COASTAL RECREATIONAL FISHING LICENSE

Final REPORT

Recipient: Antonio B. Rodriguez

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Grant Title: Defining the critical depth for intertidal oyster-reef restoration to maximize long-term ecological function

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Cost: $83,782

Description of Work**:**

The aim of this study is to increase the success of oyster-reef restoration efforts in North Carolina by quantifying reef accretion rates and cataloging internal reef composition, from initial colonization through maturity, at a variety of different water depths in Back Sound (Middle Marsh area), Carteret County. Patch reefs at intertidal and subtidal depths are the focus of this study. Our study provides critical information about oyster-reef growth that is necessary for predicting the sustainability of the fishery, as well as maximizing the ecosystem services the reef structure provides, in particular fish habitat, in a rapidly changing coastal environment by achieving three main objectives:

1. Determine the critical elevation (depth) threshold for restoration success.

Exposure stress in the intertidal increases oyster mortality and decreases growth rate during the first month of benthic life; however, the prevalence of intertidal oysters in high-salinity areas suggests oysters subsequently benefit from some duration of exposure. To determine what that ideal % exposure time is, we will examine and compare restored reefs that were constructed in 1997, 2000, and 2011 from 60 bushels of oyster shell in a 5 x 3 x 0.15 m shape. These reefs are located on different substrate elevations; hence, exposure times vary between reefs.

2. Measure reef growth, in terms of volume and area changes, from initial placement of cultch above the critical elevation threshold to 15 years.

Reef accretion is commonly expressed as the change in elevation through time, but in reality, a reef grows vertically and horizontally. Reef accretion is, in part, the result of sediment inputs (oyster shell, feces, pseudofeces, and external sediment) and sediment preservation (bioerosion, dissolution, predators, and currents). In addition, as a reef grows, sediment compaction of the reef and modification of shell size and shape contribute to changes in reef morphology. While some of the factors that define reef accretion are well constrained (e.g., individual oyster growth), few studies synthesize these parameters to calculate reef growth.

3. Evaluate restored oyster-reef sustainability with future rates of sea-level rise.

Over the next 100 years, climate change is expected to result in an average sea-level rise of ~1.4 m, including contributions from ice sheets and thermal expansion. In planning intertidal oyster reef restoration efforts and assessing the sustainability of the reef, it is essential to constrain 1) the rate of intertidal oyster reef accretion relative to projected sea-level rise, 2) the optimal elevation for placing oyster reef substrate, and 3) characteristics of optimal sites for placing substrate now such that restored oyster reefs persist and thrive under future climate-change scenarios.

Project Findings**:**

Objective 1: Physicochemical boundaries and optimal conditions characterizing the response of coastal foundation species to sea-level rise must be defined to accurately

predict sustainability. Using 15-year-old experimental oyster reefs , we examined the effects of varying inundation on vertical reef growth and oyster density, two proxies of productivity that determine the ability of reefs to maintain their position relative to sea level. These reefs were constructed adjacent to sandflat and saltmarsh habitats over a subtidal-to-intertidal depth gradient. Reefs surrounded by sandflats are defined by a strong parabolic growth pattern in relation to duration of aerial exposure. We find an abrupt switch from reef accretion to reef deterioration occurring at a critical exposure duration of 10%, an optimal reef growth zone (30-40% exposure) defined by the highest vertical accretion rates (~ 2 cm yr-1), and a growth ceiling near mean sea level (~55% exposure) where exposure stress becomes too high to support additional vertical growth. We also discover a landscape-specific response in reef growth as reefs adjacent to saltmarshes, ironically, exhibit a negative relationship between vertical accretion and aerial exposure.

Design and sampling –We addressed Objective 1 using restored *Crassostrea virginica* (eastern oyster) reefs that were constructed from cultch material (shucked oyster shell) in 1997 and 2000 by Grabowski et al. (2005) at Middle Marsh, Back Sound, North Carolina (Figure 1). Each reef was constructed from 60 bushels of cultch shell shaped in to a 3-m wide, 5-m long and 0.15-m high box and placed in the middle of sandflats (sandflat patch reefs; n=10), adjacent to *Spartina alterniflora*-dominated saltmarsh (fringing saltmarsh reefs, n=4), or fringing reefs adjacent to saltmarsh and bordering seagrass (*Zostera marina* and *Halodule wrightii*; seagrass reefs n=6). Grabowski et al. (2005) found no significant differences in oyster or reef-associated faunal densities between saltmarsh and seagrass reefs, leading us to pool them in to the "saltmarsh reef" designation for the purposes of our study.

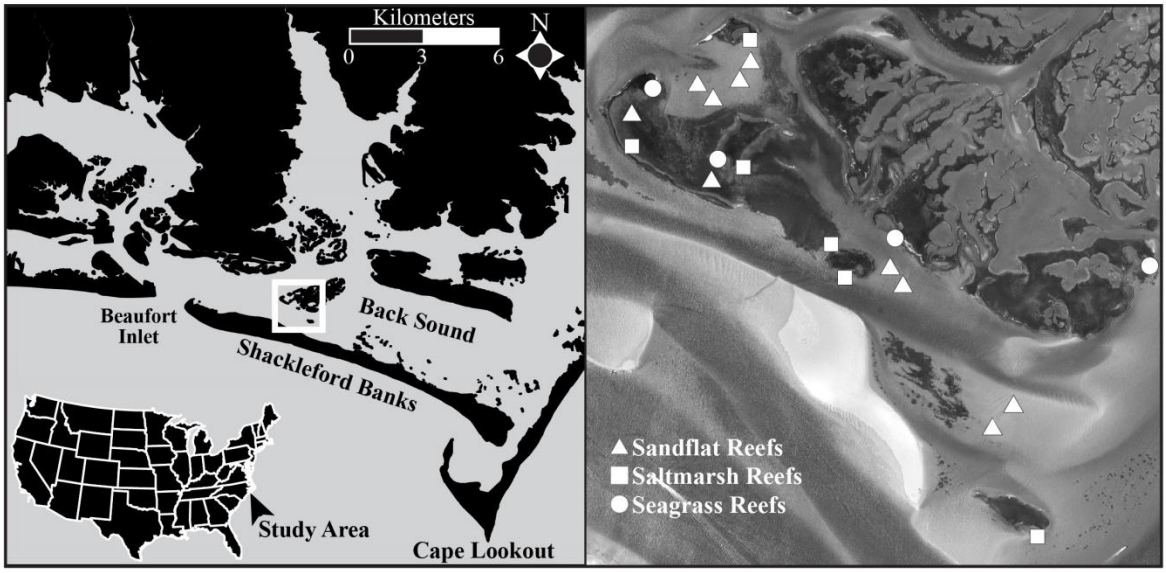

Figure 1. Study area map of Middle Marsh, a relic flood tidal delta in Back Sound, North Carolina. Study area reefs are designated by their habitat setting: sandflat (triangles), saltmarsh (squares), seagrass (circles). Oyster reefs adjacent to saltmarsh and seagrass beds were pooled for the purposes of this study.

