High carbon accumulation rates in sediment adjacent to constructed oyster reefs, Northeast Florida, USA

Jessica Veenstra¹ · Melissa Southwell¹ · Nikki Dix² · Pamela Marcum² · Jillian Jackson¹ · Cody Burns¹ · Colin Herbert¹ · Aubrey Kemper¹

Received: 9 March 2020 / Revised: 2 June 2021 / Accepted: 3 June 2021 / Published online: 26 June 2021
© The Author(s) 2021

Keywords *Crassostrea virginica* · Sediment organic matter · Constructed oyster reef · Carbon sink · Living shorelines

Introduction

Oysters are at risk; 85% of oyster cover has been lost globally over the past 130 years (Beck et al. 2011). These losses have had major effects on the oyster fisheries, but are also concerning because oyster beds have been well documented to provide important ecosystem services such as: improving water quality, stabilizing shorelines, and creating habitat for a wide variety of organisms (Grabowski et al. 2012).

Carbon sequestration is yet another ecosystem service that oyster reefs could provide, which is becoming increasingly important as global atmospheric carbon dioxide concentration rises. Although carbon sequestration research has been largely focused on terrestrial ecosystems or the open ocean (Canadell and Raupach 2008; Sabine et al. 2004), vegetated coastal ecosystems, such as seagrasses, salt marshes, and mangroves, have been identified as important carbon sinks. Although small in total area, their carbon burial rates are high, and their contribution to carbon sequestration has been termed “blue carbon”, carbon stored in coastal ecosystems (McLeod et al. 2011; Davis et al. 2015).

Oyster reefs may not seem like good candidates for carbon sequestration because they do not have an analogous vegetative component, and calcification of oyster shell releases CO₂ (Fodrie et al. 2017). However, oyster reefs support organic matter accumulation through their biodeposits

(feces and pseudofeces) which have significantly higher levels of macronutrients (C, N, P) than surrounding sediment (Newell et al. 2005; Chambers et al. 2017). In addition, the vertical structure of oyster reefs increases surface roughness, which promotes the accumulation of fine sediment and burial of organic matter (Kristmanson and Wildish 1997; Chowdhury et al. 2019). They have been shown to attenuate wave energy as well (Chowdhury et al. 2019; Kibler et al. 2019; Wiberg et al. 2019). Fringing oyster reefs can protect and stabilize salt marsh sediments and the carbon trapped within them (Ridge et al. 2017). Elevated organic matter and/or total C contents in sediments within oyster reefs provide evidence for these processes (Nelson et al. 2004; Meyer and Townsend 2000; Kellogg et al. 2013; Feinman et al. 2018; Chambers et al. 2017).

Fodrie et al. (2017) reported rates of carbon storage from 100–130 g C/m²/yr in shallow sub-tidal reefs and salt marsh fringing reefs in North Carolina, USA, whereas oyster reefs on intertidal sand flats were net sources of carbon at a rate of 710 g C/m²/yr. Oyster reefs can become net sources of carbon dioxide when organic matter storage and burial does not exceed the quantity of inorganic carbon in shell (CO₂ is released during carbonate production) (Fodrie et al. 2017). Therefore, it is important to account for both inorganic and organic carbon burial. In their study, Fodrie et al. (2017) accounted for the carbon in shell hash and sediments directly within and underneath reefs. However, to quantify the full effect, it is necessary to also include increases in organic matter burial in the sediment surrounding the reef. In our study, we quantify the carbon accumulation rates in sediment adjacent to constructed oyster reefs in northeast Florida, USA.

✉ Jessica Veenstra
jveenstra@flagler.edu

¹ Flagler College Department of Natural Sciences, 74 King St., St. Augustine, FL 32084, USA

² Guana Tolomato Matanzas National Estuarine Research Reserve, 505 Guana River Road, Ponte Vedra Beach, St. Augustine, FL 32082, USA

Methods

Constructed oyster reef study site

In 2012 and 2013, plastic mesh bags of recycled eastern oyster shells, *Crassostrea virginica*, were used to construct intertidal oyster reefs parallel to the low tide line of 315 m of the eastern shoreline of the Tolomato River within the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM Research Reserve) in Ponte Vedra, FL (Fig. 1). Twenty-eight reefs were constructed with average dimensions of 5.3 m $\times$ 1.8 m $\times$ 0.5 m with 6 m gaps between the reefs. The oyster reefs were constructed as a part of a volunteer-based “living shoreline” project to attempt to slow the shoreline erosion at an archaeological site within the reserve. Although it is common to include marsh plantings or to add fill in living shoreline designs, this project just consisted of bags of oyster shell. The Tolomato River is a part of the Atlantic Intracoastal Waterway, and the associated boat wakes accelerate the erosion of the shoreline (Herbert et al. 2018).

