Received: 9 April 2024 | Accepted: 20 May 2024

DOI: 10.1002/ecy.4385

REPORT

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

A grazing crab drives saltmarsh carbon storage and recovery

Serina S. Wittyngham[1] | **David Samuel Johnson**[2] | **Yaping Chen**[1] | **Matthew L. Kirwan**[1]

[1]Coastal and Ocean Processes, Virginia Institute of Marine Science, William & Mary, Gloucester Point, Virginia, USA

[2]Ecosystem Health, Virginia Institute of Marine Science, William & Mary, Gloucester Point, Virginia, USA

Correspondence
Serina S. Wittyngham
Email: sswittyngham@vims.edu

Present address
Serina S. Wittyngham, Department of Biology, University of North Florida, Jacksonville, Florida, USA.

Funding information
National Science Foundation, Grant/Award Numbers: 1654374, 1832221, 2012670

Handling Editor: Samantha K. Chapman

Abstract

Consumers can directly (e.g., consumption) and indirectly (e.g., trophic cascades) influence carbon cycling in blue carbon ecosystems. Previous work found that large grazers have nuanced effects on carbon stocks, yet, small, bioturbating-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 quantify how the purple marsh crab, *Sesarma reticulatum*, influenced carbon stocks, flux, and recovery in salt marshes. *Sesarma* caused a 40%–70% loss in carbon stocks as fronts propagated inland (i.e., ungrazed to recovered transition), with front migration rates accelerating over time. Despite latitudinal differences, front migration rate had no effect on carbon stocks, flux, or time to replacement. When we included *Sesarma* disturbance in carbon flux calculations, we found 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. This work showcases the significant role of consumers in carbon storage and flux, challenging the classic paradigm of plant–sediment feedbacks as the primary ecogeomorphic driver of carbon cycling in blue carbon ecosystems.

KEYWORDS
blue carbon, carbon sequestration, consumer front, herbivory front, plant–herbivore interaction, plant–soil interaction, time to replacement, top-down control

INTRODUCTION

Blue carbon ecosystems bury one to two times more carbon than their terrestrial counterparts per unit area (Mcleod et al., 2011), making them critical for mitigating climate change (Howard et al., 2017). Consumers (e.g., herbivores, omnivores, and carnivores), however, can affect carbon cycling (He et al., 2020) through their direct (e.g., consumption) or indirect (e.g., trophic cascades) interactions with plants (He & Silliman, 2016). For example, large grazers (Hogs: Persico et al., 2017; Livestock: Graversen et al., 2022) can have negative, neutral, or positive effects on carbon stocks (Davidson et al., 2017). Consumer fronts, dense aggregations of small consumers bordering a resource (Silliman et al., 2013), are becoming more prevalent worldwide (e.g., beetles in forests: Birt & Coulson, 2015; urchins in kelp forests: Lauzon-Guay & Scheibling, 2007) and can disrupt geomorphic patterning and ecosystem functioning (Hughes et al., 2009; Vu et al., 2017). Despite their impact on plant biomass (Crotty et al., 2020) and sediment properties (Farron et al., 2020), the role of small consumers in mediating carbon fluxes remains a key knowledge gap in blue carbon ecosystems (Ren et al., 2022), with He et al. (2020) stating "Whether small invertebrate herbivores in … coastal wetlands have differential effects on soil carbon sequestration is still unknown."

To address this, we used salt marshes along the US Atlantic coast as representative blue carbon ecosystems to understand how small invertebrate consumers are influencing carbon flux and storage. US Atlantic salt marshes experience consumer fronts created by the purple marsh crab, *Sesarma reticulatum* (hereafter *Sesarma*), which consumes the smooth cordgrass, *Spartina alterniflora* (hereafter *Spartina*) (Angelini et al. 2018; Vu et al., 2017; Vu & Pennings, 2021). *Sesarma* fronts are occurring more frequently in this region, covering approximately 1% of total saltmarsh area at any given time (Crotty et al., 2020). In contrast to fronts created by their large counterparts and other small invertebrate consumers (e.g., *Littoraria irrorata*, *Prokelesia marginata*), *Sesarma* graze on both above- and belowground biomass (Coverdale et al., 2012), and form burrows, which increase soil oxygenation, decomposition, and erosion (Farron et al., 2020). *Sesarma*'s top-down control on *Spartina*, combined with its burrowing activities, can negatively influence vertical accretion capacity (Schultz et al., 2016; Williams & Johnson, 2021). Given these impacts on saltmarsh features, we would therefore expect this grazer to have considerable effects on carbon storage (Coverdale et al., 2014).

