Quantifying trade-offs in ecosystem services under various oyster reef restoration designs

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ABSTRACT

Oyster populations within the coastal bays of Virginia have greatly declined, mainly due to overharvesting and disease, and past restoration efforts have largely focused on increasing their populations. Current restoration goals have now expanded to simultaneously procure the wider ecosystem services oysters can offer, including shoreline protection and ecosystem diversification. However, trade-offs exist in designing artificial reefs because it is unlikely one design will optimize all services. This study compares the services provided by reef designs varying in elevation and width located adjacent to an intertidal marsh within a coastal bay of Virginia, USA. We quantified wave attenuation to determine potential coastal protection of the adjacent marsh, and changes to sediment composition and infaunal communities before and after reef construction for three years. After construction we also quantified oyster size and population density to compare high and low elevation reef designs. High elevation reefs were more effective at attenuating waves and fostering oyster growth compared to low elevation reefs. Oysters atop high elevation reefs were on average approximately twice as dense and 20 % larger than those on low elevation designs. Reef width had a minimal effect on oyster population density; densities on high and low reefs were similar for designs with one or three rows. The presence of oyster reefs also increased infaunal diversity and sediment organic matter. Our results indicate that artificial reef design can differentially affect the services provided through restoration and elevation is especially important to consider when designing for oyster population enhancement and coastal protection.

1. INTRODUCTION

Populations of the eastern oyster, *Crassostrea virginica,* across Virginia and the mid-Atlantic region of the United States were decimated by the beginning of the twentieth century due to a combination of overharvesting, poor water quality, and disease (Rothschild et al. 1994, Kemp et al. 2005). While early restoration efforts primarily focused on enhancing populations, restoration efforts have shifted to more ecosystem-based approaches due to the increased recognition of ecosystem services (Coen and Luckenbach 2000, Ehrenfeld 2000, Grabowski et al. 2012). Ecosystem services are described as the benefits provided by natural systems to human health and well-being extending from basic provisions including food and water, to cultural and recreational benefits (MEA 2005).

The ecosystem services provided by oyster reefs have been thoroughly summarized by Grabowski and Peterson (2007) and Coen et al. (2007). These include, in addition to oyster biomass production, the services of water filtration and pseudofeces production, carbon sequestration, shoreline and habitat stabilization, ecosystem diversification, and habitat provision. The benefits of these services range from increased biodiversity and productivity benefiting fisheries and ecological communities to reduction of greenhouse gases and mitigated effects of sea-level rise through oysters sequestering carbon in their shells and stabilizing shorelines, respectively. However, due to environmental or monetary constraints associated with restoration efforts, it is unlikely that all potential ecosystem services can be fully obtained and therefore trade-offs must often be made based on restoration goals (Nelson et al. 2009).

In practice, trade-offs made by focusing on restoring different services have been quantified in coastal landscapes. For example, Bilkovic and Mitchell (2013) found that hybrid stabilization of marsh shorelines could enhance water filtration by attracting epifauna and suspension feeders. However, they also observed localized declines in benthic productivity and nutrient cycling. Additionally, North et al. (2010) used ecological modeling to find that locations where oyster harvests are optimized may not also optimize spawning, with varying results largely influenced by local hydrodynamics. Strategies to enhance ecosystem services become more complicated when varied stressors are affecting a given species or habitat (Fulford et al. 2010). Quantification of these ecosystem services (Nelson et al. 2009, Grabowski et al. 2012) can provide metrics for weighing options and finding strategies that are most effective in reaching restoration goals.

1.1 Restoration to enhance population

The recruitment of larvae and oyster growth remains substrate limited within Virginia's coastal systems and generally across the U.S. Atlantic coastline (Mann and Powell 2007, Schulte et al. 2009). Therefore, the primary objective of oyster restoration along the Virginia coast has been to provide hard substrate for oyster larvae to land, attach, and grow to viable adults. These restoration efforts have primarily relied upon the natural transport and dispersion of larvae due to tidal currents and mixing (Fuchs and Reidenbach 2013, Hubbard and Reidenbach 2015) and the deposition of oyster and other bivalve shells along intertidal regions to create suitable benthic habitat for larval settlement and oyster growth (Whitman and Reidenbach 2012). More recent restoration projects have utilized 'oyster castles', which are concrete blocks that can interlock and be stacked, allowing for flexibility in design configuration. They have proven successful and to outperform other substrates at recruiting and retaining oysters (Theuerkauf et al. 2015). Oyster castle structures have also demonstrated the ability to promote both vertical accretion and horizontal expansion of oyster habitat (Theuerkauf et al. 2015). While vertical elevation has proven to have a positive effect on the success of oyster growth and recruitment (Bartol et al.

1999, Lenihan 1999, Schulte et al. 2009) there are environmental tradeoffs. At higher elevations oysters spend less time submerged and reduce their susceptibility to predation and sedimentation (Fodrie et al. 2014, Johnson and Smee 2014, Lenihan 1999). However, emergent time exposes oysters to greater stress through temperature, desiccation, and lowered food supply which can affect growth and survivability (Johnson and Smee 2014, Byers et al. 2015). Interstitial spacing, which can be incorporated in designs with oyster castles, can be beneficial for oyster growth in the presence of predators (Soniat et al. 2004, Hill and Wiessburg 2013), but may limit benefits to aquaculture.

1.2 Oyster restoration for coastal protection

To protect shorelines from coastal erosion, past management efforts have relied heavily on shoreline armoring by using physical structures including seawalls, bulkheads, and breakwaters (Bulleri and Chapman 2010). The goal behind these techniques is to reduce the amount of energy received at the coast, because shoreline erosion is mainly attributed to incessant wave action and shear stresses that develop and suspend sediment (Fagherazzi and Wiberg 2009). However, these infrastructure techniques have ecological disadvantages including the loss and fragmentation of coastal wetland habitat and local biodiversity, and potential for enhanced transport of sediment (Bulleri and Chapman 2010).

Recent efforts have increasingly attempted to use constructed oyster reefs as natural habitat for coastal protection. These ‘living shorelines’ minimize the use of grey matter, concrete materials, and encourage the use of biologic materials such as oyster reefs and seagrass meadows to dampen wave action reaching coasts. Living shorelines have proven to be comparatively effective in mitigating coastal erosion while also enhancing local ecology (Davis et al. 2006). The dampening effects of wave energy created by the vertical obstruction caused by natural and artificial reefs, has been shown to decrease shoreline erosion and allow for increased sedimentation (Meyer et al. 1997, Piazza et al. 2005, Borsje et al. 2010, Wiberg et al. 2019). Oyster castles, which create vertical structure and interstices, can both promote oyster growth while increasing habitat complexity and enhancing local ecology (Soniat et al. 2004, Hill and Wiessburg 2013).

