Salt Marsh and Fringing Oyster Reef Transgression in a Shallow Temperate Estuary: Implications for Restoration, Conservation and Blue Carbon

Justin T. Ridge [1] · Antonio B. Rodriguez [1] · F. Joel Fodrie [1]

Abstract The importance of intertidal estuarine habitats, like salt marsh and oyster reef, has been well established, as has their ubiquitous loss along our coasts with resultant forfeiture of the ecosystem services they provide. Furthering our understanding of how these habitats are evolving in the face of anthropogenic and climate driven changes will help improve management strategies. Previous work has shown that the growth and productivity of both oyster reefs and salt marshes are strongly linked to elevation in the intertidal zone (duration of aerial exposure). We build on that research by examining the growth of marsh-fringing oyster reefs at yearly to decadal time scales and examine movement of the boundary between oyster reef and salt marsh at decadal to centennial time scales. We show that the growth of marsh-fringing reefs is strongly associated to the duration of aerial exposure, with little growth occurring below mean low water and above mean sea level. Marsh-shoreline movement, in the presence or absence of fringing oyster reefs, was reconstructed using transects of sediment cores. Carbonaceous marsh sediments sampled below the modern fringing oyster reefs indicate that marsh shorelines within Back Sound, North Carolina are predominantly in a state of transgression (landward retreat), and modern oyster-reef locations were previously occupied by salt marsh within the past two centuries. Cores fronting transgressive marsh shorelines absent fringing reefs sampled thinner and less extensive carbonaceous marsh sediment than at sites with fringing reefs. This indicates that fringing reefs are preserving carbonaceous marsh sediment from total erosion as they transgress and colonize the exposed marsh shoreline making marsh sediments more resistant to erosion. The amount of marsh sediment preservation underneath the reef scales with the reef's relief, as reefs with the greatest relief were level with the marsh platform, preserving a maximum amount of carbonaceous sediments during transgression by buffering the marsh from erosional processes. Thus, fringing oyster reefs not only have the capacity to shelter shorelines but, if located at the ideal tidal elevation, they also keep up with accelerating sea-level rise and cap carbonaceous sediments, protecting them from erosion, as reefs develop along the marsh.

Keywords Salt marsh · Oysters · Erosion · Blue carbon · Sea-level rise

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Introduction

Climate change poses a significant threat to coastal ecosystems with the expectation of increased flooding with sea-level rise (SLR) and storms. Low relief coastal environments are highly susceptible to erosion and inundation from accelerating SLR and storms, as well as anthropogenic stressors like increased development and boat wakes. While many developed areas use hardened structures to protect their shorelines in the form of bulkheads and rock revetments, there has been a movement to utilize more natural methods, such as living shorelines. Living shorelines exploit the innate ability of natural habitats (e.g., oyster reefs and salt marsh) to dissipate wave and current energy (Broome et al. 1992; Currin et al.

2010; Gedan et al. 2011; Gittman et al. 2014; Davis et al. 2015). Regaining lost shoreline habitats through restoration, which in many instances have been lost through development (salt marsh; Kennish 2001; Lotze et al. 2006) and exploitation of resources and/or disease (oyster reefs; Beck et al. 2011; zu Ermgassen et al. 2012), not only increases shoreline and property resistance to wave energy and resultant erosion but also enhances overall service delivery of the estuarine ecosystem (Coen et al. 2007; Grabowski and Peterson 2007).

Tidal wetlands provide a number of ecosystem services, making them one of the most valuable ecosystems in the world (Costanza et al. 1997). Marsh grasses form expansive platforms along estuarine shorelines of low relief and elevation, providing a number of benefits for shores under pressure from SLR and storm waves. *Spartina alterniflora* can trap sediment by baffling current and wave energy (Leonard and Croft 2006) and significantly reduce wave height (~90% decrease) within 20 m of the marsh edge (Knutson et al. 1982). Marshes can be resilient to SLR because they have the ability to increase their elevation by augmenting belowground biomass (Cahoon et al. 2004), and they can exhibit greater productivity with increased inundation (Morris et al. 2002). However, Morris et al. (2002) also describe a threshold occurring near MSL where increased inundation will result in diminished marsh productivity, and rapid SLR could destabilize many marsh shorelines. This could result in major loss of marsh services along the estuarine coastline, including wave dampening, provision of essential fish habitat, and carbon sequestration (Peterson and Turner 1994; Barbier et al. 2011; Murray et al. 2011; Möller et al. 2014).

More than 50% of wetlands have been lost in the USA alone within the last century (Kennish 2001; Lotze et al. 2006) from both natural and anthropogenic sources, with an estimated minimum global loss of 1–2% per year (Duarte et al. 2008). Along with coastal development of marshland, the combined pressure of accelerating SLR (Reed 1995; Nicholls et al. 2007; Craft et al. 2009) and sediment starvation (Syvitski et al. 2009) will lead to the eventual drowning of marshes along some coasts (Kirwan et al. 2010). An entire marsh platform can transform into a subtidal sand- or mudflat environment as conditions change, and marsh-edge erosion is pervasive along both highly productive and degraded marshes, resulting in a decrease in area and associated ecosystem services.

Oyster reefs fringe many natural salt marshes and are more resistant to erosion and positioned lower in the tidal frame than marsh platforms. With multiple stressors reducing the integrity of the marsh, the use of synergistic ecological engineering (Halpern et al. 2007; Milbrandt et al. 2015), like coupling oyster reef with marsh, is a viable coastal adaptation that should provide greater shoreline protection and stability (Cheong et al. 2013). This type of shoreline modification is applying the sequence of environments found naturally along many undisturbed, stable estuarine coastlines, encompassing subtidal sand- or mud-flat in the open bay to oyster reef and then marsh platform moving landward. The installation of substrates like oyster cultch (recycled shell) or other hard materials at the edge of vegetated habitats is commonly implemented with the expectation that a living reef will grow and protect the adjacent habitat edge from erosion. Increasing our understanding of the conditions that promote the vertical and lateral growth of reefs that fringe vegetated habitats and the subsequent evolution of the habitat boundary will better guide restoration practices for maximum return on investment in terms of time, money, and sustained shoreline protection. In addition, constraining the growth patterns and optimal growth conditions of fringing reefs will improve predictions of coastal landscape response to climate-induced changes to estuaries in the absence of intervention.

Oyster reefs are self-accreting structures through deposition of shell and biodeposits but are degraded at varying rates through predation, bioerosion, dissolution, and disturbance (Powell et al. 2006; Mann and Powell 2007; Powell and Klinck 2007; Green et al. 2009). Salinity and exposure to air during tidal cycles (aerial exposure) constitute two of the main controls on oyster reef growth (Baggett et al. 2015; Walles et al. 2016). Exposure provides a refuge from competition and predation in the high salinity lower estuary (Fodrie et al. 2014), while the fresher water of the upper estuary provides this refuge for reef growth deeper in the water column. Oysters naturally colonize hard substrate located on sand or mudflats, isolated from other habitats (patch reefs) or along the distal edge of salt marshes (fringing reefs; Grabowski et al. 2005). Previous work examining intertidal oyster patch-reef growth has shown that, like marshes, oyster reefs have the capacity to grow at rates equal to or greater than present rates of SLR (Rodriguez et al. 2014; Ridge et al. 2015).

