

Gradients In Success: The Impact of Wave Energy, Elevation and Predation on Oyster Reef Restoration

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ABSTRACT

The structure of coastal communities varies spatially and temporally in response to abiotic and biotic stressors. Local environmental conditions can be modified by the presence of a foundation species, whose dominant physical presence facilitates the growth of other organisms by ameliorating stress, providing settlement substrate and increasing resources. Oyster reefs (*Crassostrea virginica*) are an important foundation species found in estuarine environments. Oyster reefs form three-dimensional, structurally complex, biogenic habitats, that modify sediment and wave dynamics and ameliorate stress for community associates. Furthermore, they also act as a form of green-infrastructure, decreasing erosion rates and preventing shoreline loss. Because of their numerous benefits, efforts have been made to restore oyster reefs globally, with varying levels of success. Variability in the success of these restoration projects may be due to a lack of understanding of the abiotic and biotic factors that govern reef ecology. To better understand how abiotic and biotic processes regulate intertidal oyster reef community structure and their effects on restoration, we investigated the following research questions: 1) How does wave energy below 500 J/m affect oyster abundance? 2) How does reef crest height affect oyster abundance? 3) How does wave energy mediate oyster consumption? 4) How does reef relief mediate consumption of oysters?

Oyster breakwaters of two different reliefs (high vs. low) were constructed to assess how reef relief affects oyster abundance. Wave gauges were built and deployed to monitor the local wave energy environment at each site. A manipulative field experiment was used to quantify consumption with different relief and caging treatments. Results suggest that constructing reefs with high vertical relief significantly increases oyster abundance. However, the interaction between reef crest elevation and wave energy can modify this relationship, causing site-level differences in oyster abundance. Furthermore, juvenile oyster consumption was not dictated by relief and instead was site specific, most likely due to differences in predator identity at each site. This suggests that when reefs attain high oyster densities, they can support numerous community associates. The accumulation of high oyster densities on an alternative reef material, like OysterCatcher™ material, suggests that this substrate is suitable for future oyster restoration projects. However, practitioners and researchers must be aware of the effects of environmental factors such as wave energy when restoring reefs. Further research is needed to understand how human changes to the environment, such as altered wave energy due to high boating traffic, interacts with design characteristics and reef ecology to impact restoration successes and failures.

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Introduction

Most nearshore coastal ecosystems are defined by dominant foundation species that provide overall structure to the communities. Also known as habitat-forming species, foundation species have large positive effects on other community inhabitants by providing substrate, modifying environmental conditions, and increasing food supply to the area (Bruno and Bertness 2001). Referred to as “ecosystem engineers,” these organisms facilitate the establishment of other populations by providing spatial refuge through their complex structures (Bruno and Bertness 2001; Bell et al. 1991). In many cases, the physical habitat structure provided by a foundation species directly dictates the distribution and abundance of associated species through provision of critical resources such as colonization space (Underwood and Denley 1984) and refuge from predation (Huffaker 1958), competition, (MacArthur 1984), and disturbance (Dayton 1971). Therefore, for most coastal organisms, the initial presence of foundation species is necessary before the establishment of other community residents.

While foundation species ultimately modify local environmental conditions to facilitate the growth of other organisms, they too are part of that environment and are subsequently subjected to the same stresses controlling their own establishment, persistence, and distribution across the landscape (Stallins 2006; Stoffel et al. 2013). The structure of communities varies temporally and spatially in response to abiotic and biotic factors (Menge and Sutherland 1987). Understanding how factors like predation, physical stress, and habitat complexity alter the distribution, abundance, and diversity of communities has long been a research interest for ecologists. In 1957, Hutchinson proposed his multidimensional niche hypothesis, predicting that species performance is determined by a combination of multiple abiotic and biotic parameters (Hutchinson 1957). To expand upon this work, Menge and Sutherland developed a conceptual

framework to first investigate how variations in ecological processes, such as disturbance, predation and competition, influence patterns in community structure and second, how environmental stress gradients alter the magnitude of influence of those same ecological processes on community dynamics (Menge and Sutherland 1987).

Environmental stress gradients occur throughout all habitats and can be a determinant for foundation species presence and abundance across the landscape. Environmental stress can take on two forms; physical stresses exert themselves on organisms through mechanical force, like wave exposure or sediment instability, while physiological stresses, like temperature or light levels, influence the rates of biogeochemical processes (Menge and Sutherland 1987; Bowman and Hacker 2019). Total environmental stress experienced by an individual organism, or a community, is rarely due to a single factor, but typically the result of multiple environmental drivers interacting in complex, non-additive ways (Crain et al. 2008). Environmental stresses can vary spatially, with regional and local processes creating a mosaic of environmental drivers throughout the landscape (Kroeker et al. 2016). Variation in the spatial overlap and magnitude of drivers can cause major differences in species performance over relatively small scales, potentially leading to the establishment of geographic hot spots or cool spots, where species fitness and/or performance is high or low (Brown 1995).

The Menge-Sutherland Environmental Stress Model posits that the relative importance of predation, competition, and physical disturbance for regulating community structure, varies across environmental gradients (Menge and Sutherland 1987). At high levels of environmental stress, physiological limitations of individual organisms control community composition, typically creating communities consisting only of sessile organisms, who are assumed by the model to be more tolerant of environmental stress (Menge and Sutherland 1976). When

conditions are severe, mobile organisms will avoid stress by leaving the habitat or reducing their activity; therefore, in stressful conditions, predation by consumers will have no effect on basal foundation species biomass. Competition for space will also be limited by different basal species tolerance for stress. As stress decreases to intermediate levels, competition between basal species increases; this is because even in moderate conditions, top consumers are still ineffective at controlling basal species abundance, which can then attain high densities, causing sessile organisms to compete for space. Lastly, at low levels of environmental stress, predation is the dominant factor controlling community composition as consumers effectively decrease prey abundance and lessen the effects of competition (Menge and Sutherland 1987).

Intertidal oyster reefs (*Crassostrea virginica*) in North Carolina provide a model system to explore how environmental stress gradients influence the relative importance of abiotic and biotic drivers for determining a foundation species distribution and abundance (Fodrie et al. 2014). As an ecosystem engineer, oysters form 3D, structurally complex, biogenic habitats (Lenihan 1999; Lenihan et al. 2001), that modify sediment and wave dynamics and ameliorate stress for community associates (Corenblit et al. 2011). Through their physical presence, oyster reefs maintain estuarine biodiversity by providing space for colonization, foraging substrate, and refuge (Arve 1960; Bahr and Lanier 1981; Lenihan et al. 1998) supporting rich assemblages of fish and invertebrate populations (Wells 1961; Ulanowicz and Tuttle 1992; Coen et al. 1999; Peterson et al. 2003; Grabowski et al. 2005). Furthermore, oyster reefs provide essential ecosystems services to coastal communities including serving as nursery grounds for economically important fish and shellfish species (Beck et al. 2001; Coen et al. 1999), providing shoreline erosion protection and reducing marsh retreat through wave energy attenuation, and mitigating the effects of sea-level rise (Scyphers et al. 2011; Dame and Pattern 1981; Meyer et

al. 1997; Piazza et al. 2005). Unlike engineered shoreline protection approaches, such as bulkheads or seawalls, which may require repair after large storm events and cannot keep pace with sea level rise, oyster reefs bind sediments, promote vertical accretion, and maintain their own habitat, making them self-sustaining elements of coastal protection (Gittman et al. 2015; Ridge et al. 2015; Walles et al. 2016; Bruno and Kennedy 2000; Bruno et al. 2003).

Despite their numerous ecosystem services, over eighty-five percent of oyster reefs have been lost worldwide (Beck et al. 2011). Given their economic and ecological importance, coastal managers and researchers have recently focused their efforts on restoring intertidal oyster reefs with the goal of sustaining estuarine species diversity, fishery production and nature-based shoreline stabilization tactics. To meet those goals, projects must successfully restore the structurally complex biogenic habitat and recreate its functional properties (Lenihan 1999). In North Carolina, numerous attempts at restoring oyster reefs have been made over the last two decades, with some projects exceeding functional live density thresholds, while others just a few meters away have failed completely (e.g., NC Division of Marine Fisheries enhancement sites 95-965 and 96-049, J. Fodrie, *personal observations*; Fodrie et al. 2014; Keller et al. 2019). These disparities in success between restoration projects points to a lack of understanding of how stress gradients influence the production of this foundation species, leading to trial-and-error approaches without underpinning the population and community ecology dynamics that control the establishment and persistence of oyster reefs in intertidal estuarine ecosystems (Fodrie et al. 2014). To meet restoration goals and increase project success, research must address both the abiotic and biotic factors governing reef ecology.

Application of the Menge-Sutherland Environmental Stress model to oyster reef ecology may help reveal the mechanisms driving oyster restoration project failure and success.

Environmental stress, in the form of wave energy, can control the distribution of intertidal oyster reefs throughout the landscape (Corenblit et al. 2011). Wall et al. (2005) found a causal relationship between high wave energy exposure and reduced probability of reef success. Furthermore, Bahr and Lanier (1981) posited that wave energy regimes above certain thresholds can preclude the establishment of intertidal oyster reefs. Building off that research, Theuerkauf et al. (2017) found that natural intertidal oyster reefs had a narrow wave exposure threshold of approximately 500 J/m where above that, reefs did not exist. They hypothesized this was possibly due to wave energy shifting sand and moving individuals/collections of oysters, resulting in suboptimal orientation, and reducing juvenile potential for survival (Campbell 2015). In areas where wave energy is driven by boat wake waves, this threshold may be lowered, as some studies have found that boat wake waves tend to be more harmful to sediment stability when compared to tidal flow and natural wind waves (Foda 1995; Limerinos and Smith 1975; Parnell et al. 2007). This is potentially due to the increased wave height of boat wakes with larger orbital velocities and higher shear stress on the seabed that leads to greater sediment destabilization (Schroevens et al. 2011). Therefore, substrate retention in areas of high wave energy has been identified as a key determinant for maximizing juvenile oyster survival and promoting reef growth and persistence (Theuerkauf et al. 2017). Previously, oyster restoration projects typically consisted of placing loose, unconsolidated oyster shell or mesh bags filled with recycled oyster shell along an intertidal shoreline to provide settlement substrate for oyster larvae. However, many of these studies have been met with limited success, especially in areas of high wave energy. Scyphers et al. (2011) found despite adequate recruitment, substantial mortality prevented reef cementing and success; physical disturbance by wave energy caused the loose shell to expand, flatten and potentially become buried, decreasing potential settlement

substrate. Similar mechanisms were proposed in Keller et al. (2019) where the authors proposed that shifting cultch shell and wave energy increased spat mortality, preventing consolidation and further development of the reef. Therefore, in high wave energy or high boat traffic environments, many researchers are now advocating for the use of harder, alternative reef substrates for oyster restoration projects that can withstand higher thresholds of disturbance (Keller et al. 2019; Theuerkauf et al. 2017).

Multiple studies have shown how predation can be a major determinant of the structure and function of intertidal oyster reef ecosystems (Newell et al. 2000; Soniat et al 2004; Rindone and Eggleston 2011; Knights et al. 2012; Johnson et al. 2014). As habitat-forming ecosystem engineers, oyster reefs support a diverse array of organisms across trophic levels, including assemblages of basal prey (e.g., polychaetes, mollusks, decapods), intermediate predators (e.g. mud crabs) and top predators like larger bodied fish and crustaceans (Wells 1961; Ulanowicz and Tuttle 1992; Coen et al. 1999; Peterson et al. 2003; Grabowski et al. 2005). However, the strength of trophic cascades on oyster reefs is highly dependent on predator identity, habitat complexity, tidal inundation and environmental stress. Mud crabs are one of the most abundant intermediate predators found on oyster reefs (Rindone and Eggleston 2011). Morphological adaptations of Xanthid crabs allow them to utilize the interstitial space on reefs even when exposed and consume juvenile oysters with high efficiency, making them a dominant predator and a potential driver of oyster survival (McDonald 1982; Meyer 1994; Hill and Weisberg 2013; Carroll et al. 2015). The impact of mud crabs on oyster survival changes in the presence of top predators, and across environmental gradients. At intermediate and low stress levels, blue crabs readily consume mud crabs, reducing their abundance and subsequently their direct effects on oyster survival (Grabowski et al. 2008). On the other hand, in low turbulent conditions, mud

crabs can better detect and respond to blue crab chemical cues, seek refuge in the interstitial space of the reef and increase their probability of survival, creating a complex relationship between predator-prey relationships across differing environmental conditions (Pruett and Weissberg 2021). Furthermore, the presence of multiple top predators and their identity, can alter trophic cascades on oyster reefs. Grabowski et al. (2008) examined the interaction between blue crabs, toadfish, and mud crabs on oyster survival. Interference interactions between blue crabs and mud crabs reduced oyster mortality by approximately 80 percent, while toadfish suppression of oyster consumption resulted in a 95 percent reduction in oyster mortality. This relationship was further influenced by habitat complexity, with the authors finding that habitat complexity decreased both crabs' consumption of oysters independently, but increased consumption when both species were present, concluding that habitat complexity reduces the magnitude of interference interactions among predators. Thus, predator identity and habitat complexity both influence trophic cascades and subsequently oyster survival on intertidal reefs.