Ten-minute water-level data were obtained over the course of 6 months (June - December) using HOBO® U20 Water Level Loggers (Onset Computer Corporation; ± 0.3 cm accuracy) located in three areas of Middle Marsh. Loggers were placed in a stilling well (slotted PVC pipe) attached to rebar that was driven into the substrate (~3 m deep). Elevations were surveyed at both deployment and data collection, which occurred every three months, with a Trimble® RTK GPS. Pressure data were corrected for local fluctuations in barometric pressure using a fourth pressure sensor deployed on land, and water-levels were verified with independent field measurements obtained using a level measuring staff at time of deployment and readout. RTK GPS data were used to transform the water-level data in to the North American Vertical Datum established in 1988 (NAVD88) with horizontal and vertical precisions of <1.0 cm and <1.5 cm, respectively. We divided the tidal data into 1-cm bins to ascertain mean percent aerial exposure at each elevation, which we used to convert all future elevation measurements to percent exposure where appropriate. No correction was applied to account for relative SLR, because no significant trend in annual mean sea level for the past fifteen years (around the age of the reefs) exists in data from NOAA tide gauge 8656483 located 5 km northeast of the study area.

To assess the geomorphic response of the reefs over their lifetimes and determine their vertical growth limit, we collected cores from each reef's center (Figure 2). We surveyed the core location with the RTK GPS to calculate the original elevation of the substrate on which the oyster cultch was placed and measured reef thickness from the cores. To core the reefs, a 10-cm diameter aluminum pipe was driven through each reef using a jackhammer. In the lab, extracted cores were split longitudinally to allow measuring of the distance between the upper and lower extent of shell, which represents vertical reef growth (i.e., accretion). The initial elevation of each reef was determined as the top surface of the cultch pile (i.e., substrate elevation + 0.15 m cultch shell layer).

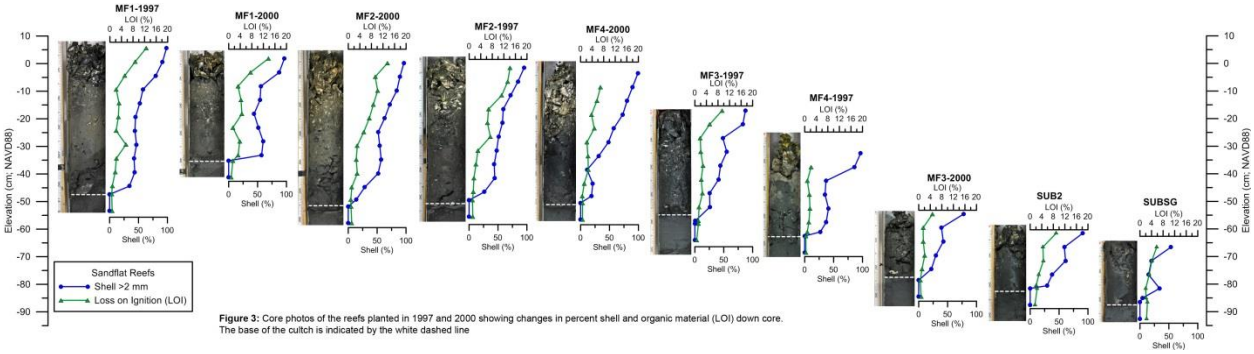

Figure 2. Core photos of the patch reefs planted in 1997 and 2000 showing changes in precent shell and organic material (LOI) down core. The base of the cultch is indicated by the white dashed line.

To assess how aerial exposure impacts oyster survivorship and recruitment (two vertical-growth mechanisms), we measured oyster density to ascertain size-abundance patterns at different elevations. Following Grabowski et al. (2005), we randomly placed 0.25-m^2 quadrats at varying elevations to obtain 2-3 quadrat samples per reef for density. Samples within reefs were not pooled because they were collected from areas with different exposure conditions, and our primary interest was to determine if exposure regulates reef dynamics. Oyster reef material was

excavated to a depth of 15 cm and quantified within each plot to establish living-oyster density. Individual shell lengths were measured from all living oysters in these plots. We recorded all plot elevations at the surface of each reef using the RTK GPS.

Finally, while reef cores estimate decadal reef growth from the middle of a reef, we supplemented these data with cm-scale vertical growth rates across the entire surface of four sandflat reefs over a 2-year period. Following methods put forth by Rodriguez et al. (2014), reefs were scanned using a Riegl three-dimensional LMSZ210ii terrestrial laser scanner in 2010 and 2012 to create two digital elevation models from 600,000 to 1,000,000 laser returns (number depends on reef size) spaced <1 cm apart. Elevation changes >1.4 cm are resolvable with this method. Point clouds were processed using RiSCAN Pro software, and we utilized Surfer 10 (Golden Software) to generate digital elevation models of the four sandflat reefs. The 2010 reef grid cells were sorted into 2-cm vertical bins and each grid-cell elevation (1 cm2) was subtracted from its 2012 counterpart (> 500,000 observations per reef) to obtain mean elevation changes between measurements for each bin (i.e., mean vertical accretion rate for every 2-cm change in reef elevation across the entire surface of the reefs). An overall mean vertical accretion rate among reefs was then calculated for each vertical bin.

In order to understand the roles elevation and aerial exposure play on vertical reef growth, we compared reef growth (reef height, log [x + 1] transformed to meet parametric assumptions) to both original cultch elevation and percent aerial exposure using regression analyses (Model II linear and nonlinear). Oyster density data were also transformed (log [x + 1]) to homogenize variances and normalize data, and regression analysis was conducted to assess its relationship with percent aerial exposure. The statistical software JMP 9.0 was used for all analyses.

Results and Discussion- Mean tidal range in Middle Marsh was 0.81 m (MLW: -0.43 m, MHW: 0.38 m); Figure 3). Regression analysis of core data yielded a significant ($F_{1,8} = 16.0$, $R^2 = 0.73$, $p = 0.004$), positive relationship between reef height and the elevation of the original cultch pile surface (Figure 3). After converting elevation data in to exposure times for nonlinear regression, we found that a significant ($F_{2,7} = 42.8$, $p < 0.001$) parabolic relationship explained 92% (adjusted $R^2 = 0.92$) of the variability between exposure of the original cultch pile and reef height for reefs (Figure 2). The greatest vertical expansion for reefs occurred between the cultch surface exposures of 10-20%.

