

A keystone grazer drives saltmarsh carbon storage and recovery

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Abstract

Ecogeomorphic theory predicts that plant-sediment feedbacks regulate carbon storage in coastal vegetated ecosystems. Yet, grazers, which remove plant biomass and alter sediment properties, remain an understudied driver of carbon cycling. We used field-derived and remote sensing data to examine how consumer fronts of the keystone grazer, *Sesarma reticulatum*, mediate carbon storage, flux, and recovery in salt marshes. We observed accelerating rates of *Sesarma* front migration that led to a decrease in carbon stocks by 40-70%. Despite latitudinal differences, front migration rate had no effect on carbon stocks, flux, or replacement time. Lastly, when we included *Sesarma* disturbance in carbon flux calculations, we found that it may take 5-100 years for marshes to replace lost carbon, if at all. Combined, we show that small grazers cause a net loss in carbon stocks as they move through the landscape, and irrespective of migration rate, these grazer-driven impacts persist for decades.

Introduction

Ecogeomorphic theory predicts that biophysical feedbacks between plant foundation species and sediment regulate carbon accumulation (Kirwan & Guntenspergen 2012; D’Alpaos et al. 2019; FitzGerald & Hughes 2019), a feature of blue-carbon ecosystems critical for climate change mitigation (Duarte et al. 2013; Howard et al. 2017). In general, aboveground plant tissues enhance sediment settling from the water column, while belowground tissues accumulate and store organic matter (Morris et al. 2002; Belliard et al. 2017). Thus, changes in primary production or decomposition can shape carbon cycling in these ecosystems (Mendelsohn & Morris 2000; Mueller et al. 2017; Tang et al. 2020).

Consumers, such as herbivores, exert top-down control on plant foundation species, suggesting that they may also influence carbon stocks. Indeed, previous work with large grazers in both terrestrial ecosystems (Elephants: Berzaghi et al. 2023; Reindeer: Stark et al. 2023; Horses, deer, and pigs: Treby & Carnell 2023) and salt marshes (Cattle: Elschot et al. 2015; Hogs: Persico et al. 2017; Livestock: Mueller et al. 2017, Harvey et al. 2019, Graversen et al. 2022) found that these consumers had a net neutral or positive effect on carbon stocks. However, consumer fronts, dense aggregations of consumers bordering a resource (Silliman et al. 2013), are becoming more prevalent worldwide (e.g., beetles in pine forests: Birt & Coulson 2015; urchins in kelp forests: Lauzon-Guay & Scheibling 2007; turtles in seagrasses: Gulick et al. 2021) and can disrupt geomorphic patterning and ecosystem functioning (Hughes et al. 2009; Vu et al. 2017). Even with their demonstrated impact on plant biomass (Crotty et al. 2020) and sediment properties (Wilson et al. 2012; Farron et al. 2020; Beheshti et al. 2021), the role of small consumers in mediating carbon fluxes has been identified as a key knowledge gap in blue-carbon ecosystems (Moore et al. 2020; Ren et al. 2022).

We used tidal salt marshes along the U.S. Atlantic coast as representative blue-carbon ecosystems to understand how consumers are influencing carbon flux and storage. Salt marshes in this region suffer from consumer fronts created by the purple marsh crab, *Sesarma reticulatum* (hereafter *Sesarma*), a keystone grazer (Crotty et al. 2020), which consumes the smooth cordgrass, *Spartina alterniflora* (hereafter *Spartina*

), a foundation species in these ecosystems (Hughes et al. 2009; Vu et al. 2017; Vu & Pennings 2021). *Sesarma* consumer fronts are occurring more frequently in U.S. Atlantic saltmarshes (Crotty et al. 2020) and in contrast to their large counterparts, *Sesarma* form consumer fronts (Vu & Pennings 2021), graze on both the above- and belowground biomass of *Spartina* (Coverdale et al. 2012), and form burrows, which increase soil oxygenation, decomposition, and erosion (Martinetto et al. 2016; Farron et al. 2020; Xiao et al. 2020). Thus, *Sesarma* 's top-down control on *Spartina* biomass, combined with their burrowing activities, can negatively impact carbon storage and vertical accretion capacity (the process by which salt marshes build elevation) (Hughes et al. 2009; Angelini et al. 2018; Crotty et al. 2020; Williams & Johnson 2021), reducing a salt marsh's ability to keep pace with sea-level rise (Holdredge et al. 2009; Schultz et al. 2016; Szura et al. 2017).