Habitat complexity on restored intertidal oyster reefs, in the form of vertical height and aerial exposure have been observed as potential factors influencing reef formation and persistence; however, the exact mechanisms and relative importance of abiotic and biotic factors are still unclear. As previously stated, habitat complexity may mediate the strength of predator-prey relationships on reefs; conversely, predation on juvenile oysters may prevent long-term growth of restored oyster reefs and therefore impact reef height and habitat complexity. Fodrie et al. (2014) found significant differences in oyster densities across depth gradients, with optimum growth at -0.6 m NAVD88 (5% daily aerial exposure). It was hypothesized that reefs below this depth failed due to increasing intensity of predation and competition with decreasing aerial

exposure. The authors suggest that similar results may be found with high relief reefs, regardless of depth, due to similar amounts of daily aerial exposure.

The impact of reef height on growth may also be due to abiotic feedbacks in the environment. Lenihan (1999) found oyster mortality to be highest in areas of sedimentation and burial, with reef height being the most important factor influencing oyster condition at a depth of 3 meters. This is potentially due to tall reefs' ability to escape the effects of poor water quality and sedimentation found near the base of reefs. Similarly, in the Delaware Bay, due to shifting sediment banks, low-relief, restored, intertidal oyster reefs became completely buried, while high relief reefs supported large oyster reef communities (Taylor and Bushek 2008). In addition, the ability of hardened shorelines to maintain vertical relief and settlement substrate in areas of high wave energy environments may explain why reefs on hardened shorelines have much higher wave energy thresholds compared to those on natural reefs, which become flattened and buried, losing crucial vertical relief overtime (Theuerkauf et al. 2017).

It is evident that the relationship between oyster reef success, habitat complexity, and abiotic and biotic processes is not linear, but is complicated and circular, with dynamic positive and negative feedbacks (Figure 1). To increase the success of oyster restoration strategies, we must first mechanistically determine how foundation species and their communities are affected by physical and biological processes. Fodrie et al. (2014) recommended further exploration of the effects of reef depth versus reef relief on the success of restored oyster reefs. Keller et al. (2019) suggests integrating ideas about how vertical reef height impacts habitat-use and foraging rates to enhance our knowledge of how constructed reefs may affect community structure. Furthermore, Scyphers et al. (2011) advocates for improving oyster reef breakwater design to include more rigid, alternative materials that can better withstand high and variable wave energy

environments and maintain structural integrity overtime. And finally, Theuerkauf et al. (2017) proposes that future research should quantify the potential interaction between wave exposure and reef elevation on intertidal reef formation by constructing reefs at varying elevations across a wave exposure gradient in order to quantify the relative importance of both variables.

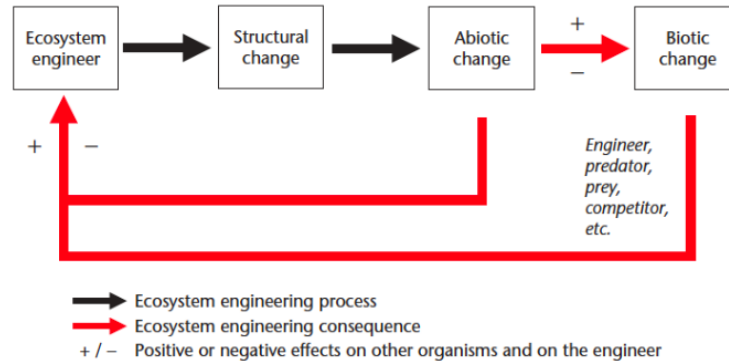


Figure 1 General pathways of physical ecosystem engineering.

Figure 1: Relationship between ecosystem engineers, habitat structure, and abiotic and biotic processes (Gutiérrez and Jones 2008)

Research Questions/Hypotheses

To begin to address the above knowledge gaps and to better understand how abiotic and biotic processes regulate ecological communities and to inform intertidal oyster reef restoration efforts, I conducted a series of observational and manipulative experiments to answer the following questions.

Research Question 1: How does wave energy below 500 J/m affect oyster abundance?

Hypothesis 1: Oyster abundance will increase with increasing wave energy below the 500 J/m threshold, defined by Theuerkauf and colleagues (2017).

Research Question 2: How does reef crest height affect abundance?

Hypothesis 2: Oyster abundance will be greater on high-relief breakwater sites compared to low relief breakwater sites.

Research Question 3: How does wave energy mediate consumption of oysters?

Hypothesis 3: Oysters at sites with the higher average wave energy will experience less consumption compared to oysters at sites with lower average wave energy. At sites with high wave energy, caged (predators excluded) and open (accessible to predators) treatments will not differ in survival, while sites with low wave energy will show greater survival in caged treatments than open treatments.

Research Question 4: How does reef relief mediate consumption of oysters?

Hypothesis 4: Low relief breakwater sites will experience greater rates of consumption than high relief sites. Therefore, low relief sites are expected to have the greatest difference in

juvenile oyster survival between caged and open treatments, compared to high relief sites, which should have a higher number of surviving oysters in the open treatment.

Methods

Study Site

The study took place in the Rachel Carson Reserve, part of the North Carolina Coastal Reserve and the NOAA National Estuarine Research Reserve, located in Beaufort, NC, United States. Taylor's Creek, an estuarine tidal creek, directly abutting the Rachel Carson Reserve, is a shallow, narrow creek with a naturally low-fetch environment influenced by twice daily tides (NC DEQ, 2022).

The study sites are located along an approximately 450 m-long stretch of salt marsh and sandy shorelines across from the Lennoxville public boat ramp, adjacent to a popular marine (Figure 2). The saltmarsh shoreline bordering Taylor's Creek is experiencing annual shoreline erosion rates of approximately 1 m yr^{-1} and RSLR of 3.1 mm yr^{-1} (Rodriguez et al. 2014; Theuerkauf et al. 2015).

Due to the proximity to a public boat ramp and boat storage facility, heavy summer boat traffic alters the wave energy environment in Taylor's Creek. In frequently trafficked, narrow, coastal waterways, boat wakes can be a predominant factor contributing to shoreline erosion (Castillo et al. 2000; Bauer et al. 2002) due to the limited distance for energy to dissipate (Bilkovic et al. 2019). Boat wakes have also been found to be especially damaging to organisms and coastal habitats in areas of small fetches that are accustomed to naturally low wave environments (Bourne 2000; Parnell et al. 2007; Soomere and Kask 2003). Previous limited research has shown that vegetated shorelines may be less effective as attenuating boat-wake waves, compared to wind-driven waves due to vessel waves having longer wave periods and greater wave heights (Houser 2010).

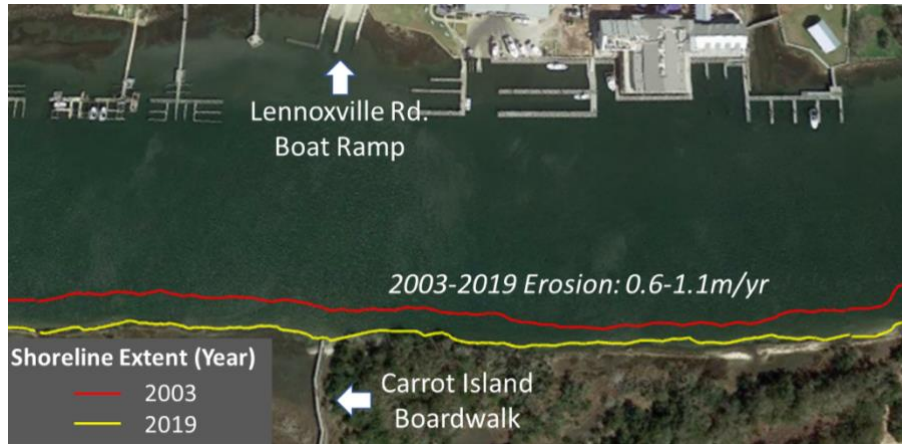


Figure 2: Aerial photograph of Taylor's Creek waterway adjacent to Lennoxville boat ramp. Red line shows shoreline position in 2003 and yellow line shows shoreline extent in 2019 after extensive erosion, likely due to heavy boat traffic

Oyster Breakwater Construction

Oyster breakwater site selection was conducted in coordination with the Rachel Carson Reserve Site Manager and the NC Coastal Reserve Coordinator. Oyster breakwaters of two different reliefs (high vs. low) were constructed to assess how reef relief and aerial exposure affects oyster abundance.

Breakwaters were constructed at 8 sites in July 2020 over a three-day period. Breakwaters were modeled after the Oyster Catcher™ design produced by Sandbar Oyster Co. and made with biodegradable material. The two experimental treatments include breakwaters of high-relief (12m * 1.5m * 0.3m) and low-relief (12m * 1.5m * 0.2m) and controls (no breakwater) (Figure 3). The bases of the reefs were initially set at approximately -0.34 North America Vertical Datum of 1988 (NAVD88), respectively, within the optimal growth zone (OGZ, -0.6 to -0.3 m NAVD88) for intertidal oysters (Fodrie et al. 2014; Ridge et al. 2015). High- and low- relief reef crests were located at approximately -0.1 and -0.2 NAVD88 respectively. Across 12 sites, each site consisted of a single treatment in a randomized block design, with four replicates per treatment (Figure 4). Treatments were placed at least 25m apart.

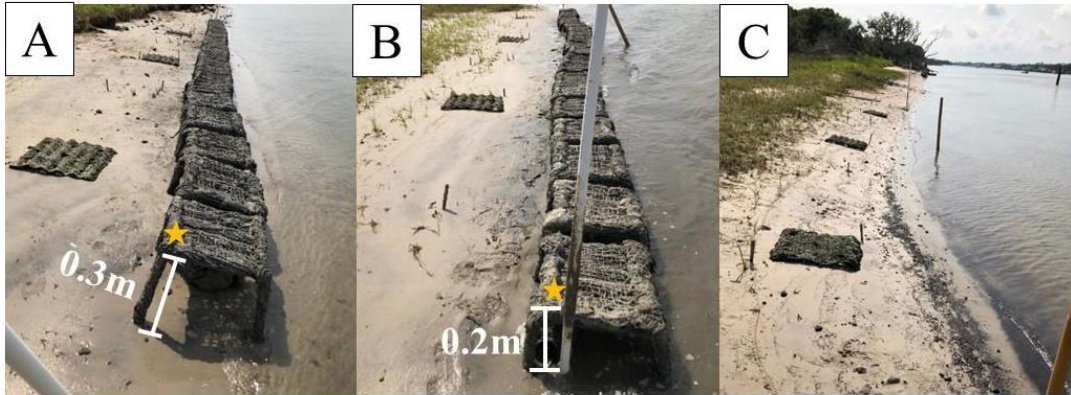


Figure 3: Oyster Catcher™ breakwater design showing A) high relief (~0.3m height) B) low relief (~0.2m height) and C) control (no breakwater). Star indicates placement of reef crest elevation measurements (Photo credit: Dr. Christopher Baillie)



Figure 4: Aerial photograph of Taylor's Creek waterway with site placements. Low relief sites (1, 4, 7, 11) shown in blue. High relief sites (3, 5, 8, 10) shown in orange. Control sites (2, 6, 9, 12) shown in yellow.