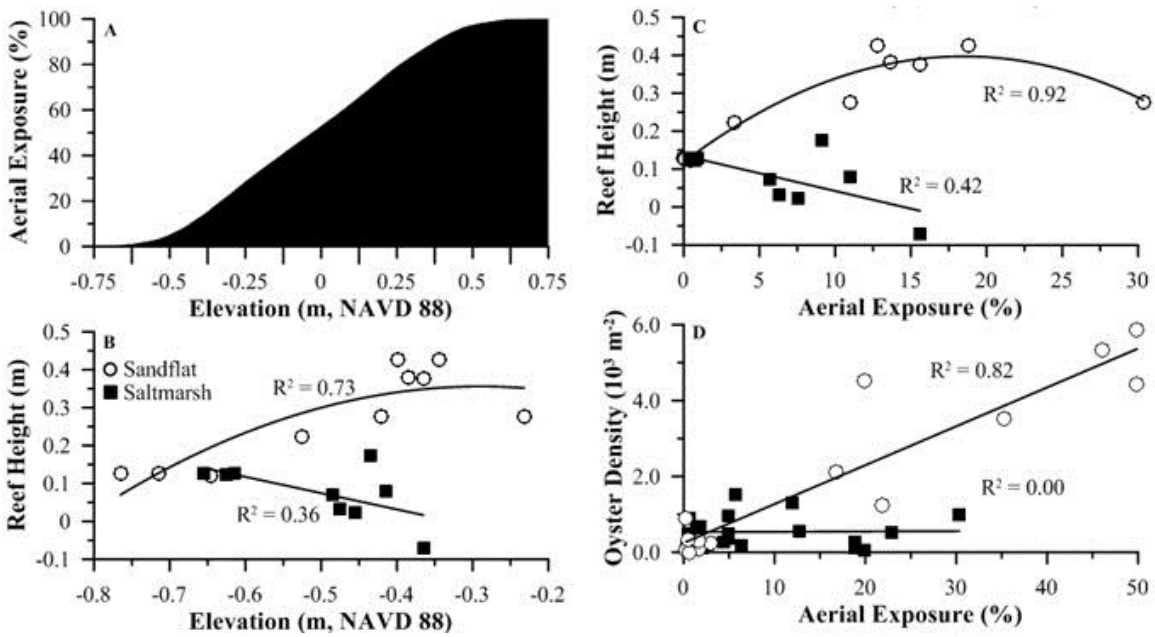

Figure 3. Water level data from study area binned by elevation (NAVD88) into percent aerial exposure (top left). Data were reconciled from three different water level loggers placed around Middle Marsh and allowed to record for six months. Reef heights measured from restored oyster reefs located on sandflats (open circles) and adjacent to saltmarshes (closed squares), with reference to elevation of the original cultch shell surface (bottom left). Reef heights measured from restored oyster reefs located on sandflats and adjacent to saltmarshes with reference to the relative aerial exposure of the original cultch surface (top right). Oyster densities for restored reefs located on sandflats and adjacent to saltmarshes with respect to the relative aerial exposure of the sample plot.

The reef plots we sampled for density were exposed between 2.05% and 49.9% of the time. We found that exposure time explained 84.2% (adjusted R^2) of the variability in oyster densities ($F_{1,13} = 44.2$, $R^2 = 0.84$, $p < 0.001$, Figure 3).

Overall, sandflat older reefs have steep sides and flat tops, while saltmarsh younger reefs have a gradual increase in elevation from substrate to reef crest. Sandflat reefs constructed in either 1997 or 2000 consistently exhibited a plateau morphology across the tops of reefs at 0.03 m NAVD88, indicating that 55% (± 1.5%) exposure is the vertical growth limit (ceiling) for reefs in this region.

From the laser scan data, we found a strong parabolic relationship between vertical-accretion rates and exposure across individual reefs (Figure 4). The areas of reefs that experienced the highest mean growth rates were exposed 30-40% of the time (Figure 4). Growth approached zero at 10% and 55% exposures at the deeper and shallower bounds, respectively. These results independently support the core and transect finding that show 55% is the exposure ceiling for oysters while 10% substrate exposure maximizes reef height.

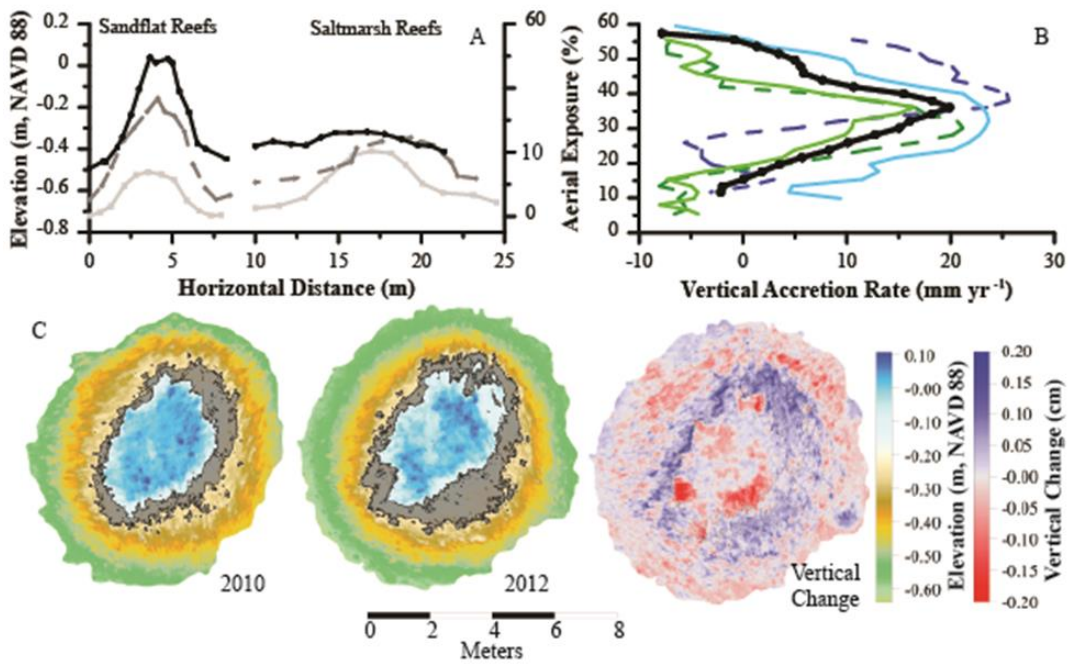

Figure 4. A) Profiles of three oyster reefs from the sandflat and saltmarsh landscape settings, constructed at different elevations. Profiles were taken with an RTK GPS on reefs created in 1997 and 2000. Dashed lines indicate reefs constructed in 1997, while solid lines are reefs built in 2000. C) Digital elevation models from 2010, 2012, and the subsequent subtraction map showing vertical change of the oyster reef over the two years. Shaded area on the 2010 and 2012 DEMs represents the 30-40% optimal growth zone. B) Mean vertical accretion rates by aerial exposure for four different sandflat reefs in Middle Marsh (colored thin lines). Black heavy line represents the mean vertical accretion rate for all five reefs. Dots on the black line represent the 2-cm vertical bin samples. Dashed lines indicate reefs constructed in 1997, solid lines are reefs built in 2000.

Aerial exposure is one of the most important factors determining lower-estuary oyster reef height, reef growth rate, and oyster density. Intertidal oyster reef productivity is optimal for areas of the reef that are exposed 30-40% of the time in euhaline waters, experiencing 2 cm yr^{-1} vertical growth on average. This growth rate returns to zero as the reef reaches its physiological ceiling at 55% exposure. While 30-40% exposure exhibits the most rapid growth, overall vertical growth since construction was greatest in cultch substrates that were exposed 10-20% of the time. This 10% exposure, occurring at -0.43 m NAVD 88, coincides with MLW and represents the critical exposure for oyster growth in which lower estuary reefs residing below that depth will exhibit debilitated vertical growth (~0 cm yr-1). Newly formed reefs that reside just below the critical exposure depth could become nonfunctional with accelerated SLR or during a year of anomalously high sea level as they are overwhelmed with biotic pressures.

Oyster density can be used as a proxy to estimate ecosystem services, and we found exceptional production of oysters (> 2000 m-2) on restored intertidal sandflat reefs above our critical depth. With up to 15 years of robust growth for the restored sandflat reefs in Middle Marsh, the exceptional oyster production associated with appropriate aerial exposure will enhance bio-filtration, habitat complexity, sediment stabilization, and larval supply. Higher relief

reefs also provide greater shoreline protection through wave attenuation throughout the tidal cycle; however, the full extent of the services provided by these reefs still needs to be established. Considering the failure of many subtidal reef restoration efforts and the headward salinity-regime shift associated with SLR, intertidal oyster reef restoration will yield a much greater and more predictable success rate in the lower estuary.