1.3 Ecosystem changes in the presence of oyster reefs

Oysters function as 'ecosystem engineers' because of their ability to influence community structure (Van der zee et al. 2012). By increasing benthic sediment stability, sediment organic matter content, and habitat heterogeneity, oyster reefs can enhance the biodiversity and trophic interactions of intertidal communities (Gutierrez et al. 2003, Van der Zee et al. 2012, Donadi et al. 2013). The increased protection and shelter from waves and predators provided by reefs can lead to increased infaunal abundance and biomass in and around reefs and increased biodiversity after restoration (Castel et al. 1989, Langlois et al 2006, Van der zee et al. 2015).

As filter feeders, oysters take in nutrients by filtering the water column and removing suspended particles (Reidenbach et al. 2013), phytoplankton, and dissolved organic matter. This filtration process aids in nutrient cycling, whereby organic matter is assimilated within oysters and inorganic nutrients are excreted into the water column as particulates (Zhang et al. 2014). Oyster filtration can lead to some remineralization of nutrients and nutrient burial, increasing organic matter in sediments nearby reefs, as well as benthic respiration (Volaric et al. 2018). Changes in sediment characteristics before and after reef restoration projects have demonstrated these differences in sediment nutrients and particle size (Southwell et al. 2017), though in areas of established reefs, organic matter can vary due to local ecosystem interactions and primary producers that utilize the inorganic material (Smaal and Prins 1993, Smyth et al. 2016).

1.4 Study objectives

Because artificial oyster reefs can alter a multitude of ecosystem services, including coastal protection and sediment transport, larval settlement, oyster growth, and local biodiversity, understanding how variations in the design of restored reefs alter the relative benefits of these services is important for successful management.

In this study, artificial oyster reefs in front of an elevated vegetated marsh platform within a coastal bay along the Eastern Shore of Virginia, U.S.A. were constructed in 2017. This site was monitored before (2017) and after construction for a three-year period (2018 – 2020). A total of eight reefs were constructed with four different reef designs differing in elevation and width. Each design was replicated twice. The questions this study addressed were:

1) How does elevation of the constructed oyster reef impact wave attenuation?
2) How does the elevation and shape of the constructed oyster reef impact larval settlement, oyster density, and growth?
3) How does the presence of constructed oyster reefs impact biomass and diversity of infauna within the surrounding sediment?
4) How does the presence of constructed oyster reefs impact sediment organic matter?

2. Methods

2.1 Study Site

Studies were performed within the Virginia Coast Reserve (VCR), a National Science Foundation (NSF) funded Long-term Ecological Research (LTER) site located on the Atlantic Ocean side of the Delmarva Peninsula, Virginia, USA (Fig 1). The VCR is located within the Volgenau Virginia Coast Reserve (VVCR) which covers over 100 km of coastline in Virginia and includes the largely undeveloped habitat encompassing upland forests, coastal bays, and barrier islands, connected to the open ocean through narrow inlets. The main driver of coastal erosion in the shallow bays, with a mean depth of 1-2 m, is wind (Mariotti and Fagherazzi 2013) and is dependent on water depth, wind direction, fetch distance, and drag on the seafloor (Fagherazzi and Wiberg 2009). In the VCR, coastal bays experience low freshwater input, a tidal range of1.2 m, (Hansen and Reidenbach 2013), and a gradient of flushing created by exchange through the inlets (Safak et al. 2015). Winds are primarily from the south in the summer and north-northeast in the winter (Wiberg et al. 2019).

Within the VCR, *Crassostrea virginica,* the eastern oyster is found fringing on marshes and in patches on mudflats, predominantly in the intertidal zone (Hogan and Reidenbach 2019). Short Prong Marsh, within Hog Island Bay of the VCR, was selected to be a new long-term research site for oyster restoration. The Nature Conservancy (TNC), along with their network of community volunteers, constructed 8 oyster castle formations along the eroding marsh edge in summer 2017 (Figure 1). Each castle block weighs approximately 16 kg and measures 30.5 cm x 30.5 cm and 20 cm high. Reef formations consisted of four different designs, each having 2 replicates, where elevation and width varied. The four designs included 1 row wide x 2 tiers high, 1 row x 4 tiers high, 3 rows x 2-tiers high, and 3 rows x 4 tiers high configurations. Rows were made approximately 1 m apart and 25 m long. In total 11,048 blocks were used; each low elevation (2-teir) row used 571 castles, while each high elevation (4-tier) row used 810 blocks.

Each design was made with rows parallel to the marsh approximately 30 m from the edge and reefs were spaced 10 m apart. Those with 2 tiers are referred to as low elevation designs, and those with 4 tiers are referred to as high elevation designs. The dimensions of the oyster castles give the 2 tier, low elevation, reefs an approximate elevation of 40 cm off the seafloor and 4 tier, high elevation, reefs an approximate elevation of 80 cm. Mean water depth surrounding the constructed reefs is approximately 1 m deep, making the crests of the oyster castles for the low and high elevation designs approximately 0.6 m and 0.2 m below local mean sea level (lmsl), respectively.

2.2 Oyster Density and Size

Oyster density was measured in-situ using randomly placed 0.25 m x 0.25 m (0.0625 m^2) quadrats to count oysters greater than 1 cm in length. Sampling took place on one of each reef design. For each of the four reef designs, 3 samples were randomly placed at the design's highest tier, giving a total of 12 replicates. For both high elevation reef designs (with either 1 or 3 rows), 3 additional replicates were also completed on the 2nd tier from the bottom (2nd of 4 stacked castles). Due to the stacked nature of the oyster castles, counts on the 2nd tiers of high elevation designs were quantified using 0.12 m x 0.25 m quadrats (6 additional quadrats). Sampling on this lower tier was completed to compare directly to the upmost tier of the low elevation designs, both at the same elevation above the seafloor. During year 3 post construction, oyster lengths were also measured to nearest 0.5 cm on the top (along the 4th tier) and mid-height (2nd tier) of the high elevation design, as well as on the top (2nd tier) of the low elevation oyster reef designs. The same reefs were sampled each year data was collected.

2.3 Wave Data

Water depth and significant wave height were analyzed through deployments of RBR TWR- 2050P wave gauges. Before construction, during the winter months (February- March) of 2017 pre-construction data were collected. Wave data were again collected during spring (April-May 2018) year 1 after construction and summer (July – August 2020) year 3 post construction. Wave gauges in year 1 and year 3 post construction were placed 10 m on either side, closer to the marsh or bay, of one high elevation (3 row x 4 tier) and one low elevation (1 row x 2 tier) design. Before reef construction, wave gauges were placed at similar distances from the marsh edge in the area where reefs were to be constructed. Deployments were approximately 4 weeks long and programmed to record waves averaged every 30 minutes with 1024 bursts taken at 4 Hz. In summer 2021 (year 4 post construction), we collected data for 3 weeks over the same high and low elevation reefs in addition to the two other designs, a high elevation design with 1 row and low elevation design with 3 rows.