Oyster Monitoring

We conducted post-construction monitoring of oyster reef characteristics in October 2020, December 2020, March 2021, June 2021, September 2021 and March 2022, to assess the impacts of wave energy, reef relief and exposure on oyster abundance. Oyster abundance was quantified by counting the number of live oysters within $\frac{1}{4}$ of a 0.0625m^2 quadrat, with the sample section (1-4) chosen randomly (Figure 5). Lengths (mm) of five oysters were also recorded in each quarter quadrat. Sampling was conducted for three breakwater ‘tables’ per site, with the quadrat placed on the landward side of the reef. Elevation points were taken on the reef crest in the middle of the sampled quadrat (Figure 3) using a Trimble R10 Real-Time Kinematic (RTK) GNSS (GPS; 0.5-1.0cm horizontal and 1.0-4.0 cm vertical resolution).



Figure 5: Oyster sampling using 0.0625m^2 quadrat. Quadrat was placed on the table surface (landward) and oyster abundance was enumerated within 1 of the 4 squares within the quadrat. Length (mm) of 5 oysters was taken within same part of quadrat using calipers (Photo credit: Anna Albright)

Wave Energy Monitoring

Pressure sensor wave gauges were based on those constructed and tested in Temple et al. (2020) using commercial plumbing parts, a pressure sensor, an Arduino micro-controller and

adapted accessories. Some changes were made to the gauges from the original Temple et al. (2020) construction for an updated version of the gauge, referred to as ‘DIY Feather Wave Gauge’, including the addition of an Adafruit Feather 32uV Adalogger and Precision RTC Featherwing in place of Arduino Uno and a data logging shield, as well as increased battery-life (Mississippi State University, 2020). Gauges were deployed seaward of the reef for approximately 3-5 days in June, July, August and September of 2021. Data from June and September was used for the oyster abundance analysis to align with oyster monitoring. Due to gauge failures, not every reef was monitored for both months (see *Wave Data Processing*)

Before deployment, the battery was plugged into the featherboard to turn on the gauge, and then the housing was sealed using a gripper cap. A cap with holes was then placed over the sensor component. Gauges were mounted vertically to sand-screws using waterproof tape with the sensor facing downward and placed approximately 15cm above the seabed, with exact height noted. Sand screws were placed approximately 2 feet in front of each reef, placed in front of the 12th table on the reef (Figure 6). After the deployment period, gauges were brought back to the lab for processing.



Figure 6: Placement of wave gauge in front of reef, mounted vertically with sensor facing downward (Photo credit: Anna Albright)

Wave Data Processing

Variations in the pressure signal due to atmospheric pressure were removed using data from the nearby NOAA-NDBC Cape Lookout station (NOAA 2022). Power spectra of detrended pressure data were calculated for 10-min time increments. Following Jones and Monismith (2007), power spectral density estimates were computed with segment lengths of 1024, with 50% overlap and a Hann window. Each resulting pressure spectrum was then converted to a water surface elevation spectrum using linear wave theory.

Three measurements of the wave environment were calculated: root-mean-square wave height (hereafter H_{rms}), energy (hereafter E), and peak wave period (hereafter T_p). H_{rms} (m) is a common statistical measure of wave height derived from significant wave height, H_s , which is the average height of the highest one-third of waves in each individual wave train (Nanson et al. 1994). H_{rms} was calculated according to Jones and Monismith (2007). E (J/m^2), defined as the integral of the wave energy density spectrum, was calculated according to Morris et al. (2021). T_p (s) is the wave period associated with the most energetic waves and was derived from equations in Morris et al. (2021) using a smoothing method to exclude outliers. Wave period refers to the time it takes for two successive crests to pass a specific point (Figure 7).

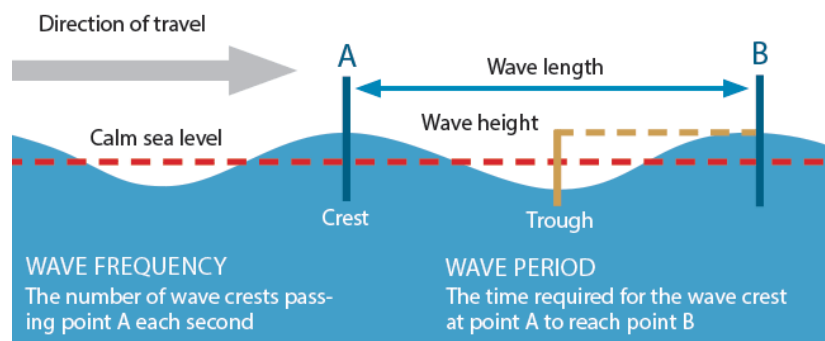


Figure 7: Description of wave metrics including length, height, frequency and period (Johnson et al. 2017)

Consumption Assays

On July 22 and 24, 2021, we conducted a manipulative field experiment used to quantify consumption with different caging and relief treatments to assess how reef crest height (high vs. low) and wave energy mediate consumption on juvenile oysters.

Juvenile oysters were purchased from Down East Mariculture based in Smyrna, NC with an average weight of 0.56 g (± 0.016 g SE) and average length of 17.2 mm (± 0.23 mm). The night before the deployment, 10 oysters were attached to ceramic plates (13.5 cm²) using Loctite SuperGlue and placed in flow-through seawater tanks at UNC Institute of Marine Sciences in Morehead City, NC, overnight. On the morning of deployment, the tiles were transported to the site in large coolers and covered with damp paper towels to prevent desiccation.

Three caging treatments were utilized including 1) plates with no cage to quantify total consumption 2) plates with a 1-cm mesh cage that fully encloses the oyster-spat plate to prevent consumption and act as a control for oyster attachment failure/dislodgement due to wave energy 3) plates with a 1-cm mesh cage that was open in the middle to use as a half cage control to account for predator attraction and changes in flow (Figure 8a). All three caging treatments were deployed at all 12 sites attached to a Vexar mesh base, oriented horizontally facing upward, mimicking spat settlement on top of the breakwater. To investigate the impact of reef crest height on consumption, 2 Vexar mesh bases were deployed at each site, one set at approximately 0.3 m height and 1 set at 0.2 m height (corresponding to our high- and low-relief breakwater original deployment height). One of each caging treatment was then zip-tied to the Vexar base (Figure 8b). To investigate how wave energy impacts consumption rates, wave gauges were deployed in front of each Vexar base pairing.

Plates were deployed at low tide. Plates were then checked 1 and 2 hours after complete inundation and no consumption was found at any site so they were left for 24 hours. After 24 hours, we recorded the number of surviving oysters on each tile. The entire consumption assay experiment was repeated twice, 2 days apart.

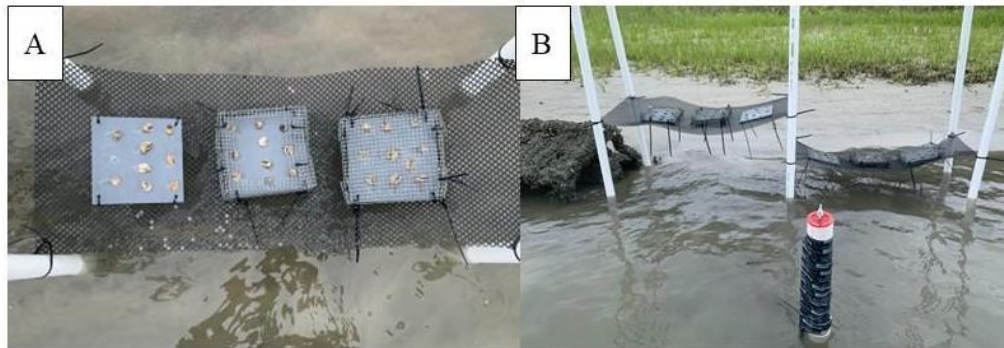


Figure 8: A) Three consumption assay caging treatments with the open/no cage (left), half cage (middle) and full cage (right). B) Two relief treatments with high (left) and low (right), and wave gauge (Photo credit: Anna Albright)

Predatory Crab Monitoring

To assess the effects of predator abundance on consumption rates and oyster abundance, crustaceans, fish, and other mobile free-living organisms were collected using two passive samplers at each site. These samplers are plastic milk crates (19 x 22 x 16 cm) filled with 3.5 lbs. of dried out oyster shells and zip-tied shut with mesh on top (referred to as “crab condos”) (Roche and Torchin 2007). These crates allow the organisms to freely move inside and outside of the crates, while being attracted to the three-dimensional habitat that the oyster shell provides. Each crate was zip-tied to wooden stakes approximately 5 meters from the middle of the oyster reef. One crate was oriented directly landward of the oyster reef and the second crate was oriented directly seaward of the oyster reef. Altogether, 24 crates were deployed: 2 per site (landward/seaward) with 12 total sites made up of 4 replicates per treatment: high-relief, low-

relief, and control (Woodard, 2022). For the purposes of this study, only predatory crab (Appendix A1-2, B1) abundances were included, and the landward and seaward totals were combined.

Summary Statistics and Statistical Analyses

Oyster abundance in the $\frac{1}{4}$ quadrat was multiplied by 4 to estimate total oyster abundance in the 0.0625m^2 quadrat. The five oyster length measurements were averaged per quadrat for three averaged measurements per site to match the three abundance estimates per site. All averages and standard errors were calculated in Excel (version 16.6). Data from site 8 was excluded in both June and September as well as site 7 in September due to pressure gauge failures.

To assess the effects of reef crest elevation, wave energy, reef relief, landward reef height, predatory crab abundance, wave energy, and their interactions, on oyster abundance, multiple models were created with the data collected in June and September 2021. For the analysis, ‘elevation’ refers to the landward reef crest elevation in m (relative to NAVD88) as measured on top of the breakwater table. ‘Relief’ refers to the reef treatment, in our case a categorical variable of high vs. low (Figure 3). ‘Height’ refers to the difference between the reef crest elevation and the reef base elevation on the landward side of the reef. Bayesian mixed effects models with the random effect of site within block and linear models using the same fixed effects but without the random effects, due to low random effect variance in the mixed models, were used. The Bayesian mixed-effect models and the linear models only differed in their wave energy measurement type (Hrms vs. E vs. Tp). All models were compared using Akaike’s

Information Criterion (AIC), after which the best model was selected. The selected model was then further explored using Analysis of Deviance Tables with type III Wald Chi Square tests.

To assess the fixed effects of caging treatment (full cage, half cage, open, Figure 8a), wave energy, reef relief, assay relief treatment (high, low, Figure 8b), oyster abundance, predatory crab abundance, and their interactions, as well as the random effect of site within block, we used a generalized linear mixed effects model on the consumption assay data. Three full models were created only differing in their wave energy measurement type. All three models were compared using AIC, with all three models fitting the data equally. Lastly, all three models were further explored using Analysis of Deviance Tables with type III Wald Chi Square tests. All modeling and subsequent analysis was conducted in the R statistical computing environment (version 4.1.3).

Results

Oyster Reef Trends Over Time

Oyster abundances and lengths differed by site, reef elevation, reef relief and time since restoration. In October 2020, 3 months post-construction, the average oyster abundance within a single quadrat across all reefs was 68.5 live individuals with a standard error of ± 8.81 (Figure 9). Site 8 (HR) initially had the highest average oyster abundance in October 2020 (126.67 ± 19.6), while site 4 (LR) had the lowest (24 ± 2.3). Average oyster abundance remained steady in December 2020 (67.3 ± 9.9), before decreasing in March 2021 (41.67 ± 6.7). Overall oyster abundance across the breakwater sites increased in June 2021 (56.67 ± 7.7). Site 8 (HR) continued to host the highest average oyster abundances (105.3 ± 5.8), while site 4 (LR) continued to have the lowest (20 ± 2.3) in June 2021. Overall, the reefs decreased in abundance in September 2021 (44 ± 7.5), with site 10 (HR) having the highest abundances (100 ± 24.4) and site 1 (LR) the lowest (13.3 ± 4.8). The greatest overall oyster abundances were recorded in March 2022, 15 months post-construction, with an average abundance of $91.3 (\pm 7.3)$ over all the reefs. In March of 2022, site 7 (LR) had the highest average abundance (121.3 ± 24.7) while site 11 (LR) had the lowest (57.3 ± 21.8).

Average oyster lengths increased over time, with the largest oysters observed in March 2022 ($48.1 \text{ mm} \pm 3.3 \text{ mm}$) (Figure 10).