The proximity of a habitat with other structurally complex habitats can alter hydrodynamics (Borsje et al. 2011; Sharma et al. 2016a; Sharma et al. 2016b) as well as predator utilization along these habitat boundaries (Irlandi and Crawford 1997; Lewis and Eby 2002; Carroll et al. 2015). Oyster reefs may produce a shadow effect, attenuating hydrodynamic energy, reducing erosion and promoting expansion of adjacent vegetated habitats (Sharma et al. 2016a, Sharma et al. 2016b). However, reduced flow around the marsh-reef complex may decrease food delivery to oysters and allogenic sedimentation in both the reef and the marsh. These interactions may ultimately result in diminished reef growth and marsh accretion, as well as changes in sediment composition within both habitats.

Vertical accretion and shoreline evolution are particularly important for carbon sequestration potential as marshes are considered a blue carbon habitat (Murray et al. 2011), capturing a disproportionately high amount of carbon compared to the global area they occupy (Chmura et al. 2003; Duarte et al.

2005). Theuerkauf et al. (2015) observed marsh shoreline erosion in North Carolina on the order of 0.65–0.76 m year^{-1}. This process has resulted in total ravinement (loss to erosion) of carbonaceous marsh sediments spanning hundreds of years, highlighting the importance of carbon export explicitly through lateral erosion when modeling marsh carbon budgets (Theuerkauf et al. 2015). During transgression, the presence of a fringing oyster reef could change the ravinement process and preservation of marsh sediments. To better understand fringing oyster reef development and the lateral trajectory of the marsh-reef boundary (and implications for the carbon-related storage services of marsh habitat), this study addresses three main questions: (1) Are fringing reefs following the same growth paradigm with regards to aerial exposure as observed on patch reefs (sensu Ridge et al. 2015)? (2) What is the trajectory of marsh-oyster reef boundaries (shorelines) in the Southeast US? and (3) What are the consequent implications for the carbon storage potential of these environments?

Conceptual Model of Estuarine Shoreline Evolution The depositional environments that exist around marsh shorelines can evolve in a number of ways depending on the local hydrodynamics, sediment supply, and rate of SLR (Mariotti and Fagherazzi 2010; Fagherazzi et al. 2012; Fagherazzi et al. 2013; Kirwan et al. 2016; Fig. 1). The stratigraphy of coastal areas preserves a record of the trajectory of the boundary between depositional environments. Assuming a productive marsh platform and the absence of a fringing oyster reef, a salt marsh may grow laterally and/or vertically with adequate sediment supply and relatively low hydrodynamic energy and rates of local SLR (LSLR). Conversely, sediment starved areas can experience wave-induced shoreline erosion even

without SLR. As a salt marsh shoreline erodes under conditions of increasing hydrodynamic energy and/or rapid SLR, salt marsh area is reduced and typically transformed into a subtidal sand- or mud-flat environment. Depending on the depth of wave- and current-induced erosion and thickness of the salt marsh, some marsh peats could be preserved under the new sandflat environment, retaining a portion of the buried carbon that accumulated in the past. Increasing the depth of erosion, or ravinement, and decreasing marsh thickness decreases the preservation potential of old marsh peat as the marsh edge transgresses.

A productive salt marsh platform fringed with oyster reef may have a different evolution under conditions of increasing hydrodynamic energy and/or accelerating SLR than the scenario described above, because an oyster reef is more resistant to erosion than the adjacent marsh. Under these conditions, the boundary between the fringing oyster reef and salt marsh could experience four different evolutionary responses including (1) regression, (2) stasis, (3) transgression, or (4) disconnection as the boundary between environments widens (Fig. 1). If the oyster reef dampens the hydrodynamic energy impacting the boundary and accretion of both environments is keeping up with the rate of LSLR, then the boundary will either regress and the marsh would expand over the oyster reef or the boundary will remain static as both environments accrete vertically. Alternatively, if the oyster reef does not sufficiently dampen the hydrodynamic energy impacting the boundary and accretion of both environments lags behind the rate of LSLR, then the boundary will either transgress, through the displacement of oyster reef on top of salt marsh, or the marsh edge will erode landward at a faster rate than the oyster reef, and the fringing reef will transform into a patch reef (disconnection).
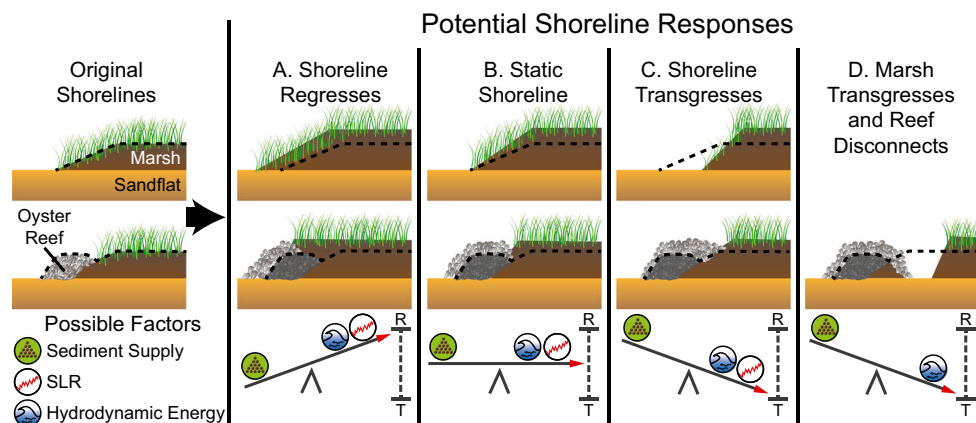

Fig. 1 Potential responses of marsh shorelines with and without adjacent oyster reefs to an increase in relative sea level, while also considering relative sediment supply and local hydrodynamics (wave and current energy). The *dashed black line* represents the original shoreline at time 1. Within each shoreline response, a combination of possible factors is included along a fulcrum to illustrate how their relative contributions will impact the balance between shoreline regression (*R*) or transgression (*T*). For example, the shoreline response *A. Shoreline regresses* can occur when sediment supply offsets the impact of SLR and/or hydrodynamic energy. As another example, response *D. Marsh transgresses and reef disconnects* may occur when hydrodynamic energy far outweighs sediment supply, regardless of the rate of SLR

Methods

Study Site and Reef Selection Back Sound and the North River Estuary, North Carolina, were chosen for the study because they contain natural and restored fringing oyster reefs (*Crassostrea virginica*) and salt marshes (*S. alterniflora*) that are experiencing edge erosion (Fig. 2). The marshes and oyster reefs included in the study are located around Middle Marsh (MM), North River Marsh (NRM), and Carrot Island (CI) (Fig. 2). Middle Marsh and North River Marsh are part of a relic flood tidal delta that formed approximately 4000–2000 years ago (Berelson and Duncan Heron 1985). It is an extensive network of salt marsh, tidal channels, natural and constructed oyster reefs, and sandflats, many of which are occupied by seasonal seagrass beds. This area experiences a semidiurnal tide with a range of 0.9 m (US Army Corps of Engineers 1976; Rodriguez et al. 2014) and salinities between 30 and 35 ppt.