Sediment sampling

In 2016, we intensively sampled the sediment landward of three constructed oyster reef segments (Reef 3, Reef 4, and Reef 5, when counting from the north). We sampled Reef 3 and Reef 4 in a 2 m $\times$ 2 m grid pattern, and Reef 5 in a 2 m $\times$ 4 m grid pattern because the footprint of that reef was larger than the other two. It was not possible to have replication in our sampling design because the entire project exists in a contiguous block. Therefore, any reefs chosen would be pseudoreplicates. Instead, we decided to intensively sample a single large plot that encompasses 3 reefs, so that we could investigate the areal extent of the reef’s effect and the spatial variation of depositional patterns between the reef segments. This approach also allowed us to focus on the oldest part of the reef, representing 4 years of depositional history. We sampled a total area of 27 m by 8 m (60 points) (Fig. 1). We sampled an equivalent number of points (60) in our control area 25 m south of the southernmost constructed reef in a 22 m by 8 m grid. No oysters were present there (Fig. 1). Both the

Fig. 1 Map of sampling site identifying the locations of the Reef Grid (light blue) and the Control Grid (light brown). The constructed oyster reefs are intertidal, and exposed just above the waterline in this satellite photo (Google Earth, 2017). The sampling site is on the eastern shore of the Tolomato River (Atlantic Intracoastal Waterway) in the GTM Research Reserve, 2 km from the mouth of the Guana River about 12 km from the nearest inlet (Inset a). We sampled sediment landward from the constructed oyster reefs in a 2 m $\times$ 2 m grid behind Reefs 3 and 4, and a 2 m $\times$ 4 m grid behind Reef 5 because it had a

slightly larger footprint than the other two reefs (Inset b). Our control grid was located 25 m south from the southernmost constructed oyster reef (light brown), and we sampled every 2 m in a 22 m $\times$ 8 m grid, to collect the same number of samples that we collected near the reefs (Inset c). Symbols within the sampling grid indicate analyses performed. On a subset of samples, we performed the organic matter analysis and on a smaller subset of 3 transects per grid, we performed particle size analysis. We measured fine sediment thickness for every sample collected (Inset b, Inset c, and Legend)

reef sampling area, and the control sampling area were entirely unvegetated.

At each sampling point, we used a 7 cm diameter clear polycarbonate push core to collect sediment when the tide was low, and the reefs were exposed. In previous observations, we had found that there was a distinctive layer of finer sediment over sandier sediment landward of the constructed reefs, which we interpret as post-construction accumulation. We base this interpretation on a time series of surface sediment characteristics at this site, which includes sediments obtained before the reef was installed (Southwell et al. 2017). We sectioned the core at the coarse–fine interface, then measured and collected the whole fine sediment layer, and at least 7–8 cm of the coarser, sandier sediment beneath it as a separate sample. Therefore, the amount of fine sediment sampled varied at each point in the grid based on the thickness of the fine sediment layer. Each core from the reef grid was split into two samples, the fine and coarse sediment layers, and placed in separate Ziploc bags. In the control area, there was no fine sediment observed, so 8 cm of coarse sediment was collected from each point within the control grid.

To determine the relationship between loss-on-ignition organic matter (%*LOI*) and organic C (%*C_{org}*), we also took four additional sediment cores (three reef and one control) in 2016–2017 from the different reefs at the same living shoreline project. We avoided reefs 3, 4, and 5 because of the disturbance caused by the previous grid sampling; each reef core was taken 2 m behind the center of the reef and the control core was taken from an equivalent elevation. The cores were 10.15 cm in diameter, 20–25 cm deep, and sectioned every 2 cm to provide data across both the fine and coarse layers we sampled in the grid. Both grid samples and core section samples were transported in a cooler and stored in a freezer until they were processed and analyzed.

Bulk density, shell content, organic matter, and organic carbon content

A subset of the sediment samples were selected for further analysis (Fig. 1b, c). Frozen samples were dried in an 80° C oven overnight, and weighed to determine bulk density (g/cm³). Dried samples were then carefully ground with a mortar and pestle to pass through a 2 mm sieve. Sediment > 2 mm diameter consisted of oyster shell and shell fragment, and was weighed to determine shell content (%). We then determined organic matter content (%) of the < 2 mm diameter (shell-free) sediment samples using the loss-on-ignition method (%*LOI*, 550° C for 12 h, Wang et al. 2011).

For the purpose of determining the relationship between %*C_{org}* and %*LOI*, the dried core section samples were transported to the Center for Marine Science at the University of North Carolina- Wilmington, where the organic carbon content

of the sectioned core samples was determined by CHN analysis on a Thermo Flash EA after vapor acidification (Hedges and Stern 1984). Using the paired data of %*C_{org}* and %*LOI* for the core section samples, we performed linear regression to determine the relationship between the two variables for this site, which we then extrapolated to the larger (grid) sample set.

Particle size analysis

We selected three transects that ran perpendicularly landward from each constructed reef, and three evenly distributed transects from the control grid (Fig. 1b, c). We analysed samples from five locations on each transect to determine the particle size distribution of the shell-free < 2 mm sediment samples. We used a pre-treatment with 30–60 mL of 30% hydrogen peroxide for 24–96 h to remove organic matter from 30 g of sediment before we performed the rapid method for particle size determination (Kettler et al. 2001). Sediment was divided into the following size fractions: coarse (2 mm–500 µm), medium (500 µm–250 µm), fine (250 µm–125 µm), and very fine (125 µm–63 µm) sands, silt and clay (< 63 µm) and reported as a percent.