Water depths from wave gauges were corrected using atmospheric pressure data provided by NOAA. For each pair of wave gauges the data were matched by timestamp and sorted by corrected water depth, based on the shallower marsh-side measurements. We eliminated records from very shallow water so that each gauge was covered by at least 0.25 m of water. Data were then split into three categories based on depth as done by Wiberg et al. (2019) for shallow (< 0.75 m), intermediate (0.75 m – 1.0 m), and deep (> 1.0 m) water. These water depths bracket the tops of the different designs considering the low elevation reefs are approximately 0.4 m off the seafloor and high elevation reefs are approximately 0.8 m off the seafloor. To determine attenuation scatterplots are made comparing significant wave heights from bay and marsh gauges. Attenuation is estimated as the relative reduction in wave height as waves propagate across the reef, measured as 1 minus the slope of the trendline, with the intercept at 0, fit through the paried data.

2.4 Infauna Collection and Processing

Infauna were collected each summer for years pre-construction (2017) to year 3 post construction (2020). Sample collection occurred in June for all years, except in year 3 post construction where collection was delayed until late August 2020 due to Covid-restricted site access. Samples were collected by inserting a cylindrical 15 cm id PVC corer into the sediment 15 cm deep. For pre-construction infauna, 8 samples were taken randomly over the area where reefs were to be constructed. For the 3 years post construction, 8 samples were also taken, with 2 in proximity to each wave gauge on either side of the high and low elevation designs. Sediment was passed through a 1 mm sieve and living infauna was removed and placed in a jar with 70 % ethanol. Infauna abundance was recorded by classifying specimens into broad taxonomic classes including worms, small crustaceans (amphipods and isopods), large crustaceans (crabs), gastropods, and bivalves. The 'worm' taxon was largely composed of polychaete species but nemerteans and acorn worms (*Enteropneusta*) have also been sampled on nearby mudflats within the VCR (Murphy and Volaric 2021). Large crustaceans collected are largely epifaunic but have been included in the infauna analysis because they are representative of important benthic organisms found near oyster reefs. For worms, all biomass was collected but only individuals with intact heads were recorded to avoid double counting broken individuals. Some methodologies count fully intact specimen due to frequent damage occurring during sieving (Gorska et al. 2019), however, we chose our methods given the limited number of samples each year. Biomass was analyzed one month after collection to standardize the procedure and reduce differences that preservation time may have on weight (Howmiller 1972, Wetzel et al. 2005). Biomass was estimated by measuring the ash free dry weight (AFDW) of each sample. Samples were dried in pre-weighed combusted tins, at 60 ºC for 48 h, weighed, and then placed in a muffle furnace at 500 ºC for 6 h (Rumohr 2009). Sample weight after time in the muffle furnace was subtracted from dry weight to obtain AFDW, the mass of the organic material in samples.

2.5 Sediment Collection and Processing

A sediment core 3 cm id and 5 cm deep was also collected adjacent to each infauna core to quantify sediment organic matter each year post construction, while 10 cores were taken randomly over the mudflat pre-construction. After collection, sediment was placed in an oven at 60 ºC until dry. Sediment was powdered, and 2 g of each sample was placed in a pre-weighed and combusted tin. Samples were placed in a muffle furnace at 500 ºC for 6 h and weighed to obtain AFDW. The percent difference in sediment weight [(ash weight – dry weight/ dry weight) *100] represents the percent organic matter within each sample.

2.6 Statistical Analysis

For density we created a generalized linear model (glm) fit with a negative binomial distribution and the predictors of tier (top of 2 tier, 2nd of 4 tier, top of 4 tier), year as a continuous variable, and an interaction term between tier and year using the MASS package in R (Venables and Ripley 2002). We also fit 2 additional glms with negative binomial distributions for both low and high elevation designs to determine differences in density between the designs with 1 and 3 rows, density as a function of number of rows, year, and their interaction. High elevation designs used combined data from 2nd and 4th tiers. A one-way ANOVA was used to determine differences in oyster shell length. One-way ANOVAs were also used to determine if infaunal abundance and biomass and sediment organic matter varied between years before and after restoration. We also computed an importance value for each infauna taxon, where relative abundance and biomass were added together. High importance values indicate that a given taxon composes a larger part of the community, whether it be through abundance, biomass or size, or a combination of both. The Anova function (type II tests) in 'car' package in R (Fox and Weisberg 2019) was used to summarize test statistics and p values, and post hoc analyses were completed using the 'emmeans' package (Length 2020). Q-Q plots and visual examination of the spread in model residuals with overall model predications and individual predictors were used to assess normality and heteroscedasticity (Zuur et al. 2009).

3. RESULTS

3.1 Oyster Density

The artificial reefs successfully fostered oyster growth on all the reef designs. All oyster counts were normalized to 0.0625 m^2, and density discussed refers to oyster counts in this area. The density on 2^{nd} tiers was lower compared to that on 4^{th} tiers of oyster castles for all years (Figure 2A, Table 1). Densities on the high elevation 4^{th} tiers averaged (± standard error) 120.8 ± 4.4, 73.5 ± 4.3, and 70.3 ± 4.5 oysters for years 1, 2, and 3 post construction, respectively. Low elevation 2^{nd} tiers averaged 55.8 ± 5.1, 31.0 ± 2.5, and 28.7 ± 1.4 oysters for years 1, 2, and 3 post construction, while for high elevation 2^{nd} tiers averaged 52.0 ± 10, 46.0 ± 6.5, and 46.0 ± 5.3 oysters (Table1). Densities were highest 1 year after construction compared to subsequent years and the greatest standard error for density on the 2^{nd} tier of high elevation designs.

Each of the explanatory variables from the linear model explained oyster density including, tier ($\chi_{2,51}$=118.8.1, $p < 0.0001$), year ($\chi_{1,50}$= 32.7, $p < 0.0001$), and the interaction between the two variables ($\chi_{2,48}$= 8.5, p = 0.01). In 2018 densities on the 2nd tiers of the high and low elevation designs were similar to one another (p = 0.89), but both were lower than that on the 4th tier (p < 0.0001) of the high elevation design. In later years, densities on the 2nd tiers remained lower than 4th tier densities, but the density on the 2nd tier of the high elevation design was greater than that on the 2nd tier of the low elevation designs in both 2019 (p = 0.01) and 2020 (p <0.001). Designs with 1 and 3 rows differed in density with year on low elevation designs ($\chi^2_{1,15}$ = 31.5, p < 0.0001) and high ($\chi^2_{1,33}$ = 1.5, p < 0.01) elevation designs, as the previous elevation analysis suggested. However, densities were similar for 1 and 3 row designs on low elevation reefs ($\chi^2_{1,16}$ = 0.003, p = 0.96) and high elevation reefs when using combined samples from all tiers for total biomass, density from 4th and 2nd tiers, ($\chi^2_{1,34}$ = 1.5 , p = 0.23) was found (Figure 3, Table 2).

