Seagrass Recovery Following Marine Heat Wave Influences Sediment Carbon Stocks

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Worldwide, seagrass meadows accumulate significant stocks of organic carbon (C), known as "blue" carbon, which can remain buried for decades to centuries. However, when seagrass meadows are disturbed, these C stocks may be remineralized, leading to significant CO_2 emissions. Increasing ocean temperatures, and increasing frequency and severity of heat waves, threaten seagrass meadows and their sediment blue C. To date, no study has directly measured the impact of seagrass declines from high temperatures on sediment C stocks. Here, we use a long-term record of sediment C stocks from a 7-km^2, restored eelgrass (*Zostera marina*) meadow to show that seagrass dieback following a single marine heat wave (MHW) led to significant losses of sediment C. Patterns of sediment C loss and re-accumulation lagged patterns of seagrass recovery. Sediment C losses were concentrated within the central area of the meadow, where sites experienced extreme shoot density declines of 90% during the MHW and net losses of 20% of sediment C over the following 3 years. However, this effect was not uniform; outer meadow sites showed little evidence of shoot declines during the MHW and had net increases of 60% of sediment C over the following 3 years. Overall, sites with higher seagrass recovery maintained 1.7x as much C compared to sites with lower recovery. Our study demonstrates that while seagrass blue C is vulnerable to MHWs, localization of seagrass loss can prevent meadow-wide C losses. Long-term (decadal and beyond) stability of seagrass blue C depends on seagrass resilience to short-term disturbance events.

Keywords: *Zostera marina*, eelgrass, disturbance, marine heat wave, blue carbon, restoration, resilience, climate change

INTRODUCTION

Seagrass meadows, salt marshes, and mangrove forests have been recognized as important sinks for carbon (C) on a global scale (Mcleod et al., 2011). This "blue" C accumulates in the anoxic sediments of these coastal wetlands; globally, blue C ecosystems store between 0.08–0.22 Pg C y^{-1}, approximately half of the total C buried in ocean sediments annually (Duarte et al., 2013). Anoxic sediment conditions preserve organic carbon from decomposition over long time-scales, from decades to centuries or even millennia (Fourqurean et al., 2012; Howard et al., 2017). However, disturbance and loss of blue C ecosystems lead to carbon emissions; not only is C stored

in the biomass of vegetation lost, but the sediment can be resuspended and organic C can be exposed to oxic conditions in the water column and/or atmosphere, leading to rapid oxidation and remineralization (Pendleton et al., 2012). In seagrass meadows, the loss of seagrass shoots can result in the loss of blue C deposits that may have accumulated over previous decades (Marbà et al., 2015).

The magnitude of seagrass blue C loss following disturbance remains uncertain. Estimates to date generally rely on simple assumptions regarding the proportion of the C stock that will be remineralized (Arias-Ortiz et al., 2018; Ewers Lewis et al., 2018). However, numerous processes will affect the vulnerability of sediment C following disturbance and vegetation loss, including sediment deposition and erosion, redox oscillations from physical and biological drivers, and plant-microbe interactions (Spivak et al., 2019). Importantly, these interacting processes occur over varying spatial and temporal scales and impact not only the preservation of existing C stocks but also the continued accumulation of new organic C inputs (Belshe et al., 2017). Greater understanding of the net effect of these processes is needed to understand the stability of seagrass blue C stocks following different kinds of disturbance. In particular, studies need to account for spatial and temporal variation in sediment C loss and recovery. Studies with repeated measurements of blue C stock before and after a disturbance event, across plot (m^2) to meadow (km^2) spatial scales, are needed to provide empirical data on blue C stability.

Seagrass resilience will influence the net effect of disturbance on blue C. We define ecosystem resilience as "the capacity to undergo disturbance without permanent loss of key ecological structures and functions" [O'Brien et al. (2018) after Holling (1973)], encompassing both the resistance to change during disturbance and the ability to recover after disturbance (Levin and Lubchenco, 2008; Standish et al., 2014). Trajectories of seagrass degradation and recovery through time represent the cumulative effect of seagrass processes that occur across spatial and temporal scales and that respond to overlapping biotic and abiotic drivers (O'Brien et al., 2018). Long-term loss of seagrass presence after disturbance has been shown to destabilize blue C stocks, leading to release of previously buried carbon (Macreadie et al., 2015; Salinas et al., 2020). However, the impact of seagrass recovery on blue C persistence remains unexplored. Seagrass meadows have emerged as priorities for marine conservation and restoration (United Nations Environment Programme [UNEP], 2020), and greater understanding of how recovery trajectories after disturbance influence blue C is needed to inform these conservation efforts.

Like other blue C ecosystems, seagrass meadows have declined in many areas of the world; estimates from a decade ago were that roughly a third of the historical extent of seagrass meadows worldwide had already been lost (Waycott et al., 2009). The magnitude of C emissions due to loss of seagrass area has been estimated at 0.01–0.09 Pg C y^{-1} (Pendleton et al., 2012). Preservation of existing meadows limits these emissions, and restoration of degraded or lost meadows can reestablish C accumulation rates on par with natural systems (Greiner et al., 2013; Marbà et al., 2015). Climate change mitigation through

blue C accumulation is one motivation for seagrass restoration efforts, and methodologies now exist to calculate and award carbon-offset credits from seagrass restoration projects (Emmer et al., 2015; Needelman et al., 2018). However, restoration of degraded meadows typically takes at least a decade (Greening and Janicki, 2006; McGlathery et al., 2012), and restored blue C stocks must persist for a period of 30 years to be eligible for carbon-offset credits (Oreska et al., 2020). Over the decadal time scales of seagrass restoration, short-term disturbance events threaten the persistence of slowly accumulating sediment C, potentially limiting the total blue C benefit from restoration. Natural meadows are also vulnerable to short-term disturbance. In particular, disturbance from high temperatures, driven more and more frequently by climate change, poses a serious threat to seagrass meadows (Orth et al., 2006; Moore and Jarvis, 2008; Thomson et al., 2015).

Rising ocean temperatures alter seagrass growth and reproduction, and particularly threaten species near the thermal boundary of their geographic range (Fraser et al., 2014; Short et al., 2016; Berger et al., 2020). Rising baseline temperatures are exacerbated by marine heat waves (MHWs), defined following Hobday et al. (2016) as periods of at least five consecutive days when temperatures exceed a climatological threshold. Recent work has shown that MHWs lead to declines in seagrass and other coastal foundation species (Lefcheck et al., 2017; Smale et al., 2019); periods of high temperatures that do not meet the MHW definition can also cause seagrass stress and decline (Moore and Jarvis, 2008). MHWs are increasing in frequency and duration (Oliver et al., 2018, 2019), increasing the risk of rapid, large-scale loss of seagrass meadows that could trigger massive losses of blue C from seagrass sediments. Previous studies have shown catastrophic dieback, with mortality of as much as 90% of shoots, following extreme high temperatures in Australian and Mediterranean seagrass meadows (Marbà and Duarte, 2009; Thomson et al., 2015; Kendrick et al., 2019). In Shark Bay, Australia, researchers recently modeled the C emissions from the sediment following a temperature-induced seagrass dieback by assuming between 10 and 50% of sediment C was exposed to oxic conditions following the dieback; their model predicted emissions of 0.5–2.5 Tg C from a 13,000 km^2 area over 3 years after the dieback (Arias-Ortiz et al., 2018). However, no study to date has empirically measured seagrass sediment C stocks before and after a temperature-induced dieback, leaving uncertainty about the spatial and temporal effects of temperature-induced seagrass loss and subsequent recovery on sediment C stocks.

Here, we address this knowledge gap using long-term data collected at the Virginia Coast Reserve Long-Term Ecological Research site (VCR). We examined sediment C storage in a restored *Zostera marina* (eelgrass) meadow that experienced a severe dieback following unusually high summer temperatures in 2015 (Berger et al., 2020). We combined long-term monitoring of seagrass and sediment metrics with intensive sediment sampling before and after the dieback to determine how losses of seagrass shoots affected sediment C stocks from the plot scale (m^2) to the meadow scale (km^2). As part of a long-term (18 years) study, we continued measurements for 3 years after the initial

loss of shoots to understand the patterns in seagrass C loss and re-accumulation over time.