Carbon accumulation rate calculations

To calculate the best estimate of the carbon accumulation rate (g C/m²/yr) in the fine sediment layer that accumulated adjacent to the reefs, we account for the organic carbon content of the organic matter in buried sediments as well as the organic carbon content and inorganic carbon content of the buried shell. Fodrie et al. (2017) discussed the concerns of buried inorganic carbon in oyster shell as a net source of carbon (CO₂ is released as a byproduct of shell production). Therefore, we use the following equation to determine total carbon stored per sediment core sample collected: where *C_{orgsed}* is the total mass of organic carbon in shell-free sediment within the core sample (sink), *C_{orgshell}* is the total mass of organic carbon in the shell within the core sample (sink), *C_{inorgshell}* is the total mass of carbon released from the calcification of the shell within the core sample (source), and *C_{total}* is total mass of carbon within the core sample.

To estimate organic carbon accumulation in shell-free sediment per core sample, we used the following equation:

$$(m_{sed} - m_{shell}) \times \%C_{org} = C_{orgsed} \quad (1)$$

where *m_{sed}* is the mass of sediment in the core sample, *m_{shell}* is the mass of shell in the core sample, and %*C_{org}* is calculated from the %*LOI* relationship determined from the elemental analysis of the dried core section samples.

From Fodrie et al. (2017), we adapted the following equation to calculate the mass of organic carbon in shell per core sample that would be considered a net sink of carbon.

$$m_{shell} \times \frac{0.0136 \text{ g organic shell material}}{1 \text{ g shell}} \times \frac{0.36 \text{ g } C_{org}}{1 \text{ g organic shell material}} = C_{orgshell} \quad (2)$$

And, we adapted the following equation to calculate the mass of carbon released during calcification of shells (Fodrie et al. 2017):

$$m_{shell} \times \left(\frac{0.95 \text{ g inorganic shell material}}{1 \text{ g shell}} \right) \times \left(\frac{0.111 \text{ g } C_{inorg}}{1 \text{ g inorganic shell material}} \right) \times 0.6 = C_{inorgshell} \quad (3)$$

Then C_{total} was determined from the following equation:

$$C_{orgsed} + C_{orgshell} - C_{inorgshell} = C_{total} \quad (4)$$

We performed the calculations above for both the reef fine sediment layer as well as the controls.

The measured C_{total} in our reef fine sediment layer was then converted to an areal deposition rate ($\text{g C/m}^2/\text{yr}$), $C_{rate-fine}$, using the area of our core sample (0.00385 m^2):

$$\frac{C_{total}}{0.00385 \text{ m}^2 \times 4 \text{ years (2012 - 2016)}} = C_{rate-fine} \quad (5)$$

However, in order to give our most conservative estimate of the additional carbon in the accumulated sediments (C_{enrich}), we subtracted the amount of carbon that would have been found in an equivalent thickness of control sediment. We used the average total mass of carbon stored per cm depth in control sediments (0.024 g/cm of core sample), the depth of fine sediment in each reef core sample (d_{sed}), and the following equation.

$$C_{total} - \left(\frac{0.024 \text{ g C}}{\text{cm}} \times d_{sed} \right) = C_{enrich} \quad (6)$$

The measured C_{enrich} in our reef sediment cores was then converted to an areal deposition rate ($\text{g C/m}^2/\text{yr}$), $C_{rate-enrich}$, using the area of our core sample (0.00385 m^2):

$$\frac{C_{enrich}}{0.00385 \text{ m}^2 \times 4 \text{ years (2012 - 2016)}} = C_{rate-enrich} \quad (7)$$

To constrain the uncertainty associated with our measurements, we calculated standard error of the carbon accumulation rate by propagating the standard deviation of sample splits of the %LOI measurement through the above calculations (Malhi et al. 2009). The standard deviation of the %LOI splits was 0.26% OM, and mass measurement uncertainty for bulk sediment samples and shell was $\pm 0.01 \text{ g}$.

Mapping

To calculate our best estimate of the overall carbon accumulation rate for the whole area sampled landward of the

constructed oyster reefs, we used a Kriging interpolation in Surfer 13 (Golden Software 2015) to create contour maps of fine sediment thickness, organic matter content, and carbon accumulation rates for the sampled grid. Using the software's volume function, we estimated the total volume of fine sediment accumulated, and the overall carbon accumulation rates for the area adjacent to individual reef segments, as well as the overall carbon accumulation rate for the whole area sampled.

Live oyster cover

National Estuarine Research Reserve staff measured live oyster cover on a subset of the 28 reef segments in Spring 2014 ($n=6$), Summer 2014 ($n=15$), and Spring 2016 ($n=16$). To determine percent live oyster cover, reefs were divided into three zones for sampling (north, middle, south). A 0.25-m^2 , 5×5 -gridded quadrat (with 25 intersecting points) was placed haphazardly within each zone. Each intersecting point was classified as live oyster, shell, or substrate. The total number of each classification was summed for each zone and zones were then averaged for each reef. Reef averages were multiplied by four to get percent cover per m^2 for each reef. Reef-level cover was then averaged for all reefs sampled and standard error was reported. Because reef segments were installed at different times, data were reported in terms of number of months after initial installation of reefs.

Statistical analysis

The linear relationship between % C_{org} and the %LOI was assessed using the Pearson correlation coefficient.