For year 3 oysters were greater in size along the high elevation reef designs (Table 1, Figure 2B). For the high elevation design the mean length (± standard error) on the 4th tier was 7.4 ± 0.1 cm and the mean for the 2nd tier was 7.1 ± 0.15 cm. For the low elevation design the mean length for oysters on the 2nd tier was 6.1 ± 0.23 cm. These data show that by the year 3 post construction oysters were largely mature (about 7.5 cm [Lenihan 1999], Figure 2B). Length differed with tier position ($F_{2,14}$ = 25.4, p < 0.0001) and oysters growing on low elevation designs were smaller than oysters growing on high elevation designs, when compared to either the high elevation 4th tier (t_{14} = -6.8, p < 0.0001) or the lower 2nd tier of the t-tier design (t_{14} = -5.5, p < 0.001) samples. Length was similar on the tiers (4th and 2nd of 4) of the high elevation design (t_{14} = -1.4, p = 0.4).

3.2 Wave Data

Mean water depths and offshore significant wave heights were similar for each deployment, before and after reef construction (Table 3). For year 1, 3, and 4 post construction average water depths were 0.91, 1.03, and 1.07 m respectively, nearing the top of the high elevation reefs. Wave height comparison between offshore and onshore before reef construction (2017) found little attenuation over the approximate 25 m distance between the gauges. Wave heights during years 1, 3, and 4 post construction (2018, 2020, and 2021) are shown in Figure 4 and wave attenuation statistics are included in Table 4. The approximately month-long sampling in years 1, 3, and 4 indicated no wave attenuation over the low elevation design. The high elevation design fostered 13 % attenuation in year 1, 21 % attenuation in year 3, and 10 % in year 4, when averaged across all wave conditions and water depths. Since reef construction was completed in 2017 after the spawning season, the year 1 data collected before the next spawning event indicate wave attenuation was caused primarily by the oyster castles, not due to the presence of oysters. The reef structure increased attenuation with increase in water depth during year 1 with no oyster growth, 5%, 14%, and 15 %, respectively for shallow, intermediate, and deep water. In years 3 and 4 after considerable oyster growth, wave attenuation was measured to be 40 %, 25 %, and 13 % for shallow, intermediate, and deep water, respectively in year 3 and 36 %, 15 %, and 1 % in year 4. While there was a reverse pattern for attenuation at different depth ranges, with additional oyster growth, the high elevation design is much more effective at attenuating waves than having either no reef (pre-construction) or solely the oyster castle structure (year 1 post construction). The additional data collected in 2021 for high and low elevation designs with different rows show that the number of rows had minimal effect on wave attenuation. The high elevation design with 1 row attenuated waves similar to (41 %, 11 %, and 6 %, for shallow, intermediate, and deep water) the high elevation design with 3 rows. The low elevation design with 3 rows had minimal wave attenuation (26 %, 2 %, and 0 % in shallow, intermediate, and deep water) and compared similarly to the low elevation design with 1 row.

3.3 Infaunal Community

Total infaunal abundance, with data combined from 8 cores, was highest before reefs were constructed (Figure 5). Year 1 post construction samples had the lowest total infaunal abundance, followed by a rebound in year 2, though still lower than the initial total, followed by a slight decrease in year 3 (Table 5, Figure 5). Abundance differed between years ($F_{3,28}$= 3.6, $p = 0.03$); pre-construction infauna were more abundant than in year 1 post construction ($t_{28} = 2.97$, $p = 0.03$), with an estimated marginal mean difference of 10.4 individuals. After construction, different taxa, other than worms, compose a larger percent of the overall fauna collected. However, the difference in abundance was driven by worm abundance, which differed before (2017) and after (2018) construction (z-ratio = 2.688, $p = 0.04$).

Total biomass (g AFDW) was also highest pre-construction compared to the 3 years post construction. Similar to abundance, biomass was lowest in year 1, followed by increasing biomass in year 2, and a slight decline in year 3 post construction (Table 5, Figure 6). However, the biomass pre-construction was heavily skewed by 1 large bivalve. This is apparent when comparing Figures 5 and 6 for abundance and AFDW. Without this single specimen the total biomass, pre-construction is similar to that in year 1, but is less than that observed in years 2 and 3 post construction. Overall, no difference in the biomass between years ($F_{3,28}$ =1.03, $p = 0.39$) was found. In years 2 and 3 post construction, crustaceans also composed larger proportions of the total biomass. The larger variation in sample biomass in year 3 post construction may be explained by the increased presence of larger fauna, with a greater proportion of crustaceans collected.

The importance of gastropods (snails) declined through time after construction, while the importance of worms remained high throughout all years (Figure 7). The importance of small crustaceans was very high the year after construction and then fell, while the importance of large crustaceans (crabs) increased throughout the years after oyster reef construction.

3.4 Sediment Composition

Sediment organic matter increased after construction of the oyster reefs (Table 5). Values ranged from 1.8 % (year 1 post construction) to 2.5 % (year 3 post construction). Despite the increasing trend after construction, analysis found the percent organic matter was not different between years ($F_{3,30}= 1.9$, $p = 0.15$).

4. DISCUSSION

4.1 Oyster Population

Oyster growth on the high elevation reef design was higher than growth on the low elevation designs. This effect of elevation was also found by other studies where higher elevations contributed to more successful recruitment and growth (Bartol et al. 1999, Lenihan 1999, Schulte et al. 2009). This has been attributed to greater flow rates occurring over more elevated reefs as well as less susceptibility to sedimentation (Lenihan 1999, O'Beirn et al. 1999). The interaction between oyster density on different tiers and year since construction makes interpretation of elevation less clear. Data from year 1 post construction of the reefs indicated clear differences between densities on low and high elevation reef designs, while densities in later years were more similar overall. However, large differences between tiers at the same elevation (tier 2 of the low elevation, and tier 2nd of 4 on the high elevation reef) were shown to exist 3 years post construction. These results emphasize that time, as the reef develops, is important to consider when monitoring overall success of reef designs. The results also indicate that the effect of sheltering provided by higher tiers may become more important as oysters grow and become more susceptible to predation and other physical factors (Bartol et al. 1999, O'Beirn et al. 2000, Whitman and Reidenbach 2012). Additionally, we found some indication that multiple rows may impact oyster densities on high elevation designs, the differences were slight and our data shows that density is more dependent on reef elevation than reef width.