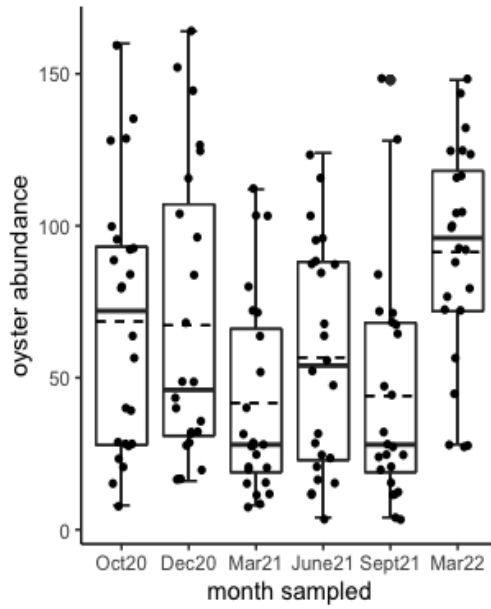


Figure 9: Oyster abundance in quadrat by month for all 8 constructed breakwaters. Dashed line represents the mean. Solid line represents the median.

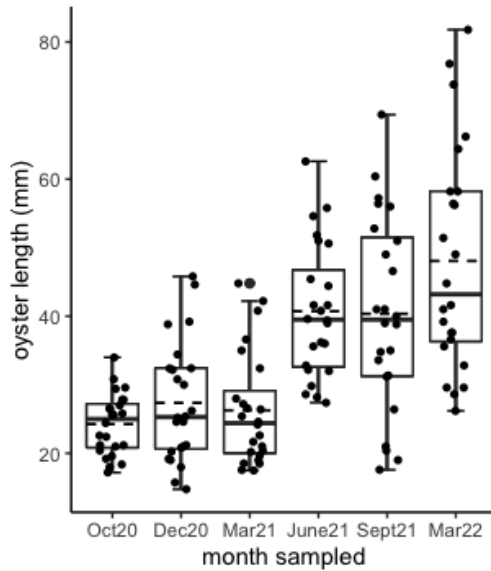


Figure 10: Oyster length (mm) by month for all 8 constructed reefs. Dashed line represents the mean. Solid line represents the median.

Oyster Reef Trends by Site

Oyster abundance varied by site. Over the entire study period, sites 8 (HR) and 10 (HR) had the highest average oyster abundances at 102.2 (± 7.9) and 99.6 (± 8.7) respectively. Sites 1 (LR), 4 (LR) and 11 (LR) had the lowest abundances at 30 (± 6.7), 30 (± 5.6), and 37 (± 5.4) respectively (Figure 11). Sites 8 (HR) and 10 (HR) also had the largest oysters, with an average length of 44.7 mm (± 4.1 mm) and 45.9 mm (± 3.9 mm) respectively while site 1 (LR) had the smallest oysters (26.7 mm ± 2.2 mm) (Figure 12).

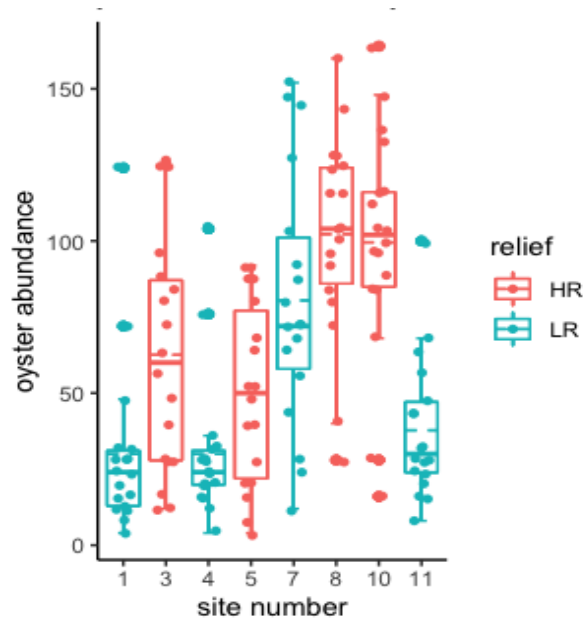


Figure 11: Oyster abundances in quadrat by site over the entire study period from October 2020 to March 2022. Dashed line represents the mean. Solid line represents the median. Low relief (LR) sites shown in blue. High relief (HR) sites shown in orange.

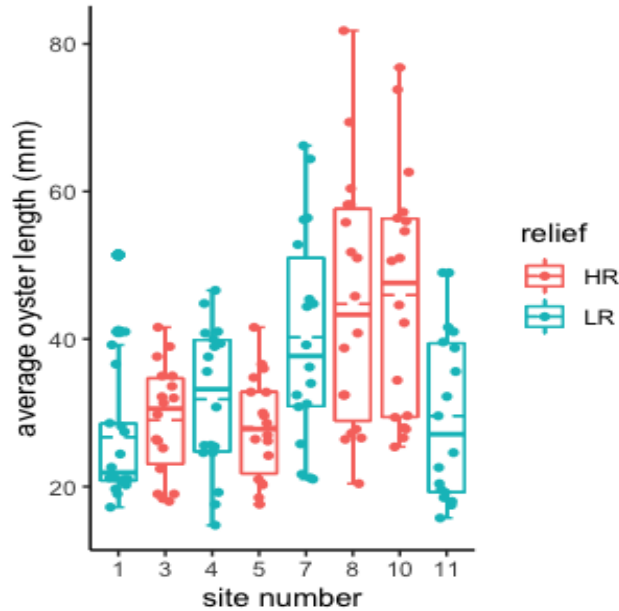


Figure 12: Oyster length (mm) by site over the entire study period from October 2020 to March 2022. Dashed line represents the mean. Solid line represents the median. Low relief (LR) sites shown in blue. High relief (HR) sites shown in orange.

Wave energy (J/m^2) and peak wave period were variable by site and month (Figure 13).

Averaged across all sites, average energy was greater in September ($0.52 J/m^2 \pm 0.017 J/m^2$) compared to June ($0.47 J/m^2 \pm 0.011 J/m^2$) ($p=0.023$). Peak wave period was slightly higher in June ($2.08 s \pm 0.03 s$) compared to September ($2.02 s \pm 0.02 s$) ($p=0.08$). Site 1 had the highest average wave energy in June ($0.52 J/m^2 \pm 2.8e-04 J/m^2$) and September ($0.66 J/m^2 \pm 4.1e-04 J/m^2$). Site 3 had the lowest average wave energy in June ($0.38 J/m^2 \pm 2.4e-04 J/m^2$), while sites 3 ($0.462 J/m^2 \pm 3.4e-04 J/m^2$) and 11 ($0.462 J/m^2 \pm 3.2e-04 J/m^2$) had the lowest wave energy in September. Site 3 had the highest peak wave period in June ($2.2 s \pm 0.03 s$) and September ($2.2 s \pm 0.02 s$). In June, site 10 had the lowest peak wave period ($1.9 s \pm 0.04s$) while in September, site 11 had the lowest peak wave period ($1.9 s \pm 0.03 s$).

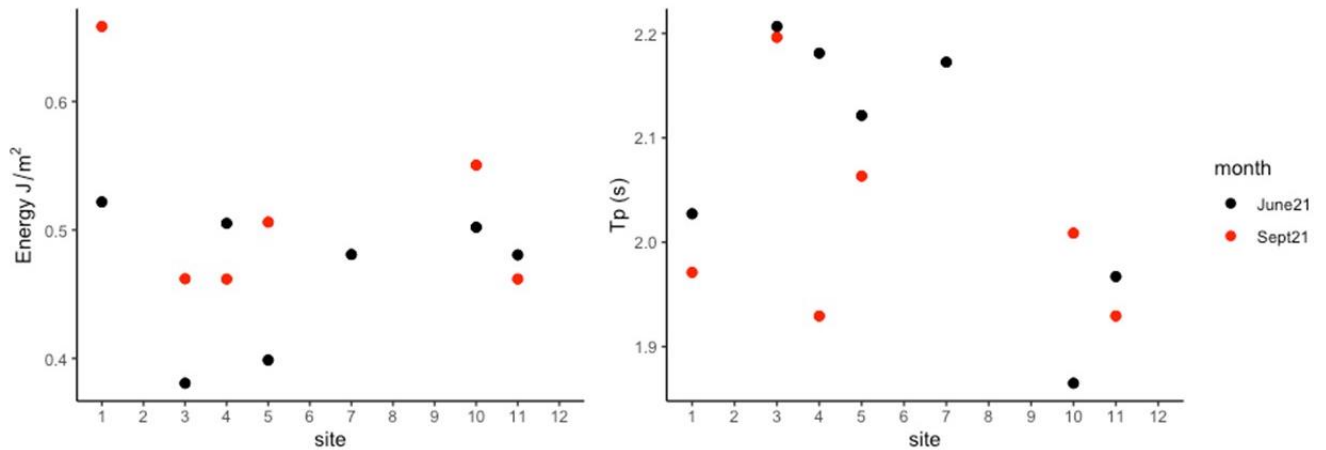


Figure 13: Average wave energy (J/m^2) (left) and peak wave period (s) by site (right) for June (black) and September 2021 (red). Hrms not depicted as it presents the same trends as Energy. Missing wave energy and peak wave period data for all control plots (2, 6, 9) and site 8 (HR) for June and September, and site 7 (LR) in September.

Oyster Reef Trends by Elevation, Reef Relief and Reef Height

Crest elevation and reef relief impacted oyster abundance with oyster abundance increasing with increasing elevation (Figure 14). The trend was stronger for low-relief reefs compared to high-relief reefs. The reefs gained crest elevation through time, with low-relief reefs increasing by an average of 0.06 m and high-relief reefs increasing by an average of 0.08 m from October 2020 to March 2022 (Figure 15). In June 2021, low-relief sites ranged in crest elevation from -0.23 m to -0.12 m, with an average crest elevation of -0.17 m (± 0.01 m). High-relief sites ranged in crest elevation from -0.17 m to -0.05 m, with an average crest elevation of -0.13 m (± 0.01 m). In September 2021, low-relief sites ranged in crest elevation from -0.23 m to -0.10 m with an average elevation of -0.16 m (± 0.01 m). High-relief sites ranged in elevation from -0.14 m to -0.04 m with an average elevation of -0.09 m (± 0.01 m).

Both high- and low-relief sites gained and then lost landward height overtime (Figure 16). In October 2020, high- and low-relief sites were significantly different in their landward reef

heights ($p=0.015$) with high-relief sites having an average height of 0.22 m (± 0.02 m) and low-relief sites having an average height of 0.15 m (± 0.02 m). By June and September 2021, high- and low-relief sites gained reef height, but no longer differed statistically from one another ($p=0.17, 0.18$). In June, high-relief reefs had an average height of 0.26 m (± 0.03 m), while low-relief reefs had an average height of 0.21 (± 0.02 m). In September, high-relief reefs were 0.28 m (± 0.02 m) in height on average and low-relief reefs were 0.24 m (± 0.02 m) in height on average. In March 2022, high- and low- relief sites lost reef height, with high-relief sites having an average height of 0.26 m (± 0.03 m) and low-relief sites having an average height of 0.16 m (± 0.02 m) ($p=0.01$).

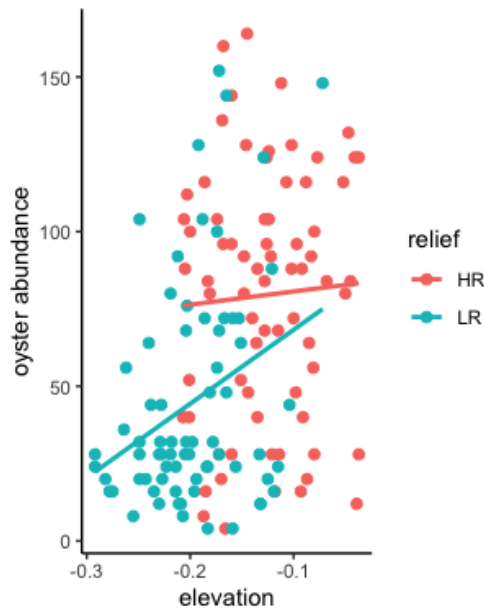


Figure 14: Oyster abundances across the elevation gradient throughout the entire study period from October 2020 to March 2022. Low relief (LR) sites shown in blue. High relief (HR) sites shown in orange. Each point represents an abundance measurement taken on the reef, with three points per site.