Results

Oyster cover

Live oyster cover on the constructed oyster reefs declined over time. Across all 28 reef segments, live cover was 66% 12 months after installation, then decreased to 23% 20 months after installation, and then increased again to 51% 25 months after installation, then declined to 12%, 47 months after installation (Fig. 2). For context, mean live oyster cover on 20 natural reefs in the Tolomato River from 2014–2016 was 27% (Marcum et al. 2018). Live oyster cover on the reefs in front of our sediment sample plot was 36% (Reef 3), 21% (Reef 4), and 28% (Reef 5) in 2014, 23 months after installation. In 2016, one month before we sampled the

sediment, live cover was 6.7% (Reef 3) and 17% (Reef 5), 46 months after installation.

Fine sediment accumulation

Four years after the reefs were constructed, the total volume of fine sediment accumulated in the treatment area was 20.2 m³ and 179 m² of the study area had an accumulated fine sediment layer of at least 2 cm (Fig. 3a). The fine sediment layer was thickest immediately behind the reef, and decreased moving landward (Fig. 3a); the silt and clay content (< 63 µm) of the fine sediment layer shows a similar pattern (Fig. 3b). Mean silt and clay content was 17% (std. dev. 6) for the fine sediment layer, 9% (std. dev. 3) for the coarse sediment layer, and 4% (std. dev. 3) for the control site. Thus, even what we labelled “coarse” sediments were still finer than those of the control site (Fig. 3b).

Organic matter content

The mean organic matter content was 2.6% (std. dev. 0.8) for the fine sediment layer, 1.8% (std. dev. 0.6) for the coarse

sediment layer that underlies the fines, and 0.8% (std. dev. 0.2) for the control (Fig. 4). The sediment located directly behind the middle of each reef segment showed the most OM enrichment, with distinctly lower OM% values in the gaps.

Carbon accumulation rate

The percent organic carbon data was significantly correlated with loss on ignition ($R^2 = 0.84$; $df = 35$; $p < 0.001$), with the linear regression equation:

$$\%C_{org} = 0.235 * \%LOI + 0.02078 \quad (8)$$

The linear relationship was consistent between control and reef samples, as well as throughout the depth of the cores. Using this relationship, the total amount of carbon accumulated in the sampling area was 84.9 kg over a 4-year period. The total carbon accumulation rate in the fine sediment layer landward of the three constructed reefs was 27.5 kg C/yr $\pm$ 0.2, or 1.0 kg C/yr $\pm$ 0.01 per meter of shoreline. The average areal deposition rate ($C_{rate-fine}$) was 170 g C/m²/yr $\pm$ 160. The spatial variability in the grid points causes this large standard deviation; this does

Fig. 2 The graph above shows mean live oyster cover (%) vs. number of months after initial installation, because reef segments were installed at different times. We have highlighted the live oyster cover for Reef 3, 4, 5 in black, because those are the reef segments that we sampled sediment behind, while the mean live oyster cover for

remainder of reef segments sampled during the study time frame is shown in grey. Standard error bars represent the variation of the replicates on each reef). For context, mean live oyster cover on 20 natural reefs in the Tolomato River from 2014–2016 was 27% (Marcum et al. 2018), represented by dashed line

Fig. 3 **a** The contour map above shows the variation in fine sediment thickness (2 cm contour intervals) landward of each of the three reefs sampled. The most fine sediment accumulated directly behind the reefs (<2 m landward from the reefs). **b** The graph shows silt and clay content (%; particle sizes <63 μ m) for the fine sediment layer,

the coarse sediment layer and the control. As distance landward of the reef increases, the silt and clay content of the fine sediment layer decreases, while the silt and clay content of the coarse sediment layer and the control remains relatively constant ($n=3$). Mean fine sediment thickness is reported for each reef sampled

not represent measurement uncertainty. Correcting for the carbon content of the control provides a more conservative estimate of the reef carbon accumulation rate of 21 kg C/yr $\pm$ 13, or 0.79 kgC/yr per meter of shoreline. The corrected areal deposition rate ($C_{rate-enrich}$) is then 131 g C/m²/yr $\pm$ 152 (Fig. 5). There are strong spatial trends within

the plot, with the points directly behind the reef exhibiting areal deposition in excess of 300 g C/m²/yr (Fig. 5). The accumulation rate for the sediment adjacent to the individual oyster reef segments varied from a minimum of 125 g C/m²/yr (Reef 3) to a maximum 154 g C/m²/yr (Reef 5).

Fig. 4 The three contour maps above show the distribution of organic matter (% determined from loss-on-ignition method) landward of the constructed reefs in the surface fine sediment layer and the coarse sediment layer below, as compared to the control site. The high-

est organic matter contents are found directly landward of the constructed reefs in the fine sediment layer. The coarse sediment layer had lower organic matter contents than the fine sediment layer, but higher organic matter contents than the control

Fig. 5 The contour map to the right shows the carbon accumulation rate (g C/m²/yr) in the fine sediment layer landward of the constructed reefs