As *Sesarma* exhaust food and suitable habitat, the front propagates inland in search of additional resources (Vu & Pennings 2021). We hypothesized that carbon stocks would be highest at the leading edge of the front, which has not yet been disturbed by *Sesarma*, lowest inside the front, which hosts active crab foraging and burrowing, and intermediate at the trailing edge where *Spartina* is revegetating (i.e., recovering from grazing). Further, we expected front migration rate to aid in carbon stock recovery, with faster migration leading to quicker replacement times. Here, we found that a keystone grazer causes a net loss in carbon stocks as it moves through the landscape, and these consumer-driven impacts are unaffected by migration rate, lasting for decades.

Materials & Methods

Study System & Front Morphology

We used a combination of field collections and remote sensing observations to assess how *Sesarma* consumer fronts are influencing carbon stocks, flux, and recovery in the salt marshes of three coastal U.S. states: Virginia, South Carolina, and Georgia (Table S1; Fig.1D). While *Sesarma* have been documented as drivers of saltmarsh erosion in northern U.S. states, such as Massachusetts (Bertness et al. 2009; Holdredge et al. 2009), Virginia marks the northernmost limit of *Sesarma* fronts which create the distinct patterning described below, while Georgia represents their southern limit.

Sesarma fronts typically form at the heads of tidal creeks (Hughes et al. 2009; Wilson et al. 2012), and their directional movement inland lowers elevation, creating favorable habitat for the revegetation of *Spartina* (Wittingham 2022). Thus, *Sesarma* fronts have three distinct zones: the leading edge of the consumer front (*Spartina* high marsh, hereafter 'ungrazed zone'), the trailing edge of the consumer front (*Spartina* low marsh, hereafter 'recovered zone'), and a narrow band (3-8 m wide) of mudflat (i.e., no *Spartina*) separating the two where *Sesarma* reside (hereafter 'denuded zone') (Fig. 1E).

Field Collections

In each of the three states, four independent consumer fronts (n=4 per state) that were at least 20 m apart were visited in August of 2022 (Table S1) and both plants and sediments were collected. At each site, five transects spanning the recovered zone to the ungrazed zone were delineated (n=20 transects per state). Along each transect, a 0.0625m² quadrat was placed on the sediment surface in each of the three zones (recovered, denuded, ungrazed; Fig. 1E). In the recovered zone, quadrats were placed 10 m away from the denuded zone edge to ensure carbon stocks reflected those of areas that had been revegetated for at least five years (assumes a maximum migration rate of 2 m yr⁻¹ (Hughes et al. 2009)). In the ungrazed zones, quadrats were placed 3 m from the denuded zone edge. Within each quadrat, all aboveground *Spartina* biomass was removed with garden shears and placed in a resealable plastic bag. In the same quadrat, a Russian peat borer (AMS, Inc. U.S.A.) was used to take sediment cores to a depth of 30 cm. Each core was immediately sectioned into 5 cm segments (n=6 sections per core) and each portion was placed in its own resealable plastic bag. All plant and sediment samples were kept on ice until transported to the Virginia Institute of Marine Science (VIMS) for processing.

Plant samples were rinsed to remove sediments and separated into live and dead aboveground tissues. All plant and sediment samples were dried at 60°C to a constant mass. Bulk density (BD) was calculated as

the dry mass in grams divided by the sediment core volume. Dried samples were then homogenized, and a 5 g subsample was muffled at 550°C for 6 hours to analyze organic matter content (loss on ignition (LOI)). Representative subsamples of collected sediments from each depth, plant zone, and state were acidified with 10% hydrochloric acid (HCl), ran on a Thermo FlashEA system, and compared to an acetanilide standard curve to derive carbon fraction.