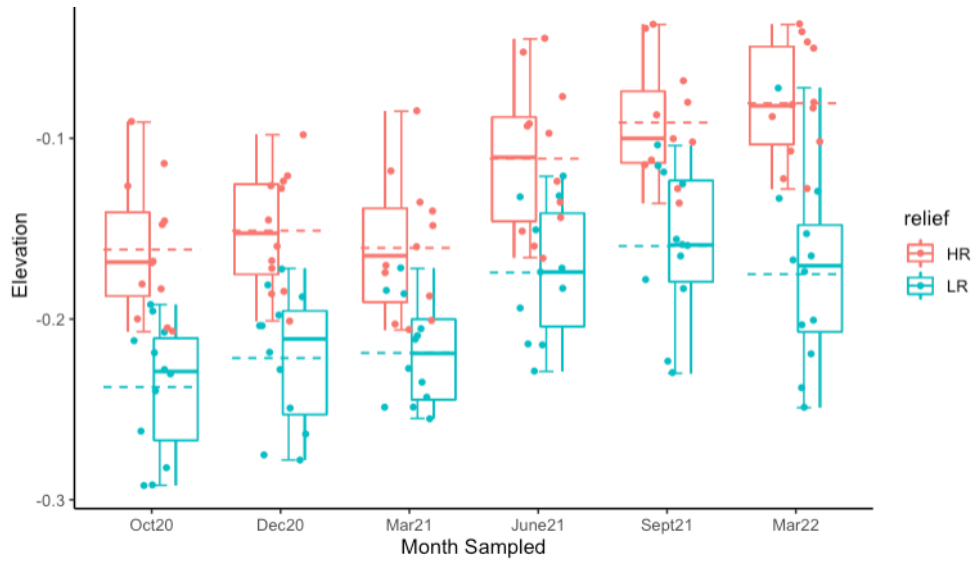


Figure 15: Reef crest elevation from October 2020 to March 2022. Low relief (LR) sites shown in blue. High relief (HR) sites shown in orange.

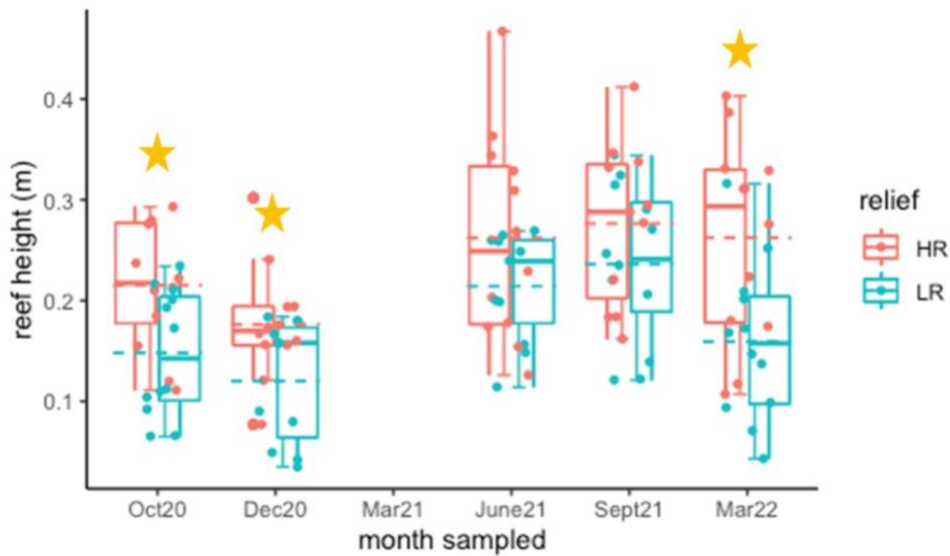


Figure 16: Landward reef height from October 2020 to March 2022. Low relief (LR) sites shown in blue. High relief (HR) sites shown in orange. Stars represent high and low relief heights are significantly different ($p < 0.05$). March 2021 missing data.

June & September 2021 Predatory Crab Abundances

Predatory crab abundances varied by site and month for high and low-relief reefs

(Appendix A1-2). In June 2021, there was an average of 10.125 (± 1.3) oyster predators per site

captured within our crab condos. Site 11 (LR) hosted the most, capturing 16 crabs ,while site 7 (LR) hosted the least, with 4 individuals captured. A greater number of organisms were collected in September, with an average of 16.25 (± 2.0) per site. Again, the greatest number of predatory crabs were observed at site 7, with 23 individuals, while site 3 only hosted 5.

Oyster Abundance Model Output

Three linear models fit the oyster abundance data from June and September 2021 equally. The first model (named “newlinTp”) included interactions between elevation and Tp, predatory crab abundance, landward reef height and reef relief (Appendix A3). The second model (named “newlinTp4”) included terms for interactions between elevation and Tp, predatory crab abundance, and landward reef height (Appendix A5). The third model (named “newlinE2”) included terms for interactions between elevation and energy, height, and reef relief (Appendix A7). All three models found landward reef height to be an important predictor for oyster abundance ($p= 0.008119, 0.014187, 0.01347$) (Appendix A4, A6, A8). Each unit increase in height resulted in approximately 16-17 less oysters per quadrat (Appendix A3, A5, A7). Models newlinTp and newlinE2 found reef relief to be an important predictor ($p= 0.025348, 0.02565$), with low relief reefs predicted to have approximately 29-36 less oysters per quadrat compared to high relief reefs (Appendix A3-4, A7-8). Only model newlinTp4 found crest elevation by itself (no interaction) to be a significant predictor ($p=0.005258$) with oyster abundance increasing by 12.97 with each increase in elevation (Appendix A5-6). Both model newlinTp and newlinTp4 found the effect of Tp to be dependent on elevation, with an effect size estimate of 33.08 ($p=0.004804$) and 32.078 ($p=0.007447$) (Appendix A3-6, Figure 17). Both those models also found the effect of predatory crab abundance to be also dependent on elevation, with an effect size estimate of 26.27 ($p=0.002734$) and 26.67 ($p=0.002054$) (Appendix A3-6). Model newlinE2

suggested that the effect of energy was dependent on elevation, with an effect size estimate of -24.207 ($p=0.02122$) (Appendix A7-8, Figure 17).

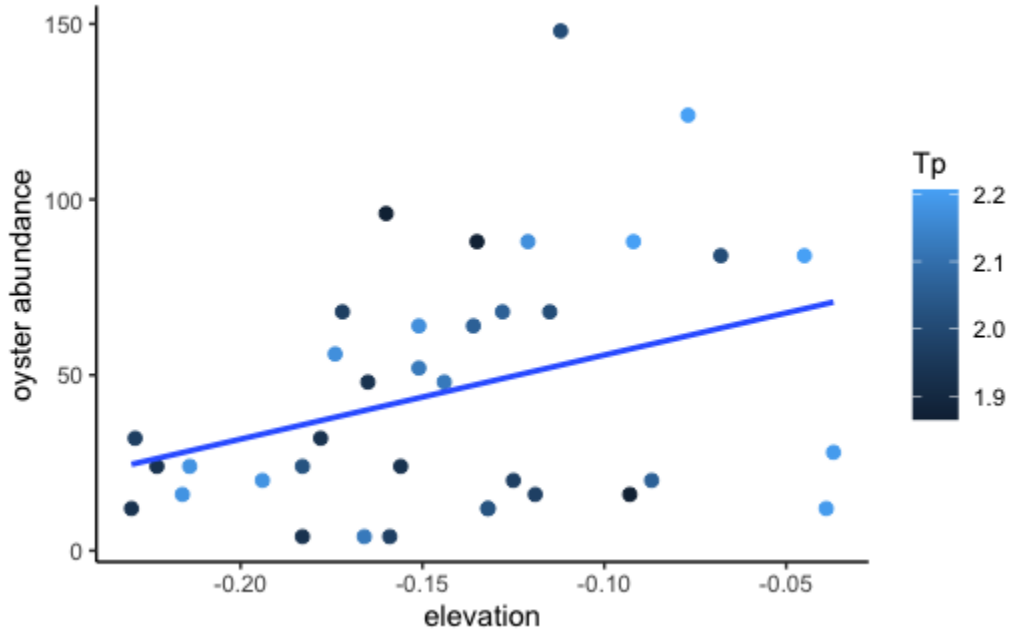


Figure 17: Oyster abundances by elevation (m) in June and September 2021. Peak wave period (“Tp”) (s) shown in color gradient.

Consumption Assays

The outcome of the consumption assays was highly variable by site and caging treatment (Figure 18). Sites 5-10 had the highest consumption, while sites 1-4 and sites 11-12 had low to no consumption across both trials. Across both trials, open assays (those with no cage) experienced 100% consumption at sites 5, 6, 7, 9 and 10. Consumption did not differ between high and low relief assays.

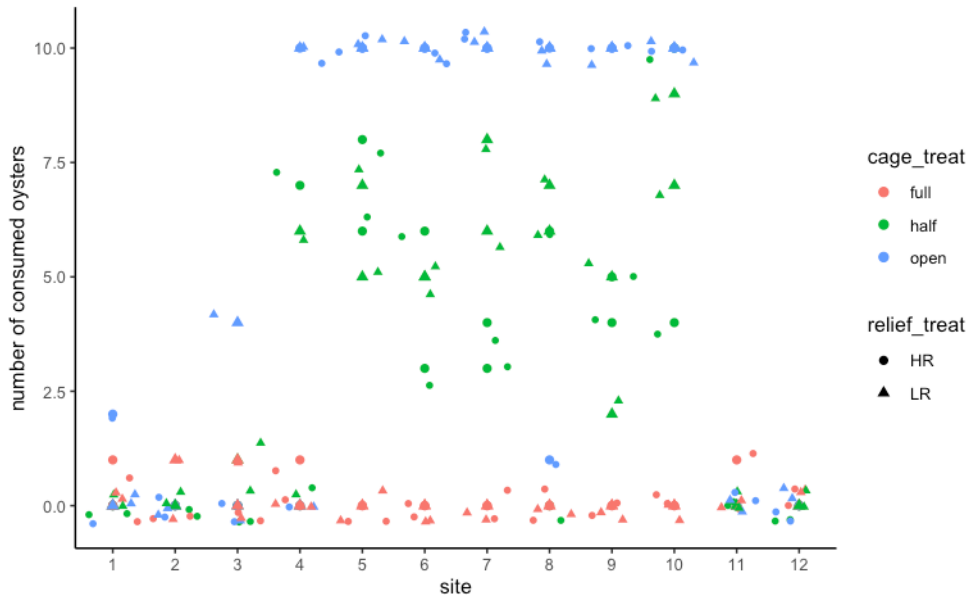


Figure 18: Number of consumed oysters (out of 10) by site after 24 hours. Consumption assay relief treatment ('relief_treat') shown in the shape of the point. High relief (HR) shown by circular points. Low relief (LR) shown by triangular points. Caging treatment ('cage_treat') shown by color. Full cage shown in pink. Half cage shown in green. Open (no cage) shown in blue.

Wave energy measurements differed by trial and site (Figure 19). During trial 1, sites 6 and 9 were the most energetic experiencing an average energy of 0.77 J/m^2 and 0.76 J/m^2 respectively during the 24 period. The lowest average energy was recorded at site 2 (0.44 J/m^2). Also during trial 1, sites 4 and 9 had the highest peak wave periods at 2.035 s and 1.98 s respectively, while site 12 had the lowest peak wave period at 1.80s. During the second trial again, site 9 (0.87 J/m^2) and 2 (0.44 J/m^2) had the highest and lowest average wave energies respectively. Sites and 11 and 12 had the lowest peak wave periods during the second trial at 1.79 s and 1.77 s respectively. Although none of the three energy measurements were considered significant by the model, a positive correlation between energy and number of consumed oysters was observed (Figure 20).