Oyster-reef growth and evolution of the reef-marsh contact were studied using natural and constructed reefs (Table 1). The natural fringing reefs and back-reef marshes examined were along straight portions of the marsh shoreline and along marsh headlands. The oyster reefs at marsh headlands were narrow (~10 m) and long extending (20–40 m) off the headland into the adjacent estuary (groin reefs). The other natural marsh-fringing reefs are oriented with their long axis parallel to the marsh shoreline extending ~100 and 10 m in the along- and cross-shore directions, respectively. Constructed fringing reefs were built from recycled oyster shell placed at the edge of the salt marsh in 3 m × 5 m × 0.15 m boxes (long dimension oriented parallel to the marsh shoreline) around Middle Marsh in 1997 and 2000 (Grabowski et al. 2005) (Fig. 2).

Fig. 2 Study area map of Back Sound and North River Estuary in North Carolina. Marsh sites with reefs (natural and constructed) and without reefs are indicated with *symbols*. *Black filled symbols* represent reefs that were scanned using terrestrial lidar. All reef sites were cored and oyster densities sampled. Labels are placed at sites mentioned in the text
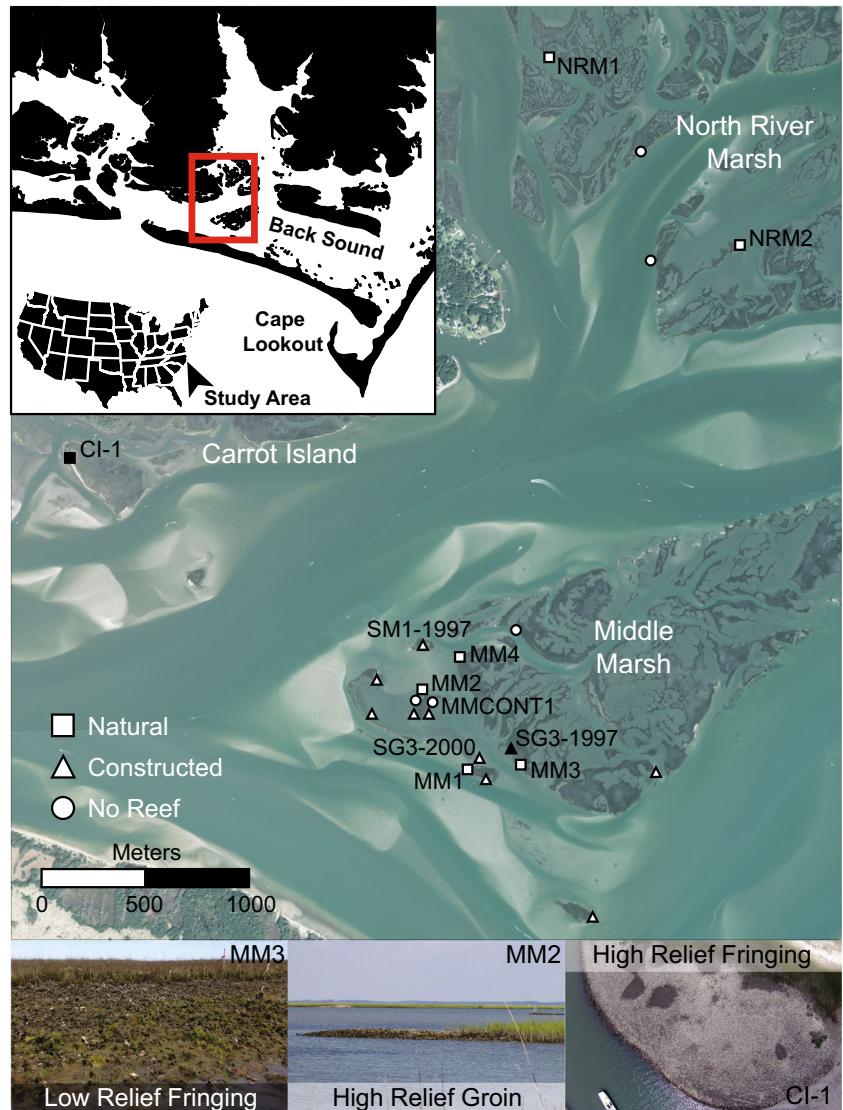
Table 1 Description of study reefs and sampling conducted on each

Reef	Type	Vertical relief[a]	Sampling methods			
			Laser scan	Core	Core transect	Density
Natural reefs						
MM1	Fringing	High		X	X	X
MM2	Groin	High		X	X	X
MM3	Fringing	Low		X	X	X
MM4	Fringing	Low		X	X	X
NRM1	Disconnect	High		X	X	
NRM2	Groin	High		X	X	X
CI-1	Fringing	High	X	X	X	X
Constructed reefs						
SG3-1997	Fringing	Low	X	X		X
SG3-2000	Fringing	Low		X		X
SM1-1997	Fringing	Low		X		X

[a] Low relief fringing reefs are less than 0.25 m in vertical relief, while high relief reefs are greater than 0.25 m in vertical relief

Reef Growth Growth of natural and constructed fringing reefs was assessed using remote sensing and coring. Terrestrial laser scanning has proven to be a highly accurate method for measuring reef growth and elevation changes >1.4 cm (Rodriguez et al. 2014; Ridge et al. 2015). This method only works for areas exposed during a tidal cycle, and data were collected during spring low tides when the maximum reef area was exposed. The natural and constructed fringing reefs were scanned twice between 2010 and 2015 using a RIEGL three-dimensional LMSZ210ii terrestrial laser scanner to create digital elevation models (DEM) from 600,000 to 1,000,000 laser returns spaced <1 cm apart. Point clouds were processed using RiSCAN Pro software (RIEGL LMS), extraneous points were removed using the MARS 7 software package (Merrick® Advanced Remote Sensing Software), and DEMs of the reefs were generated at a 5-cm grid-cell spacing using Surfer 11 (Golden Software, Inc.) (Fig. 3). Reef grid cell elevations were subtracted from its second-scan counterpart to obtain elevation changes between measurements, then those differences were sorted into 2-cm elevation bins, based on the first scan for each bin, and averaged (i.e., mean vertical accretion for every 2-cm reef elevation bin across the entire surface of the reefs; Ridge et al. 2015). Intertidal elevations were converted to percent aerial exposure or relative amount of time spent out of the water during an average tidal cycle, as described by Ridge et al. (2015), because aerial exposure is an important determinant of reef growth in the high-salinity seaward portions of estuaries (Walles et al. 2016). This provided fine-scale vertical growth measurements for determining if aerial exposure impacts the growth of fringing reefs similarly to patch reefs. All elevations are reported in reference to the North American Vertical Datum of 1988 (NAVD88).

To supplement the laser scan data, we took cores through the middle of 10 constructed reefs to coarsely measure reef growth from date of construction to 2010. Core locations were surveyed using a Real-Time Kinematic Global Positioning System (RTK-GPS) to determine the exact elevations of the reef surface relative to mean sea level (MSL). To core the reefs, a 10-cm diameter aluminum pipe was driven into the surface using a jackhammer. In the lab, cores were split longitudinally, sectioned continuously in 5-cm increments from the top, photographed, and described. In addition to the date of oyster-reef construction, we used the distance between the reef surface and the top of oyster cultch shell to calculate vertical growth rates. The oyster cultch shell is morphologically distinct and easily discernable from new oyster growth because the cultch shell was sourced from subtidal oyster beds that have wider and thicker shells compared to the narrower thinner shells of intertidal reefs.