Remote Sensing

We used high resolution (~1.0 m) aerial images acquired from Digital Orthophoto Quadrangle (DOQ, USGS EROS Archive between 1987 and 2006) and National Agriculture Imagery Program (NAIP, Google Earth Engine, 2003-present) to assess consumer front migration over the course of ~25 years (between 1993/1994-2018/2019). In each state, we selected ~50 consumer fronts within a 10 km area of our field sites. These fronts were randomly sampled from the latest aerial images (i.e., 2018 or 2019) to ensure we captured consumer fronts of variable sizes and that were at least 20 m apart from one another. For each site, we manually delineated the leading edge of the consumer front in 1993 (or 1994), 2008 (or 2009), and 2018 (or 2019) based on the year of image availability (Fig. 1A-C; Table S2).

To quantify the magnitude of front migration between time periods, we generated three random points at each consumer front identified in 2018/2019 and created perpendicular lines (i.e., transects) to intersect the fronts in 1993/1994 and 2008/2009. We computed the average length (m) of the three transects connecting fronts of different years, which represented the distance of consumer front migration between time periods. The rates of front migration (m yr^{-1}) were then calculated by dividing the mean distance of front migration by the number of years between delineations (Fig. 1A-C, Table S2). In some cases (~7% of all sites, Table S2), consumer fronts emerged only recently, thus they were absent in earlier images. For these sites, we measured the distance between the trailing and leading edges of the consumer front to make a conservative (minimal) estimate of front migration between time periods. If a consumer front was absent in two consecutive years of delineation (~2% of all sites), an “NA” value was assigned to represent no front migration over the entire time period. Migration rates were then averaged by state and used to calculate carbon flux as described below. All geoprocessing was performed in ArcGIS (v10.7) following the methods of Chen & Kirwan (2022).

Carbon Calculations

We plotted carbon fraction against loss on ignition (LOI) for each plant zone in each state to generate best-fit equations describing the relationship, following the methods of Craft et al. (1991) (Table S3). Using the equations generated for each plant zone and state, we calculated carbon fraction for all remaining sediment samples at each depth interval. Sediment carbon stock (kg m^{-2}) was then calculated as:

$$\bar{\rho} \text{fraction} \text{ stock} (\text{kg m}^{-2}) = \sum \text{fraction} (BD * d)(1)$$

where C fraction is the carbon content calculated for each depth increment (6 sections per core), BD is the bulk density (g cm^{-3}), and d is the depth interval (cm). Values were converted to kg m^{-2} and summed to derive a carbon stock per sediment core. Plant carbon stocks (kg m^{-2}) were derived using *Spartina* carbon fractions from Ho & Pennings (2013) and dry biomass. Carbon flux (C) was calculated as:

$$\Delta C (\text{kg m}^{-2} \text{ yr}^{-1}) = \frac{r_{cf}}{s} (2)$$

where C is a given carbon stock (sediment only, or sediment + plants), r_{cf} is the average migration rate of consumer fronts (calculated per state from remote-sensing observations above), and s is the distance traveled by each consumer front. When the difference in carbon stocks between ungrazed zones and denuded zones (i.e., ungrazed to denuded transition) is substituted for C , the resulting change shows how much carbon is lost as a *Sesarma* front migrates inland (i.e., carbon loss). Conversely, when the difference in carbon stocks between recovered zones and denuded zones (i.e., denuded to recovered transition) is substituted for C , the resulting change represents how much carbon is gained as *Spartina* revegetates (i.e., carbon gain). The net change in carbon stock as a *Sesarma* front migrates is then calculated as the difference between carbon gain and loss.