MATERIALS AND METHODS

Site Description and Study Design

South Bay, VA, United States, contains one of four eelgrass meadows restored by seeding in the shallow bays of the Virginia Coast Reserve Long Term Ecological Research site[1]. The depth in the coastal bays ranges from 0.8–1.6 m below mean sea level and the tidal range is 1.2 m (Fagherazzi and Wiberg, 2009). Sediments in South Bay are dominated by fine sands and dry bulk density is 1.4 g cm^{-3} (McGlathery et al., 2012). Seagrass plots in South Bay were seeded in 2001; the original 0.4 ha plots have since expanded into a continuous meadow, approximately 20 km^2 by 2018 (Orth et al., 2020). Our monitoring efforts targeted the area of the original restoration, a region of the larger meadow that was approximately 7 km^2 by 2015 (Oreska et al., 2017; **Figure 1**). This area has been monitored annually since 2007 at six of the original 0.4 ha restoration plots, located in the center of the meadow; these plots reached a stable, mature-meadow density of 400–600 shoots m^{-2} within 6–8 years after seeding (McGlathery et al., 2012). We labeled these long-term plots as "inner" meadow plots, and we leveraged the long-term data set in order to compare measurements of seagrass shoot density and sediment C stock before and after the MHW disturbance. In addition to the six inner plots, we measured shoot densities and sediment C stocks at nine additional sites, located between the inner plots and the meadow edge in areas that were colonized as the meadow expanded from the original seeded plots. We labeled these younger meadow sites as "outer" meadow plots (see **Figure 1**). The configuration of outer and inner meadow plots enabled us to understand possible variation in the impact of the MHW on sediment C stocks in the 7-km^2 meadow region. Each plot was at least 200 m from the nearest neighboring site. The full set of nine outer plots was sampled in 2013; however, in the years after the MHW, subsets of four (2016) or six (2017–2018) outer plots were sampled.

Marine Heat Wave

During June 2015, the South Bay meadow experienced high temperatures, followed by loss of seagrass shoots at the inner meadow sites (Berger et al., 2020). Following Hobday et al. (2016), we defined a marine heat wave as when water temperatures exceed the 90th percentile relative to local, long-term climatology for five consecutive days. We analyzed a long-term (24 years) record of hourly water temperature from a NOAA tide station located in Wachapreague, VA, United States, approximately 38 km from the South Bay meadow, in order to confirm that the June 2015 water temperatures qualified as a MHW. We also analyzed sea surface temperatures (SSTs) acquired from AVHRR satellite imagery of the Chesapeake Bay region[2] to show patterns of SST associated with heat wave and non-heat wave conditions
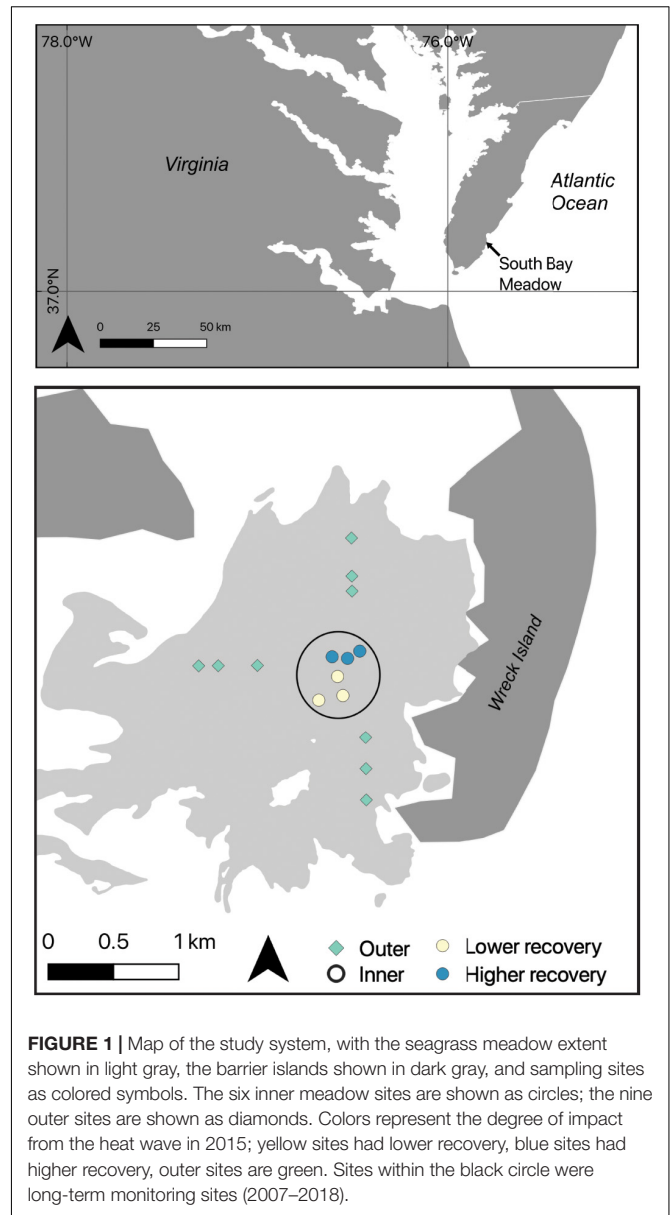
FIGURE 1 | Map of the study system, with the seagrass meadow extent shown in light gray, the barrier islands shown in dark gray, and sampling sites as colored symbols. The six inner meadow sites are shown as circles; the nine outer sites are shown as diamonds. Colors represent the degree of impact from the heat wave in 2015; yellow sites had lower recovery, blue sites had higher recovery, outer sites are green. Sites within the black circle were long-term monitoring sites (2007–2018).

throughout the VCR. Satellite-derived SST images, available up to nine times per day, had a resolution of 1 km^2 and were masked to eliminate cloudy regions and locations where the data did not meet data quality criteria. Details of the processing of the satellite data are available from (see text footnote 2). We used the available SST imagery from June 2015 to contrast MHW and non-MHW conditions during the observed seagrass die-off.

Seagrass Disturbance and Recovery

We used a combination of aerial imagery and field surveys to assess the effect of the June 2015 MHW on the seagrass meadow. Aerial images of the meadow were collected by researchers at the Virginia Institute of Marine Science from 2015–2018 as part of their annual Submerged Aquatic Vegetation survey[3]. Details of

the image collection and processing are available elsewhere (Orth et al., 2012). We report seagrass shoot density data from 2014 (pre-dieback) to 2018 (post-dieback) that are part of a longer monitoring effort from 2008–2018. Seagrass shoot densities were measured at the six inner meadow sites during early summer (late June to early July). To measure shoot densities, we laid a 50 m transect from the center of the site and counted shoots within 10 evenly spaced 0.25 m^2 quadrats. In the nine outer meadow sites, we counted shoot densities in 10 haphazardly distributed 0.25 m^2 quadrats in 2014, as part of a related study (Oreska et al., 2017). Shoot densities were not measured at the outer sites in 2015 or 2016. In 2017 and 2018, we measured shoot densities at a subset of six outer sites, following the same protocol as for the six inner meadow sites. At the inner meadow sites, we quantified seagrass shoot recovery each year after the disturbance by calculating the annual shoot density as a percentage of the pre-disturbance (2014) shoot density.

Sediment C Stocks

We measured sediment C stocks in the upper layers of sediment (0–5 cm depth) annually from 2013–2018 at the inner meadow sites, consistent with the long-term study, to understand how seagrass disturbance and recovery affected the sediment stock in the upper sediments. Previous work has shown that seagrass restoration in South Bay had enhanced sediment C stocks to a depth of 12 cm by 2014; however, the bulk of the effect occurs between the sediment surface and 6 cm depth (Greiner et al., 2013; Oreska et al., 2017). At each of the six inner meadow sites, we collected five replicate 5-cm deep cores using a cut-off syringe corer (inner diameter 2.5 cm) at 10 m intervals along the transects used for shoot densities. A second set of 5-cm deep sediment cores was also collected for bulk density analysis. In order to understand how C loss differed across the 7-km^2 meadow, we used data from comparable sediment cores collected at the outer sites; all nine outer sites were sampled in 2013 as part of a related study (Oreska et al., 2017), and in later years, subsets of four (2016) or six (2017–2018) outer plots were sampled. We compared areal C stocks in g C per m^2 over time.

