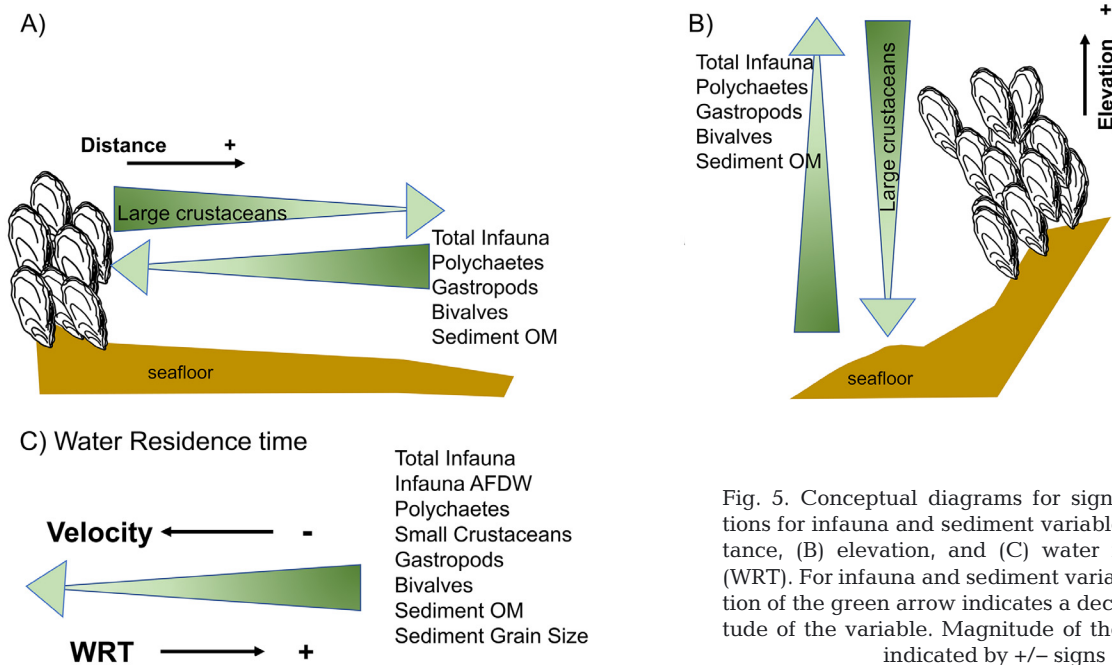


Fig. 5. Conceptual diagrams for significant correlations for infauna and sediment variables with (A) distance, (B) elevation, and (C) water residence time (WRT). For infauna and sediment variables, the direction of the green arrow indicates a decreasing magnitude of the variable. Magnitude of the site variables indicated by +/- signs

also increased at lower elevations, and with lower WRT (faster flows). By contrast, large crustaceans (i.e. crabs) were found in greater abundance closer to reefs and at higher elevations (Figs. 4A & 5A,B). Small crustacean abundances did not vary significantly with distance from reefs or elevation but were more abundant with lower WRT (Fig. 5C). Neither

infauna abundances nor AFDW for each sample varied with oyster percent cover or mean oyster reef area (Table 2). However, sites with patchier oyster reefs exhibited weaker spatial patterns in infauna abundance as a function of distance from the reefs, as well as lower variability in infauna abundance (Fig. S1).