Live Oyster and Salt Marsh Density Oyster density is an indication of oyster population, recruitment and survivorship, while size provides additional information on the age structure of a reef (Kraeuter et al. 2007). Along natural reefs, at least four transects running from the reef crest to base were spaced 1 m apart. Each transect was divided into four zones down the reef slope, and a random sample was taken within each zone using a 0.06-m² quadrat. Quadrats were excavated to the depth that all living oysters were collected, typically where the reef became anoxic (Baggett et al. 2015). All plot elevations were recorded at the surface of the reef using the RTK-GPS. Along with oyster density, the shell heights of all oysters were measured to ascertain the number of adult oysters (>2.5 cm).

Marsh-grass densities were measured using a 0.25-m² quadrat at the farthest extent of grass adjacent to the fringing reef, the marsh platform levee, and the interior of the marsh (5–10 m from the levee). Stem heights of 10 grass blades were recorded within each plot. These measurements were also taken at five non-reef marsh sites for reference (Fig. 2).

Reef-Marsh Evolution To assess the evolution of the reef-marsh interface, we collected a core transect perpendicular to
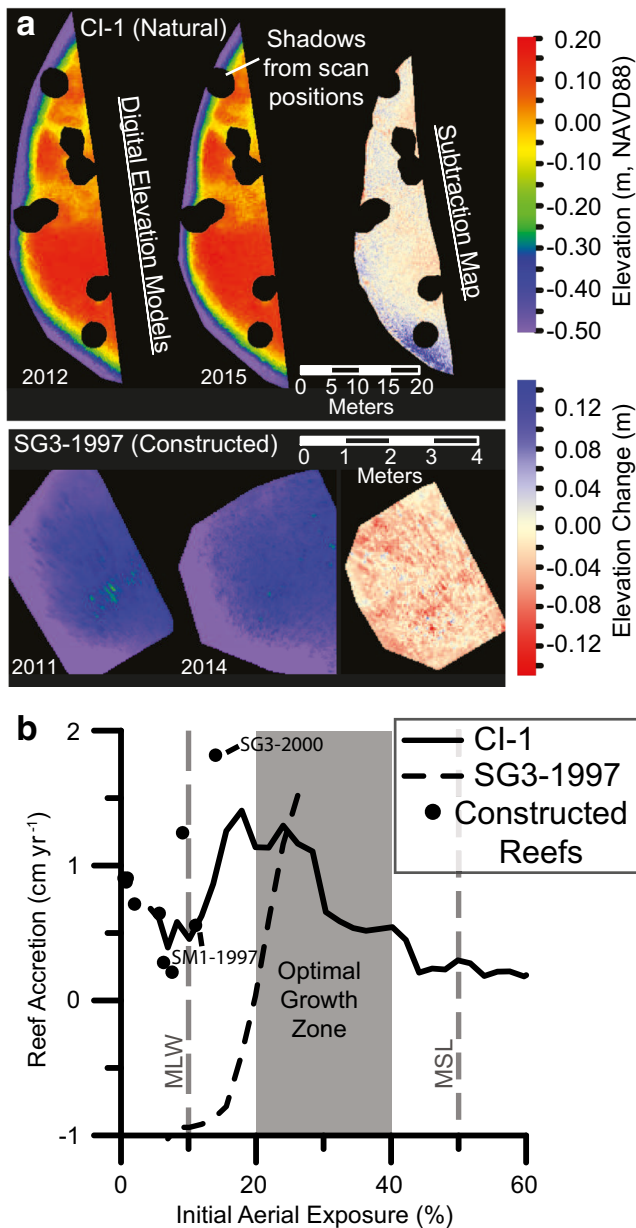
Fig. 3 a Digital elevation models (DEMs) constructed from laser scans of natural (CI-1) and restored fringing reefs (SG3-1997). Subtraction maps (*right panels*) denote elevation change between the two scans. Holes on maps (*left panels*) represent scan shadows with insufficient data to accurately construct the DEMs. **b** Mean vertical growth rate across a natural fringing oyster reef (CI-1, *solid line*) and constructed fringing oyster reef (SG3-1997, *dotted line*) based on consecutive laser scans and binned by the aerial exposure of initial scan. *Dots* represent growth rates of constructed oyster reefs based on core data and plotted by the initial aerial exposure of the cultch shell surface at construction. Mean low water (MLW) occurs at 10% aerial exposure, and the optimal growth zone (OGZ) spans 20–40% aerial exposure as established in Ridge et al. (2015)

the reef-marsh contact across seven natural fringing-reef shorelines. Each transect is composed of four cores (10-cm aluminum pipe) collected at the seaward edge of the reef, at the reef crest, in the zone occupied by both living oysters and

marsh grass and in the marsh beyond the extent of living oysters. Using the RTK-GPS, we collected elevation profiles by walking from the bayward edge of the reef into the marsh to demark the boundaries and overlap of habitats. For reference, we also cored areas of marsh with no oyster occurring on the shoreline using two cores 1 m from the marsh edge in both directions. Concurrently, transects of push cores were taken at non-reef marsh sites progressing away from the marsh edge (furthest extent of living grass) at 1-m intervals. This provided the thickness and extent of marsh sediments preserved following marsh shoreline retreat. We used the jackhammer method of collecting cores on the reef, and some salt marshes were cored using a sledgehammer to drive the 10-cm diameter aluminum pipe into the subsurface.

Once taken, cores were processed similarly to the oyster-reef cores obtained to measure vertical reef growth. The similar depth of strata between adjacent cores indicates that what little compaction was introduced during the coring process (<5 cm, defined as the distance between the top of the core and the adjacent substrate measured before the core was extracted) is ubiquitous within and among the cores. For the natural reefs, we estimated the timing of first oyster colonization and lateral reef expansion by obtaining carbon-14 dates from shell fragments cut from the umbo of articulated oysters sampled at the base of reefs. Additionally, we radiocarbon dated marsh material collected just below the reef-marsh contact in the mid-reef core of two natural groin reefs (MM2 and NRM2). The National Ocean Sciences Accelerator Mass Spectrometry Facility at the Woods Hole Oceanographic Institution provided the radiocarbon ages. Ages were calibrated to years before present (AD 1950 = 0 BP) and calendar years at the 95.45% confidence interval (2 sigma) obtained by using the CALIB 7.1 program (Stuiver and Reimer 1993; Reimer et al. 2013).

Sedimentary Analyses Coastal depositional environments form distinct lithofacies, arranged in a vertical succession dictated by the evolution of an area through time with laterally shifting habitats. In addition to visual description, we measured grain size on each 5-cm section of the cores to aid in defining lithofacies. Samples were wet sieved to separate the >2-mm size fraction, which was weighed. The remaining finer-grained sediment was dried, weighed, subsampled, and processed through a Cilas 1180 laser particle size analyzer to obtain a grain size distribution from 0.04 to 2000 μm split into 100 bins.