Smith & Kirwan (2021) developed a novel method for determining how long it will take an ecosystem to reaccumulate carbon stocks following a loss. Using this method, the time to replacement (t_r) was calculated as:

$$t_r \text{ (yr)} = \frac{C}{CAR} \quad (3)$$

where C is the carbon stock lost (kg m^{-2}) during the ungrazed to denuded transition (i.e., carbon loss), and CAR is the carbon accumulation or gain rate ($\text{kg m}^{-2}\text{yr}^{-1}$). For this study, we calculated time to replacement in two ways: 1) using a regional carbon accumulation rate of $0.1236 \text{ kg m}^{-2} \text{ yr}^{-1}$ for the South Atlantic-Gulf from Wang et al. (2019), and 2) using our site-specific carbon gain rates calculated during the denuded to recovered transition (Table S4). The use of each rate comes with limitations. Our approach is local and site-specific, but not based on radiometric dating. In contrast, the Wang et al. (2019) carbon accumulation rate is not local and does not factor in consumer disturbance, but is better quantified. For each rate, we then calculated two separate time to replacement values, the first using sediment only carbon loss, and the second using sediment + plant carbon loss.

Statistics

Statistical analyses were conducted in RStudio version 4.2.2 (R Core Team, 2022). Linear mixed models quantified differences in responses with state (Virginia, South Carolina, Georgia) and zone (ungrazed, denuded, recovered) as fixed effects, and sampling site as a random effect when applicable. Response variables were transformed when necessary to meet model assumptions. Statistical significance was determined at a level of $p < 0.05$.

Results

The bulk density (BD) and loss on ignition (LOI) of sediment cores collected in this study displayed a similar correlation to those found in Morris et al. (2016) (Fig. S1). Morris et al. (2016) evaluated this relationship for 33 wetlands within the continental U.S., which suggests that our results are broadly applicable to U.S. salt marshes.

South Carolina had a total carbon stock (i.e., sum of sediment + plant stocks across zones) of $5.93 \pm 0.40 \text{ kg C m}^{-2}$ (mean ± 1 standard error), which was 62% higher than cumulative stocks in Georgia ($3.12 \pm 0.18 \text{ kg C m}^{-2}$; $p < 0.0001$) and 80% higher than those in Virginia ($2.55 \pm 0.24 \text{ kg C m}^{-2}$; $p < 0.0001$) (Fig. 2A-C). Regardless of whether plants were included, ungrazed zones in all three states (sediment only: Virginia: $1.24 \pm 0.04 \text{ kg C m}^{-2}$; South Carolina: $1.73 \pm 0.09 \text{ kg C m}^{-2}$; Georgia: $0.95 \pm 0.02 \text{ kg C m}^{-2}$; sediment + plants: Virginia: $1.33 \pm 0.04 \text{ kg C m}^{-2}$; South Carolina: $1.93 \pm 0.09 \text{ kg C m}^{-2}$; Georgia: $1.16 \pm 0.02 \text{ kg C m}^{-2}$) had higher stocks than denuded zones (sediment only, no plant growth; Virginia: $0.64 \pm 0.05 \text{ kg C m}^{-2}$; South Carolina: $1.30 \pm 0.04 \text{ kg C m}^{-2}$; Georgia: $0.69 \pm 0.02 \text{ kg C m}^{-2}$), although the magnitude of difference varied by state ($p < 0.0001$; Fig. 2A-C). Surprisingly, South Carolina carbon stocks in the recovered zones were 33% higher (sediment + plants: $2.70 \pm 0.20 \text{ kg C m}^{-2}$) than ungrazed zones (sediment + plants: $1.93 \pm 0.09 \text{ kg C m}^{-2}$) (Fig. 2B) and recovered zones in Georgia had 51% higher stocks when plant carbon was included (sediment only: $0.75 \pm 0.03 \text{ kg C m}^{-2}$; sediment + plants: $1.27 \pm 0.03 \text{ kg C m}^{-2}$) (Fig. 2C).