Discussion

Our dataset shows that constructed oyster reefs alter the depositional environment of the intertidal zone, up to 6 m landward of the boundaries of the reef itself. In fact, the area with fine sediment accumulation greater than 2 cm (179 m^2), was more than four times the area of the constructed reefs themselves (40 m^2 , Fig. 3a). The total volume of fine sediment deposited in our treatment area over the four-year time span is 20.2 m^3 , or 0.75 m^3 of sediment per linear m of the shoreline. Others have made observations of increases in silt and clay content with the construction of oyster reefs (Meyer and Townsend 2000; Wilber et al. 2012; Kellogg et al. 2013; Chowdhury et al. 2019). Constructed oyster reefs are frequently designed as this project was, breakwater or sill structures specifically engineered to disrupt wave energy, increase sedimentation, and reduce erosion (Currin et al. 2010; Gittman et al. 2016; Smith et al. 2018; Chowdhury et al. 2019). Chowdhury et al. (2019) found similar deposition rates, $0.11 \text{ m}^3/\text{m}^2$, 5–35 m landward of constructed oyster reefs. As we did not quantify the deposition within the oyster reef itself, the substantial sedimentation that occurs within the reef would likely augment the total reef-induced deposition value.

Finer particles have a larger total surface area to attract and accumulate organic matter, and rates of organic matter accumulation often have been linked to sediment surface area (Rhoads and Boyer 1982; Keil et al. 1994). For this reason, it is not surprising that silt and clay content is correlated with organic matter content in our dataset ($R^2 = 0.8615$). It is likely that oyster biodeposits comprise part of the sedimentary organic carbon content as well. Ninety-five percent of biodeposit material is $< 3 \text{ }\mu\text{m}$ in diameter, the majority of which is mineral material and 4–12% of which is organic matter (Haven and Morales-Alamo 1966). Some studies have shown that detritus-feeding invertebrates preferentially consume particles $10 \text{ }\mu\text{m}$ –1 mm. (Rhoads and Boyer 1982). Increased activity and processing/pelletization by benthic organisms can increase the stabilization of the sediment and organic matter (Rhoads and Boyer 1982).

The thickness of fine sediment accumulated landward of the constructed reefs was the lowest behind Reef 3 and the highest behind Reef 5 (Fig. 3a). We relate this to the condition of the reefs fronting those sections (Fig. 2). When we sampled these sediments, Reef 3 had 6.7% live oyster cover, while Reef 5 had 17% live oyster cover, and generally seemed to be taller and in better shape than Reef 3 and 4. This suggests that deposition is sensitive to reef health. In fact, the rapid accumulation that we observed in our study site may very well be more reflective of the early years of the reef, when live oyster cover was higher (Fig. 2).

Accumulation and storage of organic carbon

At our site, the organic matter content of the fine sediment layer was much higher than the coarse sediment layer and control (Fig. 4). This aligns with and expands upon previous studies that observed similarly elevated organic matter or total C content within constructed reef sites (Meyer and Townsend 2000; Kellogg et al. 2013; Fodrie et al. 2017; Feinman et al. 2018). Some have found even higher organic matter contents (8–10%) in the surface sediments adjacent to restored oyster reefs (Chambers et al. 2017) suggesting that the potential for organic matter storage may be even higher in some locations. It is worth noting that coarse reef sediment underlying the fine layer in our study has higher organic matter contents and higher silt and clay content than the control. The values are also higher than the pre-construction surface sediments measured at this site (Southwell et al. 2017.) This suggests downward translocation of fine particles and organic carbon into the coarse underlayer, perhaps by bioturbation. If this is true, our accumulation rates are underestimates, as they exclude the coarse layer.

Carbon accumulation rate

Our data demonstrate that the effect of oyster reefs on the carbon budget can extend well beyond the boundaries of the reefs themselves. The area sampled with an accumulation rate higher than $100 \text{ g C}/\text{m}^2/\text{yr}$ was 90 m^2 , which is more than two times as large as the area of associated oyster reefs and the gaps between them, 40 m^2 ($1.5 \text{ m} \times 27 \text{ m}$, Fig. 5). The overall carbon accumulation rate in the treatment area was $131 \text{ g C}/\text{m}^2/\text{yr}$ (Fig. 5). It is comparable to the average rates reported for salt marshes, mangroves and seagrasses, and it considerably exceeds the rates reported for terrestrial forest ecosystems (McLeod et al. 2011). Unlike those systems, our study site does not have high rates of autochthonous production from vegetation in situ; the organic carbon in this study is likely a mix of allochthonous inputs. Nevertheless, filtration of phytoplankton and deposition of oyster feces and pseudofeces may provide a mechanism for sequestration of some new carbon (Newell et al. 2005; Chambers et al. 2017). Furthermore, the rapid burial of organic-rich sediments protects this organic matter from photolysis and oxygen, which might otherwise lead to release and recycling (Hartnett et al. 1998; Mayer et al. 2006; Kieber et al. 2006; Southwell et al. 2011). Thus, the high rates of carbon accumulation are meaningful in the context of carbon cycling and suggest that the sediments adjacent to oyster reefs could be important carbon sinks.