Predatory crab abundance captured by our crab condos during our July sampling was relatively low across our reefs with an average of $9 (\pm 1.34)$ organisms per site. Site 3 (HR)

hosted the greatest number of crabs with a total of 22 individuals. Site 4 (LR) hosted the least number of individuals, only capturing 3 total (Appendix B1)

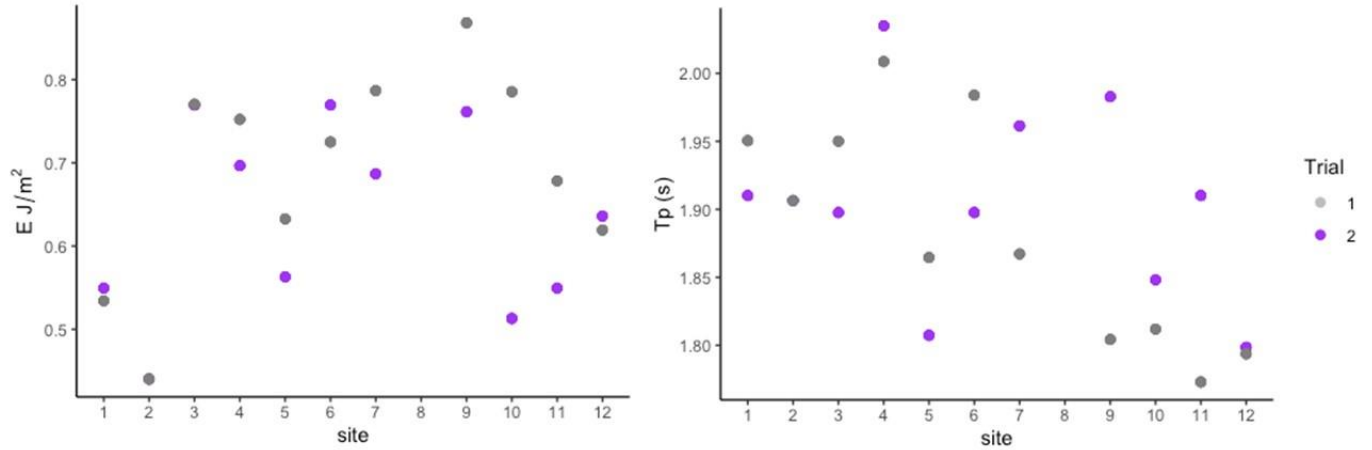


Figure 19: Average wave energy (J/m^2) (left) and peak wave period (s) by site (right) during July Consumption Assays. Trial 1 shown in gray. Trial 2 shown in purple. Missing data for site 8 due to gauge failure

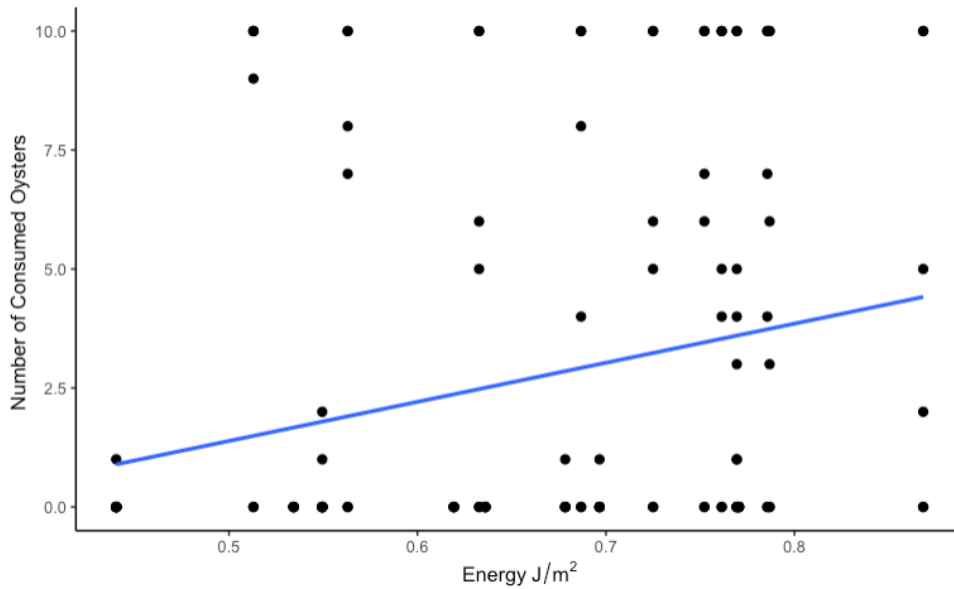


Figure 20: Number of consumed oysters (out of 10) as Energy (J/m^2) increases.

All three constructed models were within 1.4 AIC of one another and therefore all equally represent the data. All three mixed models included terms for relief treatment (the relief of the assay), total predatory crab abundance, caging treatment, and the interaction between oyster abundance and reef relief (that of the constructed reef adjacent to the assay) but differed in their wave energy measurement (Appendix B2-4). The model including Hrms (hereafter “mHrms”) had the highest weight (0.44), followed by the model using Energy (hereafter “mE”) (0.34), with the lowest weighted model being that using Tp (hereafter “mTp”) (0.24).

Total crab predator abundance ($p=0.059$, 0.054 , 0.031) and caging treatment ($p<2.2e-16$) were the most important predictors for consumption for all three models (Appendix B5-7). A one unit increase in total crab predator abundance led to 1.18, 1.23, 1.34 decrease in oyster consumption for mHrms, mE and mTp respectively (Figure 21). The mean number of consumed oysters in the half cage treatment was 4.2 times higher than that of those consumed in the full cage for all three models. The mean number of consumed oysters in the open treatment (no cage) was 6.6 times higher than that of the full cage for all three models. 85% of the random effect variance was explained by block itself, while 15% of the random effect variance was attributed to the nested effect of site within block.

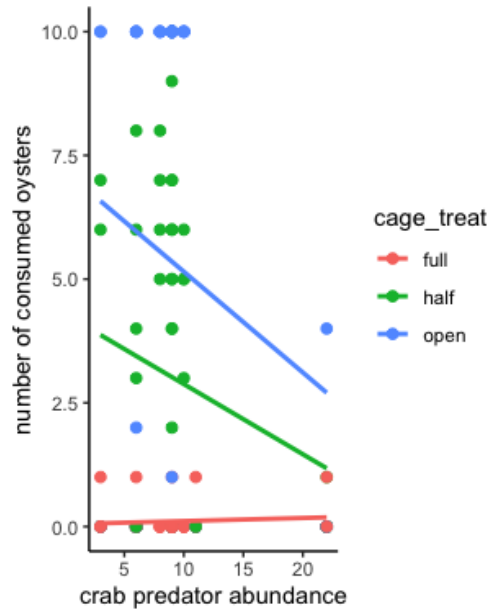


Figure 21: Number of consumed oysters (out of 10) by predatory crab abundance. Full cage shown in pink. Half cage shown in green. Open treatment shown in blue.

Discussion

Our results suggest that the establishment of successful oyster reef restoration projects depends on complex interactions between abiotic and biotic factors. The high variation in oyster abundances both temporally (Figure 9) and spatially (Figure 11) suggests that even small-scale changes in environmental factors can have large effects on reef functionality. High abundances of oysters as early as three months post-construction at some sites promotes the feasibility of using Oyster Catcher™ material as a substrate for future breakwater construction in similar environments to that of Taylor's Creek. At only three months post-construction, there were obvious spatial patterns in oyster abundances; those sites that accumulated the highest abundances of oysters early on (sites 8 and 10) continued to host the highest abundances throughout the entire study period, while those that had the lowest abundances in the beginning (site 1 and 4), never accumulated high abundances (Figure 11). However, this cannot be attributed to a failure in design of the breakwaters, but possibly due to small-scale variation in environmental characteristics not monitored during the study period, with the eastward reefs potentially experiencing more favorable conditions for oyster accumulation and growth compared to the westward reefs (Figure 4). Research by Kroeker et al. (2016) showed how interactions between environmental drivers creates a complex environmental mosaic that alters species performances even over small spatial scales. Their research revealed that individuals on adjacent reefs may differ drastically in their fitness, even in naturally formed reef environments (Lester et al. 2007). This suggests that oyster restoration project designs need to be adapted to local conditions and that pre-project monitoring for preferable conditions need to be at fine scales.

Effect of Reef Relief, Elevation and Reef Height on Oyster Abundance

Understanding how reef relief, elevation and wave energy interacted to impact oyster abundance was key to our research goals. Our results show that reef relief (high vs. low) was extremely important for increasing oyster abundance, with high relief reefs having a mean estimate of 29-36 more oysters per quadrat compared to low relief reefs, based on model outputs (Appendix A3, A7). Although not all high-relief reefs had higher oyster abundances than all low-relief reefs, our results did show that increasing vertical relief may help mitigate poor environmental conditions brought on by small-scale spatial variations. This was exemplified through site 3 (HR); despite adjacent sites (1 and 4, LR) doing poorly, presumably due to less favorable conditions on the western side of the creek, site 3 was able to accumulate oysters to match that of site 7 (LR) and surpass that of site 11 (LR), despite their potentially better conditions on the eastern side of the creek. These results follow similarly to that of Lenihan (1999) who found initial reef height to be the most important factor in oyster condition, most likely due to tall reefs' ability to escape sedimentation or poor water quality (Scyphers et al. 2011, Lenihan 1999).

Constructing reefs with high vertical relief not only increases oyster abundance, but also increases reef accretion (as measured by increased elevation). High-relief reefs increased in reef crest elevation more than low relief reefs did from October 2020 to March 2022. This could either be due to high-relief reefs hosting larger and more abundant oysters, and/or their ability to retain more sediment when compared to low-relief reefs. Reef accretion results from interactions between abiotic and biotic factors, including oyster-shell production (abundance and length) and allogenic sedimentation (Rodriguez et al. 2014). Our initial increase in reef crest elevation October to December 2020 is likely due to the accumulation of oysters 3 months post-

construction (Figure 15). However, increases in reef crest elevation due to increases in oyster abundance can become limited overtime, as oysters exhibit an upper zero-growth boundary (growth ceiling), above which oyster accumulation is limited due to inundation requirements (Ridge et al. 2015, Rodriguez et al. 2014). It is possible that the upper boundary of reef crest elevation can be surpassed, not by the accumulation of more oysters, but by the growth of larger oysters. This is supported by the fact that despite oyster abundances decreasing in December 2020, March 2021 and September 2021 (Figure 9), elevation and oyster lengths continued to increase (Figure 15, 10). Therefore, high-relief reef's tendency to host larger oysters may help overcome some reef accretion limitations caused by oyster growth ceilings.

Disentangling the effects of reef relief (initial, categorical) versus crest elevation (continuous) versus height (continuous) on oyster abundance can be difficult. "Height" in our study refers to the difference between the reef crest elevation, and the landward reef base elevation. Looking just at the model outputs, it appears as though increased height negatively affects oyster abundance, with an estimate of approximately 17 less oysters per quadrat with every unit increase in height (Appendix A3, A5, A7). However, this is somewhat misleading and ignores the mechanisms by which oyster reefs grow. In October and December 2020, high and low relief sites had significantly different heights (Figure 16). However, overtime, this difference dissipated, with high- and low-relief sites not differing significantly in height in June and September 2021. This is potentially due to high-relief sites accumulating more sediment landward of the reef, decreasing the difference between the base elevation and the crest elevation. High-relief sites have greater structure than low relief sites, both initially, with a greater base log diameter, and through time, with higher oyster abundances. Greater physical structure can lead to higher rates of sedimentation, trapping the outgoing sediment with the tides

(Ridge et al. 2015). This idea falls in line with that of Ridge et al. (2015), who observed that even at low oyster densities at their highly exposed sites (i.e. lower tidal inundation), reef accretion at the base of the reef was driven by sediment accumulation, not oyster growth. Roughly one year post-construction, in June and September of 2021, the reefs may not be increasing in reef crest elevation as much as they are in reef base elevation, due to sedimentation rates being higher than oyster growth rates. This is possibly due to some of the reefs hitting the growth ceiling around June-September 2021. This is supported by the fact that reef heights decreased between September 2021 and March 2022 (Figure 16). It also could explain why increasing reef crest elevation was more tightly correlated with increases in oyster abundance for low-relief reefs than high relief reefs, which maintained somewhat similar oyster abundances across elevation gradients (Figure 14). It is likely the high-relief reefs hit the growth ceiling elevation earlier and could not continue to increase oyster abundances due to inundation requirements (Rodriguez et al. 2014, Ridge et al. 2015, Bost et al. 2022).