Percent organic carbon in reef and marsh sediments was obtained using a combination of loss on ignition (LOI) and a Perkins-Elmer CHN analyzer. CHN analysis was conducted on 6–10 samples (<2-mm size fraction) from most cores, and LOI was used on the >2-mm size fraction for each sample. We also used LOI to further supplement this dataset from the remaining cores, which consisted of separately combusting

sediments <2 mm and organic material >2 mm (mainly blades, stems and roots) at 550 °C for 4 h. A calibration (Craft et al. 1991) was applied to more accurately estimate the organic C content from organic matter combusted during LOI, making these results directly comparable and combinable with CHN data. Mean percent organic carbon (sediment + organics, mass by volume) was calculated for marsh strata in each core and then averaged across sites for the interior marsh carbon inventory (kg m^{-2}). Next, using the dimensions of marsh sediment preserved below oyster reef obtained from the cross sections, we calculated average carbon inventory below each study reef. Finally, prior to the formation of these fringing reefs, marsh shorelines likely stretched beyond the present extent of their preserved sediments, and we determined the percent carbon conserved at each shoreline using respective carbon inventories and the trapezoidal area bounded by the two oyster-reef cores with marsh sediments (cross sections) at relevant sites (MM2, MM3, and NRM2). Our study areas fall along the edges of historical aerial imagery, and the distance from reliable benchmarks for georectification makes it difficult to reliably track shoreline changes at each of our sites. Therefore, for a conservative estimate of percent carbon preserved by the reefs, we assumed the greatest erosion scenario in that the current lateral extent of marsh sediment along eroding shores was once occupied by a fully formed marsh platform.

Results and Interpretation

Reef Growth and Density Elevation measurements from the laser scans of the natural fringing reef (CI-1) yielded a parabolic growth response with elevation (Fig. 3), having the greatest growth (1.4 cm year^{-1}) between 18 and 28% aerial exposure (−0.35 and −0.25 m NAVD88, respectively). Overall, the entire reef area examined exhibited growth, which dropped to <0.5 cm year^{-1} at 10% (mean low water, MLW) and 52% exposure (−0.43 and −0.1 m NAVD88,

respectively). Scans of the constructed fringing reef (SG3-1997) revealed a similar trend in the 3-year time step, but in the first scan (2010), reef substrate only incorporated elevations up to −0.25 m NAVD88. Most of SG3-1997 experienced little or no growth (predominantly loss), with growth spiking at the highest elevations (Fig. 3a).

The cores from constructed reefs in Middle Marsh sampled the cultch surfaces of all but two reefs (SG3-2000 and SM1-1997) below MLW, and the mean thickness of the reefs above the cultch were only 10.5 ± 5.7 cm (mean ± SD). Thus, we observed the same pattern as the laser scanning results with little growth below MLW, based on the overall reef growth since their construction (mean growth rate of 0.89 ± 0.51 cm year^{-1}). Greatest growth (20 cm or 2.0 cm year^{-1}) occurred on constructed reef SG3-2000 (Fig. 3b), which had the highest cultch surface exposure (14%).

Adult oyster density increased with exposure, with greatest densities occurring near the tops of natural reefs around MSL (Fig. 4). Constructed fringing reefs mainly occupy areas at below MLW, and oyster densities in those lower tidal zone regions, while being less abundant, followed the pattern found on natural reefs.

Salt marsh density and average stem height between reef and non-reef sites were not significantly different (density $t = −0.966$, df = 34, $P = 0.34$; height $t = 1.88$, df = 34, $P = 0.069$; Supplemental Fig. 1). Mean stem densities in non-reef and reef marshes were 128 ± 49.2 and 112 ± 50.2 m^{-2} (mean ± SD), respectively, while mean stem heights were 48.2 ± 10.2 cm (non-reef) and 54.5 ± 9.93 cm (reef).

Sedimentary Units and Stacking Patterns Cores sampled the same three sedimentary units in all transects along natural shorelines. The deepest unit was a fine-grained silty sand (mean grain size ~150 μm) with less than 1% shell fragments. This unit was interpreted as a sandflat and is similar to the modern sandflat that exists throughout Middle Marsh. Above
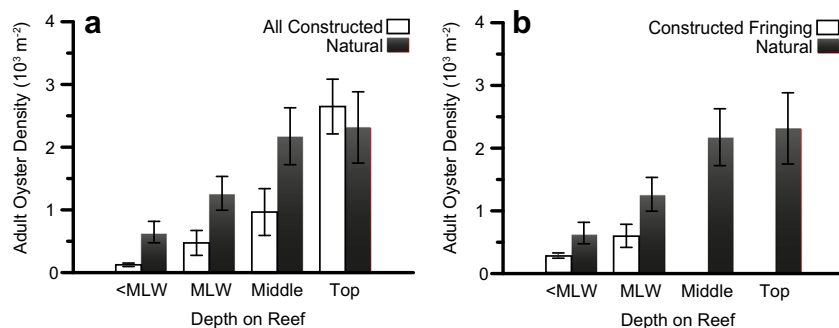

Fig. 4 Adult oyster densities on **a** natural and Middle Marsh constructed reefs (adapted from Ridge et al. 2015) and **b** comparing constructed fringing reefs with natural reefs. Elevation exposure bins for depths on

reef include <*MLW* (<10% exposure), *MLW* (10–20% exposure), *middle* (20–40% exposure), and *top* (>40% exposure)

the sand flat, we sampled a carbonaceous muddy sand (mean grain size ~100 μm) to sandy mud (mean grain size ~50 μm) with abundant roots and stems of *S. alterniflora*. This unit was interpreted as salt marsh peat and extends below and in direct contact with all but the natural reef NRM1 (Fig. 5, Supplementary Fig. 2). While older, deeper marsh sediments were uniformly muddy sand, inner marsh cores (core 1 for each transect) all exhibited a fining upward trend (the transition from coarse-dominant to fine-dominant sediment up core). Marsh cores closer to the reef (core 2 of each transect) were sandier overall. In most transects, the marsh unit was continuous and thickened toward the reef-marsh boundary.

Oyster reef strata were composed of >15% shell with sandy mud or muddy sand filling the pore space, and the taphonomically active zone (zone of living oysters) having between 80 and 98% shell with relatively open pore space. Similar to the marsh cores, reef cores exhibited a fining upward trend in grain size. Laterally, reefs experienced a midpoint peak thickness and thinned toward both the sandflat and salt marsh boundaries. The maximum thickness of the reefs varied, with the groin reefs MM2 and NRM2 being the thickest reefs sampled (0.6 and 0.85 m thick, respectively).

Radiocarbon dates from the deepest section of North River reef NRM2 revealed the reef first formed 110–208 cal years BP (~1819 AD). Dates from the base of the Middle Marsh reef MM2 suggested it formed after 1950 AD (Fig. 5), and aerial photography from the USA Department of Agriculture (USDA) in 1958 indicated that a smaller precursor reef was present. For both groin reefs, MM2 and NRM2, dates taken up the slope of the reef-marsh contact demonstrated that these reefs expanded over the marsh after 1950. Similar to NRM2, shell material from CI-1 showed the reef was as old as 65–211 cal years BP (~1877 AD).