Sesarma fronts in the mid-Atlantic and Southeastern United States typically form at the heads of tidal creeks (Hughes et al., 2009), and as *Sesarma* exhaust food and suitable habitat, the front propagates inland in search of additional resources (Vu & Pennings, 2021). Their directional movement inland lowers elevation, creating favorable habitat for *Spartina* revegetation and allowing for recovery of many sediment and invertebrate properties (Wu et al., 2021). *Sesarma* fronts have three distinct zones: the leading edge (*Spartina* high marsh, hereafter "ungrazed zone"), the trailing edge (*Spartina* low marsh, hereafter "recovered zone"), and a band (3–8 m wide) of mudflat separating the two where *Sesarma* reside (hereafter "denuded zone") (Figure 1A). 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. Further, we expected front migration rate, calculated via remote sensing, to aid in carbon stock recovery, with faster migration potentially leaving some *Spartina* belowground biomass behind, aiding in revegetation and leading to quicker replacement times.

MATERIALS AND METHODS

Field collections

We evaluated *Sesarma* front influence on saltmarsh carbon cycling in three coastal US states: Virginia, South Carolina, and Georgia (Appendix S1: Table S1; Figure 1B). While *Sesarma* impact salt marshes in the Northeastern United States (Holdredge et al., 2009), Virginia is the northern limit of *Sesarma* fronts which create this distinct patterning, South Carolina is an intermediate, and Georgia is the southern limit. In each state, four independent consumer fronts that were at least 20 m apart were visited in August 2022 (Appendix S1: Table S1). At each front, five transects spanning the recovered zone to the ungrazed zone were delineated and a 0.0625-m^2 quadrat was placed in each of the three zones (recovered, denuded, ungrazed; Figure 1A) along each transect ($n = 60$ quadrats per state). In recovered zones, quadrats were 10 m from the denuded zone edge to ensure carbon stocks reflected areas that had been revegetated for at least five years (assumes a migration rate of 2 m $year^{-1}$; Hughes et al., 2009; see also Wu et al., 2021 for a similar space-for-time substitution) (Figure 1F–H). Quadrats were placed in the center of denuded zones, and 3 m into ungrazed zones. Within each quadrat, aboveground *Spartina* biomass was collected and 30-cm-deep sediment cores (Russian peat borer, 6 cm diameter; AMS, Inc., USA) were taken and sectioned into 5 cm segments ($n = 6$ sections per core). Plant and sediment samples were dried at 60°C for biomass and bulk density (BD), respectively, and sediment was muffled at 550°C for 6 h for organic matter content (loss on ignition [LOI]). Subsamples of sediments from each depth, zone, and state were acidified and ran on a Thermo FlashEA system to derive carbon fraction.

Remote sensing

We assessed front migration over ~25 years (between 1993/1994 and 2018/2019) using 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). In each state, we