Effect of Wave Energy, Peak Wave Period and Elevation on Oyster Abundance

While the positive feedback between the abiotic (elevation, inundation, wave attenuation, sedimentation) and biotic (oyster abundance) components of oyster reefs (Figure 1) make them a useful, self-maintaining system for coastal protection (Piazza et al. 2005), there is a conflict between the optimal elevation for shoreline protection benefits and oyster growth (Morris et al. 2021). From an engineering perspective, researchers suggest setting reef crest heights at or above water levels to attenuate the greatest amount of wave energy (Chauvin 2018, MacDonald 2018, Wilberg et al. 2018, Chowdhury et al. 2019, Zhu et al. 2020). However, despite Morris et al. (2021) finding that reefs whose crest were inundated for less than 50% of the time were 14 times

more effective at decreasing wave heights, Ridge et al. (2015) found that oysters do not colonize substrates with less than 50% inundation duration. Researchers suspected that this was due to desiccation stress; however, based on our model outputs (Appendix A3, A5, A7), elevation and wave energy/peak wave period interact with another, modifying their direct effects on oyster abundance. One of our models predicted that increasing elevation of a reef positively effects oyster abundance (Appendix A5). However, in areas of higher wave energy, this relationship may be modified. Generally, reefs set higher in elevation or those with taller reef crests, are more exposed to wave driven shear stress (Morris et al. 2021). Therefore, while increasing elevation could increase oyster abundance, it may also increase the probability of coming in contact with crashing surface waves, dampening the positive effect of elevation in certain areas depending on the local wave energy environment (Kamphuis 2000).

The interaction we see between wave energy/peak wave period and elevation may also help explain our site level differences in oyster abundance. Taylor's Creek is a naturally low-fetch environment, influenced by twice daily tides (NC DEQ, 2022). However, its proximity to a public boat ramp and popular marina has altered its energy environment, causing site level differences in the wave environment (Figure 13). The area near the boat ramp has a tumultuous environment, with boats revving their engines in order to get on and off trailers, causing the adjacent shoreline to have the highest rates of erosion. Because of this, we were unable to build reef sites directly across from the boat ramp (Figure 4), as the shoreline was too unstable, with maritime forest falling into the water (*Dr. Rachel Gittman, personal observation*). As boats leave the boat ramp, they tend to exit towards site 4-6, and hit a cruising 'no-wake' speed around sites 7-12 (*Anna Albright, personal observation*). This difference in the kind of wave energy (revving vs. cruising) may be why site 4 and 5 performed poorly, while sites 7-8 and 10 accumulated

many oysters, despite their differences in relief. More research is required in this area to understand how the different properties of waves, especially those made by boat wakes, impact oyster abundances.

Interactions Between Predator Abundance, Consumption and Oyster Abundance

Combining the results from the oyster abundance models and the consumption assay models may help us understand how oyster restoration impacts estuarine communities. Similar to other research studies, we found that oyster survival was highly dependent on predator access to juvenile oysters, with uncaged and half-caged treatments experiencing higher consumption rates than those of caged controls at sites 5-10 (Grabowski et al. 2020). However, despite the ability of predators to consume oysters efficiently at some sites, surprisingly, when excluding other factors, as oyster abundance on the reef increased, consumption rates on the assay increased (Figure 22). Furthermore, in our oyster abundance models, we saw that the interaction between predatory crab abundance and elevation had a positive impact on oyster abundance (Appendix A3, A5). To understand this, we must reconsider how the abiotic and biotic components of an oyster reef ecosystem interact with one another in a dynamic relationship, as shown in Figure 1. Model newlinTp4 showed how increasing elevation increases oyster abundance (Appendix A5). Reefs with better structure (i.e. higher oyster abundances) frequently hold higher densities of mud crabs (Grabowski et al. 2005, Ziegler et al. 2018) as mud crabs not only consume juvenile oysters, but also use the reef as refuge from predation (Grabowski et al. 2004). The increase in crab abundance then drives the increase in consumption that we see at sites with higher oyster abundance. This further supports the idea that when constructed reefs can obtain

sufficient live-oyster abundances, they can support and enhance local communities, building thriving ecosystems where they did not previously exist.

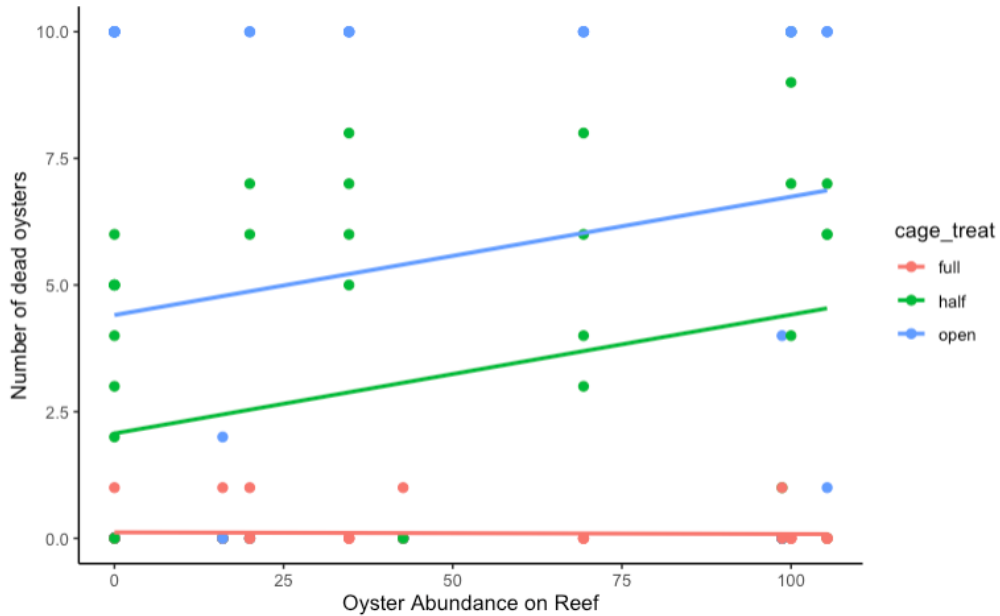


Figure 22: Number of dead oysters as oyster abundance on the reef increases. Full cage shown in pink. Half cage shown in green. Open (no cage) shown in blue

Consumption and Potential Predator Identity

Interactions between our sampling methodology and environmental conditions may help clarify the reasoning behind the patterns seen in our consumption assays, especially as it relates to predator identity. Our consumption models predicted that a decrease in predatory crab abundance led to an increase in consumption (Appendix B2, B4, B6). Crab condos are relatively small, and only provide adequate space for small organisms, making them biased towards small crustacean species or juveniles. While not significant in the model, we did see a positive correlation between wave energy and oyster consumption (Figure 20), with sites with the highest wave energy (6-9) also having high consumption. Small mobile organisms are unable to

withstand high wave energy areas and tend to leave the habitat during high stress periods (Menge and Sutherland 1987). Therefore, the high consumption rates at some of the sites may be driven by a few, larger crab species (e.g. blue crab, stone crabs), instead of small mud crabs, as the larger crustaceans can better withstand the higher stress conditions. Stone crabs (*Menippe* spp.) have recently expanded their range into several sounds in North Carolina, and their impact on estuarine food webs is not fully known (Rindone and Eggleston 2011). While not fully documented throughout the course of this study, large stone crabs were noted to be present at sites 3 (HR), 5 (HR) and 8 (HR) in August 2021 (Albright, *personal observation*). Rindone and Eggleston (2011) found that at low oyster densities (like that of the assays), stone crab predation on oysters could lead to local extinction of oyster populations. The total consumption of oyster on the open tiles at sites 5-10 during the assay period could be due to similar stone crab feeding observed by those authors.

Examining the effect of caging treatment on oyster consumption may provide an alternative explanation to our consumption rate patterns and give us insight into predator identity. While both the uncaged and the half-caged treatments had higher consumption rates than the full caged treatment, fewer oysters were consumed in the half cages compared to the full cages (Figure 18, Appendix B2-4). The half cages, while mostly open, did provide a small barrier to the oysters on the perimeter of the tile, for which a predator would need to go around a lip to access the spat. For a predatory crab, this may be possible, reaching within the confines of the cage to handle the oyster. However, for a predatory fish species, like sheepshead, this would not be possible. Despite it being well known that sheepshead prey on oysters, they are notoriously hard to capture using conventional passive sampling methods (Sedberry 1987). Therefore, the differences in consumption seen between our two caging treatments and between

our sites could be due to differences in sheephead abundances at our reefs, despite not capturing them in our condos.

Lastly, we did not observe an effect of reef relief on oyster consumption (Appendix B5-7). This is in contrast to other studies that have suggested that oysters at lower elevations experience greater predation pressures (Fodrie et al. 2014, Keller et al. 2019). This is possibly due to the low densities of juvenile oysters on our assays, for which predators had ample time during the 24-hour period to consume all 10 oysters. However, this further supports our idea that consumption is not the driving force behind the differences we see in oyster abundances between high and low relief sites.

Conclusions

Throughout our investigation, we aimed at understanding how elevation, reef relief and wave energy impacted oyster abundance and mediated oyster consumption. We found that increasing elevation and reef relief positively impacted oyster abundance, but that small-scale spatial variations in other environmental characteristics heavily influenced reef success. Furthermore, in contrast to our hypothesis, we found that for our reefs, relief did not impact consumption, but instead that potentially predator identity and predator access to juvenile oysters, controlled consumption rates. Our work also suggests that when reefs attain higher oyster abundances, it leads to increasing consumption, possibly due to the successful creation of a complex habitat that can support numerous community associates.

From our research it is evident that creating breakwaters with high vertical relief is a necessary element to oyster restoration design. High-relief breakwaters not only host high oyster abundances but potentially help mitigate effects of erosion by accumulating more sediment

overtime, compared to those of lower relief breakwaters. Going forward, it is important to investigate how reef relief and elevation impact wave attenuation capabilities of restored reefs at fine scales.

Widespread use of oyster reef restoration for shoreline protection has been hindered by the public's perception that nature-based infrastructure cannot withstand high wave energy environments, especially that of artificial boat wake waves (Scyphers et al. 2010, Theurekauf et al. 2017). While our models do show that wave energy, especially those with short-periods, can negatively affect oyster abundance, this impact is only significant when interacting with elevation. This does not mean that nature-based infrastructure cannot be used, but that practitioners may need to design breakwaters more in favor of oyster growth, with longer inundation durations, rather than for engineering purposes (<50% inundation), in order to increase long-term reef success. The ability of our high-relief reefs to maintain vertical relief, accumulate oysters, and induce sediment accumulation makes them a great candidate as an alternative to bulkheads for shoreline protection. Their ability, once formed, to maintain abundance while supporting predators makes them both ecologically and structurally advantageous. While the public should be aware of the negative impacts boating can have on oyster reef restoration, it should not be a deterrent for constructing hybrid breakwaters as a greener option for shoreline protection. Moving forward, it is important to test the designs across higher wave energy environments and further disentangle the environmental characteristics that lead to restoration success.

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Appendix A

Table A1: Predatory Crab Abundance for high (HR) and low relief (LR) sites in June 2021.

Site	Relief	Total predatory crab abundance	Organism identification
1	LR	12	<i>P. herbstii</i> (8), <i>D. sayi</i> (3), unknown crab sp. (1)
3	HR	15	<i>P. herbstii</i> (7), unknown crab sp. (6), oyster drill (1)
4	LR	8	<i>P. herbstii</i> (4), unknown crab sp. (3), stone crab (1)
5	HR	9	<i>P. herbstii</i> (3), <i>R. harrisii</i> (1), <i>D. sayi</i> (3), unknown crab sp. (1), stone crab (1)
7	LR	4	<i>P. herbstii</i> (4)
8	HR	7	<i>P. herbstii</i> (5), <i>R. harrisii</i> (1), unknown crab sp. (1)
10	HR	10	<i>P. herbstii</i> (8), <i>D. sayi</i> (1), unknown crab sp. (1)
11	LR	16	<i>P. herbstii</i> (6), <i>R. harrisii</i> (4), <i>D. sayi</i> (1), unknown crab sp. (5)

Table A2: Predatory Crab Abundance for high (HR) and low relief (LR) sites in September 2021

Site	Relief	Total predatory crab abundance	Organism identification
1	LR	12	<i>P. herbstii</i> (8), <i>R. harrisii</i> (1), <i>D. sayi</i> (1), stone crab (2)
3	HR	5	<i>E. depressus</i> (1), stone crab (4)
4	LR	19	<i>P. herbstii</i> (5), <i>D. sayi</i> (6), unknown crab sp. (3), stone crab (2), oyster drill (3)
5	HR	19	<i>P. herbstii</i> (8), <i>D. sayi</i> (3), unknown crab sp. (7), oyster drill (1)

7	LR	23	<i>P. herbstii</i> (7), <i>D. sayi</i> (7), unknown crab sp. (6), stone crab (3)
8	HR	21	<i>P. herbstii</i> (5), <i>R. harrisii</i> (6), unknown crab sp. (7), stone crab (3)
10	HR	14	<i>P. herbstii</i> (10), <i>D. sayi</i> (2), unknown crab sp. (2), stone crab (2)
11	LR	17	<i>P. herbstii</i> (10), unknown crab sp. (6), stone crab (2)

Table A3: Oyster Abundance model (“newlinTp”) summary output. ‘Scale(elevation)’ is the reef crest elevation (in meters). ‘Scale(Tp)’ is the peak wave energy estimate (in seconds). ‘Scale(total_crab)’ is the predatory crab abundance. ‘Scale(height)’ is the landward height of the reef (in meters) ReliefLR is the low relief reef oyster abundance estimate. ‘Scale(elevation): scale(Tp)’ is the interaction between reef crest elevation and peak wave period. ‘Scale(elevation): scale(total_crab)’ is the interaction between reef crest elevation and total predatory crab abundance. ‘Scale(elevation): scale(height)’ is the interaction between reef crest elevation and reef height. ‘Scale(elevation): reliefLR’ is the interaction between elevation and low relief reef category.