Salinity and aerial exposure gradients coupled with landscape setting provide a complex intersection of physicochemical and biotic processes promoting spatial heterogeneity in oyster-reef habitats. In euhaline parts of estuaries, oyster-reef growth on sandflats follows the rocky intertidal paradigm unlike reefs adjacent to saltmarshes that exhibit opposite weaker growth patterns relative to those driven by aerial exposure. The marsh shoreline is less favorable for robust vertical growth yielding only a thin veneer of oysters, while more extensive reefs will develop away from the influence of the marsh. Considering the consistently greater growth and relatively high densities of oysters on intertidal sandflat reefs, restoration efforts should consider the benefits of placing substrate in relation to the critical exposure depth and the optimal growth zones in euhaline waters. These favorable depth zones will be moving targets with rising sea level. However, the governing exposures will be widely applicable geographically across astronomical and meteorological tidal gradients, and excluding additional future stressors, the persistence of existing intertidal oyster reefs on sandflats above the critical exposure depth will be ensured because of their high growth rates.

Objectives 2 and 3: In the high-salinity seaward portions of estuaries, oysters seek refuge from predation, competition and disease in intertidal areas, but this sanctuary will be lost if vertical reef accretion cannot keep pace with sea-level rise (SLR). Oyster-reef abundance has already declined ~85% globally over the last 100 years, mainly from over harvesting, making any additional losses due to SLR cause for concern. Before any assessment of reef response to accelerated SLR can be made, direct measures of reef growth are necessary. On the basis of our measurements, we developed a globally-testable empirical model of intertidal oyster-reef accretion. We show that previous estimates of vertical reef growth, based on radiocarbon dates and bathymetric maps may be >1 order of magnitude too slow. The intertidal reefs we studied should be able to keep up with any future accelerated rate of SLR and may even benefit from the additional subaqueous space allowing extended vertical accretion.

Design and sampling – Oyster reefs were constructed in 1997 (n=3), 2000 (n=2) and 2011 (n=6) on 6 separate intertidal sand flats in and around Middle Marsh, North Carolina, (Figure 5). Prior to planting the 2011 reefs, we surveyed seafloor elevations at the reef sites with a Trimble 5800 global positioning system (GPS; 0.5 cm horizontal and 1.5 cm vertical error on average) to use as a base from which to measure growth. For the older reefs, we assumed that the substrate elevations were the contact between the cultch and sandflat sediment measured from the cores.

Core collection involved driving a 10-cm diameter aluminum pipe through the center of reefs with a jackhammer. Core location and elevation was surveyed with the Trimble GPS. To vertically characterize the reef sediment, we divided each core into 5-cm bins (= 392 cm3) downward from the reef top and 2-cm^3 subsamples from bins below the reef base. To separate

the shell material >2 mm, we washed each core sample through a sieve, collecting all of the sediment-laden water in a bucket. Shells were dried in an 80°C oven, weighed, photographed, and identified (>90% *Crassostrea virginica*). When all of the sediment settled out of suspension in the bucket, we decanted the water, dried the sediment in an 80°C oven, and weighed the sample. We subsampled the dry <2 mm size fraction, sonicated the subsample to break up agglomerations, and particle sizes from 2000 to 0.04 µm were measured using a Cilas laser particle-size analyzer.

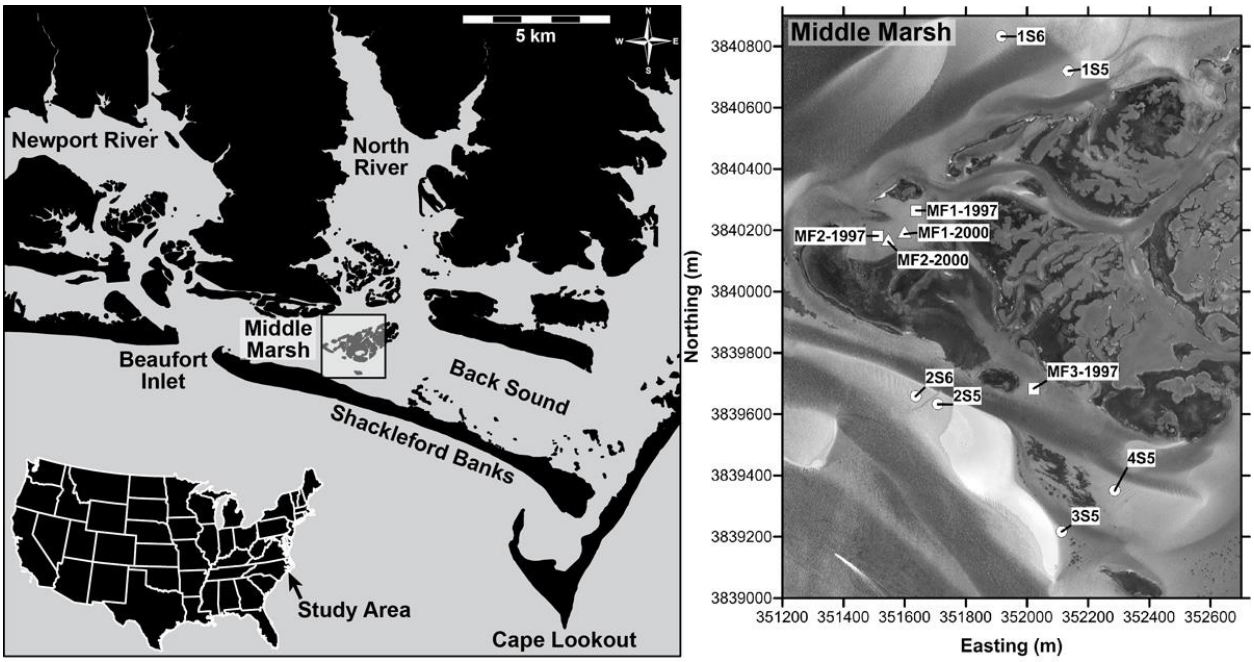

Figure 5. Maps showing reef locations. Symbols denote year of reef construction. The older reefs were constructed in 1997 (squares) and 2000 (triangles) and the younger reefs in 2011 (circles).

Each reef was surveyed three times; the first during placement of the cultch using a level and measuring tape, and subsequent surveys between 2010 and 2013 using the terrestrial laser scanner. The laser scanner, mounted on a tripod adjacent to the reef, rotated 360° while collecting up to 2 million spatial (x, y, and z) data points from laser returns. To sample entire reefs, we scanned from 2-3 different positions around each reef's perimeter during the 30 minutes before and after a spring low tide. Laser returns were transformed into the Universal Transverse Mercator coordinate system by positioning 8 reflectors in the scan area and surveying them with the Trimble GPS. The reefs were imaged from 600,000 - 1,000,000 laser returns (number depended on reef size) spaced <1 cm apart. Laser returns from the oyster reefs and surrounding sandflats were isolated from the entire point cloud using the manual classification tools included in the Merrick Advanced Remote Sensing® software suite. We used Golden Software's Surfer 11.0 to generate grid files (1-cm spacing) of the reefs and surrounding sandflat with the Kriging algorithm, which given the high density of points resulted in nearly identical maps as those made using the Nearest Neighbor algorithm. All reef measures including height, area, and volume were made from the DEMs.