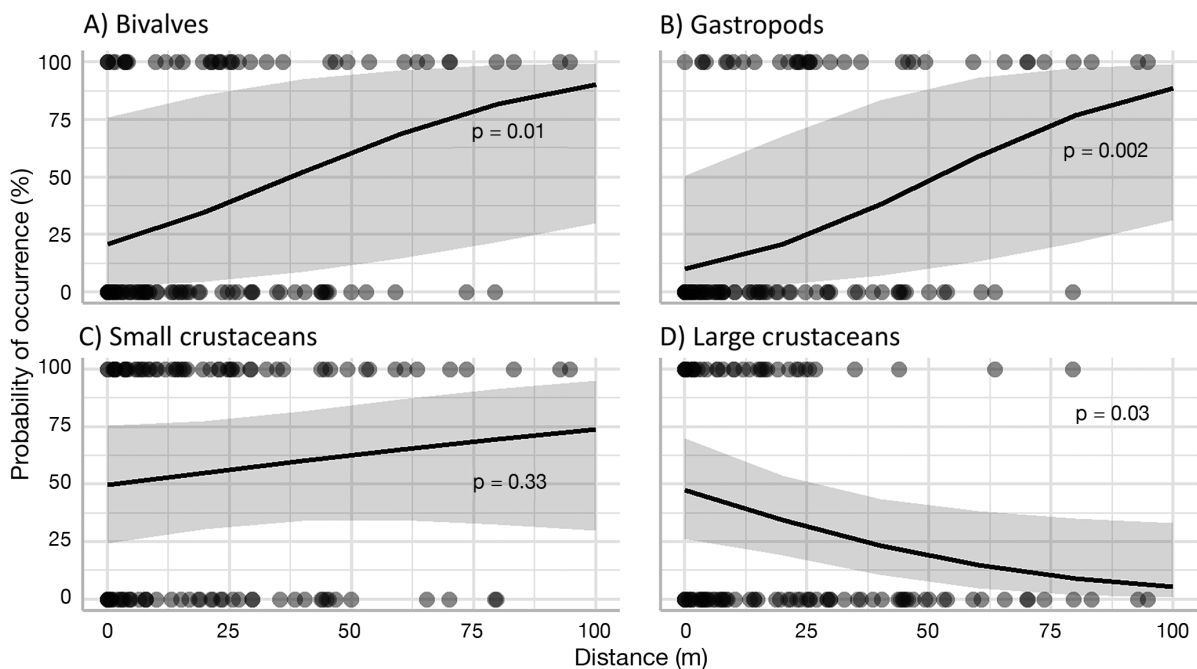


Fig. 6. Distance effects plots for (A) bivalves, (B) gastropods, (C) small crustaceans, and (D) large crustaceans. Shaded area: 95% confidence intervals using ggeffects package (Lüdtke 2018); filled circles: raw data



Table 3. Regression analyses predicting the presence of taxa and richness using distance and elevation. Number of observations: 108.  $\beta$ : estimated coefficients; P/A: presence/absence

Taxa (P/A)	Distance				Elevation			
	$\beta$	SE	<i>z</i>	<i>p</i>	$\beta$	SE	<i>z</i>	<i>p</i>
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
Small crustaceans	0.01	0.01	0.98	0.33	-1.79	-1.83	-0.98	0.33
Large 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

Predicted values from the regression models showed bivalves (Fig. 6A) and gastropods (Fig. 6B) had similar distributions out to 90 m from reefs and were on average 70% more likely to be found 90 m from a reef than immediately adjacent to a reef. Contrary to other infauna, there was a predicted general decrease in probability of observing large crustaceans away from reefs, decreasing from 48% adjacent to a reef to 7% at a distance of 90 m (Fig. 6D). Small-crustacean presence was highly variable and there was no measurable trend in their occurrence (Fig. 6C). The richness (number of broad taxa represented) was not measurably affected by distance ( $p = 0.27$ ) from the reef or local elevation of the mudflat at the location infauna were collected ( $p = 0.67$ ) (Table 3).

### 3.3. Sediment

Utilizing the interpolated surfaces from sediment distributions, visual patterns suggested that sediment organic matter tended to be higher closer to reefs (Figs. 3B & S2). Sites with patchier oyster reefs showed less variability. These patterns were supported statistically by Spearman's rank correlations, which showed that organic matter decreased further from oyster reefs at higher elevations, and with lower WRT (i.e. faster flows; Table 4, Figs. 5 & 7). Kriging analysis suggested a trend for smaller sediment grain size nearer to the reef (Figs. 3C & S3), but this was not borne out by the regression analysis, which showed no trend with distance ( $t = 2.3$ ,  $p = 0.13$ ) or other site characteristics (elevation:  $t = 1.6$ ,  $p = 0.21$ ; or WRT:  $t = 1.9$ ,  $p =$

0.26). Kriging also showed that for one of the 8 sites (site 4), this spatial pattern reversed. However, Spearman's rank correlations found that grain size decreased with increasing WRT and sediment organic matter (Table 4, Fig. 5), suggesting that finer sediment particles are associated with high organic matter and slower moving flows. These findings for organic matter and grain size are congruent because organic matter is negatively related to grain size (Southwell et al.

2017), and with slower flows that retain smaller sediment grain sizes. Greater mean oyster reef size was positively correlated with sediment organic matter and negatively with grain size. Organic matter was also positively correlated with percent oyster cover.