We collected additional sediment samples in 2017 and 2018 to further investigate the impact of seagrass loss and recovery on sediment C stocks. After the widespread loss of shoots in 2015, seagrass recovery was patchy at the plot (m^2) scale, with large patches of bare sediment persisting through 2018 in some areas. In 2017, we assessed small-scale (m^2) patchiness at the six inner meadow sites; at each site, we collected five replicate 5-cm deep sediment cores from bare patches, and five cores from adjacent seagrass patches. We compared areal sediment stocks in g C per m^2 in bare and seagrass patches by integrating C content over the 5 cm core depth. To determine the extent of C loss deeper in the sediment profile, in 2018 we collected four replicate 10-cm deep sediment cores at each of the six inner meadow sites and segmented the cores into three depth increments, 0–2.5, 2.5–5, and 5–10 cm. We compared bulk C content in mg C per cm^3 of sediment across the three depth intervals.

All sediment samples were transported on ice to the laboratory and were frozen immediately. Bulk density analysis was conducted by sub-sampling thawed cores; three cm^3 of

sediment was weighed and then dried to a constant weight. Bulk densities were calculated from the wet and dry weight and sample volume. For the sediment C analyses, frozen samples were defrosted and dried to constant mass at 60°C. Visible fragments of rhizomes, roots, and shells were removed and the samples were homogenized and stored in glass scintillation vials. Carbon content was measured on 25 mg subsamples using a Carlo Erba Elemental Analyzer with a 1,020°C combustion tube and 650°C reduction tube, and helium as a carrier gas. Bulk C stocks in the sediment were calculated by multiplying C content (mg C per mg sediment) by the sediment bulk density to calculate C stock in g C per cm^3. Stocks were converted to g C per m^2 by integrating over the 5 cm depth of the core. These sediments are siliciclastic and contain negligible carbonate (Saderne et al., 2019), so total C is a suitable measure of organic C in this system.

Statistical Analysis

The initial seagrass shoot recovery, calculated as the 2016 shoot density as a percentage of the pre-disturbance 2014 shoot density, varied between the inner meadow sites. Three out of six sites had initial shoot recovery >49% and were classified as "higher" recovery sites. The remaining three sites had initial shoot recovery <35% and were classified as "lower" recovery sites. We compared recovery over time between the higher and lower recovery sites using linear mixed models (LMMs, Zuur et al., 2009) with shoot density modeled as a function of two fixed effects, the years since disturbance and the recovery status, with site as a random effect.

To assess the impact of seagrass loss and recovery on sediment C stocks, we used LMMs to analyze the long-term record of upper sediment C stock (g C m^{-2}) from the six inner meadow sites. We modeled upper sediment C stock through time as a function of year, including two pre-disturbance years (2013–2014), the year of the MHW (2015), and three post-disturbance years (2016–2018). Site was included as a random effect. During model selection, we determined that sediment C in the upper 5 cm did not vary through time based on recovery status (higher versus lower recovery sites); therefore, recovery status was not included in the final model.

We performed additional analyses to understand the effect of seagrass loss and recovery on sediment C in more detail. At the plot scale (m^2), we compared upper sediment C stocks (g C m^{-2}) in bare and seagrass patches in 2017 using a paired t-test; samples collected from bare and seagrass patches within the same sites were paired in order to account for site-level effects on C stock. To assess sediment C loss below 5 cm, we compared sediment C content (mg C cm^{-3}) from 0–10 cm depth between the higher and low recovery sites in 2018 with LMMs, with recovery status, sediment depth, and the interaction as fixed effects and site as a random effect. By using subdivided sediment cores, sediment C content from each successive, neighboring depth interval may have been correlated. However, including an auto-regressive (AR-1) correlation structure to account for this possible autocorrelation (Zuur et al., 2009) did not improve the model, based on a log-likelihood comparison of the model with and without the AR-1 structure ($L = 0.0008$, $df = 1$, and $p = 0.978$). We therefore did not include the AR-1 correlation structure in

the final model. Finally, to look at landscape-scale spatial patterns over time, we used LMMs comparing sediment C stocks (g C m^{-2}) at the inner meadow sites with stocks at the outer meadow sites over 4 years; location (inner/outer), sampling year (pre-disturbance: 2013; post-disturbance: 2016, 2017, and 2018) and the interaction between location and year were fixed effects and site was a random effect.

For all LMMs, we used the package *nlme* in R (Pinheiro et al., 2018; R Core Team, 2018). We assessed homogeneity and normality of residuals graphically, and we added heterogeneous covariance structures to models when necessary to achieve homoscedasticity. We used backward model selection based on Akaike Information Criterion (AIC) and we evaluated the significance of model terms with *F* tests. Final model results are shown in **Table 1**. We used the function *glht* from the package *multcomp* to compare effect levels using *post hoc* contrasts, with adjusted p-values to account for multiple comparisons (Hothorn et al., 2008). Differences were considered significant for $p < 0.05$; means are reported with $\pm$ SE, $n = 6$ except where noted otherwise.

RESULTS

Temperature Exposure

Analysis of temperature data from the NOAA station in Wachapreague showed that a marine heat wave occurred from 12–25 June 2015 (**Figure 2A**). The heat wave affected waters throughout the Virginia coastal bays, with SST of ∼28–30°C during the MHW days, compared to ∼23–24°C during the non-MHW days in June 2015 (**Figure 2B**). The satellite sea-surface temperature imagery shows that under both MHW and non-MHW conditions, water temperatures in the Atlantic Ocean, east of the barrier islands, were lower than temperatures in the sheltered bays (**Figure 3**). Where the seagrass dieback occurred in South Bay, there was a clear difference between average ocean and bay temperatures during both MHW and non-MHW conditions (**Figure 3D**). During the MHW, mean temperatures were 26.1°C at the Atlantic Ocean site and 27.6°C in the seagrass meadow. During non-MHW conditions, mean temperatures were 25.3°C in the Atlantic Ocean and 26.4°C in the seagrass meadow. Throughout June 2015, seagrass meadow waters were on average 1.1–1.5°C warmer than the Atlantic Ocean waters under both MHW and non-MHW conditions.
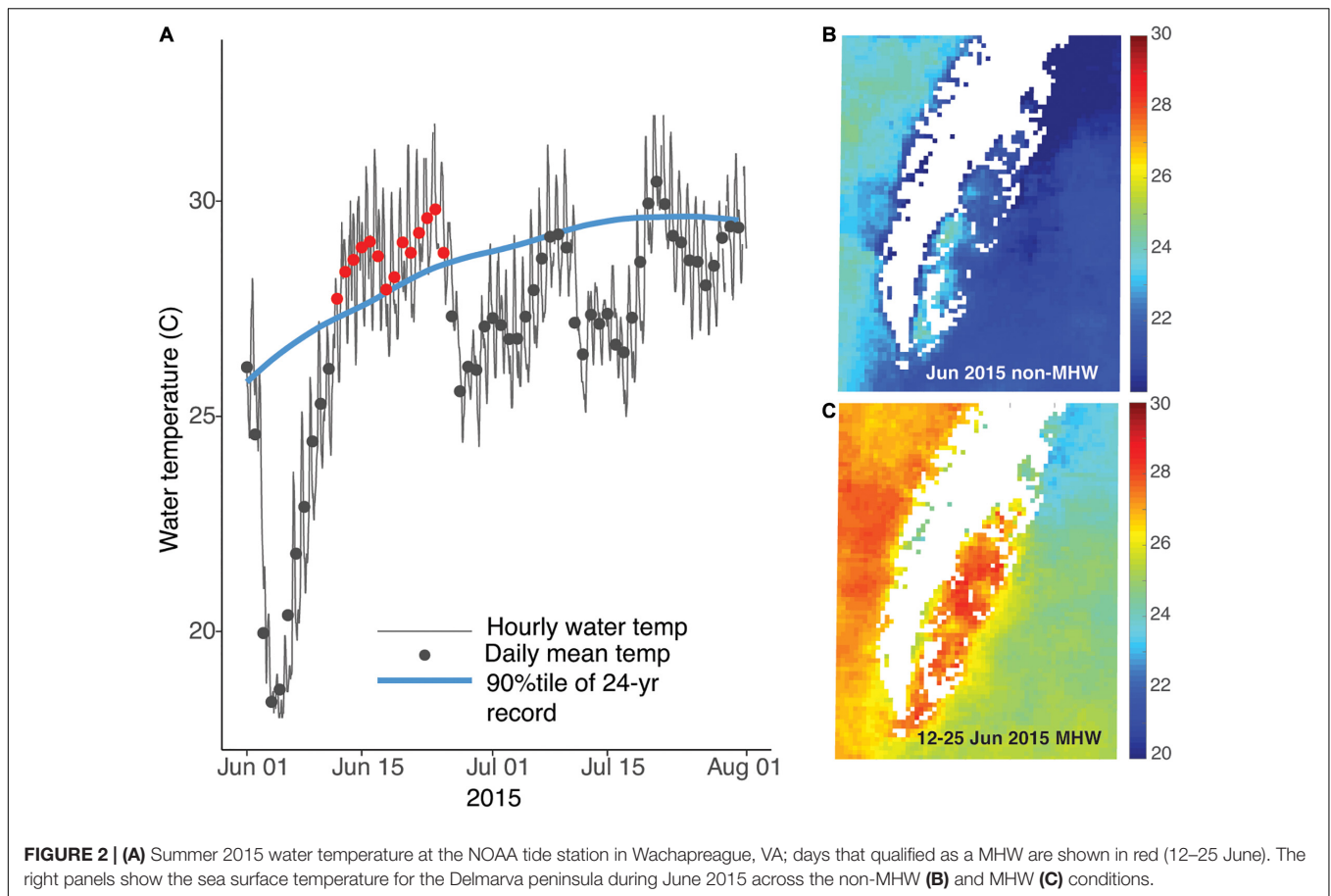
Seagrass Loss and Recovery