The potential sources of error that could have impacted our ability to measure oyster-reef growth, included: 1) GPS error, 2) laser-scanner instrument error, 3) error with manually leveling the reflectors and associating them with the surveyed points, 4) error associated with manually editing the point cloud, and 5) error associated with using algorithms to create the DEMs. We quantified error experimentally from a synthetic reef, which was a pile of oyster shell in a 1.2 x 1.2 x 0.15 m shape (Figure 6). The morphology of the synthetic reef was measured three times using two scan positions. Each setup included repositioning and resurveying the reflectors. Those three data sets were processed in the same manner as outlined above to create DEMs and vertical error was estimated by subtracting grid cells (Figure 6). The mean of those 25,662 observations was zero, indicating that no bias exists, and error was therefore defined as the mean standard deviation or 0.014 m (Figure 6).

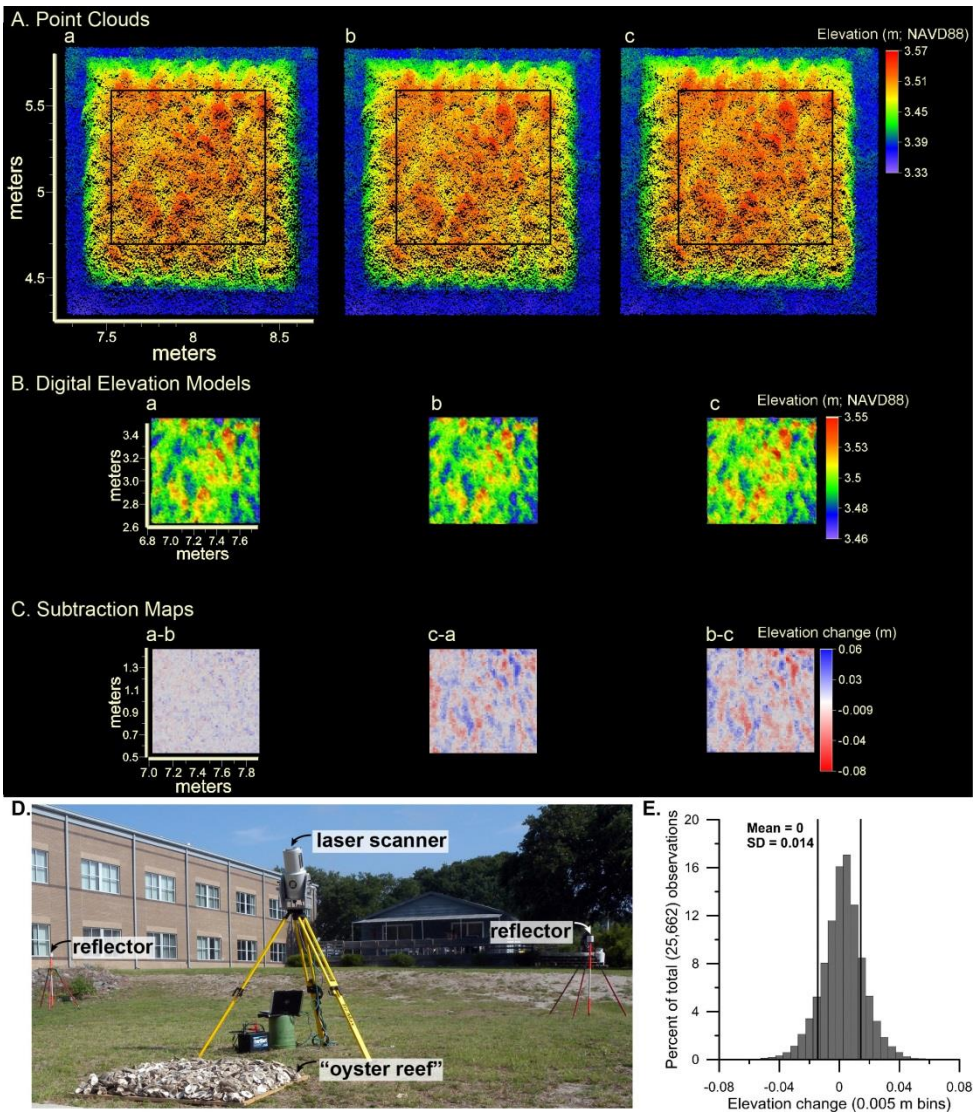

Figure 6. Measurement error was quantified using a synthetic reef. A) Point clouds of the synthetic reef, which was created with oyster cultch; B) DEMs created from the point clouds; C) Difference maps of the DEMs; D) Photograph of the synthetic reef and instrument set up; and E) Bar chart of the difference-map

cells binned every 0.005 m illustrating one-standard deviation around the mean with vertical black lines, which is the vertical measurement error.

Reef area and surface area were measured using Golden Software's Surfer 11.0 by digitizing the perimeter from DEMs and the perimeter was defined as the transition from smooth sandflat to irregular oyster reef. We estimated the error associated with choosing that boundary by having three individuals perform the analysis, independently, using the same DEM. Error was defined as the standard deviation of those measures or 0.88 m2. The error associated with the volume measure was calculated as the product of the vertical error (0.014 m) and the surface area of the reef.

Results and Discussion- Sea-level rise, threatens oyster reefs in the high-salinity seaward portions of estuaries because there, oysters seek refuge from biofouling (space competition), predation, and disease in intertidal areas. The importance of the intertidal to individual oyster growth in lower estuaries is apparent from experimental work that has shown intertidal oysters grow 34% faster and exhibit an order of magnitude less fouling (% cover) than subtidal oysters (Bishop and Peterson, 2006). Constructed subtidal reefs in no-harvest sanctuaries (North Carolina, USA) were also found to have few if any live oysters (mean density of 0-92 live oysters m^{-2}) after six years in euhaline waters, while intertidal reefs faired significantly better (200-225 live oysters m^{-2}; Powers et al., 2009).

Although an oyster reef hosts a variety of organisms, reef structure is primarily composed of the biogenic sediment of oysters, including skeletal shell material and biodeposits, and allogenic sediment (e.g. from resuspension, shoreline erosion, and river discharge). Reef structure is controlled largely by reef accretion rates and erosion rates. Reef accretion is the result of sediment inputs including oyster-shell production, biodeposition, and allogenic sediment, while reef erosion is mainly a function of bioerosion, dissolution, predation, and hydrodynamic processes (Figure 7). Allogenic sedimentation contributes to reef accretion; however, if the sedimentation rate is too high, reef structure will be lost due to burial and a decrease in oyster-shell production through a reduction in oyster settlement, survival, and growth.