Preservation of the marsh sediment under the study reefs reached 5–15 m from the farthest extent of living marsh (Figs. 5 and 6), while marsh sediments at all non-reef sites were completely absent at some distance within 5 m of the marsh edge (Fig. 6). Interior marsh cores had an average soil carbon density of 0.0208 ± 0.004 g C cm^{-3} and organic carbon inventory of 12.5 ± 2.41 kg C m^{-2} (average of four cores and standard deviation). Carbon inventories for marsh sediments below reefs ranged from 0.382 to 9.72 kg m^{-2} among individual cores and reef sites with an overall average below-reef inventory of 5.29 ± 2.69 kg C m^{-2} and soil carbon density of 0.0199 ± 0.007 g C cm^{-3}. The natural low-relief fringing reefs, MM3 and MM4, yielded average below-reef marsh carbon inventories of 3.50 ± 2.37 and 1.81 ± 2.01 kg C m^{-2}, respectively (averages of two cores each). Marsh sediments under the high-relief fringing reef, MM1, contained 8.27 kg C m^{-2} (one core), while the marsh sediments below the groin reefs NRM2 and MM2 contained 7.44 kg C m^{-2} (one core) and 5.44 ± 3.78 kg C m^{-2} (three cores), respectively.

To calculate the percent carbon preserved by the reefs during transgression, we used a conservative date for oyster-reef presence on the marsh shorelines (1950 AD, moderned by radiocarbon analysis). This meant the marsh platform would have been approximately 15-cm lower at historical rates of LSLR (2.8 mm year^{-1}, Beaufort, NC; NOAA Tides and Currents, station ID 8656483). The corresponding interior marsh core at each site was used to estimate the potential carbon within the hypothetical marsh platform bounded by the relevant oyster cores. Compared to the current extent of buried marsh sediment and corresponding carbon inventories, carbon preservation under reefs MM3, NRM2, and MM2 equaled 22.2, 28.3, and 58.4%, respectively. Just relating the interior marsh cores to cores taken within the reef-marsh interface indicated that an average of $64.4\% \pm 13.4\%$ (standard error) was capped by the transgressing reef.

Discussion

Reef Growth Natural fringing reefs appear to be following a parabolic exposure-growth curve, with a peak in reef growth between MLW and MSL. This growth pattern follows previous fine-scale examinations of constructed intertidal patch-reef growth, which exhibited a parabolic growth pattern with greatest rates occurring in the mid-low intertidal (optimal growth zone, OGZ; Ridge et al. 2015) with zero-growth boundaries forming near MLW and MSL (growth ceiling). However, unlike constructed patch-reef growth curves, the natural fringing reef exhibited growth lower in the tidal range from 15 to 30% as opposed to the 20–40% previously described. It also experienced net accretion across all elevations sampled, only decreasing to 3.9 mm year^{-1} around MLW and 2.3 mm year^{-1} near MSL, roughly the rate of local LSLR (2.8 ± 0.37 mm year^{-1}). This inconsistency may indicate that natural reef growth behaves differently than constructed reef growth due to a variety of factors. Growth may manifest differently with varying levels of reef maturity (Rodriguez et al. 2014). The fringing reef's location adjacent to salt marsh may impact the growth curve due to flow modification (Leonard and Croft 2006) and/or predator accessibility and behavior (Irlandi and Crawford 1997; Lewis and Eby 2002; Carroll et al. 2015). While proximity to the marsh would not change the tidal exposure-elevation gradient, baffled flow near the marsh could reduce food delivery, and the higher elevations of the reef nearer the marsh edge may experience increased predation. This reef may have also experienced a different aerial exposure regime during this study period than the elevation-exposure calibration we derived from Middle Marsh water levels earlier in 2011 as a result of annual fluctuations in sea level between 2012 and 2015, with annual mean sea level changing ±4 cm between years (Beaufort, NC, mean sea level trends; NOAA Tides and Currents, station
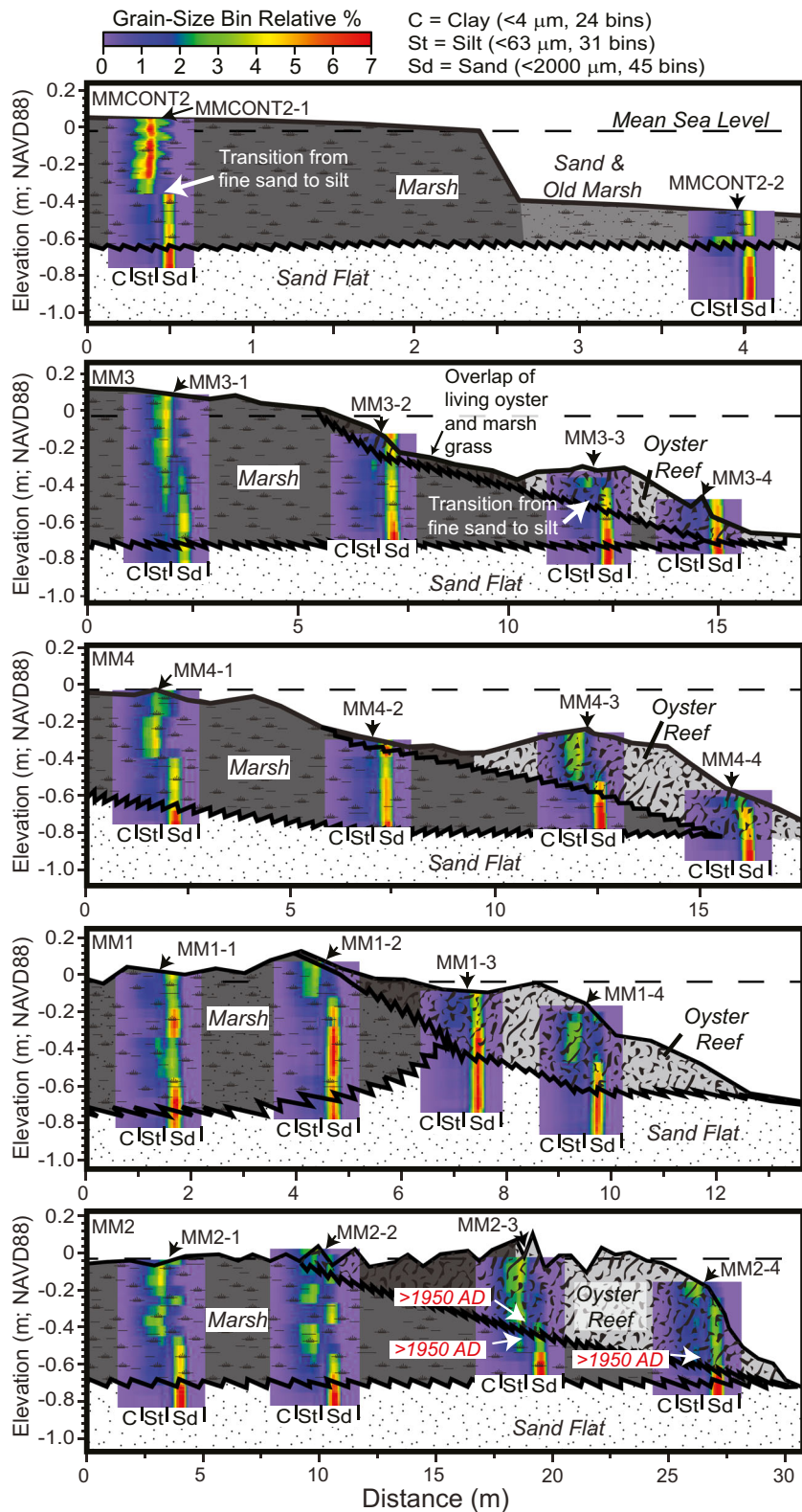
Fig. 5 Cross sections of five study sites with corresponding grain size color maps from labeled cores. *Shaded oyster reef* represents units that are mix oyster and marsh sediments (overlap of living marsh and oyster). Radiocarbon dates are labeled in *red* with *arrows* pointing to approximate depths sampled. Grain size composition with depth was transformed into a colored grid using a relative percentage histogram of the 100 grain size bins. Within each color map, the *y*-axis corresponds to the core depth embedded in the cross-section, and the *x*-axis is divided into the 100 grain size bins from 0.04 to 2000 μm. The *x*-axis has been subdivided into the grain size categories of clay (C; < 4 μm), silt (St; < 63 μm), and sand (Sd; < 2000 μm) for ease of reference. Grain size maps exclude the gravel fraction (>2 mm) from each section, which is predominantly shell material in oyster reefs and plant material in the marsh sediments
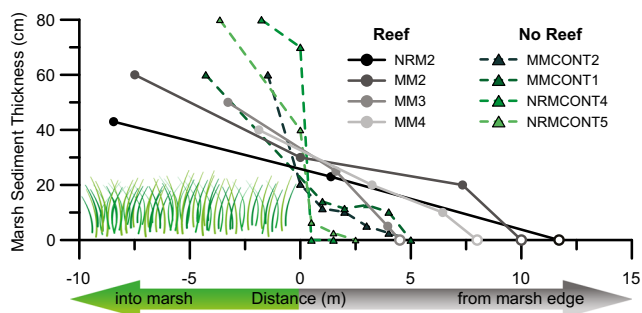
Fig. 6 Preservation of marsh sediments in both oyster reef (*gray solid lines*) and non-reef (dashed green lines; ±0.5 m) shorelines. Reef site data to the left of zero were obtained from cores taken in the overlapping zone of living oyster and marsh grass. Using the cross sections (Fig. 5), a midpoint value was chosen between the outermost core that sampled marsh sediment under the reef and the presumed extent of marsh sediment assuming the continuous depth of the marsh-sandflat contact (represented by the *open circles* along the *x*-axis)