4.2 Coastal Protection Potential

Observed wave data were captured pre-construction, after construction with little growth (year 1), and after construction with mature oysters (years 3 and 4). While minimal changes in significant wave height from bay to marsh occurred over the low elevation oyster reefs, wave attenuation increased over time due to enhanced oyster growth for the high elevation reef designs. Because the data from year 1 come from a time when there was minimal oyster growth on the reefs, the difference between the year 1 and years 3 and 4 post construction data show the difference in wave attenuation between the structure itself and with the addition of oysters. Therefore, not only are the structures acting to reduce wave height, and consequent energy from reaching the marsh, but oysters themselves are adding to this service of coastal protection. Little variation in attenuation was observed at the low elevation reef design under intermediate (0.75 m to 1 m water depth) and deep water (> 1 m depth), likely because at these deeper water levels minimal reduction in wave orbitals and interaction with the reef structure occurred. Attenuation was affected most by design elevation, while reef width (1 or 3 rows) had minimal effect. The data from 2021, which examined attenuation over one of each design, found that attenuation was similar for reefs that were the same in elevation even though they differed in the number of rows. It should also be noted that for the high elevation reef designs, we observed a greater amount of attenuation in shallower water compared to deeper water. Similar findings were found within the VCR at different locations (Wiberg et al. 2019) and this is likely due to the increased ability of oysters to interact with wave orbitals in shallow water, causing greater frictional resistance, as well as initiate wave breaking before reaching the marsh edge. The low elevation designs, even with increased width (of 3 rows), had little effect on attenuation, although some moderate wave attenuation was observed for the low elevation design with 3 rows when in deep water.

4.3 Infaunal Community Responses

The infaunal community and sediment composition experienced change as the oyster reefs matured. While worms dominated the infauna community both before and after restoration, larger infauna began to compose greater proportions of biomass and abundance as time since post construction increased. However, abundance of taxa other than worms was relatively sparse, and some of the species collected are generally epifauna. The sparse abundances of the other taxa limits the interpretation of their overall increase from amounts collected prior to restoration and different sizes and species of worms were also not accounted for. However, increases in large crustaceans (such as crabs) near reefs was likely due to increased habitat and shelter and/or that reefs may act as a foraging location (Harwell et al. 2011, Hill and Weissburg 2013). Increases in higher order species can alter community dynamics influencing populations of fish and other transient species (Rodney and Paynter 2006, Gregalis et al. 2009). The first summer of sampling after restoration also saw the lowest abundance of infauna, indicating ta disturbance effect observed in year 1 post construction. Sampling in year 3 also occurred the last week of August 2020, rather than early June as in the previous 3 years due to lab accessibility due to Covid-restrictions. Therefore, some patterns observed in year 3 were possibly affected by seasonality and variability of infauna within coastal estuaries (Harwell et al. 2011).

Oyster restoration studies have reported rapid responses to sediment enrichment as soon as a year after oyster restoration (Davis et al. 2006, Southwell et al. 2017), while others have reported benefits of restoration, such as infaunal community enhancement, to lag behind the growth of oysters (Liu et al. 2018). Infaunal communities are also subject to great variability both spatially and temporally (Grabowski et al. 2005, Ziegler et al. 2017). Habitats with muddy sediments can take longer time to recover biotic communities compared to cleaner sands (Dernie et al. 2003). This could explain the general increase in infaunal abundance and biomass in the years after restoration observed (Figures 5 and 6). Similarly, change in sediment composition is also likely to be a more gradual process taking place over longer periods of time, especially within our samples using cores taken 5 cm deep. Our findings therefore support previous literature that suggests different services are likely to respond at different timescales (La Peyre et al. 2014, Volaric et al. 2020), with oyster growth and wave attenuation observed more quickly than the responses observed in infaunal communities and sediment composition. This emphasizes the need for long-term monitoring. While the high elevation design in our study worked best to promote multiple ecosystem services, managers should examine reef design for relative elevation compared to marsh elevation and water depth.

4.4 Study Limitations

Although we found greater oyster densities and oyster lengths with higher reef elevations, presumably a maximum height exists above which oyster densities and growth rate will decrease, due to decreases in submergence time and increased exposure to atmospheric conditions. An analysis of existing oyster reef elevation throughout the VCR (Hogan and Reidenbach 2019) found that the oyster reef crests ranged from -0.7 to 0.1 m lmsl. Considering the mean water depth in year 1 post construction was 0.91 m, 1.03 year 3, and 1.07 m in year 4, at 80 cm above the seafloor the high elevation reefs were found to be approximately -0.1 to -0.3 m below the msl calculated from wave gauges, placing them about 0.2 m below this maximum elevation range. Future studies could construct reefs both above and below this elevation to test limits on oyster growth. Still, these data indicate that perhaps elevation in addition to tier position are both important in determining oyster growth and survivability. Although there may be some change in elevation due to structure settlement, there is a need to continuously monitor reef elevation because oyster growth adds to the elevation with time. This also highlights an advantage that green nature-based solutions have over traditional solutions, where green solutions can adapt and grow to meet changes such as rising sea levels, continuously buffering coasts, while traditional concrete structures are made to adjust and fit an environment for only a snapshot in time.

We recognize the additional limitations established by the sampling procedure set in 2018 for oyster density analysis. Initially we were primarily concerned with reef elevation on wave attenuation and sampled just 1one reef of each design. Our 2018 oyster density sampling was limited in replication due to the constraints on the construction of restored oyster reefs and field logistics. However, we collected 3 subsamples from each reef design and sampled reefs over time (3 years), yielding a total oyster density sample size of n = 9 for each design. We believe that this degree of replication is sufficient to test our hypotheses, however, increased sampling including both replicates of designs and repeated measures over time would provide more robust results. Because this is an un-replicated local study, it would also be beneficial to replicate the study design in different locations to see if general conclusions made from one site can be made for other regions and site conditions.

Other biological factors could also affect the outcome of oyster restoration success. We observed the appearance of algal cover on top of tiers and between rows of different designs. Although differences in algal cover were not quantified in this study, algal cover presents another factor that can affect oyster growth and benthic processes not reflected in our data (Thomsen and McGlathery 2006, Volaric et al. 2019). Density was higher year 1 compared to year 2 and 3 post construction, which reported similar oyster densities. This could be due to a growth response, where there is a greater amount of recruitment and development of juveniles early on, but density is reduced as fewer oysters successfully reach maturity (Gosselin and Qian 1997), even though overall biomass may have increased with fewer, larger oysters. Although we did not take length measurements year 1 post construction, it is likely that the oysters were not mature at this time, and therefore although densities were greater, biomass was likely less at this time based upon oyster shell length to biomass ratios reported in the literature (Southworth et al. 2010).