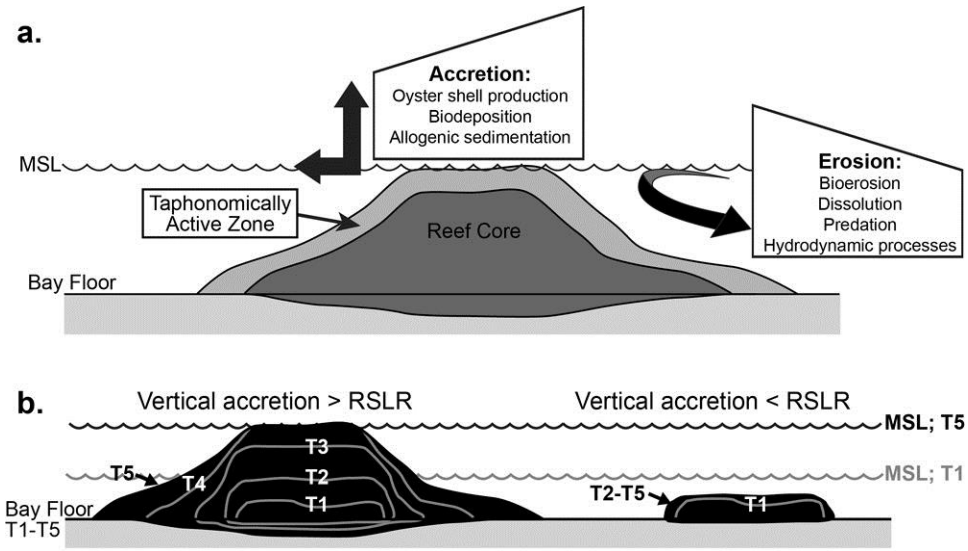

Figure 7. Conceptual model of oyster-reef growth. A) The factors that influence reef accretion and erosion are modulated by exposure time. B) If reef accretion cannot keep pace with sea-level rise, the exposure time will decrease and erosional processes will increase, which will ultimately result in loss of biogenic structure. T1-T5 denotes time lines. RSLR= relative sea-level rise and MSL= mean sea level.

To investigate reef composition and growth, we examined cores collected in 2010-2011 from five intertidal experimental reefs constructed on sandflats in 1997 (n=3) and 2000 (n=2). Experimental reefs colonized on 60 bushels of oyster shell (cultch) with initial dimensions of 3 x 5 x 0.15 m (W x L x H). The cores showed that the upper 15 cm of the reefs are primarily composed of live oysters, shell material, and open pore space of the taphonomically active zone (TAZ), the zone where shell modification or destruction is highest (Figures 7 and 8). Below the TAZ we observed the reef core, where pore space between the oyster shells is filled with sediment and shell preservation is highest. On average (by mass; ± 1 SD), the reef core consists of 48 ± 9% shell (>2 mm in size), 30 ± 12% sand (allogenic sediment; no agglomerates), and 19 ± 6 % silt and clay (biodeposits + allogenic sediment). Based on the similarity of the grain-size distributions, the sand in the reef is likely sourced from the surrounding sandflat.

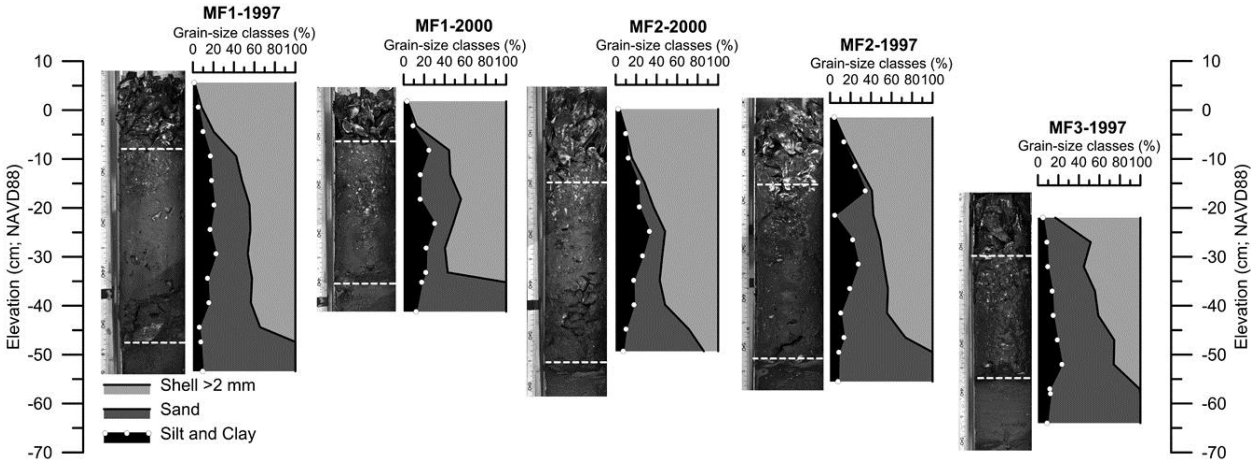

Figure 8. Oyster-reef compositional changes with depth. Core photos and sample depths plotted relative to the NAVD88 datum. Dashed lines on photos bracket the reef core.

Reef accretion rate is commonly expressed as the change in elevation through time (cm/yr). Based on the reef heights measured from the top of the core to the top of the cultch (assuming the top of the cultch was 15 cm above the substrate), those five reefs grew 2.7 ± 0.7 cm/yr (mean ±1 SD). Examining reef growth rates exclusively using core data, however, does not scale up to whole-reef evolution given the irregular and complex patterns of oyster settlement, growth, and survivorship over a range of scales (<1 to 10's of m) within reefs. In addition, maximum potential reef height and thickness depend on the elevation of the substrate and the upper limit of the tidal range where oysters cannot grow because the stress from limited inundation is too high. We name that upper limit the growth ceiling, which likely varies across tidal ranges and climates. If the top of the reefs reached their growth ceiling sometime in the past, then those reef-height measurements from coring might underestimate vertical reef-growth rate.

Core data indicated that reefs grow at a rate that should be resolvable using direct measuring techniques across relatively short time periods. In order to examine changes in growth, from initial colonization to maturity, our approach shifted towards the use of remote sensing applied to those reefs constructed in 1997 and 2000 plus six experimental reefs constructed in 2011. The 2011 reefs were constructed in the same coastal research reserve and to the same specifications as the older reefs. Thus, we were able to closely examine changes in reef height, area, and volume during the first two years and after ~10 years of reef development. To image the shape of the older and younger reefs we used a Riegl terrestrial laser scanner (LMSZ210ii) and reef growth was measured from high-resolution DEMs created from the laser returns.

Reef height is defined here as the distance between the elevation of the substrate on which the cultch was placed and the elevation of a horizontal plane intersecting the highest 1-2% of the reef's surface area quantified from the DEM. Based on linear regression, the 2011 reefs grew vertically 11.5 ±1.4 cm/yr (Figure 9). The older reefs, with the exception of MF3-1997, did not gain more than 2.0 ±1.4 cm in elevation over the two-year observation period. The elevation across the crest of the 5 older reefs in 2012 was 0.6 ±4.0 cm NAVD88 (mean ±1 SD), which is close to local mean sea level (8.5 ±3.7 cm NAVD88) and is the growth ceiling. All of the 2011 reefs were constructed >36 cm below the ceiling, and therefore were not growth limited during our study period. Most of the older reefs were constructed on substrates of similar elevations as the 2011 reefs and based on the average growth rate of the 2011 reefs, the older reefs likely reached their present heights rapidly within their first 4 years of growth. Reef MF3-1997 was constructed at an elevation similar to the 2011 reefs; however, the top of the reef was still 6 cm below the growth ceiling 14 years after construction. Reef MF3-1997's vertical growth was limited by some external stress, possibly recreational harvesting, which explains why the reef gained elevation between 2011 and 2012 (Figure 9). When a reef reaches the growth ceiling, the top is limited by aerial-exposure stress and vertical accretion of the reef crest is reduced to the rate of sea-level rise.