Images of the South Bay meadow acquired in May 2015 showed the healthy state of the meadow, weeks prior to the June 2015 dieback (**Figure 4A**). Aerial images of the meadow condition in July 2015, after the MHW, were not available. However, measurements of seagrass densities were conducted every 2 weeks from early June-early July at three of the inner sites in a related study (Aoki and McGlathery, 2018), and these measurements showed a rapid decline from 356 ($\pm$19, $n = 3$) shoots m^{-2} in early June 2015, before the MHW, to 151 ($\pm$11, $n = 3$) shoots m^{-2} in early July 2015, roughly 3 weeks after the MHW. Measurements of ecosystem metabolism, conducted using *in situ* aquatic eddy covariance at one inner site, also showed a significant decline in ecosystem respiration and gross primary production during this period, as well as a shift to net heterotrophy, indicating the substantial impact of the MHW and subsequent shoot density decline on the seagrass ecosystem (Berger et al., 2020). No aerial images were acquired in 2016; however, the 2017 images showed the unevenness of the recovery in the meadow 2 years after the initial dieback (**Figure 4B**). The central area of the meadow, where the inner sites were located, remained patchy in 2017, while areas further from the center did not have visible bare areas in 2017. By 2018, 3 years after the MHW, the patchiness was no longer visible in the aerial images, indicating recovery of the seagrass meadow in terms of canopy cover (**Figure 4C**).

Shoot density counts revealed site-specific patterns in shoot loss and recovery. Shoot losses were comparable at all six inner meadow sites, with mean shoot densities dropping from 599 ($\pm$20) shoots m^{-2} in July 2014 to 43 ($\pm$19) shoots m^{-2} in July 2015, just weeks after the MHW (**Figure 5**). Initial recovery varied by site; higher recovery sites had densities of 379 ($\pm$47, $n = 3$) shoots m^{-2} whereas low recovery sites had densities of 175 ($\pm$25, $n = 3$) shoots m^{-2} in 2016. However, shoot recovery converged somewhat over time, with densities of 503 ($\pm$16, $n = 3$) shoots m^{-2} at higher recovery sites compared to 406 ($\pm$44, $n = 3$) shoots m^{-2} at low recovery sites by 2018. Both recovery status and years since disturbance were significant effects in the model (**Table 1**). Shoot densities from the outer meadow sites were not included in the model, because densities were only available for 2014, 2017, and 2018. However, shoot densities were

TABLE 1 | Summary of model results for the spatial and temporal analyses of sediment C stocks.

Model	Explanatory variable	df	F	P
Seagrass recovery over time				
	Initial recovery status	1	14.48	**0.02**
	Years since disturbance	1	87.57	**<0.0001**
	Residual	17		
Upper C stock over time				
	Sample year	5	49.84	**<0.0001**
	Residual	25		
Depth profile of C stock				
	Initial recovery status	2	70.65	**0.0001**
	Sediment depth	1	0.66	0.42
	Recovery × depth	2	3.93	**0.04**
	Residual	15		
C stock at inner and outer sites over time				
	Location	1	1.13	0.30
	Year	3	8.68	**0.000**
	Location × year	3	14.60	**<0.0001**
	Residual	28		

Bold values indicate p < 0.05.

FIGURE 2 | (A) Summer 2015 water temperature at the NOAA tide station in Wachapreague, VA; days that qualified as a MHW are shown in red (12–25 June). The right panels show the sea surface temperature for the Delmarva peninsula during June 2015 across the non-MHW **(B)** and MHW **(C)** conditions.

comparable between the outer sites in 2018 and 2014 [mean densities of 580 ($\pm$59) shoots m^{-2} in 2018 compared to 542 ($\pm$29) shoots m^{-2} in 2014]. Without knowing the extent of seagrass loss at these sites in 2015, we cannot determine if the outer sites recovered faster or experienced less loss, but it is clear that the outer sites had robust shoot densities in 2018.

Loss of Upper Sediment C Stock

At the inner meadow sites, carbon stocks in the upper 5 cm of sediment varied significantly over time (**Table 1**). During the 2 years before disturbance, areal C stocks were constant in the restored meadow, at 399 ($\pm$29) g C m^{-2} in 2013 and 386 ($\pm$37) g C m^{-2} in 2014 [mean ($\pm$SE), **Figure 6A**, Tukey contrast, $p = 0.99$]. In 2015, sediment samples were collected approximately one month after the MHW; at this sampling point, the C stock had increased significantly to 571 [$\pm$27 g C m^{-2} (Tukey contrast, $p < 0.001$)]. However, by the following summer, the C stock declined substantially; C stock in 2016 was 303 ($\pm$19, $n = 6$) g C m^{-2}, significantly lower than the pre-disturbance value in 2013 (Tukey contrast, $p < 0.001$). The C stock declined to a minimum of 250 ($\pm$21, $n = 6$) g C m^{-2} in 2017 but began to re-accumulate, with a value of 317 ($\pm$16, $n = 6$) g C m^{-2} in 2018, 3 years after the dieback. The C stock 3 years after the dieback was significantly greater than the minimum in 2017 (Tukey contrast, $p = 0.040$), but remained significantly
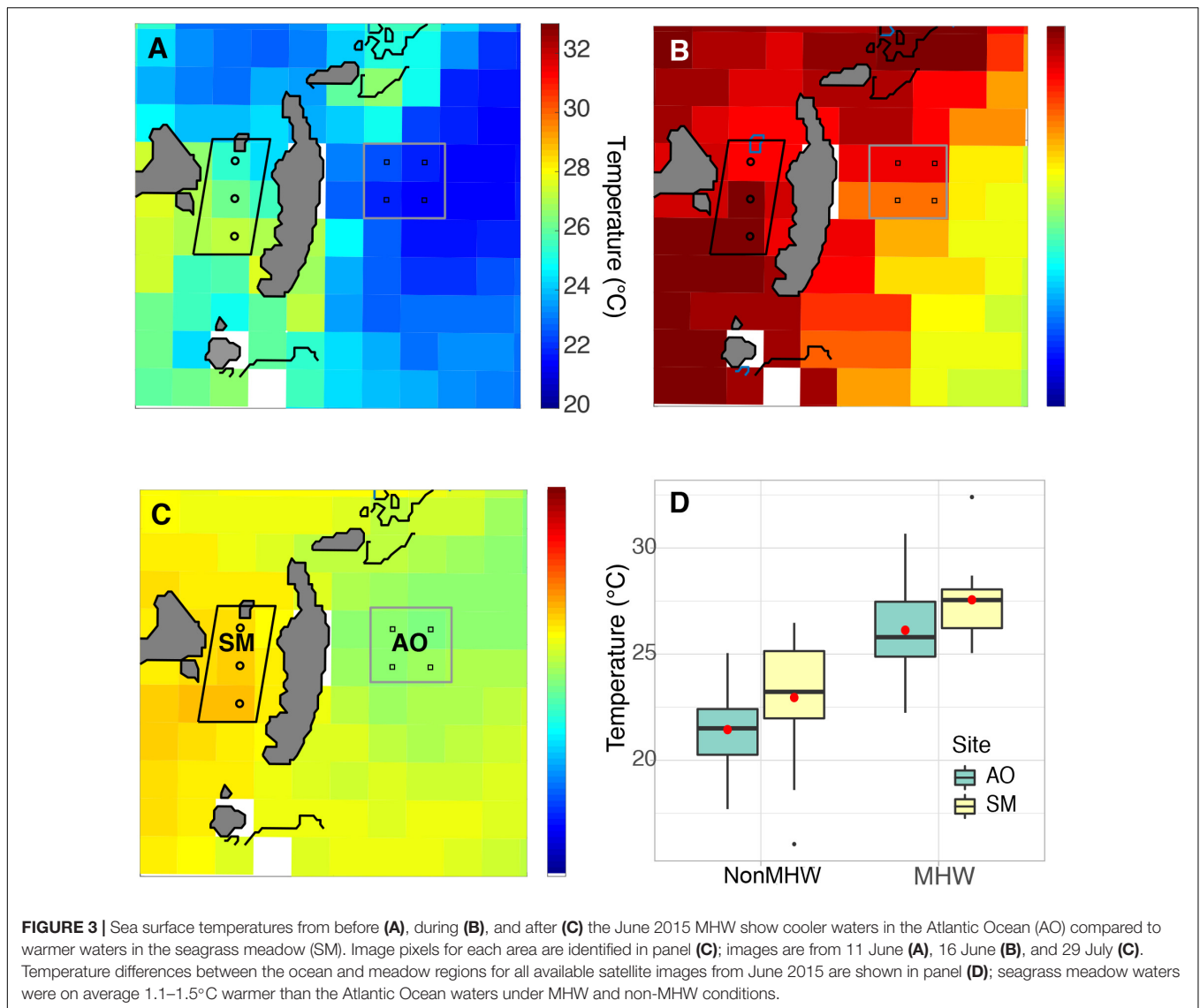
lower than the pre-disturbance meadow stock (Tukey contrast, $p = 0.042$), indicating the lag in recovery of sediment carbon stocks following seagrass loss. At the outer meadow sites, C stocks showed no significant change from pre-disturbance stock of 249 ($\pm$ 25, $n = 9$) g C m^{-2} in 2013 to post-disturbance stock of 256 ($\pm$18, $n = 4$) g C m^{-2} in 2016. By 2018, outer meadow sites had accumulated C stock of 372 ($\pm$40, $n = 6$) g C m^{-2}, significantly greater than the 2013 pre-disturbance stock (Tukey contrast, $p = 0.0035$).