Although other studies of deposition that quantify deposition *within* oyster reefs may not be directly comparable to our work, they do provide some context. Reported

depositional rates for subtidal oyster reefs range from 26.9–115 g C/m²/yr (Fodrie et al. 2017; Westbrook et al. 2019). Westbrook et al. 2019 also found that shallow reefs (< 1 m depth) generally had higher organic matter contents than deep water reefs (> 1 m depth), and those adjacent to salt marshes showed higher rates of C burial as well. Based on their definition, the reefs sampled in this study would be shallow water reefs, and they are adjacent to a salt marsh, so depth and surrounding nearby ecosystems may play a role in the magnitude of carbon trapping potential of oyster reefs. Furthermore, this oyster reef was designed as a breakwater, so it is not surprising that it exhibits higher deposition compared to natural oyster reefs and/or constructed reefs with different configurations.

Previous studies of living shoreline construction indicate that carbon sequestration is highest in the early stages of the project (Davis et al. 2015). Similarly, it is unlikely that such high sedimentation rates at our site could persist over the long term; the sediment accumulating behind the reef would eventually raise the level of the sediment surface and diminish the protection from wave energy. At some point, the sediment deposition would therefore be controlled by the vertical growth rate of the oysters. Our site is especially unlikely to maintain these sedimentation rates, given the decline in live oyster cover over time. That fate of the carbon already deposited is also uncertain. Given the negative trend of the live oyster cover over time, it is possible that the vertical structure that facilitated sediment deposition may break down, rendering the sediment susceptible to erosion.

It is not clear why live oyster cover declined. Initially, live oyster cover was much higher than on natural reefs in the area, possibly because there was no other structure available in nearby areas of this shoreline. This was followed by a reduction in cover potentially due to overcrowding (Fig. 2). At 24 months, there was additional recruitment observed, followed by a downward trend. By 48 months, the plastic mesh bags began to start breaking down, and the reefs began falling apart. In a high energy environment, where boat wake or wave energy is high, plastic mesh oyster bags may not be an effective way to build sustainable constructed oyster reefs (Chowdhury et al. 2019).

Rodriguez et al. (2014) showed that oysters in newly established reefs can grow at an astonishing 11.5 cm/yr, but that reef height, in turn, becomes constrained by sea level in mature reefs. Therefore, in some sense, the carbon and sediment trapping potential of reefs seems limited. However, there is much still to learn about the longer-term interactions between oyster reefs, sediments, and adjacent salt marshes, particularly with regard to carbon storage in sediments. For example, a marsh fronted by an oyster reef sill or breakwater may show greater accretion or decreased erosion (Gittman et al. 2016; Smith et al. 2018; Chowdhury et al. 2019). Restored or constructed oyster reefs have been

shown to reduce erosion of salt marsh edges as well or better than natural oyster reefs, showing that they contribute to shoreline stabilization (Stricklin et al. 2010; Ridge et al. 2017) while others have shown that they may only be effective under certain conditions (La Peyre et al. 2017; de Paiva et al. 2018). Nonetheless, if restored or constructed oyster beds can protect salt marsh sediments, they will protect the carbon stored within that ecosystem as well, improving the carbon sequestration of the entire coastline (Ridge et al. 2017).

There are three assumptions in our approach that may affect the calculated value of organic carbon deposition in our study. If those assumptions are false, they would lead us to underestimate the carbon deposition rate. First, we assume that only the finer, upper layer of sediment in the treatment site contains post-reef deposition; the carbon content of the coarse lower layer is assumed to pre-date the reef. However, as discussed above, our results suggest potential translocation of fine particles and carbon to the lower coarse layer. The second assumption is that the thickness of the post-reef sediment in the control area is equal to that of the treatment area. This assumption leads us to subtract the carbon content of the control sediment within an equivalent depth. This assumption is almost certainly false, as the sediment surface is visibly raised behind the oyster reefs, and not in the control. Without subtracting the control, our carbon deposition rate would be 170 g C/m²/yr. The third assumption is that the oyster shell in our study area was grown in situ, and must therefore be accounted for as a carbon source. In reality, much of that shell was likely derived from the bags of cultch; the calcification of that shell, and the carbon fluxes resulting from that calcification, did not result from the installation of the constructed reef. The shell was collected from restaurants; therefore, if the reef had not been built, the shell would have simply been buried in a landfill instead of in the mud. Therefore, the inclusion of this shell (which represents a carbon source upon calcification) may cause a further underestimation of the real value. We made these assumptions in order to render our calculation conservative, but it should be noted that the real value is likely to be higher.

Conclusion

Oyster reefs are ecosystems at risk and with their wide variety of ecosystem services, they are an ecosystem worthy of protection and restoration. With restoration or construction, biogeochemical properties can respond quickly, including carbon accumulation in as little as one year after construction (Chambers et al. 2017). Our study shows that oyster reef construction alters the surrounding sedimentary system in ways that dramatically enhance carbon accumulation over a surprisingly large area in the first few years

after construction. Areal accumulation rates are higher than those of terrestrial ecosystems, and comparable to the rates reported for other coastal ecosystems (McLeod et al. 2011 and Fodrie et al. 2017). Constructed oyster reefs can also reduce the erosion rates of nearby salt marshes, protecting the carbon there, as well (Ridge et al. 2017). Thus, the construction of a relatively small area of oyster reef can have a relatively large impact on the carbon within the whole system. However, the persistence of that carbon is likely dependent on the stability of the constructed reefs.

Author contributions JV and MS designed the study, analysed the data, and wrote the manuscript, ND and PM collected and analysed live oyster cover data, and provided feedback on the manuscript, JJ, CB, CH, and AK helped with field work, lab work, data analysis, and literature review.