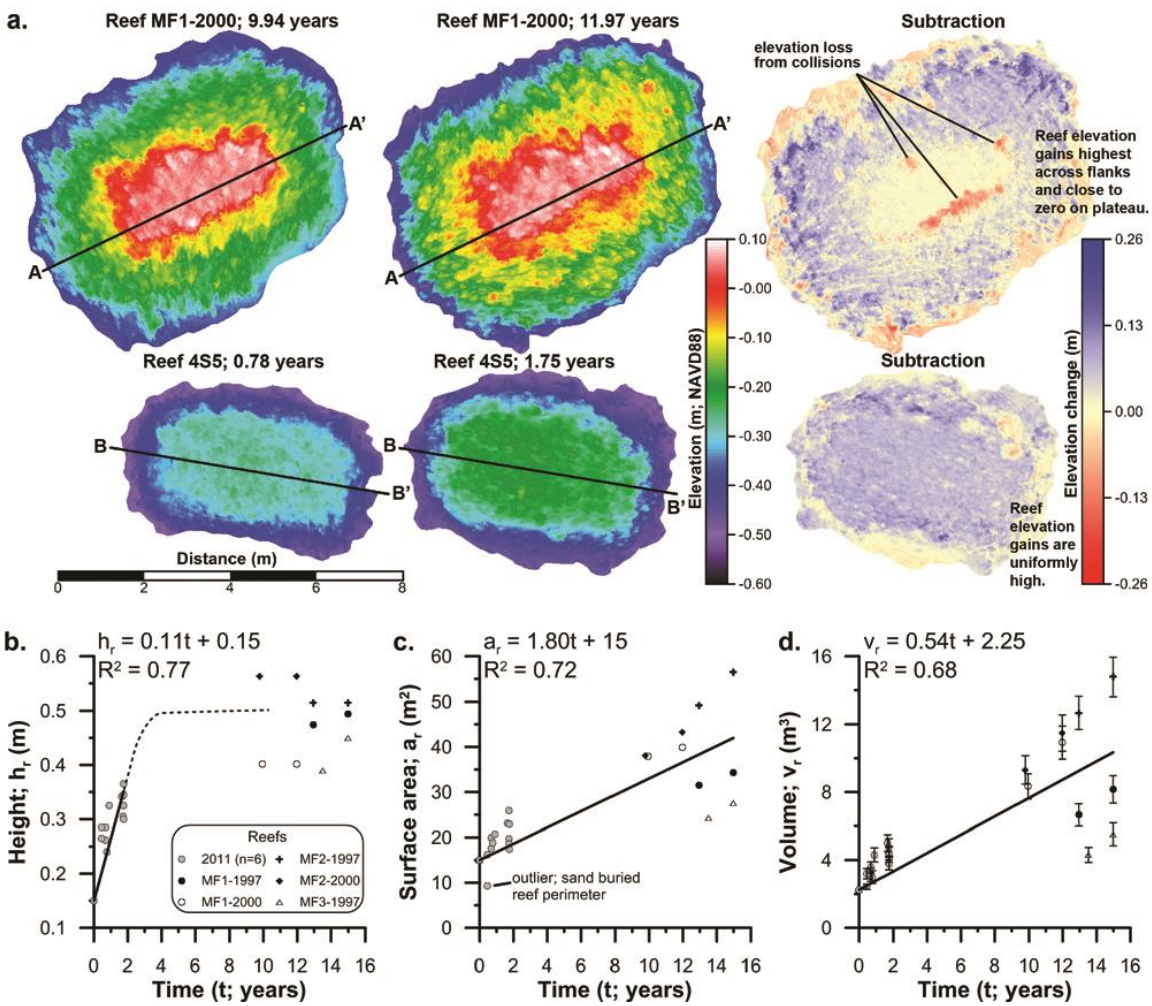

Figure 9. a) DEMs and difference maps of an older reef, MF1-2000, and a young reef, 4S5. Regression lines of b) vertical growth (± 0.014 cm; dashed line is an extrapolation), c) areal growth (± 0.88 m2) and d) volume change (± surface area x 0.014 cm).

Reef growth is important to quantify in three dimensions because lateral accretion ensures continual vertical growth by providing space below the ceiling for larval settlement and subsequent accumulation of oyster biomass. Reef lateral accretion decreased with increasing reef age: average radial expansion was 30.1 ±10.5 cm/yr, for the 2011 reefs, and 10.3 ±3.5 cm/yr, for the older reefs (mean ±1 SD). Lateral accretion is likely facilitated by the transport of shell from the reef's crest to perimeter and impeded by the transport and deposition of sand from the surrounding area burying the edge of the reef. Both of those processes were observed in the DEMs generated during 2010 and 2012 and were likely associated with coastal storms (e.g. Hurricane Irene; 2011). Over the relatively short time frame of our study, linear regression was the best model to explain rates of surface area and volume change. Reef surface area increased 1.8 m^2/yr and volume increased 0.54 m^3/yr, indicating that the reefs double in area and volume from their original cultch dimensions about every 9.5 and 4.0 years, respectively. Intertidal oyster reefs below the vertical growth ceiling grow rapidly in all directions.

Reef accretion is a complex mix of oyster biology, taphonomy, and depositional/erosional processes that cause growth rates to vary over time and space. The crests of the older reefs showed little vertical change through time, except for small pockets of erosion due to collisions (earlier coring and observed impacts from floating debris), predation, and currents. Elevation gains on the older reefs were highest across the perimeters of the reefs, where the oysters are likely experiencing less stress from aerial exposure, but still benefit from reduced competition, predation, and disease by being situated intertidally (Figure 10). Our results suggest that intertidal reefs have the potential to match even the highest predictions of SLR by the year 2100, provided SLR does not coincide with or create additional stresses on oyster reefs that reduce productivity.

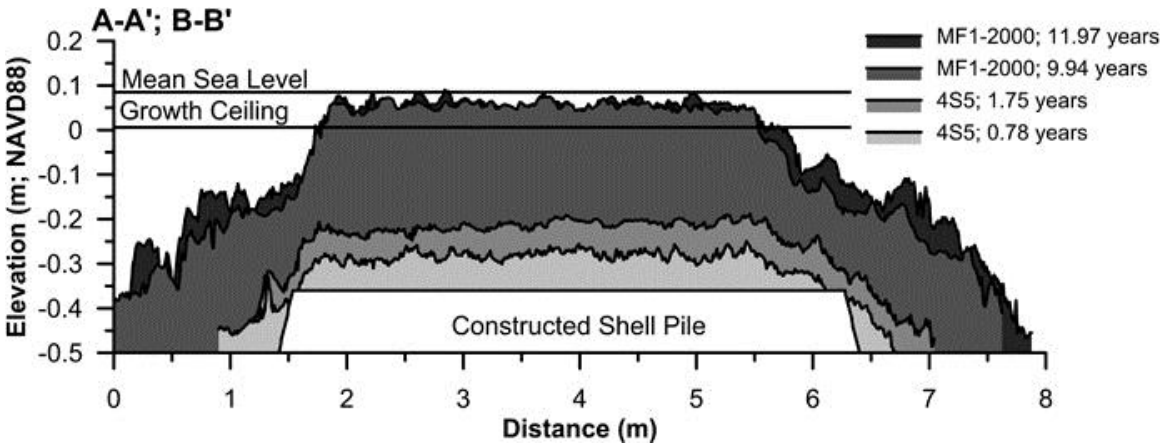

Figure 10. Transects across the reefs at different growth stages. See Figure 9 for transect locations.