ID 8656483). Because the tidal range in this area is just below a meter, each centimeter change in water level would correspond to a shift of slightly more than 1% aerial exposure when referencing our baseline water level data. A 4-cm drop in water level could explain the OGZ appearing at 15% aerial exposure instead of 20% when compared to the same 2011 baseline water levels.

Constructed fringing reefs in Middle Marsh are experiencing little to no growth, and in some instances, substantial elevation losses as the substrate is slowly redistributed (e.g., the abundant loss on SG3-1997; Fig. 3). The scanned constructed reef (SG3-1997) experienced a growth peak at its highest elevation (26% exposure). While that peak did occur within the previously defined OGZ for constructed patch reefs (Ridge et al. 2015), the critical exposure boundary (the depth at which growth is equivalent to LSLR) of this constructed fringing reef also falls within the previously defined OGZ. Therefore, from a restoration standpoint, it appears that the optimal placement of material along some marsh shorelines could be defined by an even narrower depth range than previously suggested from examining patch reefs.

In comparison to constructed patch reefs in Middle Marsh (Rodriguez et al. 2014; Ridge et al. 2015), many of these constructed fringing reefs were placed lower in the tidal range, with much of their surface below MLW (Figs. 3 and 4). A detailed inspection of the shell material within each core section (Supplementary Fig. 3) reveals that the "growth" displayed by most of these reefs is only a cluster of oysters that spans one to two generations. When we exclude the taphonomically active zone (zone of living oysters), which is the top 5–10 cm of each core, the only reef that showed growth is SG3-2000. Reef SG3-2000 was the only constructed-fringing-reef site where cultch material was placed near the OGZ, which further supports the paradigm that reef material placed too low in the water column will not produce a prolific reef in lower estuarine systems.

Oyster recruitment, growth, and survival collectively mediate oyster-reef accretion rates, and therefore, oyster density should generally be correlated with reef accretion. Adult oyster density in both natural and restored fringing reefs matched the observed reef-growth pattern, increasing growth with exposure, except at the highest elevations of the reef (>OGZ), where oyster densities were high but growth rates were low. These areas of the reef near MSL are most likely older sections of the reef that have been confined by the growth ceiling (~55% aerial exposure in this area). Over time, oyster recruitment within the interstitial space has increased density (Fig. 4), while oyster growth is still being limited by desiccation stress. Most of the restored fringing reefs included in this study fall on the deeper end of the growth spectrum and thus have markedly lower densities than the more mature, natural fringing reefs.

It is possible that the constructed-reef locations along marsh shorelines, which did not have substantial natural oyster reefs prior to cultch placement, are not suitable for reef development due to factors other than aerial exposure. Recent work has indicated that some shorelines may be unsuitable for oyster reef growth due to high wave exposure (Theuerkauf et al. 2016). Flow and sedimentation, which were not measured here, have been used to model reef development (Jordan-Cooley et al. 2011; Housego and Rosman 2015), primarily for subtidal oyster reefs. Flow has a major influence on the growth and condition of oysters (Grizzle et al. 1992; Lenihan et al. 1996; Lenihan 1999), and the baffling of flow around the marsh may inhibit food delivery to oysters and increase sediment deposition. Several studies (MacKenzie 1981; Colden and Lipcius 2015) have linked sedimentation to oyster mortality, and studies conducted by Lenihan (1999), Taylor and Bushek (2008), and Colden and Lipcius (2015) found that sediment burial could be detrimental to reef development. Solomon et al. (2014) found that sedimentation was positively correlated with increased inundation in the intertidal; thus, low flow and high sedimentation could explain why the constructed reef SM1-1997, which was placed just above MLW but in a very sheltered area, still exhibited little growth (Fig. 3). This coupled with the high growth of SG3-2000, which had the greatest cultch material thickness (i.e., highest relief; Supplementary Fig. 3), may indicate that the importance of flow and sedimentation with relation to subtidal reef height (Lenihan 1999; Schulte et al. 2009; Jordan-Cooley et al. 2011) could be applicable to intertidal reefs. While it is possible that we are witnessing a localized effect, these data still support the need for proper siting of oyster restoration projects.

Reef-Marsh Evolution Core transects revealed that most of the natural fringing reefs in Back Sound are in a state of transgression (Fig. 1, response C), as old marsh sediment was found beneath five of the seven natural reefs studied.

Radiocarbon dating of marsh-sandflat contacts from around Back Sound indicates that marsh grass colonized and fully occupied intertidal sandflats as early as the sixteenth century (Theuerkauf et al. 2015). The increased rate of SLR during the last two centuries combined with anthropogenic disturbances has driven marsh area loss along our coasts (Nicholls et al. 1999). Lateral retreat of marsh shorelines in response to these changes in estuarine conditions is associated with some degree of ravinement of old marsh sediment from waves and currents. Prior to oyster-reef formation, it is likely that the areal extent of the marsh platform extended seaward. This assumption is supported by core transects across marsh shorelines in this study that sampled marsh below oyster reef (Fig. 6) and other research conducted in nearby areas (Mattheus et al. 2010; Theuerkauf et al. 2015) that showed over 20 m of shoreline erosion since 1958 (the oldest, discernable shoreline from aerial photographs). In places of eroding marsh, the non- or sparsely vegetated, shoreface may have provided an intertidal surface for deposition of shell material allowing reefs to gain a foothold. Radiocarbon dating of basal oysters from three reefs suggests that these reefs occupied their present position within the last 200 years, and dates obtained from the reef/marsh sediment contact in cores 3 and 4 of the natural groin reef MM2 (Fig. 5) show that transgression has primarily happened within the last century.