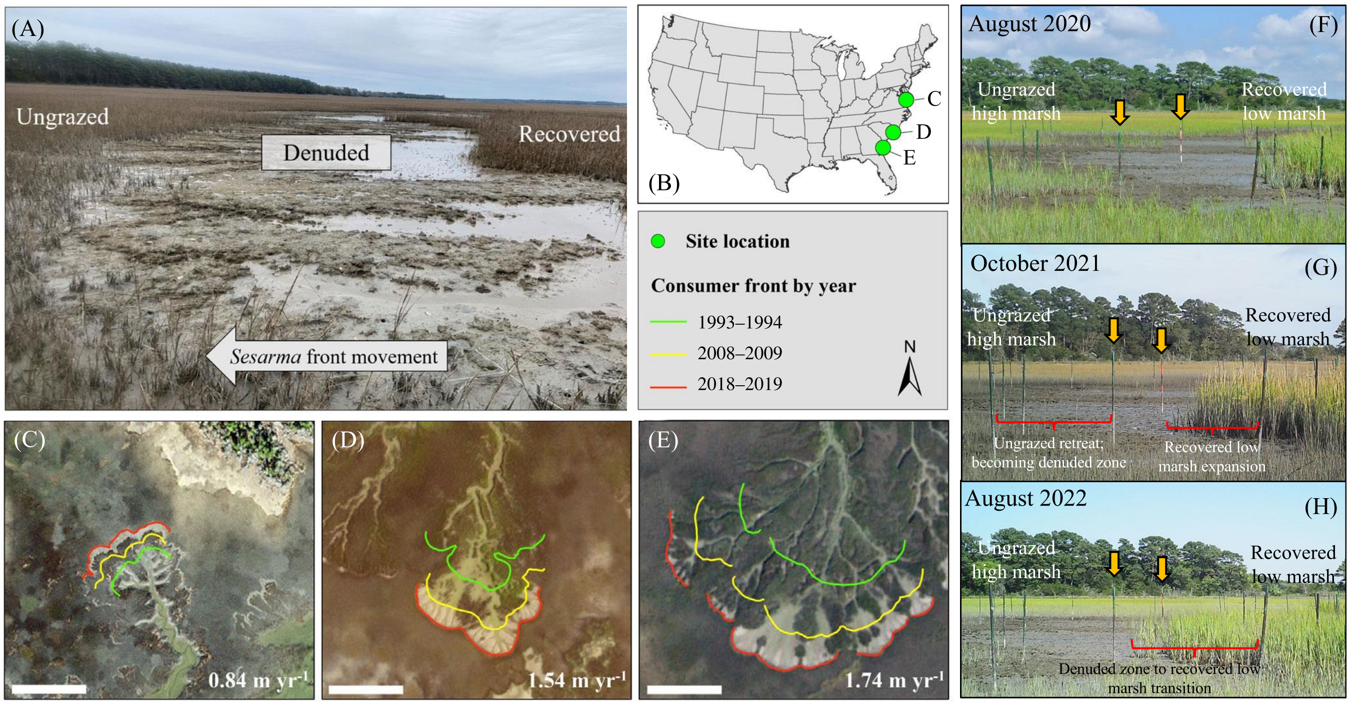

FIGURE 1 (A) Cross-sectional view of a representative consumer front depicting the three distinct zones: ungrazed, denuded, and recovered. Arrow indicates inland migration of consumer fronts. (B) Map of sampled US states (C: Virginia; D: South Carolina; E: Georgia). Location by year (1993–1994: green; 2008–2009: yellow; 2018–2019: red) at representative fronts in (C) Virginia, (D) South Carolina, and (E) Georgia. The values (in meters per year) shown in white on panels C–E refer to average migration rates per state (i.e., average of all calculated rates, $n = \sim 50$; Appendix S1: Tables S2–S4) between 1993/1994 and 2018/2019. The white scale bars correspond to 50 m. Photos of a migrating *Sesarma* front in (F) August 2020, (G) October 2021, and (H) August 2022. Gold arrows point to focal PVC poles and red brackets highlight the ungrazed high marsh retreat and low marsh recovery and expansion that formed the basis of the space-for-time substitution method used in this study. All photos (A, F, G, H) were taken by Serina S. Wittyngham.

randomly selected ~50 fronts of variable sizes from the latest aerial images (i.e., 2018 or 2019) within 10 km of our field sites. We manually delineated the leading edge of each front in 1993 (or 1994), 2008 (or 2009), and 2018 (or 2019) (Figure 1C–E; Appendix S1: Tables S2–S4). To quantify front migration between time periods, we generated three random points at each front identified in 2018/2019 and created transects to intersect the fronts in 1993/1994 and 2008/2009. The average length (in meters) of the transects represented the distance of front migration between time periods. Front migration rates (in meters per year) were calculated by dividing distance by the number of years between delineations (Figure 1C–E, Appendix S1: Tables S2–S4). In some cases (~7% of sites, Appendix S1: Tables S2–S4), fronts recently emerged and were absent in earlier images. For these, we measured the distance between the trailing and leading edges to make a conservative (minimal) migration estimate between time periods. If a front was absent in two consecutive delineation years (~2% of sites), an "NA" value was assigned to represent no migration. Rates were averaged by state and used to calculate carbon flux as described below. Geoprocessing was performed in ArcGIS (v10.7) following the methods of Chen and Kirwan (2022).