As *Sesarma* fronts migrated inland, all three states experienced significant carbon stock loss (i.e., ungrazed to denuded transition, Fig. 3A) (Virginia: $-1.02 \pm 0.04 \text{ kg C m}^{-2}\text{yr}^{-1}$; South Carolina: $-1.44 \pm 0.25 \text{ kg C m}^{-2} \text{ yr}^{-1}$; Georgia: $-0.97 \text{ kg C m}^{-2} \text{ yr}^{-1}$), with South Carolina experiencing the greatest loss, though carbon losses were not statistically different between states ($p = 0.069$, Fig. 3A). Interestingly, South Carolina had the largest carbon gain (i.e., denuded to recovered transition, Fig. 3B) ($0.95 \pm 0.16 \text{ kg C m}^{-2} \text{ yr}^{-1}$; $p = 0.046$) when compared with Georgia ($0.15 \pm 0.02 \text{ kg C m}^{-2}\text{yr}^{-1}$) and Virginia ($-0.08 \pm 0.01 \text{ kg C m}^{-2} \text{ yr}^{-1}$), which, in contrast, experienced an additional loss of carbon. When assessing carbon flux, despite slight gains in South Carolina and Georgia, all three states experienced a net loss in carbon stocks (i.e., ungrazed to recovered transition, Fig. 3C) (Virginia: $-1.10 \pm 0.04 \text{ kg C m}^{-2}\text{yr}^{-1}$; South Carolina: $-0.49 \pm 0.20 \text{ kg C m}^{-2} \text{ yr}^{-1}$; Georgia: $-0.82 \pm 0.09 \text{ kg C m}^{-2} \text{ yr}^{-1}$).

Our time-series remote-sensing analyses revealed that *Sesarma* fronts are migrating at different rates along

a latitudinal gradient, and this migration has accelerated by ~30% in each state since the early 1990s (Table S2). *Sesarma* fronts in Virginia are migrating the slowest (0.84 m yr⁻¹), South Carolina at an intermediate pace (1.54 m yr⁻¹), and Georgia the fastest (1.74 m yr⁻¹) (Fig. 1A-C). Despite *Sesarma* fronts in Georgia moving more than two times faster than those in Virginia, migration rate had no effect on carbon loss ($p = 0.556$) or carbon gain ($p = 0.609$) (Fig. S2A, B). Further, migration rate had no effect on time to replacement, regardless of whether the regional carbon accumulation rate ($p = 0.947$, Fig. S2C) or local carbon gain rate was used for calculations ($p = 0.499$). Lastly, approximately 20% of the *Sesarma* fronts tracked through remote sensing observations in each state recently emerged (i.e. ‘minimal’; Table S2), providing further evidence that *Sesarma* fronts are increasing in prevalence over time.

Time to replacement varied greatly depending on whether carbon accumulation or gain rate was used in calculations. Using the average carbon accumulation rate for the South Atlantic-Gulf regions (0.1236 kg m⁻² yr⁻¹; Wang et al. 2019), replacement times were longest in Virginia (29 ± 2.6 yrs), followed by South Carolina (22.51 ± 8.05 yrs), and Georgia (13.55 ± 2.62 yrs), although these differences were not statistically significant ($p = 0.109$) (Fig. 4A). When using site-specific carbon gain rates calculated in this study (Table S4), carbon stocks in Virginia never recover from herbivory, as both its losses and “gains” were negative, while carbon stocks in South Carolina recover in 5.33 ± 2.31 yrs, and Georgia in 110.20 ± 93.47 yrs ($p = 0.0268$) (Fig. 4B).

Discussion

Historically, the relationship between plant foundation species and sediments is viewed as the primary driver of carbon accumulation and storage in blue-carbon ecosystems (Kirwan & Mudd 2012; Gonneea et al. 2019). Thus, any alteration to primary production or decomposition can influence carbon stocks. Consumers, such as herbivores, remove plant biomass and disrupt sediment properties (Wilson et al. 2012; Crotty et al. 2020), yet their influence on carbon storage and flux remains a distinct knowledge gap (Ren et al. 2022). Here, we found that consumer fronts created by the keystone grazer, *Sesarma*, substantially reduced carbon stocks in salt marshes of the mid-Atlantic and southeastern U.S., and that despite differences in front migration rates, their impacts can last for decades.