Data availability Raw data will be provided.

Declarations

Conflicts of interest The authors do not have any conflicts of interest to disclose.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Beck MW, Brumbaugh RD, Airolidi L, Carranza A, Coen LD, Crawford C, Defeo O, Edgar GJ, Hancock B, Kay MC, Lenihan HS, Luckenbach MW, Toropova CL, Zhang G, Guo X (2011) Oyster Reefs at Risk and Recommendations for Conservation. Restoration, and Management, *BioScience* 61(2):107–116
- Canadell JG, Raupach MR (2008) Managing forests for climate change mitigation. *Science* 320:1456–1457
- Chambers LG, Gaspar SA, Pilato CJ, Steinmuller HE, McCarthy KJ, Sacks PE, Walters LJ (2017) How Well Do Restored Intertidal Oyster Reefs Support Key Biogeochemical Properties in a Coastal Lagoon? *Estuaries Coasts* 41(3):784–799
- Chowdhury MSN, Walles B, Sharifuzzaman SM, Hossain MS, Ysebaert T, Smaal AC (2019) Oyster breakwater reefs promote adjacent mudflat stability and salt marsh growth in a monsoon dominated subtropical coast. *Sci Rep* 9(1):8549
- Curran, CA, Chappell WS, Deaton A (2010) Developing alternative shoreline armoring strategies: The living shoreline approach in North Carolina, in Shipman H, Dethier M, Gelfenbaum G, Fresh KL, and Dinicola RS, eds. (2010) Puget Sound Shorelines and the Impacts of Armoring—Proceedings of a State of the Science Workshop, May 2009: U.S. Geological Survey
- Davis JL, Curran CA, Brien CO, Raffenburg C and Davis A (2015) Living shorelines: coastal resilience with a blue carbon benefit. *PloS One* 10(11), p.e0142595.
- de Paiva JN, Walles B, Ysebaert T, Bouma TJ (2018) Understanding the conditionality of ecosystem services: The effect of tidal flat morphology and oyster reef characteristics on sediment stabilization by oyster reefs. *Ecol Eng* 112:89–95
- Feinman SG, Farah YR, Bauer JM, Bowen JL (2018) The Influence of Oyster Farming on Sediment Bacterial Communities. *Estuaries Coasts* 41(3):800–814
- Fodrie FJ, Rodriguez AB, Gittman RK, Grabowski JH, Lindquist NL, Peterson CH, Piehler MF, Ridge JT (2017) Oyster reefs as carbon sources and sinks. *Proc R Soc B* 284:20170891. <https://doi.org/10.1098/rspb.2017.0891>
- Gittman RK, Peterson CH, Curran CA, Joel Fodrie F, Piehler MF, Bruno JF (2016) Living shorelines can enhance the nursery role of threatened estuarine habitats. *Ecol Appl* 26(1):249–263
- Grabowski JH, Brumbaugh RD, Conrad RF, Keeler AG, Opaluch JJ, Peterson CH, Piehler MF, Powers SP, Smyth AR (2012) Economic Valuation of Ecosystem Services Provided by Oyster Reefs. *Bioscience* 62(10):900–909. <https://doi.org/10.1525/bio.2012.62.10.10>
- Haven DS, Morales-Alamo R (1966) Aspects of Biodeposition by Oysters and Other Invertebrate Filter Feeders. *Limnol Oceanogr* 11(4):487–498
- Hartnett HE, Keil RG, Hedges JJ, Devok AH (1998) Influence of oxygen exposure time on organic carbon preservation in continental margin sediments. *Nature* 391:572–575
- Hedges JJ, Stern JH (1984) Carbon and nitrogen determinations of carbonate-containing solids 1. *Limnol Oceanogr* 29(3):657–663
- Herbert D, Astrom E, Bersosa AC, Batzer A, McGovern P, Angelini C, Wasman S, Dix N, Sheremet A (2018) Mitigating Erosional Effects Induced by Boat Wakes with Living Shorelines. *Sustainability* 10(2):436
- Keil RG, Tsamakis E, Bor Fuh C, Calvin Giddings J, Hedges JJ (1994) Mineralogical and textural controls on the organic composition of coastal marine sediments: hydrodynamic separation using SPLITT-fractionation. *Geochim Cosmochim Acta* 58(2):879–893
- Kellogg ML, Cornwell JC, Owens MS, Paynter KT (2013) Denitrification and nutrient assimilation on a restored oyster reef. *Marine Ecology Press Series* 480:1–19. <https://doi.org/10.3354/meps10331>
- Kettler TA, Doran JW, Gilbert TL (2001) Simplified Method for Particle Size Determination to Accompany Soil-Quality Analyses. *Soil Sci Soc Am J* 65:849–852
- Kibler KM, Kitsikoudis V, Donnelly M, Spiering DW, Walters L (2019) Flow-Vegetation Interaction in a Living Shoreline Restoration and Potential Effect to Mangrove Recruitment. *Sustainability* 11(11):3215
- Kieber RJ, Whitehead RF, Skrabal SA (2006) Photochemical production of dissolved organic carbon from resuspended sediments. *Limnol Oceanogr* 51(5):2187–2195
- Kristmanson DD, Wildish D (1997) Benthic Suspension Feeders and Flow. Cambridge University Press, Cambridge, UK
- La Peyre MK, Miller L, Miller S, Melancon E (2017) Comparison of oyster populations, shoreline protection service, and site characteristics at seven created fringing reefs in Louisiana. In *Living Shorelines: The science and management of nature based coastal protection*, 363–82. Boca Raton, FL: CRC Press, Taylor & Francis
- McLeod E, Chmura GL, Bouillon S, Salm R, Björk M, Duarte CM, Lovelock CE, Schlesinger WH, Silliman BR (2011) A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front Ecol Environ* 9(10):552–560. <https://doi.org/10.1890/110004>