Carbon calculations and statistics

Following the methods of Craft et al. (1991), plots of carbon fraction by LOI were used to generate best-fit equations for each zone in each state (Appendix S1: Table S5). Using these equations, we calculated carbon fraction for all remaining sediment samples at each depth interval. Sediment carbon stock (in kilograms per square meter) was then calculated as:

$$\text{Carbon stock}\left(\text{kg}\,\text{m}^{-2}\right) = \Sigma\,\text{C fraction}\,(\text{BD} \times d), \tag{1}$$

where C fraction is the carbon content calculated for each depth increment (six sections per core), BD is the bulk density (in grams per cubic centimeter), and d is the depth interval (in centimeters). Values were converted to kilograms per square meter and summed to derive a carbon stock per core. Plant carbon stocks (in kilograms per square meter) were derived using *Spartina* carbon fractions from Ho and Pennings (2013) and dry biomass. Carbon stock results are presented as sediment only or as sediment + plant to reflect cumulative stocks. Carbon flux (ΔC) was calculated as:

$$\Delta \mathrm{C}\left(\mathrm{kg\,m}^{-2}\,\mathrm{year}^{-1}\right) = \mathrm{C}\frac{r_{\mathrm{cf}}}{s}, \tag{2}$$

where C is a given carbon stock (sediment only, or sediment + plants), r_{cf} is the average front migration rate (calculated from remote sensing observations), and s is the distance traveled by each front. When the difference in carbon stocks between ungrazed and denuded zones (i.e., ungrazed to denuded transition) is substituted for C, the resulting change shows how much carbon is lost as a front migrates (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 (i.e., carbon flux) in carbon stock as a *Sesarma* front migrates is the difference between gain and loss.

Using the method of Smith and Kirwan (2021) for determining how long it will take an ecosystem to reaccumulate lost carbon, time to replacement (t_r) was calculated as:

$$t_r\,(\mathrm{year}) = \frac{\Delta \mathrm{C}}{\mathrm{CAR}}, \tag{3}$$

where ΔC is the carbon stock lost (in kilograms per square meter) during the ungrazed to denuded transition (i.e., carbon loss) and CAR is the carbon accumulation or gain rate (in kilograms per square meter per year). We calculated time to replacement in two ways: (1) using a regional CAR of $0.1236\,\mathrm{kg\,m}^{-2}\mathrm{year}^{-1}$ for the South Atlantic-Gulf from Wang et al. (2019) and (2) using our site-specific carbon gain rates (i.e., denuded to recovered transition) (Appendix S1: Table S6). There are limitations to each calculation. Our carbon gain rate 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.

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

RESULTS

Total carbon stocks (sum of sediment + plant stocks across zones; Equation 1) in South Carolina were 62% higher than those in Georgia and 80% higher than in Virginia (Figure 2A–C; Appendix S1: Tables S7 and S8). Whether plants were included or not, in all three states, ungrazed zones had higher stocks than denuded zones, although the magnitude of difference varied by state (Figure 2A–C; Appendix S1: Tables S7 and S8). In contrast to other states, recovered zone carbon stocks (sediment + plant) in South Carolina were 33% higher than ungrazed zones (Figure 2B). Recovered zones in Georgia had 51% higher stocks when plant carbon was included (sediment only vs. sediment + plant; Figure 2C; Appendix S1: Tables S7 and S8). All three states experienced significant carbon stock loss with front migration (i.e., ungrazed to denuded transition, Figure 3A; Appendix S1: Table S8), though losses were not statistically different between states (Figure 3A; Appendix S1: Table S7). South Carolina had the largest carbon gain (i.e., denuded to recovered transition, Figure 3B), and Virginia experienced an additional loss of carbon (Appendix S1: Table S8). 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; Equation 2; Figure 3C; Appendix S1: Table S8).

Sesarma front migration has accelerated by ~30% in each state since the early 1990s (Appendix S1: Tables S2–S4). *Sesarma* fronts in Virginia are migrating the slowest at $0.84\,\mathrm{m\,year}^{-1}$, South Carolina at $1.54\,\mathrm{m\,year}^{-1}$, and Georgia the fastest at $1.74\,\mathrm{m\,year}^{-1}$ (Figure 1C–E). Despite fronts in Georgia moving more than two times faster than those in Virginia, migration rate had no effect on carbon loss or carbon gain (Appendix S1: Figure S1A,B; Table S8). Migration rate also had no effect on time to replacement, regardless of whether the regional CAR (Appendix S1: Figure S1C) or local carbon gain rate was used for calculations (Appendix S1: Table S8). Approximately 20% of the fronts tracked through remote sensing observations in each state recently emerged (i.e., "minimal"; Appendix S1: Tables S2–S4), providing additional support that *Sesarma* fronts are increasing in prevalence over time (Crotty et al., 2020).