4.5 Conclusion

Our study provides evidence that oyster reef design differentially affects ecosystem services provided by oyster restoration. Specifically, higher elevation reefs had more dense oysters with greater lengths on upper tiers compared to lower tiers and wave attenuation was also greatest over the higher elevation design. Wave attenuation increased as the reef matured. Together these data indicate that the higher elevation reef design at Short Prong Marsh works best to foster both oyster growth and coastal protection. The width of the reef (1 row vs. 3 rows) had minimal effect on oyster densities. The presence of restored oyster reefs increased the incidence of higher trophic level species, with crustaceans composing larger proportions and having greater importance of total infauna collected as oyster reefs matured, although abundances were sparse before and after restoration. Additionally, we observed an increasing trend in organic matter with time following restoration. While our results agree with literature that higher elevation reefs better foster oyster growth and wave attenuation, the data also emphasize the need for continued monitoring over long periods of time as reefs mature and accrete vertically.

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6. TABLES

Table 1. Oyster density (per 0.0625 m^2) ± standard error (se) on high and low tiers completed years 1, 2, and 3 post construction and mean oyster length (cm ± se) for data collected in year 3 post construction. Mean length was calculated after 1 outlier was removed

Year	Elevation	Mean Count (±se)	Mean length (cm ± se)
2018	2	55.8 ± 5.1	--
	2 of 4	52.0 ± 10.0	--
	4	120.8 ± 4.4	--
2019	2	31.0 ± 2.5	--
	2 of 4	46.0 ± 6.5	--
	4	73.5 ± 4.3	--
2020	2	28.7 ± 1.4	6.1 ± 0.235
	2 of 4	46.0 ± 5.3	7.1 ± 0.15
	4	70.3 ± 4.5	7.4 ± 0.10

Table 2. Oyster density (per 0.0625 m^2) ± standard error (se) on high and low elevation designs with 1 or 3 rows for years 1, 2, and 3 post construction

Year post construction	Design	Number of Rows	Mean Density (± se)
1	High	1	88.2 ± 19.5
		3	84.7 ± 14.5
	Low	1	53.3 ± 6.8
		3	58.3 ± 4.0
2	High	1	67.2 ± 8.3
		3	52.3 ± 6.9
	Low	1	34.3 ± 1.2
		3	27.7 ± 3.0
3	High	1	63.8 ± 7.2
		3	52.5 ± 6.5
	Low	1	27.3 ± 0.62
		3	30.0 ± 1.9

Table 3. Mean and maximum values for water depth and significant wave height (Hs) from combined marsh and bay- side wave gauges for each of the sampling periods including pre-

construction (2017) and year 1 (2018) and 3 (2020) and 4 (2021) post construction. Values were calculated from data collected when the marsh-side gauges were in at least 0.25 m of water

	Location	Depth (mean ±se /max) m	Hs (mean ± se/max) m
Pre-construction	Bay	1.34 ±0.01/2.07	0.06± 0.003/0.37
	Marsh	0.63± 0.01/1.38	0.06± 0.003/0.38
Year 1	Bay	0.99 ±0.006/ 2.05	0.09± 0.001/0.40
	Marsh	0.83 ±0.006/1.98	0.09± 0.001/0.36
Year 3	Bay	1.19± 0.01/2.47	0.06± 0.001/0.49
	Marsh	0.87 ±0.01/1.87	0.06± 0.001/0.44
Year 4	Bay	1.19±0.01/2.19	0.04±0.001/0.23
	Marsh	0.95 ±0.01/1.91	0.04±0.001/0.23

Table 4. Percent attenuation from trendlines and R^2 values for scatterplots comparing marsh and bay-side significant wave heights for all data and each water depth (shallow (< 0.75 m), intermediate (0.75 – 1.0 m), and deep (> 1.0 m)) for each deployment, including pre-construction (2017) and years 1 (2018) and 3 (2020) and year 4 (2021) post construction. An asterisk indicates marginal wave growth (slope greater than 1) as indicated by the data.

	Water Depth	Pre-construction	Year 1		Year 3		Year 4			
Bay vs marsh		No reef	Low	High	Low	High	Low 1 row	Low 3 row	High 1 row	High 3 row
Attenuation	All	2 %	1 %	13 %	0 %	21 %	0%*	2%	14%	10%
R^2		0.99	0.98	0.95	0.98	0.93	0.91	0.94	0.91	0.94
Attenuation	Shallow		1 %	5 %	0 %	40 %	11%	26%	41%	36%
R^2			0.98	0.85	0.98	0.91	0.88	0.89	0.85	0.93
Attenuation	Int.		1 %	14 %	0 %	25 %	0%*	2%	11%	15%
R^2			0.98	0.98	0.98	0.95	0.92	0.95	0.96	0.96
Attenuation	Deep		0 %	15 %	0 %	13 %	0%*	0%*	6%	1%
R^2			0.99	0.99	0.98	0.95	0.93	0.97	0.94	0.96

Table 5. Mean infaunal abundance, biomass (g AFDW), and percent sediment organic matter (OM)) ± standard error (se) for samples collected pre-construction (2017) through year 3 (2020) post construction

Year	Abundance (count ± se)	AFDW (g ± se)	OM (% ± se)
Pre-construction	18.8 ± 2.9	0.11 ± 0.02	2.05 ± 0.11
1	8.4 ± 1.8	0.12 ± 0.02	1.77 ± 0.28
2	12.5 ±1.8	0.18±0.03	2.15 ± 0.34
3	9.4 ±3.1	0.17 ± 0.05	2.52 ± 0.13

7. FIGURES

Fig 1 Study site showing a) the VCR located on the eastern side of the Delmarva Peninsula and the location of Short Prong Marsh located within the VCR (black circle) and the VCR in the context of the surrounding states, b) the random arrangement of the reef designs running parallel to the Short Prong Marsh edge(reef designs are indicated as 1 = 1 row x 2 tiers, 2 = 1 row x 4 tiers, 3 = 3 row x 3 tiers, and 4 = 3 rows x 4 tiers), and c) oyster castles before settlement in 2017 and d) year 3 post construction (2020)

Fig 2 Barplots for oyster a) densities during years 1 – 3 post construction (2018 – 2020) computed from counts within 0.25 m x 0.25 m quadrats and oyster b) lengths measured for a subset of oysters with quadrats year 3 (2020); one outlier was removed from the length dataset. Tier 2 is from the second tier of low elevation designs, while tiers 2 of 4 and 4 are from corresponding tiers of the high elevation designs.