Table 4. Spearman's rank correlation coefficients ( $\rho$ ) and *p*-values for sediment grain size and percent organic matter (OM) with site variables (distance, elevation, water residence time [WRT], percent oyster cover, mean reef area in  $m^2$ ), and each other (sediment grain size and sediment organic matter)

Site variable	Percent OM		Grain size	
	$\rho$	<i>p</i>	$\rho$	<i>p</i>
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

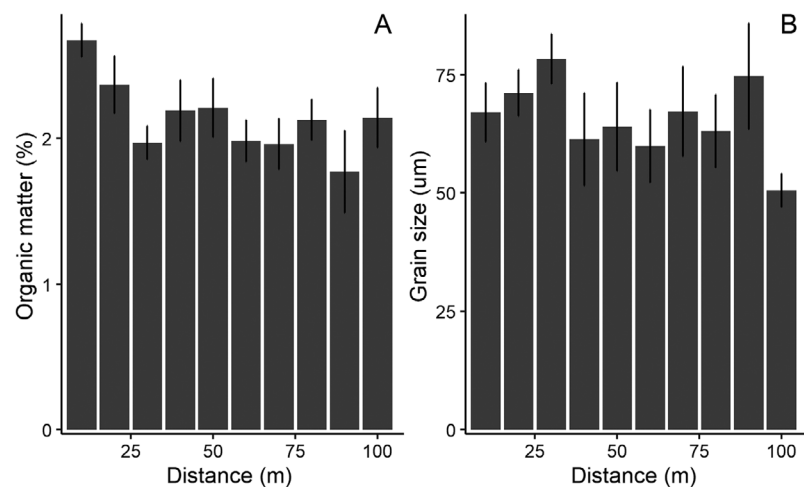


Fig. 7. (A) Organic matter and (B) grain size at varied distances from oyster reefs. Bars: mean ( $\pm$ SE) from binned data every 10 m from oyster reefs

## 4. DISCUSSION

### 4.1. Site characteristics and physical variables

Oysters have been previously found to alter mudflats by modifying fauna communities and sediment composition (Lenihan 1999, Grabowski et al. 2005, Colden et al. 2016). We found that distance, elevation, and local flow are important variables in determining infauna and sediment distributions. Our analysis utilizing interpolated surfaces demonstrated that gradients in infauna and sediment distributions are less distinct when oysters are patchy throughout the region, compared to regions composed of a few large intact oyster reefs (Fig. 2). This result supports the idea that distance from a reef, along with flow, may indeed alter the distributions of sediment and infauna because oyster cover and size can influence site characteristics, including flow and consequent sediment composition. Larger reefs were also associated with reduced flows. Although our work cannot determine the extent to which oysters form within reduced-flow regions, or oysters reduce the flow directly, previous work has shown that oyster reefs can significantly reduce local flow rates due to the drag imposed by their rough topography (Lenihan 1999, Whitman & Reidenbach 2012, Reidenbach et al. 2013, Colden et al. 2016). This reinforces the role that oysters may play in engineering their physical environment, and helps explain our findings that reefs alter sediment composition and the infaunal community. It also builds upon previous findings within our study region showing that WRT and sediment characteristics are strongly linked (Wiberg et al. 2015).

### 4.2. Sediment analyses

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

negative correlations found with WRT and organic matter, emphasizing the importance of the local flow in altering sediment characteristics and agreeing with studies suggesting that finer sediments hold more nutrients (Nedwell et al. 1999).

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

### 4.3. Infauna communities

Bivalves and gastropods were more common and abundant further from reefs. This result agrees with previous findings of 'halos' of low faunal density around oyster reefs (Posey & Ambrose 1994, Reeds et al. 2018). Reeds et al. (2018) found an infauna abundance halo 30 m around an artificial reef outside Sydney Harbour, Australia. Our results build upon this earlier finding by characterizing infauna communities around multiple, patchier oyster reefs over 2 years. Our results indicate a halo of approximately 40 m for bivalves and gastropods (using an increase in ~25% of observance as the halo criterion), a similar distance observed by Reeds et al. (2018). Reeds et al. (2018) determined a footprint of 15 $\times$  reef area, which is similar for oyster reefs in our study.

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

Predation by crabs and other predators may have reduced mollusk and worm densities closer to reefs

or caused them to move farther from reefs through a 'landscape of fear' behavioral response observed in coastal environments (Langlois et al. 2005, Madin et al. 2011, Bilodeau et al. 2021). Reefs are generally higher in elevation compared to their surrounding mudflat (Hogan & Reidenbach 2019); therefore, if infauna predators are more likely found on reefs, they will also be found at higher elevations. Large crustaceans also represented the only taxonomic grouping where WRT data was not significantly correlated to density. This could be because crabs are more transient and mobile than worms and mollusks, spending less time in — and less dependent upon — sediment, and more tolerant to environmental disturbances (Davis et al. 1982, Langlois et al. 2006).