Using the South Atlantic-Gulf region CAR ($0.1236\,\mathrm{kg\,m}^{-2}\,\mathrm{year}^{-1}$; Wang et al., 2019), replacement times were longest in Virginia at 29 ± 2.6 years, followed by South Carolina at 22.51 ± 8.05 years and Georgia at

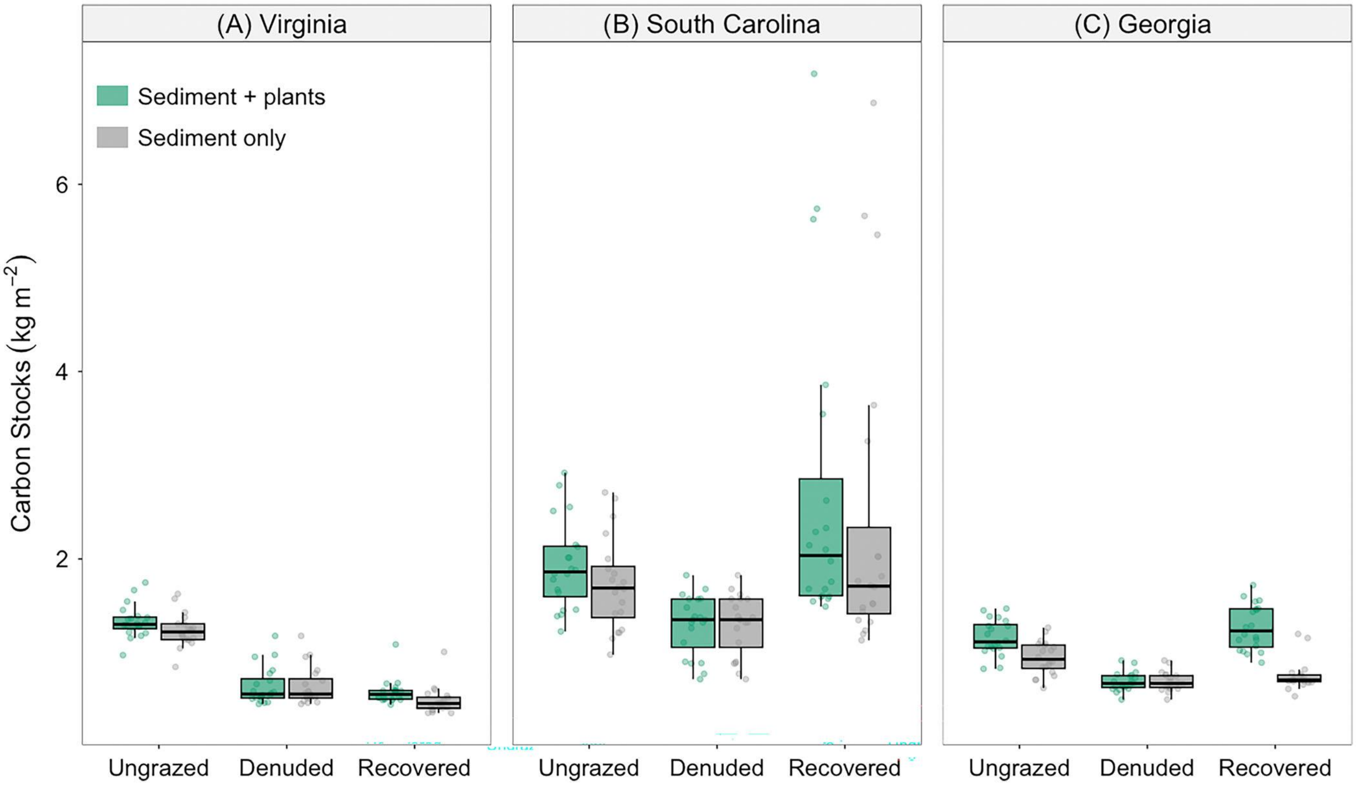

FIGURE 2 Carbon stocks in kilograms per square meter in ungrazed, denuded, and recovered zones in (A) Virginia, (B) South Carolina, and (C) Georgia. Green boxes are cumulative carbon stocks (sediment + plants), and gray boxes are sediment-only stocks. Sediment-only and sediment + plants are equal in denuded zones, as there were no plants. Data are shown as mean ± SE.