Fig 3 Densities of oysters analyzed each year post construction for designs with 1 and 3 rows of A) high elevation and B) low elevation designs

Fig 4 Scatterplots showing the attenuation for the low (1 row x 2 tiers; left panel) and high (3 rows x 4 tiers; right pannel) elevation designs for years 1 (2018), year 3 (2020) , and year 4 (2021) post construction with attenuation analyzed for shallow (< 0.75 m, blue), intermediate (0.75 – 1.0 m, orange), and deep (> 1.0 m grey) water. Trendlines and R^2 values for each water depth range are displayed. Attenuation is estimated as the relative reduction in wave height as waves propagate across the reef, measured as 1 minus the slope of the trendline, with the intercept at 0. A 1:1 line (black) was added for comparison and its slope of 1 would indicate that bay and marsh wave heights were the same

Fig 5 Infaunal abundance (count) for a) each taxon from combined 8 samples each year and b) the proportion of each taxon from the combined data

Fig 6 Infaunal AFDW (ash free dry weight) for a) each taxon for combined 8 samples each year and b) the percent of AFDW for each taxon for combined samples. In pre-construction data (2017) the outlying single bivalve (1.251 g) was removed when analyzing differences in sample abundance between years in the one-way ANOVA

Fig 7 Importance value for each taxon found in each year’s samples. Importance value was calculated by adding the proportion of each taxon’s abundance and biomass in the combined 8 samples collected each year. A) For pre-construction samples (2017), the importance value was only calculated for 1 bivalve, because AFDW was combined for worms and small crustaceans that year. b) The years after restoration (2018 – 2020, right) emphasize the increasing importance of large and small crustaceans

Figure 1:

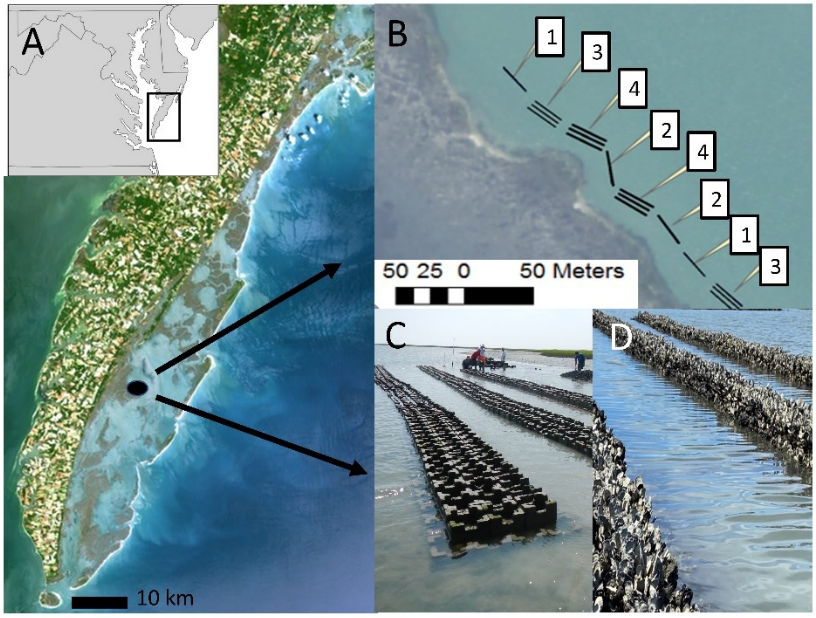
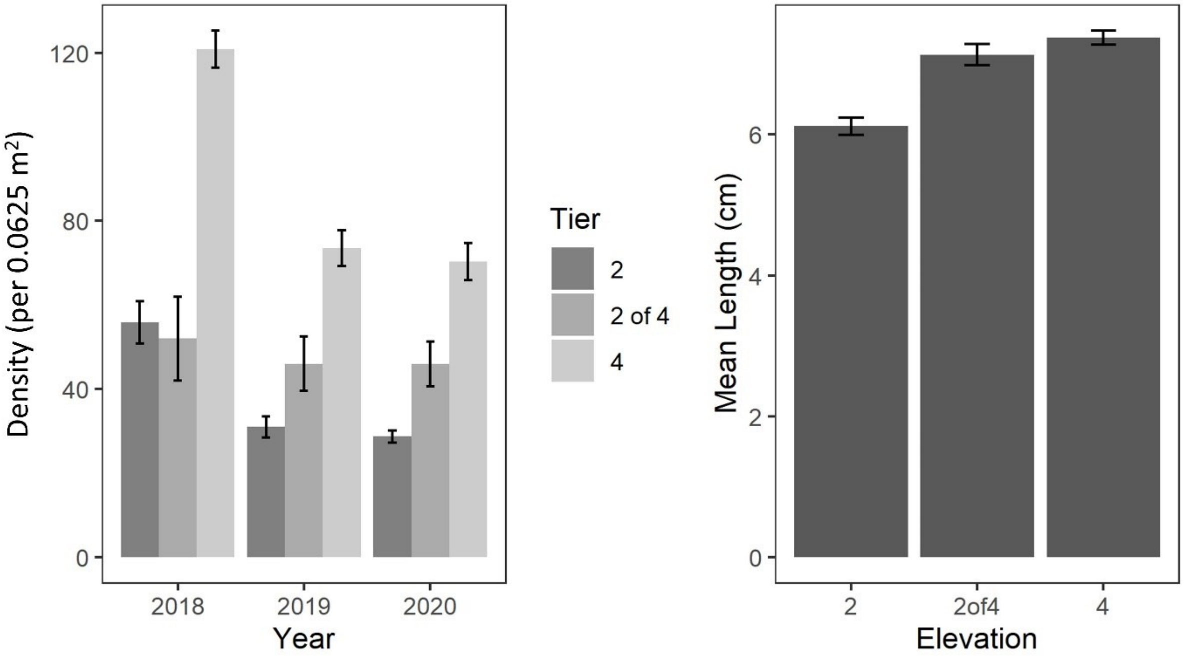


Figure 2:



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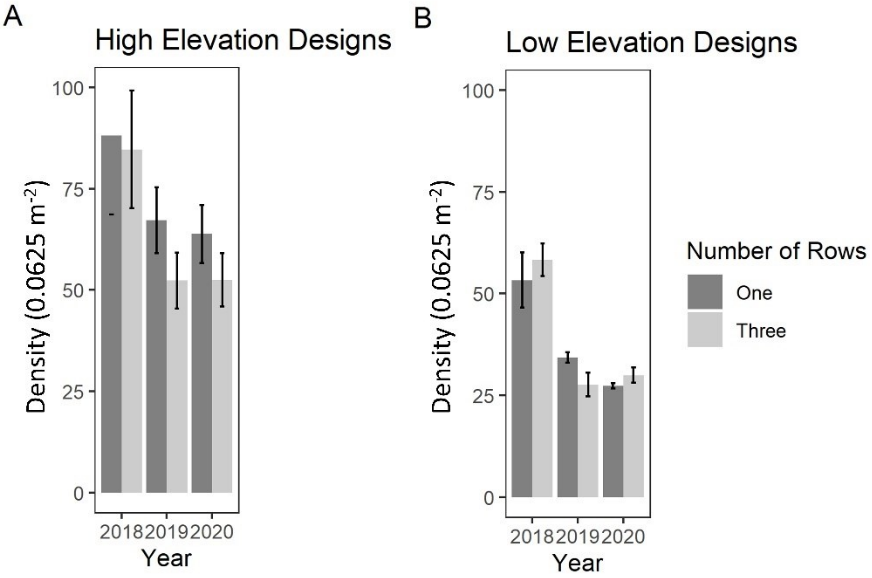