- Malhi Y, Aragao L, Metcalfe DB, Paiva R, Quesada CA, Almeida S, Anderson L, Brando P, Chambers JQ, DaCosta ACL, Huttyra LR, Oliveira P, Patino S, Pyle EH, Robertson AL, Teixeira LM (2009) Comprehensive assessment of carbon productivity, allocation, and storage in three Amazonian Forests. *Glob Change Biol* 15(5):1255–1274
- Marcum P, Dix N, Monroe M (2018) Guana Tolomato Matanzas National Estuarine Research Reserve 2014–2016 Oyster Monitoring Summary. Guana Tolomato Matanzas National Research Reserve Technical Report
- Mayer LM, Schick LL, Skorko K, Boss E (2006) Photodissolution of particulate organic matter from sediments. *Limnol Oceanogr* 51(2):1064–1071
- Meyer D, Townsend E (2000) Faunal Utilization of Created Intertidal Eastern Oyster (*Crassostrea virginica*) Reefs in the Southeastern United States. *Estuaries* 23(1):34–45
- Nelson KA, Leonard LA, Posey MH, Alphin TD, Mallin MA (2004) Using transplanted oyster (*Crassostrea virginica*) beds to improve water quality in small tidal creeks: a pilot study. *J Exp Mar Biol Ecol* 298:347–368
- Newell RIE, Fisher TR, Holyoke RR, Cornwell JC (2005) Influence of Easter Oysters on Nitrogen and Phosphorus Regeneration in Chesapeake Bay, USA. In *The Comparative Roles of Suspension Feeders in Ecosystems*. 93–120. Springer
- Rhoads DC, Boyer LF (1982) The effects of marine benthos on physical properties of sediments. *Animal-Sediment Relations*. Springer, Boston, MA, pp 3–52
- Ridge JT, Rodriguez AB, Fodrie FJ (2017) Salt Marsh and Fringing Oyster Reef Transgression in a Shallow Temperate Estuary: Implications for Restoration, Conservation, and Blue Carbon. *Estuaries Coasts* 40:1013–1027
- Rodriguez AB, Fodrie FJ, Ridge JT, Lindquist NL, Theuerkauf EJ, Coleman SE, Grabowski JH, Brodeur MC, Gittman RK, Keller DA, Kenworthy MD (2014) Oyster reefs can outpace sea-level rise. *Nat Clim Chang* 4(6):493
- Sabine CL, Feely RA, Gruber N et al (2004) The oceanic sink for anthropogenic CO₂. *Science* 305:367–371
- Smith CS, Puckett B, Gittman RK, Peterson CH (2018) Living shorelines enhanced the resilience of saltmarshes to Hurricane Matthew (2016). *Ecol Appl* 28(4):871–877
- Southwell MW, Veenstra JJ, Adams CD, Scarlett EV, Payne KB (2017) Changes in Sediment Characteristics upon Oyster Reef Restoration, NE Florida, USA. *J Coast Zone Manag* 20(442):2
- Southwell MW, Mead RN, Luquire CM, Barbera A, Avery GB, Kieber RJ, Skrabal SA (2011) Influence of organic matter source and diagenetic state on photochemical release of dissolved organic matter and nutrients from resuspendable estuarine sediments. *Mar Chem* 126(1–4):114–119
- Stricklin AG, Peterson MS, Lopez JD, May CA, Mohrman CF, Woodrey MS (2010) Do Small, Patchy, Constructed Intertidal Oyster Reefs Reduce Salt Marsh Erosion As Well As Natural Reefs? *Gulf and Caribbean Research* 22(1):21–27
- Wang Q, Li Y, Wang Y (2011) Optimizing the weight loss-on-ignition methodology to quantify organic and carbonate carbon of sediments from diverse sources. *Environ Monit Assess* 174(1–4):241–257
- Westbrook P, Heffner L, La Peyre MK (2019) Measuring carbon and nitrogen bioassimilation, burial, and denitrification contributions of oyster reefs in Gulf coast estuaries. *Mar Biol* 166:4. <https://doi.org/10.1007/s00227-018-3449-1>
- Wiberg PL, Taube SR, Ferguson AE, Kremer MR, Reidenbach MA (2019) Wave Attenuation by Oyster Reefs in Shallow Coastal Bays. *Estuaries Coasts* 42:331–347
- Wilber DH, Hadley NH, Clarke DG (2012) Resident Crab Associations with Sedimentation on Restored Intertidal Oyster Reefs in South Carolina and the Implications for Secondary Consumers. *North Am J Fish Manag* 32(5):838–847

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.