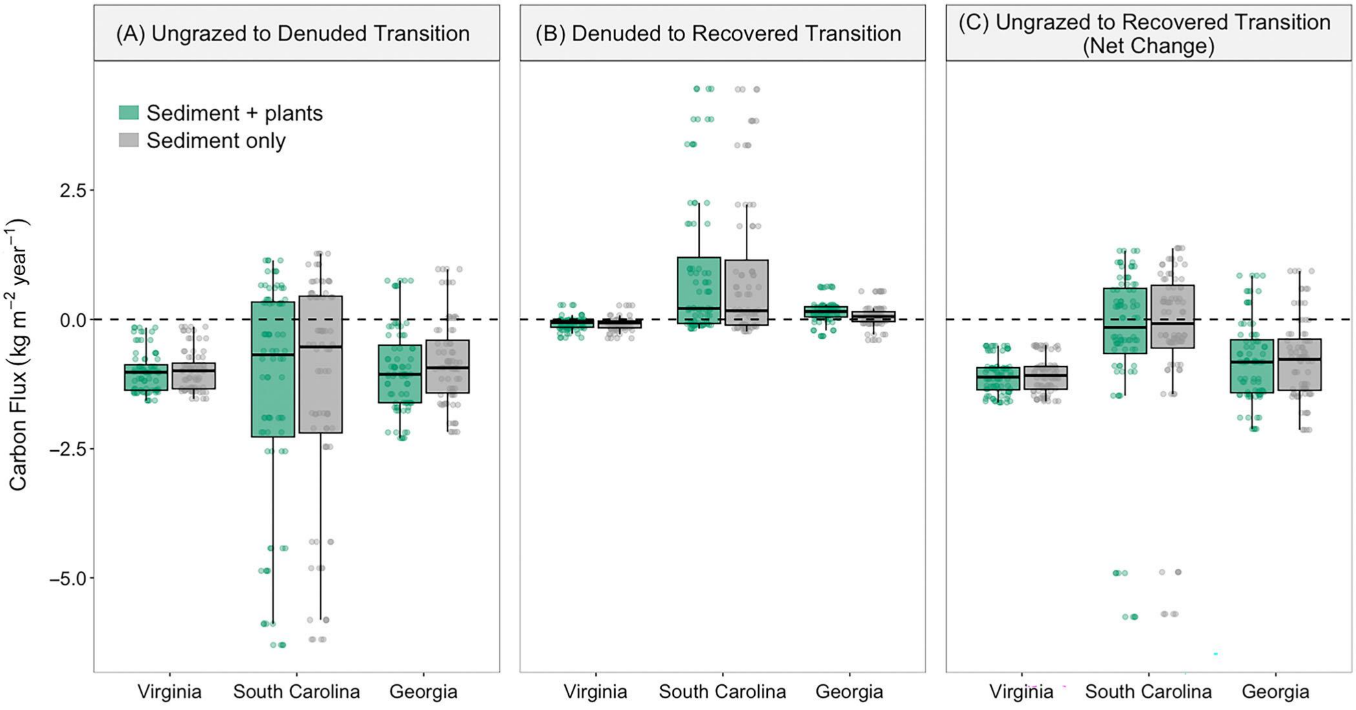

FIGURE 3 Carbon flux in kilograms per square meter per year in Virginia, South Carolina, and Georgia as (A) ungrazed zones transition to denuded zones, (B) denuded zones transition to recovered zones, and (C) overall net change from ungrazed to recovered zones. Green boxes are cumulative carbon flux (sediment + plants), and gray boxes are sediment-only flux. Values below the dashed line represent carbon losses, and those above the dashed line represent carbon gains. Data are shown as mean ± SE.