Previous work in both terrestrial ecosystems (Berzaghi et al. 2023; Stark et al. 2023; Treby & Carnell 2023) and salt marshes (Elschot et al. 2015; Mueller et al. 2017; Persico et al. 2017; Harvey et al. 2019; Graversen et al. 2022) found that large consumers had a net neutral or positive effect on carbon stocks. In contrast, we found that the small consumer, *Sesarma*, negatively impacts carbon stocks (Fig. 2). In terrestrial ecosystems, large consumers will preferentially browse for aboveground, low-density plants, which can cause reallocation to belowground biomass (Elschot et al. 2015; Harvey et al. 2019) as well as allow dense, woody vegetation to accumulate carbon (Berzaghi et al. 2023). Further, large consumers trample underlying sediments, which decreases soil oxygenation and thus decomposition (Mueller et al. 2017; Persico et al. 2017; Tang et al. 2020; Graversen et al. 2022). Contrary to its large counterparts, *Sesarma* form consumer fronts (i.e., high densities bordering a resource; Vu & Pennings 2021), graze on both above- and belowground biomass (Coverdale et al. 2012), prohibiting plant compensation, and form burrows, increasing decomposition and erosion (Martinetto et al. 2016; Farron et al. 2020; Xiao et al. 2020), ultimately causing a net loss of carbon in U.S. mid-Atlantic and southeastern salt marshes.

As ungrazed zones transitioned to denuded zones with *Sesarma* front migration, carbon stocks declined across all three states (Fig. 2A-C). This supports our hypothesis and demonstrates an initial impact of *Sesarma* on carbon storage. In both Virginia (Fig. 2A) and Georgia (Fig. 2C), sediment-only carbon stocks in the recovered zones were less than or equal to those in denuded zones. Recovered zones in Georgia, however, had 51% higher stocks when plant carbon was included (sediment only: 0.75 ± 0.03 kg C m⁻²; sediment + plants: 1.27 ± 0.03 kg C m⁻²), suggesting that labile carbon may be an important source in this system (Fig. 2C), a finding similar to previous work in sediment-limited lagoons (Else-Quirk & Unger 2018). Surprisingly, South Carolina carbon stocks in the recovered zones were 33% higher (2.70 ± 0.20 kg C m⁻²) than ungrazed zones (1.93 ± 0.09 kg C m⁻²), indicating rapid carbon accumulation following consumer disturbance (Fig. 2B). This quick recovery is most likely driven by the tight coupling between *Spartina* productivity and

elevation (Morris et al. 2002; Fitzgerald & Hughes 2019). Across the three states evaluated in this study, *Sesarma* fronts caused a decline in elevation as they migrated inland, with recovered zones occurring at lower elevations than both denuded and ungrazed zones (Smith, *unpublished data* ; Wittingham 2022). In South Carolina, this lowered elevation potentially positioned the recovered *Spartina* at an ideal tidal height such that its productivity, and thus carbon capture and storage, was maximized, allowing it to recover carbon stocks faster than any other site. Despite this large recovery of carbon stocks in South Carolina, there was still a net loss of carbon associated with *Sesarma* fronts in all three states (Fig. 3C).

Sesarma front migration rates are largely unknown, but often assumed based on a single study in South Carolina (Hughes et al. 2009). We found high latitudinal variation in front migration (Fig. 1A-C), most likely driven by seasonality in primary production and *Sesarma* foraging. Fronts in Georgia moved more than two times faster than those in Virginia (Fig. 1A-C), and fronts in all three states accelerated over time (Table S2). Thus, we expected that migration rate would be a determinant of recovery following *Sesarma* disturbance, with faster-moving fronts having quicker recovery. However, we found that there were no significant relationships between front migration rate and carbon stocks, flux, or time to replacement (Fig. S2A-C). Thus, this lack of correlation suggests that our findings are broadly applicable across the mid-Atlantic and southeastern U.S.

As *Sesarma* fronts propagate through the marsh, they lower elevation and create conditions unfavorable for continued crab colonization, yet favorable for *Spartina* revegetation (Vu & Pennings 2021; Wittingham 2022). In fact, *Spartina* can reoccupy denuded zones within a single growing season (Wittingham 2022), suggesting potential for rapid recovery of carbon stocks. However, when considering *Sesarma* disturbance in time to replacement calculations (equation 3; Smith & Kirwan 2021), we found that *Sesarma* -driven impacts to carbon stocks can persist for decades (Fig. 4), despite quick *Spartina* revegetation. Specifically, when using the local carbon gain rate from this study (i.e., denuded to recovered transition), we found the inclusion of grazing caused a ten-fold increase in Georgia's recovery time, while Virginia will never replace its lost carbon (Fig. 4B). Interestingly, the sizable carbon stock of the recovered zone in South Carolina (Fig. 2B) shortened its replacement time (Fig. 4B) when compared to those calculated using the carbon accumulation rate for the South Atlantic-Gulf region (Wang et al. 2019). This suggests that if marshes in South Carolina can maintain elevation, then carbon accumulation following consumer disturbance is rapid.