Model: newlinTp	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	58.6858	9.6003	6.113	1.57e-06***
scale(elevation)	6.1901	11.2549	0.550	0.58684
scale(Tp)	0.5829	7.8798	0.074	0.94158
scale(total_crab)	-5.5709	7.4484	-0.748	0.46097
scale(height)	-16.7681	6.3249	-2.651	0.01326 *
reliefLR	-29.3903	12.5636	-2.339	0.02697 *
scale(elevation): scale(Tp)	33.0877	10.7681	3.073	0.00480 **
scale(elevation): scale(total_crab)	26.2681	7.9647	3.298	0.00273 **
scale(elevation): scale(height)	-11.6895	7.4920	-1.560	0.13034
scale(elevation):	-6.0688	16.2381	-0.374	0.71152

reliefLR				
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Table A4: Anova output for model newlinTp

Model: newlinTp	Sum Sq	Df	F value	Pr (>F)
scale(elevation)	655.7	1	0.8464	0.365708
scale(Tp)	653.4	1	0.8435	0.366521
scale(total_crab)	1280.9	1	1.6535	0.209399
scale(height)	6326.2	1	8.1665	0.00819 **
relief	4340.9	1	5.6037	0.025348 *
scale(elevation): scale(Tp)	7314.1	1	9.4417	0.004804 **
scale(elevation): scale(total_crab)	8426.1	1	10.8772	0.002734 **
scale(elevation): scale(height)	1885.9	1	2.4344	0.130342
scale(elevation): relief	108.2	1	0.1397	0.711517

Table A5: Oyster abundance model (“newlinTp4”) summary output.

‘Scale(elevation)’ is the reef crest elevation (in meters). ‘scale(Tp)’ is the peak wave energy estimate (in seconds). ‘Scale(total_crab)’ is the predatory crab abundance. ‘scale(height)’ is the landward height of the reef (in meters). ‘Scale(elevation): scale(Tp)’ is the interaction between reef crest elevation and peak wave period. ‘Scale (elevation): scale(total_crab)’ is the interaction between reef crest elevation and total predatory crab abundance. ‘Scale(elevation): scale(height)’ is the interaction between reef crest elevation and reef height.

Model: newlinTp4	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	44.708	5.317	8.408	2.88e-09 ***
scale(elevation)	12.973	5.873	2.209	0.03522 *
scale(Tp)	1.308	7.953	0.164	0.87054
scale(total_crab)	-3.281	7.485	-0.438	0.66439

scale(height)	-16.011	6.712	-2.385	0.02381 *
scale(elevation): scale(Tp)	32.078	11.148	2.878	0.00745 **
scale(elevation): scale(total_crab)	26.669	7.876	3.386	0.00205 **
scale(elevation): scale(height)	-10.793	7.338	-1.471	0.15210

Table A6: Anova model output for newlinTp4

Model: newlinTp4	Sum Sq	Df	F value	Pr(>F)
scale(elevation)	7966.4	1	9.1081	0.005258 **
scale(Tp)	538.3	1	0.6154	0.439113
scale(total_crab)	1913.6	1	2.1879	0.149884
scale(height)	5956.8	1	6.8105	0.014187 *
scale(elevation): scale(Tp)	7242.3	1	8.2802	0.007447 **
scale(elevation): scale(total_crab)	10028.2	1	11.4653	0.002054 **
Scale(elevation): scale(height)	1892.3	1	2.1634	0.152096

Table A7: Oyster abundance model (“newlinE2”) summary output

‘Scale(elevation)’ is the reef crest elevation (in meters). ‘Scale(E)’ is wave energy (J/m²). ‘Scale(height)’ is the landward height of the reef (in meters) ReliefLR is the low relief reef oyster abundance estimate. ‘Scale(elevation): scale(E)’ is the interaction between reef crest elevation and wave energy. ‘Scale(elevation): scale(height)’ is the interaction between reef crest elevation and reef height. ‘Scale(elevation): reliefLR’ is the interaction between elevation and low relief reef category.

Model: newlinE2	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	68.868	10.497	6.561	3.46e-07 ***
scale(elevation)	-2.542	12.223	-0.208	0.8367
scale(E)	1.523	6.702	0.227	0.8218
scale(height)	-17.737	7.025	-2.525	0.0173 *
reliefLR	-36.717	15.518	-2.366	0.0249 *

scale(elevation): scale(E)	-24.207	9.937	-2.436	0.0212 *
scale(elevation): scale(height)	-3.606	6.335	-0.569	0.5736
scale(elevation): reliefLR	9.294	16.306	0.570	0.5731

Table A8: Anova output for model newlinE2

Model: newlinE2	Sum Sq	Df	F value	Pr(>F)
scale(elevation)	833.7	1	0.9002	0.35056
scale(E)	579.2	1	0.6254	0.43546
scale(height)	6413.0	1	6.9249	0.01347 *
relief	5125.1	1	5.5342	0.02565 *
scale(elevation): scale(E)	5496.0	1	5.9346	0.02122 *
scale(elevation): scale(height)	300.1	1	0.3241	0.57356
Scale(elevation): relief	300.9	1	0.3249	0.57306

Appendix B

Table B1: Predatory crab abundance for July 2021

Site	Total predatory crab abundance	Organism identification
1	6	<i>P. herbstii</i> (2), <i>R. harrisii</i> (2), unknown crab sp. (2)
2	9	<i>P. herbstii</i> (3), <i>R. harrisii</i> (2), unknown crab sp. (4)
3	22	<i>P. herbstii</i> (8), <i>D. sayi</i> (5), unknown crab sp. (7), stone crab (2)
4	3	<i>D. sayi</i> (2), stone crab (1)
5	8	<i>P. herbstii</i> (3), <i>R. harrisii</i> (3), unknown crab sp. (1), stone crab (1)
6	10	<i>P. herbstii</i> (5), unknown crab sp. (4), stone crab (1)
7	6	<i>P. herbstii</i> (2), <i>R. harrisii</i> (3), unknown crab sp. (1)
8	9	<i>P. herbstii</i> (5), <i>R. harrisii</i> (2), stone crab (2)
9	9	<i>P. herbstii</i> (3), <i>R. harrisii</i> (1), <i>D. sayi</i> (1), unknown crab sp. (4)
10	9	<i>P. herbstii</i> (5), <i>D. sayi</i> (2), unknown crab sp. (2)
11	11	<i>P. herbstii</i> (6), unknown crab sp. (3), stone crab (2)
12	6	<i>P. herbstii</i> (5), unknown crab sp. (1)

Table B2: Consumption Assay ‘mHrms’ model summary output. ‘Relief_treatLR’ is the low-relief assay estimate. ‘Scale(total_crab)’ is the predatory crab abundance. ‘Cage_treathalf’ is the half-cage treatment. ‘Cage_treatopen’ is the open cage treatment. ‘Scale(oyster_abundance)’ is the oyster abundance on the reef. ‘Reef_reliefhigh’ is the estimate for assays next to high relief breakwaters. ‘Reef_relieflow’ is the estimate for assays next to low relief breakwaters. ‘Scale(Hrms)’ is the wave energy measurement (as RMS wave height).

‘Scale(oyster_abundance): reef_reliefhigh’ is the interaction between oyster abundance and the reef relief of the adjacent breakwater.

Model: mHrms	Estimate	Std. Error	Z value	P (> z)
(Intercept)	-6.7372	2.1142	-3.187	0.00144**
relief_treatLR	0.1602	0.2126	0.754	0.45097
scale(total_crab)	-1.1817	0.6259	-1.888	0.05901
cage_treathalf	4.2234	0.4844	8.719	< 2e-16 ***
cage_treatopen	6.6247	0.5294	12.513	< 2e-16 ***
scale(oyster_abundance)	0.8709	1.4397	0.605	0.54525
reef_reliefhigh	0.3277	2.1445	0.153	0.87853
reef_relieflow	-1.6218	1.8735	-0.866	0.38667
scale(Hrms)	-0.2722	0.2223	-1.224	0.22085
scale(oyster_abundance):reef_reliefhigh	1.9847	1.6643	1.193	0.23305

Table B3: Consumption Assay ‘mE’ model output summary

Model: mE	Estimate	Std. Error	Z value	P (> z)
(Intercept)	-6.6777	2.1108	-3.164	0.00156**
relief_treatLR	0.1601	0.2125	0.753	0.45117
scale(total_crab)	-1.2315	0.6339	-1.943	0.05203
cage_treathalf	4.2145	0.4836	8.716	< 2e-16 ***
cage_treatopen	6.6146	0.5285	12.516	< 2e-16 ***
scale(oyster_abundance)	0.9155	1.4675	0.624	0.53274
reef_reliefhigh	0.3184	2.1818	0.146	0.88398
reef_relieflow	-1.7123	1.9003	-0.901	0.36756
scale(E)	-0.1983	0.2170	-0.914	0.36062

scale(oyster_abundance):reef_reliefhigh	1.9042	1.7100	1.114	0.26547
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Table B4: Consumption assay ‘mTp’ model output summary

Model: mTp	Estimate	Std. Error	Z value	P (> z)
(Intercept)	-6.55538	2.05660	-3.187	0.00144**
relief_treatLR	0.15984	0.21228	0.753	0.45148
scale(total_crab)	-1.34723	0.62549	-2.154	0.03125*
cage_treathalf	4.20309	0.48227	8.715	< 2e-16***
cage_treatopen	6.60135	0.52703	12.526	< 2e-16***
scale(oyster_abundance)	1.05149	1.46634	0.717	0.47332
reef_reliefhigh	0.28818	2.20388	0.131	0.89596
reef_relieflow	-1.84241	1.90470	-0.967	0.33340
scale(Tp)	-0.08456	0.17150	-0.493	0.62196
scale(oyster_abundance):reef_reliefhigh	1.65449	1.70515	0.970	0.33190

Table B5: Anova output for model mHrms

Model: mHrms	Chisq	Df	Pr(>Chisq)
(Intercept)	10.1547	1	0.001439 **
relief_treat	0.5682	1	0.450971
scale(total_crab)	3.5651	1	0.059006
cage_treat	173.0530	2	< 2.2e-16 ***
scale(oyster_abundance)	0.3659	1	0.545252
reef_relief	2.1486	2	0.341536
scale(Hrms)	1.4989	1	0.220846

scale(oyster_abundance):reef_relief	1.4221	1	0.233054
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Table B6: Anova output for model mE

Model: mE	Chisq	Df	Pr(>Chisq)
(Intercept)	10.0078	1	0.001559 **
relief_treat	0.5677	1	0.451170
scale(total_crab)	3.7749	1	0.052028
cage_treat	173.0668	2	< 2.2e-16 ***
scale(oyster_abundance)	0.3892	1	0.532739
reef_relief	2.2577	2	0.323405
scale(E)	0.8357	1	0.360615
scale(oyster_abundance):reef_relief	1.2400	1	0.265468

Table B7: Anova output for model mTp

Model: mTp	Chisq	Df	Pr(>Chisq)
(Intercept)	10.1600	1	0.001435**
relief_treat	0.5669	1	0.451485
scale(total_crab)	4.6392	1	0.031249*
cage_treat	173.2313	2	< 2.2e-16 ***
scale(oyster_abundance)	0.5142	1	0.473322
reef_relief	2.4369	2	0.295695
scale(Tp)	0.2431	1	0.621964
scale(oyster_abundance):reef_relief	0.9415	1	0.331903