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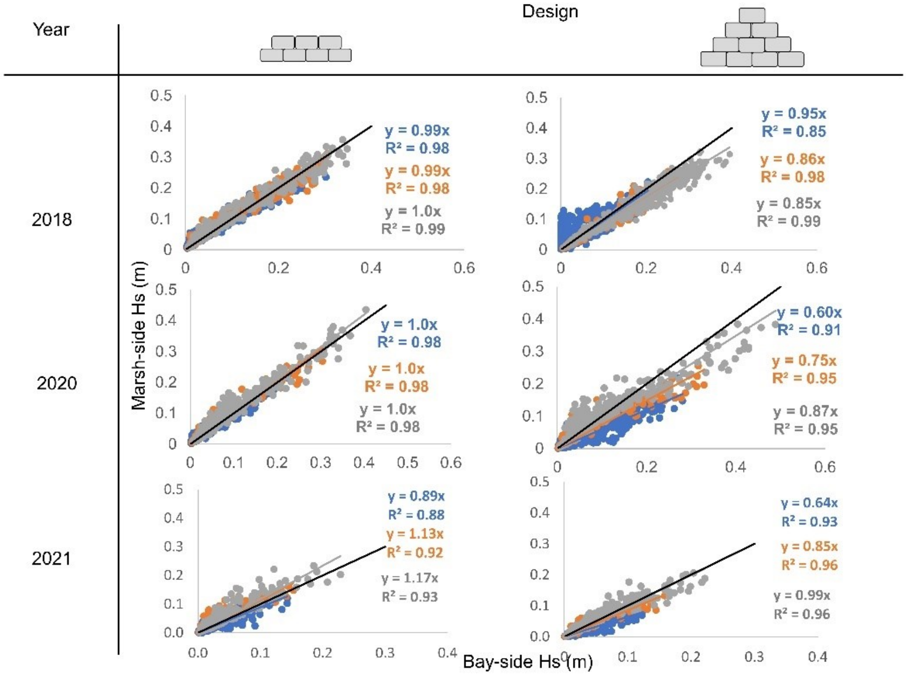

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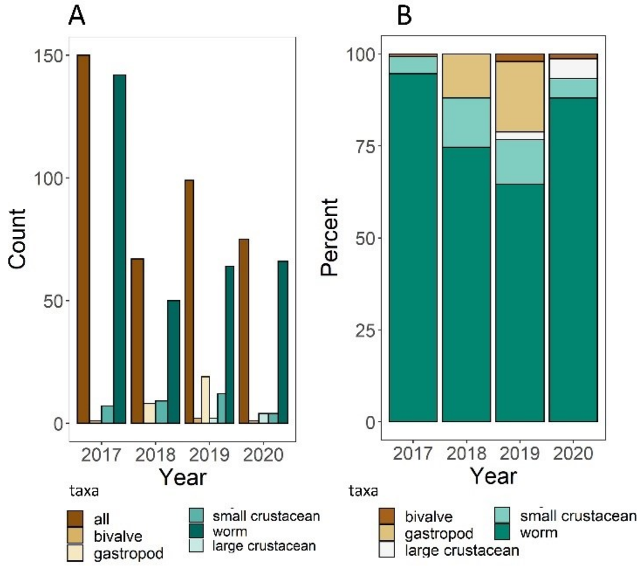

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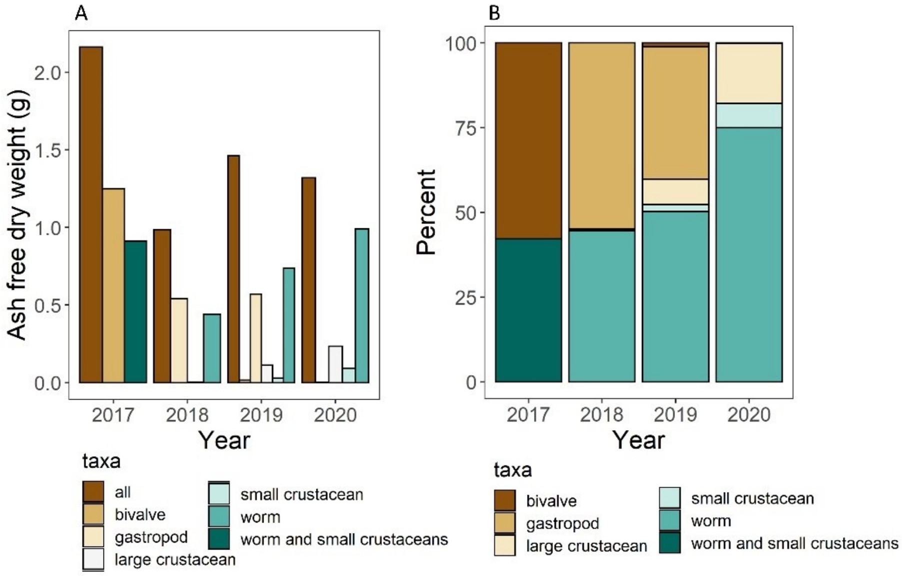
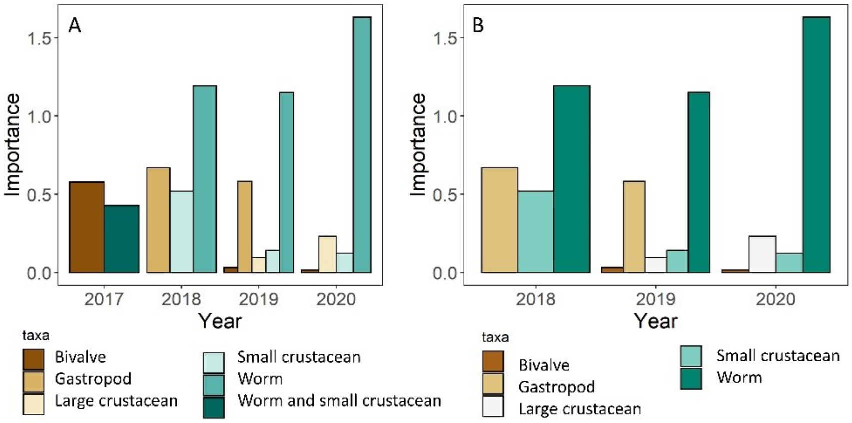


Figure 7:


A
B
Importance
0.0
0.5
1.0
1.5
2017
2018
2019
2020
Year
taxa
Bivalve
Gastropod
Large crustacean
Small crustacean
Worm
Worm and small crustacean