Overall, our findings show that a small, keystone grazer is having substantial, negative effects on carbon stocks, a finding contrary to previous work focused on large consumers (Elschot et al. 2015; Mueller et al. 2017; Persico et al. 2017; Harvey et al. 2019; Graversen et al. 2022; Berzaghi et al. 2023; Stark et al. 2023; Treby & Carnell 2023). Further, this study demonstrates that consumers play a significant role in carbon storage and flux, challenging the classic paradigm of plant-sediment feedbacks as the primary ecogeomorphic driver of coastal carbon cycling (Kirwan & Mudd 2012; FitzGerald & Hughes 2019). Plant-sediment feedbacks that stabilize wetlands in the face of sea-level rise are governed by tidal channel evolution (D'Alpaos et al. 2019), yet observations of tidal channel elongation are typically restricted to locations with consumer fronts or other sources of vegetation disturbance (Kirwan et al. 2008; Hughes et al. 2009). Our observation of accelerated rates of *Sesarma* front migration suggests that both the direct (carbon consumption) and indirect (marsh stability) impacts of consumers on carbon cycling will intensify under accelerated sea-level rise. Given *Sesarma* 's disproportionate impact on carbon stocks despite their small size, and the slow recovery associated with their disturbance, it is critical to include consumer impacts in future estimates of carbon flux and accumulation. This study uniquely combines and advances our knowledge of both ecology (e.g., impacts of a keystone grazer) and geomorphology (e.g., drivers of carbon storage and flux), highlighting the importance of interdisciplinary work in revealing controls on ecosystem function.

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Figure Captions

Fig 1 . Location by year (1993-1994: green, 2008-2009: yellow, 2018-2019: red) at representative consumer fronts in A) Virginia, B) South Carolina, and C) Georgia. The values (m yr⁻¹) shown in white on panels A-C refer to average migration rates per state (i.e., average of all calculated rates, n = ~50; Table S2) between 1993/1994 and 2018/2019. The white scale bars correspond to 50 m. D) U.S. map of sampled U.S. states (A: Virginia, B: South Carolina, C: Georgia). E) Cross-sectional view of a representative consumer front depicting the three distinct zones: ungrazed, denuded, and recovered. Arrow indicates inland migration of consumer fronts.

Fig. 2 . Carbon stocks in kilograms per meter squared in ungrazed, denuded, and recovered zones in A) Virginia, B) South Carolina, and C) Georgia. Green bars represent cumulative carbon stocks in both sediments and plants, whereas gray bars represent stocks in sediment only. Note that values for sediment only and sediment + plants are the same in denuded zones, as there were no plants to consider. Data are shown as mean $\pm$ 1 standard error.

Fig. 3 . Carbon flux in kilograms per meter squared per year in Virginia, South Carolina, and Georgia as A) ungrazed zones transition to denuded zones, B) denuded zones transition to recovered zones, and C) an overall net change from ungrazed to recovered zones. Green bars represent cumulative carbon flux in both sediments and plants, whereas gray bars represent flux in sediment only. Data are shown as mean $\pm$ 1 standard error.

Fig. 4 . Time to replacement in years for Virginia, South Carolina, and Georgia calculated using A) carbon accumulation rates from Wang et al. (2019) and B) carbon gain rate calculated in this study. Note that in panel (B), carbon gain rate in Virginia is zero, thus shaded bars indicate a replacement time of infinity. Green bars represent cumulative carbon replacement in both sediments and plants, whereas gray bars represent replacement in sediment only. Data are shown as mean $\pm$ 1 standard error.