Small-Scale Patchiness

At the patch scale (m^2), uneven shoot recovery at the six inner meadow sites affected the amount of C retained in the sediments in 2017, 2 years after the dieback. The paired t-test showed that seagrass patches retained significantly more C in the upper 5 cm of sediment compared to bare patches, 268 ($\pm$23, $n = 6$) g C m^{-2} compared to 199 ($\pm$21) g C m^{-2} [mean ($\pm$SE), **Figure 6B**; $t = -4.248$, df = 5, and $p = 0.008$].

Retention of Deeper Sediment C Stock

Analysis of the deeper (10 cm) sediment cores showed that sites with faster initial recovery (higher recovery sites) retained significantly more sediment C than lower recovery sites (**Table 1**). Sediment profiles of the deeper sediment cores from 2018 are shown in **Figure 7**. C content (mg C cm^{-3}) was not significantly

FIGURE 3 | Sea surface temperatures from before **(A)**, during **(B)**, and after **(C)** the June 2015 MHW show cooler waters in the Atlantic Ocean (AO) compared to warmer waters in the seagrass meadow (SM). Image pixels for each area are identified in panel **(C)**; images are from 11 June **(A)**, 16 June **(B)**, and 29 July **(C)**. Temperature differences between the ocean and meadow regions for all available satellite images from June 2015 are shown in panel **(D)**; seagrass meadow waters were on average 1.1–1.5°C warmer than the Atlantic Ocean waters under MHW and non-MHW conditions.

different in the surface sediments (0–2.5 cm interval) between the three higher and three lower recovery sites (5.4 ± 0.7 g cm^{-3} and 4.1 ± 0.5 g cm^{-3} respectively, Tukey contrast, $p = 0.26$). However, higher recovery sites had significantly greater C content than lower recovery sites in the 2.5–5 cm interval (6.8 ± 2 g cm^{-3} and 4.2 ± 0.7 g cm^{-3} respectively, Tukey contrast, $p < 0.001$) and the 5–10 cm interval (6.7 ± 0.2 g cm^{-3} and 3.6 ± 0.2 g cm^{-3} respectively, Tukey contrast, $p < 0.001$). Integrating these C concentrations by each depth interval, the higher recovery site stored 636 g C m^{-2}, while the lower recovery sites stored 384 g C m^{-2} in the upper 10 cm of sediment.
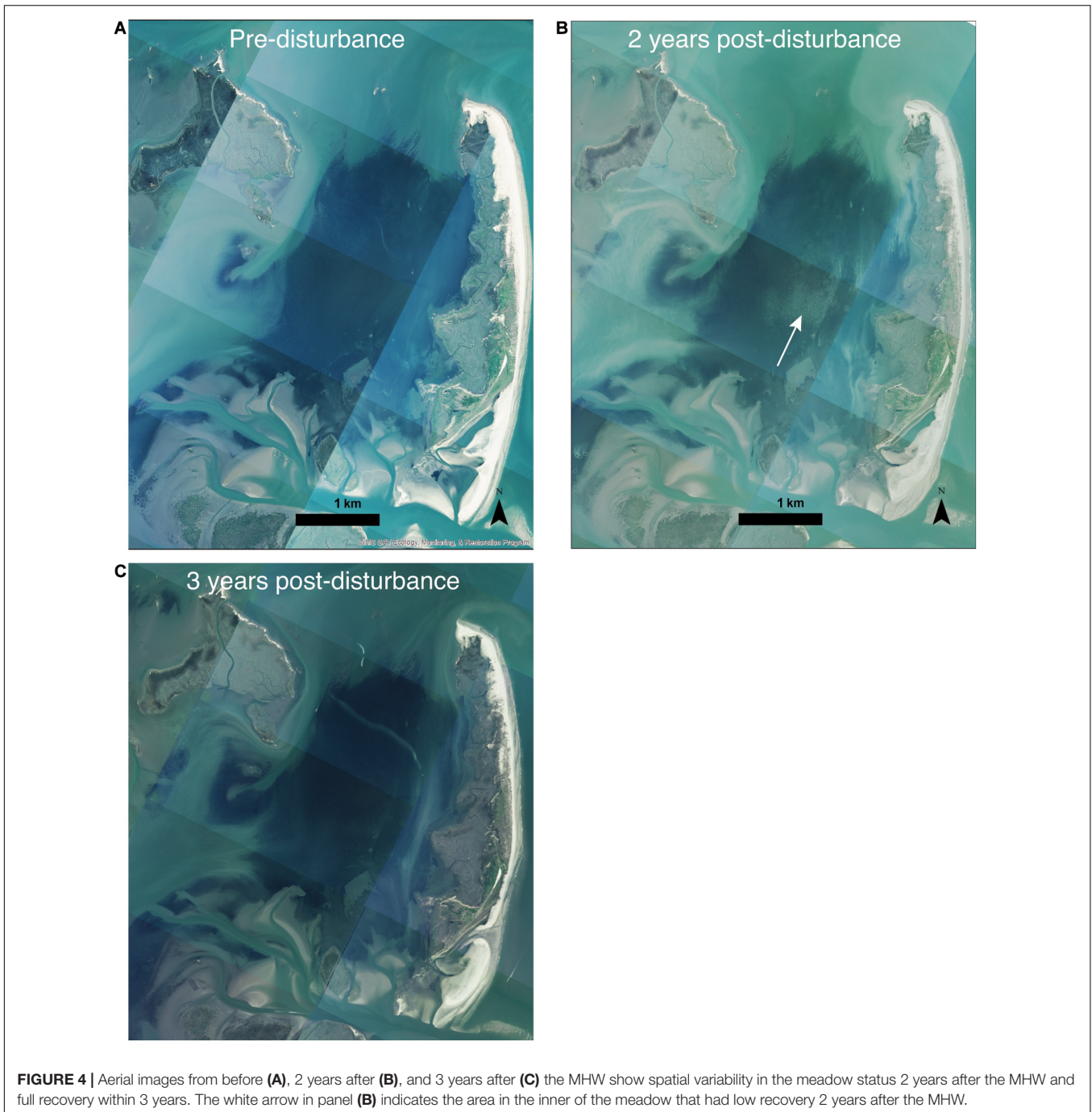
Landscape-Level Spatial Effects