All infauna correlation coefficients with WRT were negative, indicating faster flows increased infauna abundances, richness, and biomass. This suggests that WRT represents an important variable in species distributions. In fact, WRT was the only variable tested that explained small crustacean abundance. WRT is highly correlated with flow and tidal currents, with decreases in the residence time of water correlating strongly with high mean water velocities (Safak et al. 2015), which have been shown to impact small crustacean distributions and possibly limit their abundance at other locations (Grant 1981). Local hydrodynamics can also create microtopographic features (such as sediment ripples) that affect distributions of infauna (Barros et al. 2004, Besterman et al. 2021).

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

#### 4.4. Future considerations

Future efforts to understand how infauna and sediment are affected by oyster reefs would benefit from repeated measurements at these mudflats to see if the spatial distributions we found are representative, and possibly to identify longer-term, seasonal, and year-to-year variations. While each of the sampling events in 2016 and 2019 were completed during the summer months, there is likely variation within and among seasons (Zajac & Whitlatch 1982, Harwell et al. 2011). The 10–15 cm depth to which cores were sampled may affect taxa presence, abundance, and biomass in samples. However, it has been found in our region that estuarine macrofauna are relatively rare below 15 cm (Hines & Comtois 1985), resulting in

the recommended depth range of 10–15 cm (Raz-Guzman & Grizzle 2001). We were also unable to address the size and age of oysters needed to affect communities due to patchy areas with multiple reefs of unknown age in proximity to sampling locations. The nearness of reefs to one another could explain some of the effects we observed, as other studies have found that isolation from reefs alter infauna abundances and sediment characteristics (Zalmon et al. 2014). Knowing how these variables affect infauna and sediment distributions could be informative in designing future oyster restoration projects to maximize biodiversity and overall ecosystem function.

#### 4.5. Conclusions

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

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## Appendix.

Table A1. Studies on the effects of infauna and sediment with distance to hard structured reefs. Arrows: magnitude of change for the variables listed; GS: grain size; NA: not applicable; NM: nautical mile; OM: organic matter. Modified from Langlois et al. (2006) with sediment analysis and additional sources added

Study	Location	Sampling zone	Scale	Distance and small infauna	Distance and large infauna	Distance and GS	Correlation: infauna and GS	Correlation: infauna and OM
Langlois et al. (2006)	NE New Zealand	Shallow ~10 m, open coast	2–30 m	No	NA	No	Weak	NA
Langlois et al. (2005)	NE New Zealand	Shallow ~10 m, open coast	2–30 m	NA	Crabs ↑ distance ↓ Urchin, bivalve ↓, distance ↑	No	Abundance ↑, GS ↓	NA
Davis et al. (1982)	SW USA	Shallow ~13 m, open coast	Transects 4–100 m	No	Yes Polychaetes ↑, distance ↓ Sea pen ↓, distance ↓	Yes GS ↑, distance ↓	Yes	No
Ambrose & Anderson (1990)	SW USA	Shallow ~13 m, open coast	Transects 10s of m	Yes, Differed per species	NA	Yes GS ↑, distance ↓	Yes	Yes
Barros et al. (2004)	SE Australia	Rocky subtidal	Close vs. far, 4 vs. 15 m	0.5 mm sieve Taxa ↑, distance ↓ Polychaetes ↑, distance ↓	NA	GS ↑, distance ↓	Yes	NA
Barros et al. (2001)	SE Australia	Shallow rocky reefs	1, 5, 10 m	NA	NA	GS ↑, distance ↓	Weak	NA
Dahlgren et al. (1999)	N. Carolina, USA	50 km offshore	10–75 m transects	NA	1.5 cm 1 species ↓, distance	NA	NA	NA
Posey & Ambrose (1994)	N. Carolina, USA	~32 m, deep offshore	10s of m, up to 75 m transects	0.5 mm sieve	Total infauna, polychaete, bivalve, isopod, amphipod, abundance ↑ with distance ↑	NA	Yes	NA
Van der Zee et al. (2012)	Netherlands, Wadden Sea	Intertidal	100 m grids	Species abundance ↑ distance ↓	NA	Yes	Yes	Yes
Zalmon et al. (2014)	Brazil	9 m deep	0–15 m	0.5 mm sieve Different functional groups respond differently with distance	NA	GS ↓, distance ↑ not significant	Yes	NA
Fabi et al. (2002)	Adriatic Coast	1.2 NM offshore, 11 m deep	10s of m, up to 50 m	0.5 mm sieve Densities in/out of reef similar Diversity ↑, distance ↓	NA	GS ↓, distance ↓	Yes	NA

Table A2. Polychaete families collected during 2016 sampling, total number in each family over 44 cores (25 cm diameter). Polychaete identifications made using Bartholomew (2001)

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

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