Grain size data reinforce that the upper portions of the marsh sediment column were eroded prior to or during transgression of the fringing oyster reef. Cores from the marsh interior show that basal marsh sediment is sandy, and this old marsh was deposited during initial colonization of the sandflat, when allogenic marsh sediment was being sourced from the surrounding sandflats. As the marsh accreted and increased in areal extent, the allogenic sediment source transitioned from the adjacent sandflat to the finer grains suspended in the water column, demonstrated by the fining upward sequence present in interior marsh cores. This process is mirrored in the oyster reefs, with the pore space in less developed reefs being predominantly filled with sandy allogenic sediment. Pore space of the higher relief, mature reefs is fining upward (Fig. 5). The tops of those reefs are now disconnected from the adjacent sandflat, and pore space is primarily being filled with fine-grained sediments, likely biodeposits of oyster feces and pseudofeces. Marsh sampled below the oyster reefs show the same fining upward sequence as the interior marsh cores, but upper muddy marsh sediment is thinner than what was sampled in the marsh interior, and we interpret the difference in thickness between the interior marsh and the marsh preserved below the oyster reef being due to ravinement processes.

Cores taken within the transition area between the marsh and oyster reef (core 2 in most transects) display a sandier marsh unit throughout except in the high-relief natural reefs MM1 and MM2. This is most likely due to the reconnection of the allogenic sediment sourcing from the adjacent sandflat as the shoreline retreated and probably further mixed by bioturbation from burrowing organisms. The siltier mid-transect cores (core 2) from MM1 and MM2 are likely due to the fringing reefs being more mature with greater vertical relief than other sites. The mature fringing reefs reduced the connection of the marsh with the adjacent sandflat, protecting that marsh sediment from reworking through exposure to erosive forces. This provides further evidence that larger reefs with higher relief exhibit enhanced protection of the shoreline.

At the point of reef maturation, when the reef reaches its growth ceiling, the transition zone between reef and marsh reaches peak stabilization. The ravinement of marsh sediment has been reduced or halted as seen in MM1 and MM2, but it is unlikely that the reef-marsh transition zone will remain static with both habitats accreting at the same rate. Rather, it is more likely that the reef will consolidate as it intrudes into the marsh and increased oyster density crowds out the marsh grass as rising sea level elevates the growth ceiling and the transition zone transgresses. In many cases, it is improbable that the rate of oyster reef transgression would supersede upland migration of the marsh, but in instances where the marsh cannot traverse the upland boundary or has no upland to expand upon (Middle Marsh), this will result in the loss of the marsh platform area over time, gradually decreasing its carbon sequestration potential.

Carbon Reservoir Marsh-carbon inventories from our study sites (both interior marsh and below reef) were the same magnitude as inventories obtained in nearby salt marshes (5–8 kg C m^{-2}, Theuerkauf et al. 2015). These values are also equivalent to carbon inventories observed in Florida in middle and high marsh areas (10 ± 5 kg C m^{-2}) but less than low marsh observations (25 ± 4 kg C m^{-2}) (Choi and Wang 2004). Likewise, our soil-carbon densities from interior marsh and below the reefs were on the low end of the marsh-carbon density spectrum (see review in Chmura et al. 2003).

Ravinement of the marsh shoreline results in export of stored carbon to the estuary that can far outweigh the marsh's capacity to trap carbon (Theuerkauf et al. 2015). Fringing reefs, regardless of morphology, did not impact marsh grass density or overall stem height (Supplementary Fig. 1), and thus the natural hardening of the shoreline by oyster reefs is principally responsible for mitigating the depth of ravinement and consequent loss of carbonaceous marsh sediment. This study indicates that, from a fringing reef's inception, it can preserve a quarter to half the carbon stored within an eroding marsh shoreline. These percent preservation values are conservative, because it is possible that the marsh was already eroded prior to oysters colonizing the shoreline, which would increase the relative percent carbon preserved by the reefs. In the process of a reef growing vertically and laterally along the marsh edge, erosion of marsh sediments was likely reduced

correspondingly to the maturity of the reef. This is further evidenced by the cores taken within the habitat overlap (the reef-marsh interface), which indicate that nearly two thirds of the marsh carbon is being preserved under recently transgressed areas; the highest preserved carbon values being in the reefs with the greatest relief.

No marsh sediment was preserved >5 m bayward of the marsh edge at reference sites where no oyster reef was present, indicating total ravinement of carbonaceous sediments. When compared to the annual rate of carbon being lost from nearby eroding marsh sites without oyster reefs (annual shoreline retreat 0.65 m; average carbon inventory 6.79 kg C m^{-2}; Theuerkauf et al. 2015), carbon preservation under the reefs MM1 and MM2 is equivalent to approximately 1.5 and 18.9 years of unimpeded marsh erosion, respectively (6.70 ± 7.16 years, average for all sites). This presents a new view of how reefs can help enhance ecosystem services of marshes by preserving buried marsh carbon during transgression. This process is likely occurring throughout the Southeastern USA and other parts of the world where oyster reefs fringe wetland environments.

Beyond capping carbonaceous marsh sediments, there still remains the question of what role oyster reefs play in estuarine carbon budgets. It has been speculated that reefs can act as carbon sinks (Peterson and Lipcius 2003; Grabowski and Peterson 2007), although there is a lack of empirical evidence to support this postulation. As seen in the marsh, finer sediments (silts and clays) are generally richer in organic carbon, and the fine sediments trapped in the pore space of upper sections of mature reefs may be evidence for the reef's capacity to trap large amounts of carbon within the reef matrix. However, most of that carbon is likely allogenic, and it is yet to be determined if this burial is enough to offset overall reef respiration and the CO_2 produced during the calcification process (Ware et al. 1992).

Conclusions

Salt marshes and oyster reefs are highly threatened habitats but are crucial components to a coastal landscape that has experienced alarming changes since the end of the nineteenth century (Beck et al. 2001; zu Ermgassen et al. 2012). This study demonstrates that marsh shorelines in central North Carolina, and likely other locations along the Southeast coast of the USA, are in a general state of retreat and that fringing oyster reefs naturally transgress these habitats. Natural fringing oyster reefs exhibit a similar pattern of growth to highly productive constructed patch reefs, having a peak in growth occurring between MLW and local MSL, and we have also shown that constructing fringing reefs above MLW in lower estuaries is important for promoting reef growth. As reefs mature, they not only slow marsh retreat but also preserve

buried marsh carbon during transgression. Careful consideration of tidal placement and hydrodynamic conditions will help promote growth of constructed reefs, and coupled restoration and preservation of reef and marsh environments will help ensure prolonged ecosystem functioning in impacted estuaries.

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