Compared to the inner sites, the outer sites did not experience a net loss of carbon after the MHW (**Figure 8**). The outer sites had significantly greater C stocks in 2018 (3 years post-disturbance) compared to 2013 (pre-disturbance meadow); the net change in C stock was an increase of 56% over the 6 years. In contrast, the

inner meadow sites had lost significant amounts of C compared to 2013 levels by 2017, and only partially re-accumulated that C in 2018, with a net loss of 18%. The pattern of C loss and re-accumulation at the inner sites was consistent across the sites with higher and lower recovery. By 2018, there was no significant difference in C stock between the inner and outer sites (317 ± 16 and 372 ± 40 g C m^{-2} respectively, Tukey contrast, $p = 0.98$). However, the stock at the inner sites remained below the 2013 pre-dieback stock of 399 ± 29 g C m^{-2} and likely below the amount that would have accumulated, had the meadow not been disturbed in 2015.
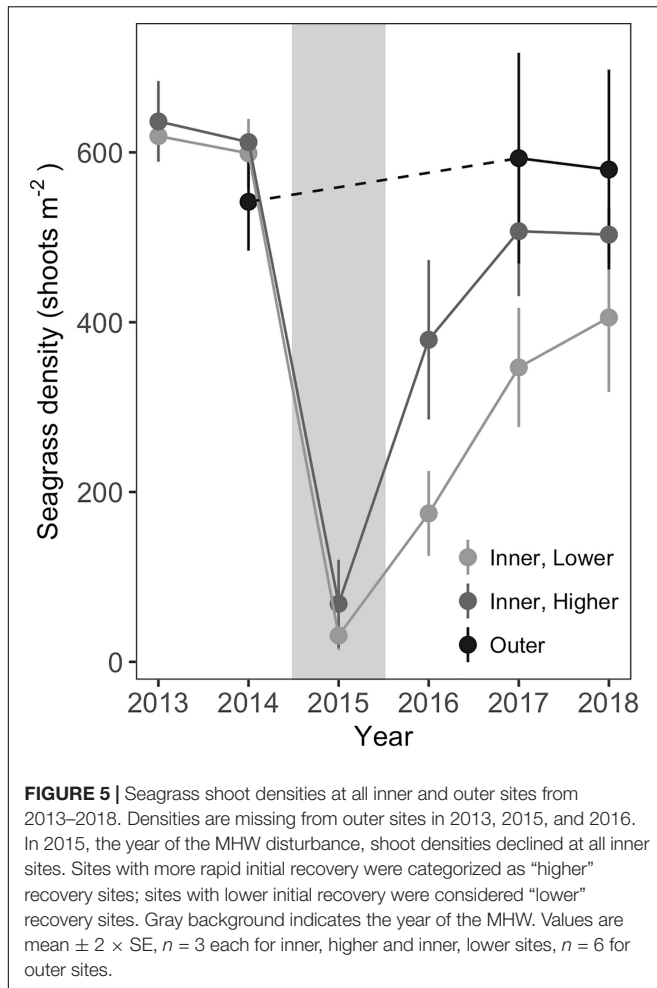
DISCUSSION

To our knowledge, this is the first study to directly quantify the impact of a marine heat wave on sediment C stocks in a seagrass meadow. Using long-term data from a landscape-scale

FIGURE 4 | Aerial images from before **(A)**, 2 years after **(B)**, and 3 years after **(C)** the MHW show spatial variability in the meadow status 2 years after the MHW and full recovery within 3 years. The white arrow in panel **(B)** indicates the area in the inner of the meadow that had low recovery 2 years after the MHW.

restoration project that spanned the period before, during, and after the MHW, we report that inner meadow sites experiencing extreme shoot density declines of 90% during the MHW also showed net losses of 20% of C in upper sediments (0–5 cm) over the three following years. However, this effect was not consistent across the 7-km^2 meadow; outer meadow sites showed no change in shoot densities before and after the disturbance and experienced net increases of 60% of C in upper sediments (0–5 cm) over the 3 years after the disturbance. These outer meadow sites may have experienced less disturbance or they may
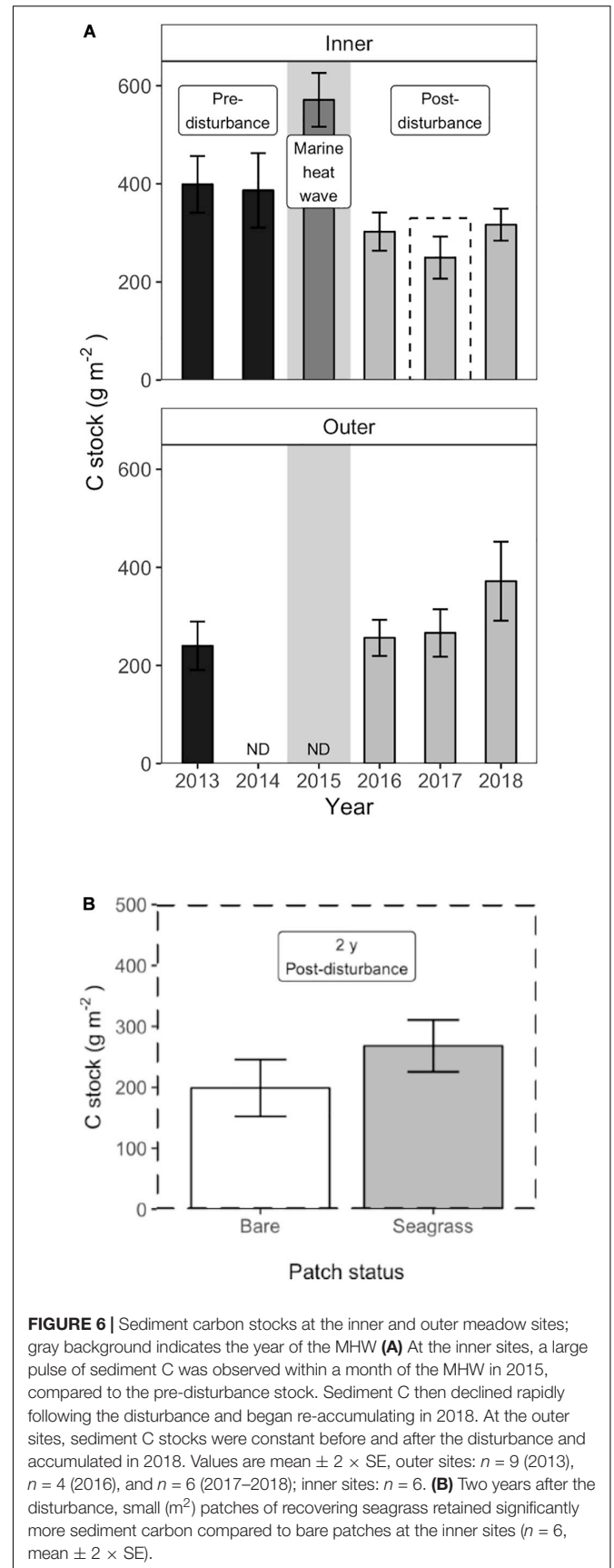
have recovered more quickly. Regardless, the effects of a regional MHW were not uniform over a large seagrass meadow. Our study further documents that the unevenness of seagrass recovery had a clear impact on the preservation of sediment C stocks. Inner sites that had faster initial shoot recovery maintained C at deeper depths (down to 10 cm) compared to inner sites with slower initial shoot recovery (**Figure 7**). Seagrass patches (m^2) also retained more sediment C than adjacent bare patches (**Figure 6B**). Together, these findings indicate that the long-term stability of seagrass sediment C stocks – over decades or
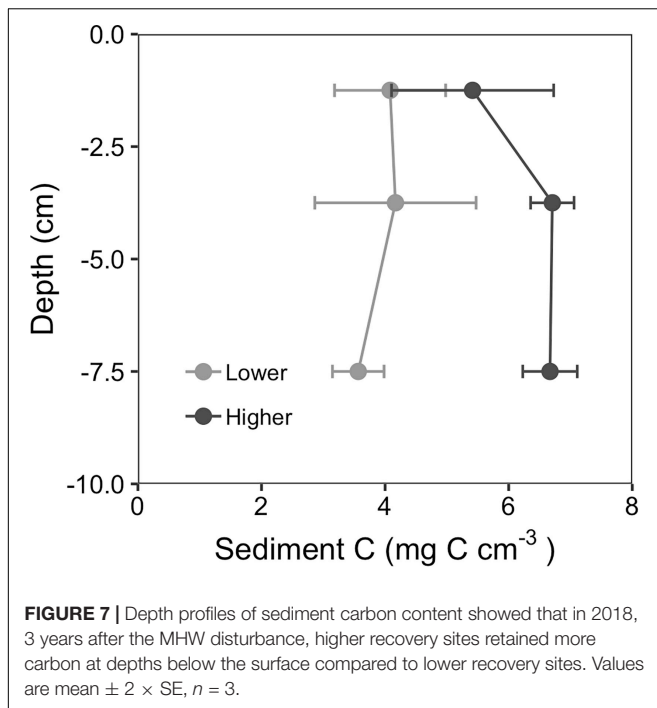
FIGURE 5 | Seagrass shoot densities at all inner and outer sites from 2013–2018. Densities are missing from outer sites in 2013, 2015, and 2016. In 2015, the year of the MHW disturbance, shoot densities declined at all inner sites. Sites with more rapid initial recovery were categorized as "higher" recovery sites; sites with lower initial recovery were considered "lower" recovery sites. Gray background indicates the year of the MHW. Values are mean $\pm$ 2 $\times$ SE, n = 3 each for inner, higher and inner, lower sites, n = 6 for outer sites.