The high growth rates we document are from the oysters growing rapidly in large clusters on the reefs (Figure 11). In addition, the reefs show high preservation of oyster shell in the reef core (low taphonomic loss), which is supported by our measurements (mean ±1 SD) of carbonate in the TAZ (301 ± 142 kg/m3) being similar to the reef core (369 ± 94 kg/m3). Excluding shell material, the composition of the reef core is mostly allogenic sediment, making reefs efficient sediment traps as they grow. Reef rugosity likely promotes sediment trapping by reducing shear stresses between the clusters of oysters and sedimentation helps bind the reef together by filling pore space. Some of the older reefs may have been at their growth ceiling for ~10 years; however, they are not buried by allogenic sediment. Maintenance of pore space in the absence of vertical reef growth suggests shear stresses are reduced along an increasing-depth gradient in the TAZ.

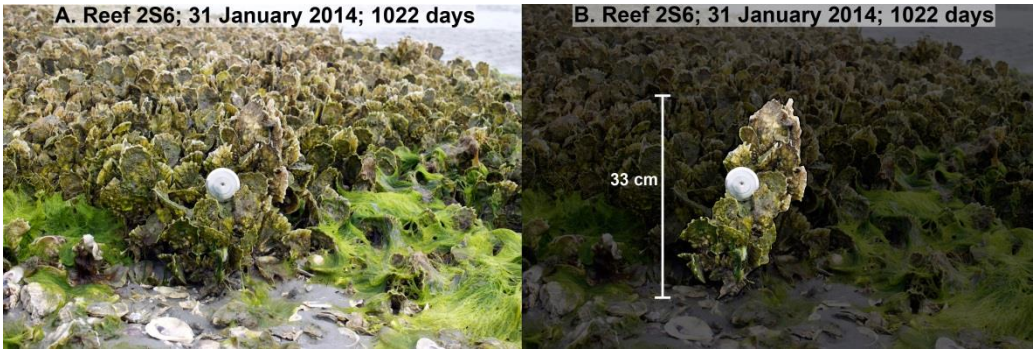

Figure 11. The intertidal reefs examined here a primarily composed of long and slender oysters that grow in closely-spaced clusters. Clusters of oysters are much longer than individuals (A) and a 33-cm long cluster Is highlighted in B (same photo as shown in A).

With global warming resulting in higher rates of SLR, existing intertidal oyster reefs that have reached their growth ceiling could respond to SLR and the associated reduction in aerial exposure time by demonstrating enhanced vertical accretion. The high rates of reef growth suggest that the intertidal high-salinity portions of estuaries can be hot spots for oyster-reef productivity. Restoring reefs on intertidal sandflats could help preserve vegetated estuarine ecosystems sensitive to SLR and coastal structures by dampening waves and reducing estuarine shoreline erosion. Buffering shorelines from erosion is an ecosystem service reefs provided more widely in the mid-19th century, prior to massive exploitation. The subsequent increase in coastal development, often at the shoreline, commonly uses riprap revetments and bulkheads as reef substitutes for shoreline stabilization, which is an inferior alternative because of the great natural capital reefs provide, including the maintenance of elevation in reference to mean sea level.

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The Atlantic
Pacific Standard
Carteret News Times
The News and Observer
Public Radio East
WCTI 12 News
Coast Watch
Endeavors

Appendix A “Core_locations” data dictionary

Column #	Field Name	Units	Limits	Comments
1	Core name	N/A	N/A	
2	Easting	meters UTM	N/A	
3	Northing	meters, UTM	N/A	
4	Elevation	meters, NAVD88	N/A	
5	Horizontal error	meters	N/A	
6	Vertical error	meters	N/A	

Appendix B "Core_data" data dictionary

Column #	Field Name	Units	Limits	Comments
1	Reef	N/A	N/A	Reef Name
2	Core Elevation	cm, NAVD88	N/A	The elevation the core was collected At.
3	Sample Depth	cm, NAVD88	N/A	The midpoint of the 5 cm sample, reported relative to NAVD88
4	Loss on Ignition	%	100	
5	Shell > 2 mm	%	100	Sieve data
6	< 2 mm (% $CaCO_3$)	grams	N/A	Acid digestion data
7	Mean grainsize	phi	100	Mean of the fraction < 2 mm. Cilas laser particle size analyzer
8	Standard Deviation	phi	N/A	Of the fraction < 2 mm in size.

Photomosaic images of the cores, and photos of the shell >2 mm in size sampled in each 5 cm interval down the core are organized in folders labeled by reef name. All depth intervals indicated in the photos are relative to the top of the core.

Appendix C "Reef_Densities_Elevations" data dictionary

Column #	Field Name	Units	Limits	Comments
1	Collection Date	N/A	N/A	YearMonthDay
2	Landscape	N/A	N/A	mf-mudflat; sm-saltmarsh; sg-seagrass
3	Quadrat	N/A	N/A	5 x 5 matrix. Quadrat is 0.25 m square.
4	Elevation	Meters NAVD88	N/A	
5	# *Crassostrea virginica*	Live individuals	N/A	
6	wt (g)	grams	N/A	
7	Exposure	%	100	Percent time the sample site is exposed.

Appendix D “Reef_fauna_Densities” data dictionary

Column #	Field Name	Units	Limits	Comments
1	Collection Date	N/A	N/A	YearMonthDay
2	Landscape	N/A	N/A	
3	Northing	UTM	N/A	
4	Easting	UTM	N/A	
5-80	Species name	Live individuals	N/A	

Appendix E "Water_level_data" data dictionary

Column #	Field Name	Units	Limits	Comments
1	Easting	UTM	N/A	Location of logger
2	Northing	UTM	N/A	Location of logger
3	Time	GMT-04:00	N/A	Month/day/year time
4	Water Level	meters NAVD88	N/A	

Appendix F "Spatial_data_inventory" data dictionary

Column #	Field Name	Units	Limits	Comments
1	Reef Name		N/A	
2	Date		N/A	Month/day/year time
3	Ground Points	UTM	N/A	File located in reef folder.
4	Geo tif	UTM, meters NAVD88	N/A	File located in reef folder.
5	Google .kmz	Geographic, meters NAVD88	N/A	File located in reef folder.
6	Grid file	UTM, meters NAVD88	N/A	File located in reef folder.

Maps are organized by reef in folders. All maps are in the UTM coordinate system and elevations are in meters relative to NAVD88. The grid cell size of the maps is 5 cm.

Appendix G "Reef_growth" data dictionary

Column #	Field Name	Units	Limits	Comments
1	Reef Name		N/A	
2	Observation Date		N/A	Month/day/year
3	Height	meters	N/A	Distance between reef top and substrate.
4	Area	$meters^2$	N/A	
5	Surface Area	$meters^2$	N/A	
6	Volume	$meters^3$	N/A	
7	Volume Error	$meters^3$	N/A	
8	Substrate Elevation	meters NAVD88	N/A	
9	Reef thickness from cores	meters	N/A	