longer – depends on seagrass resilience to and recovery from short-term disturbance events.
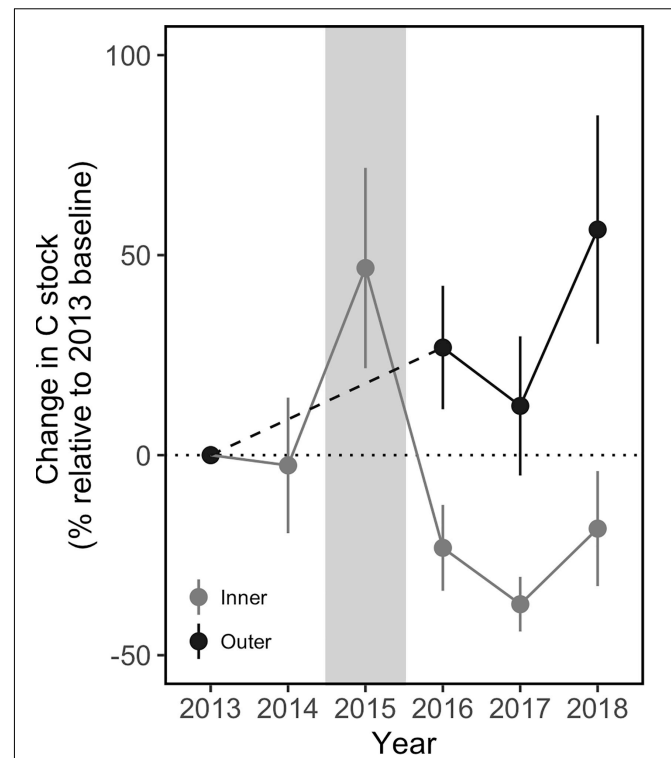
Spatial and Temporal Patterns in Blue C Loss

This case study highlights that sediment C loss following disturbance can be localized. Seagrass loss, and subsequent sediment C loss, was clear at the inner sites following the MHW disturbance. However, the effects of the MHW on the outer sites were not as evident. Both the aerial images of the meadow and the shoot density counts at the outer sites showed high seagrass cover in 2017 and 2018, and the sediment C stocks increased between 2013 (pre-disturbance) and 2016 (1 year post-disturbance) (**Figure 8**). Given the limited data available, we cannot determine whether the temporal stability of shoot densities and C stocks at the outer sites resulted from less disturbance compared to the inner sites, greater resistance to the effects of the MHW, more rapid recovery, or a combination. We hypothesize that disturbance from temperature stress was more limited at the outer sites as a result of ameliorating effects of tidal exchange with cooler ocean water. The inlet north of the meadow is the main source of tidal exchange for the bay, and there was a

FIGURE 6 | Sediment carbon stocks at the inner and outer meadow sites; gray background indicates the year of the MHW **(A)** At the inner sites, a large pulse of sediment C was observed within a month of the MHW in 2015, compared to the pre-disturbance stock. Sediment C then declined rapidly following the disturbance and began re-accumulating in 2018. At the outer sites, sediment C stocks were constant before and after the disturbance and accumulated in 2018. Values are mean $\pm$ 2 $\times$ SE, outer sites: n = 9 (2013), n = 4 (2016), and n = 6 (2017–2018); inner sites: n = 6. **(B)** Two years after the disturbance, small (m^2) patches of recovering seagrass retained significantly more sediment carbon compared to bare patches at the inner sites (n = 6, mean $\pm$ 2 $\times$ SE).

FIGURE 7 | Depth profiles of sediment carbon content showed that in 2018, 3 years after the MHW disturbance, higher recovery sites retained more carbon at depths below the surface compared to lower recovery sites. Values are mean ± 2 × SE, $n = 3$.

FIGURE 8 | Change in sediment carbon stocks in the surface sediments (0–5 cm) at the inner and outer meadow sites before and after the MHW, compared to a pre-disturbance 2013 baseline. Despite a pulse in sediment C observed within one month of the MHW, the inner sites lost sediment C and took 3 years to begin re-accumulating, with a net loss of 18% by 2018. In contrast, the outer sites showed a net increase of 56% in sediment C within 3 years after the MHW. Gray background indicates the year of the MHW. Values are mean ± 2 × SE, outer sites: $n = 9$ (2013), $n = 4$ (2016), and $n = 6$ (2017–2018); inner sites: $n = 6$.

gradient of cooler temperatures from the ocean through the inlet to the meadow during both MHW and non-MHW conditions (**Figure 3**). There may be a temperature gradient within the meadow; the northernmost pixel identified as seagrass meadow was consistently cooler than the more southern meadow pixels, a difference of up to 0.5°C, which may be meaningful given the sensitivity of eelgrass in this region to temperatures above 28°C (Moore and Jarvis, 2008; Berger et al., 2020) and the 15-day duration of the MHW. However, the coarse spatial resolution of the SST data (1 km^2 pixels) limits further inference. Temperature measurements are needed at finer spatial scales (<1 km) to understand differences in exposure to thermal stress, and any cooling effects of tidal exchange, across the meadow. Spatial patterns in sediment conditions may also have contributed to localized C loss at the inner sites; the inner sites had higher organic matter content before the dieback (Oreska et al., 2017), potentially leading to greater intrusion of toxic sulfide during the seagrass dieback (Holmer and Kendrick, 2013). Regardless of the exact mechanism, the net gain of sediment C at the outer sites shows that the meadow-wide MHW did not cause meadow-wide C losses. A related study mapping blue C in this meadow showed an increase in meadow-wide sediment C stocks from 2013 to 2016, despite the localized loss of sediment C in the inner meadow (Oreska et al., 2020). Our study confirms these findings and shows that disturbance from a MHW can have non-uniform effects on seagrass loss and recovery and on sediment C stock persistence at the meadow-scale (km^2). These spatial patterns highlight the need to understand meadow-scale dynamics and landscape-scale drivers of seagrass loss and recovery after disturbance.

Within the inner sites that experienced net sediment C loss, patterns in sediment C to depths of 10 cm indicate the importance of shoot recovery. Previous work has shown that the major enhancement of sediment C following seagrass restoration occurs from 3–6 cm depth, in part due to contributions from belowground biomass (Greiner et al., 2013), whereas surface sediments (0–3 cm) have lower C content (Oreska et al., 2017). At sites with higher (more rapid) shoot recovery, seagrass shoots would reduce erosion, resuspension, and oxidation of sediment C and would support sediment accretion through deposition of particulates (de Boer, 2007; van Katwijk et al., 2010; Hansen and Reidenbach, 2012); shoots would also add organic matter to the root zone (3–6 cm depth). In contrast, sites with lower shoot recovery would experience less C accumulation at depth, less surface accretion, and greater rates of erosion and oxidation. Our measurements of change in C stocks do not differentiate these simultaneous processes, but previous measurements of accretion rates show that sediment C in the 0–10 cm interval had accumulated over the last decade of the restoration (Greiner et al., 2013; Oreska et al., 2017). Greater stocks of C below 2.5 cm at the higher recovery sites, as shown in **Figure 7**, indicate at least partial retention of the deeper C stores that had accumulated prior to the disturbance, whereas

the reduced C stock at the lower recovery sites, consistent across the 0–10 cm depth profile, suggests extensive erosion and re-suspension. A similar dynamic would explain the lower stocks of C in bare patches compared to adjacent seagrass patches (**Figure 6B**); patchy shoot recovery stabilized the local sediments, preventing resuspension and oxidation. Previous work in this study system has found that seagrass restoration converted erosional sediments to an environment of net deposition and that seagrass effects on hydrodynamics and sediment suspension were density dependent (Hansen and Reidenbach, 2012). Other studies assessing sediment C after long-term seagrass loss have also highlighted the role of erosion (Serrano et al., 2016; Salinas et al., 2020). Thus, although the shoot losses after the MHW were comparable at all the inner meadow sites, site-specific patterns in shoot recovery mediated the impact of disturbance on C loss by influencing erosion rates.

This case study suggests that rapid shoot recovery following disturbance may be key to minimizing the net loss of seagrass blue C; however, there are several contrasts in the temporal records of shoot recovery and sediment C. First, there is a clear peak in sediment C at the inner sites in 2015, the year of the MHW (**Figure 6**). This peak likely results from the dieback of seagrass shoots and an associated pulse of detritus and organic matter to the sediments. Sediment sampling in 2015 was conducted within one month of the MHW; the peak in sediment C coincided with the minimum shoot densities, showing a contrasting immediate effect of the MHW on seagrass shoots versus C stocks. However, by the following summer (2016), the sediment C stock had fallen well below the pre-disturbance value whereas seagrass shoots had recovered by 26–77%. The contrast between rapid shoot recovery and continued C loss indicates the importance of erosion during fall and winter, before seagrass regrowth in spring. Other processes, such as stimulation of decomposition through the input of detritus, may also have contributed to the large decline in C stock from 2015 to 2016 (Liu et al., 2020). Second, the time lag between shoot recovery and recovery of C stocks persisted over time; C stocks did not begin to re-accumulate until 2018, 3 years after disturbance (**Figure 8**). The time lag shows that while rapid shoot recovery can minimize net loss of C at depth, recovery of sediment C stocks occurs over longer time scales than shoot recovery. Finally, it is important to note that the difference in C stock between higher and lower recovery sites is evident in the depth profiles (**Figure 7**) but was not significant in the temporal record of surface C stock (0–5 cm depth, **Figure 6**). Competing effects of erosion and accretion, as well as the changing shoot densities over time, complicate the comparison of sediment C in the surface interval (Belshe et al., 2017). Overall, seagrass shoot recovery trajectories indicate general but not exact patterns in net sediment C change after disturbance.

Implications for Seagrass Blue C Under Climate Change

Under a changing climate, baseline sea surface temperatures are rising, and MHWs are predicted to increase in severity, duration, and frequency (Oliver et al., 2019). These conditions will hamper rapid shoot recovery following diebacks and may increase loss of sediment C from disturbed seagrass meadows. In our case study, sediment C loss was offset temporally from seagrass shoot loss. At the inner sites, minimum shoot densities occurred in the year of the MHW (**Figure 5**), but sediment C stocks in the upper five cm declined over the 2 years following the MHW (**Figure 6**). Re-accumulation of sediment C did not occur until 2018, 3 years after disturbance. Cooler conditions, and no MHW, during June of the years following the dieback provided conditions to support seagrass recovery (Berger et al., 2020), likely contributing to sediment C retention and eventual re-accumulation. Repeated disturbance from MHWs in successive years, or within the same year, would likely have disrupted the shoot recovery and delayed or prevented the preservation and re-accumulation of C stocks. Seagrass populations near the thermal boundary of their geographic range will be most vulnerable to future temperature stress (Short et al., 2016); blue C stocks in these areas, including the *Z. marina* meadows in coastal Virginia, are therefore at greater risk of disturbance and C loss. Climate change projections suggest that the southern range limit of *Z. marina* may shift northward by 1.4–6.5 degrees of latitude by 2100 (Wilson and Lotze, 2019), potentially leading to loss of the Virginia coastal meadows and total exposure of the C stocks over time.

At the landscape scale, seagrass resilience to MHW disturbance, including both resistance and recovery, is a function of many environmental parameters. In particular, interactions between multiple stressors, including temperature, turbidity, and sulfide intrusion, can limit recovery (Lefcheck et al., 2017), as was the case in Shark Bay, Australia (Kendrick et al., 2019). The effects of interacting stressors are likely to become more pronounced under a changing climate, but management that minimizes non-temperature stressors can increase seagrass resilience and thereby protect seagrass blue C stocks. Regulations aimed at improving water quality have supported the recovery of seagrass in Chesapeake Bay, VA (Lefcheck et al., 2018) and have helped to stabilize seagrass area in Europe (de los Santos et al., 2019). In South Bay, long-term monitoring has shown consistently high water quality over the last 20 years (McGlathery and Christian, 2020); these favorable conditions likely benefited the seagrass recovery in South Bay, leading to the retention of sediment C in most areas of the meadow. Persistence of seagrass blue C stocks, along with the other services provided by seagrass meadows, will require maintaining these favorable environmental conditions.

Understanding the potential for climate change mitigation through restoration of blue C ecosystems requires knowledge of the stability of blue C stocks. Carbon offset credits may provide an avenue to finance seagrass restoration; voluntary credits are now available under a seagrass offset-credit accounting framework administered by Verra (formerly the Verified Carbon Standard Program). Assigning credits under this framework requires knowledge of the net carbon offset that a seagrass restoration project can generate over the project period, typically 30 years (Needelman et al., 2018; Oreska et al., 2020). As we show here, short-term disturbances can interrupt restoration trajectories,

potentially altering the net carbon offset through time. Long-term monitoring is therefore critical to understand seagrass sediment C dynamics, and managers should not necessarily expect continuous seagrass blue C accumulation throughout a restored meadow over multi-decadal timescales. Unfortunately, seagrass restoration projects are typically monitored for 12 months or less (van Katwijk et al., 2016). Additional empirical and longitudinal studies are needed to document the impact of disturbance on seagrass C stocks and to better understand the persistence of seagrass blue C through time.

With increasing pressures on ocean ecosystems from climate change and other anthropogenic stressors, a narrow window exists to rebuild resilient and sustainable coastal habitats, including seagrass meadows (Duarte et al., 2020). Given the long time horizon for seagrass restoration success, projects started now will take at least a decade to realize their potential, and as MHWs become more prominent in the future ocean, seagrass C stocks will be more vulnerable to disturbance. Greater understanding of the landscape-scale drivers of blue C persistence is urgently needed to inform habitat suitability and risk assessments. Large-scale restoration projects, such as at this study site, are key to these efforts, and they can also provide compelling examples of restoration success. This study site is part of a hugely successful seagrass restoration project, with a total area of more than 36 km^2 as of 2018 (Orth et al., 2020). Despite the localized loss of C resulting from the 2015 MHW disturbance, these restored meadows continue to expand, accumulate sediment C, and provide many additional benefits to water quality and biodiversity. Against the backdrop of accelerating climate change, large-scale and long-term restoration projects are needed more than ever to maximize the benefits of blue C sequestration in seagrass meadows.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

LA collected and analyzed data, led data interpretation, and drafted and revised the manuscript. KM, MO, and AB collected data, contributed to data interpretation, and commented on the manuscript. PW analyzed data, contributed to data interpretation, and commented on the manuscript. PB contributed to data interpretation and commented on the manuscript. RO collected data and commented on the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

ACKNOWLEDGMENTS

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