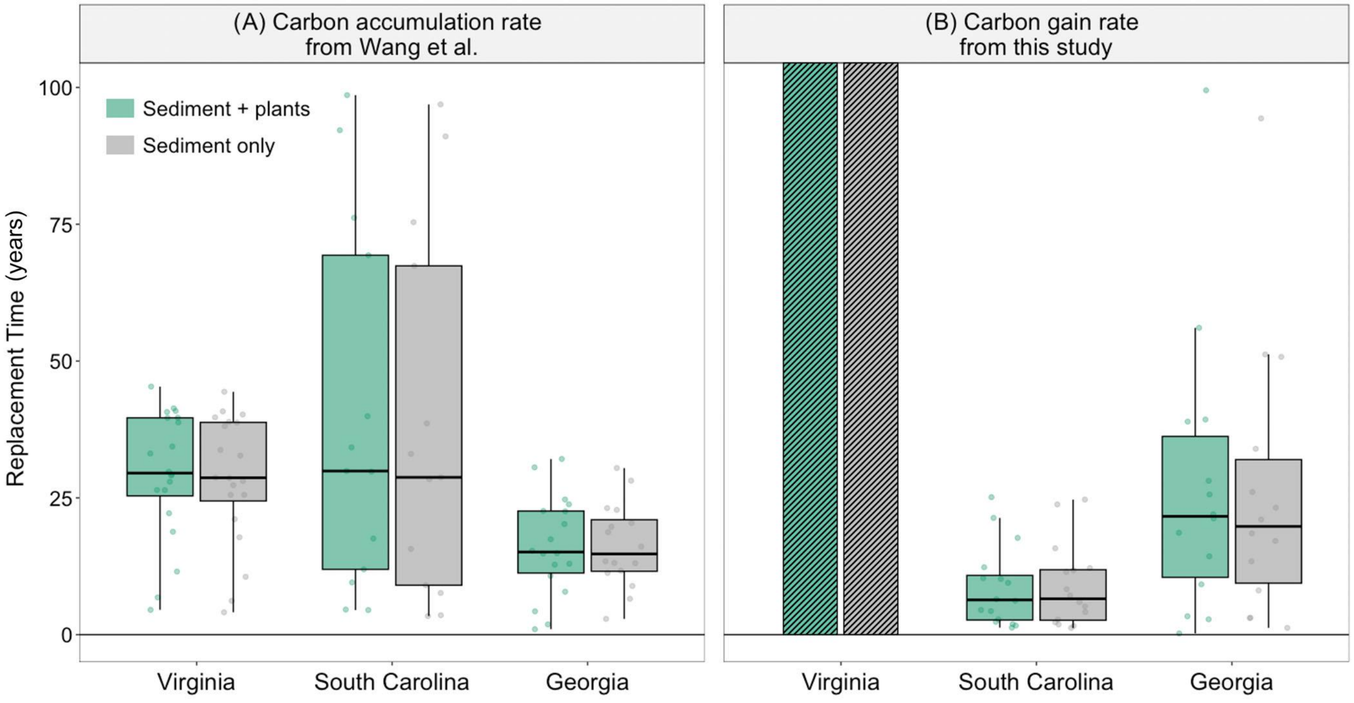

FIGURE 4 Time to replacement in years for Virginia, South Carolina, and Georgia calculated using (A) regional carbon accumulation rate (CAR) from Wang et al. (2019) and (B) carbon gain rate calculated in this study. In panel (B), carbon gain rate in Virginia is zero, thus shaded bars indicate an infinite replacement time. Green boxes are cumulative carbon replacement (sediment + plants), and gray boxes are replacement in sediment only. Data are shown as mean ± SE.

13.55 ± 2.62 years, although these differences were not statistically significant (Figure 4A; Appendix S1: Table S8). When using site-specific carbon gain rates calculated in this study (Appendix S1: Table S6), 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 years and Georgia in 16.94 ± 6.51 years (Figure 4B).

DISCUSSION

Small, bioturbating herbivores remove plant biomass and disrupt sediment properties (Angelini et al. 2018; Crotty et al., 2020; Wilson et al., 2012), yet their influence on carbon flux and recovery is a distinct knowledge gap (He et al., 2020; Ren et al., 2022). Here, we found that fronts created by the small invertebrate grazer, *Sesarma*, cause carbon loss in US mid-Atlantic and southeastern salt marshes, a finding similar to previous work in New England (Coverdale et al., 2014). In contrast to New England marshes, where grazing can cause marsh edge loss without recovery, fronts at lower latitudes experience low marsh revegetation, thus we were uniquely able to quantify carbon loss, gain, and recovery, all of which varied by state. Despite a latitudinal gradient in migration rates, they were not a significant predictor of carbon flux or recovery. This suggests that front-driven decreases in elevation, which can alter primary production rates (Morris et al., 2002), most likely explain these variations in carbon flux and recovery. Although *Sesarma* fronts only cover 1% of total marsh area at any given time, their increased prevalence (Crotty et al., 2020) and ability to cause permanent state change (Wu et al., 2021), combined with accelerating migration rates and slow carbon recovery rates, suggest their influence exceeds this limited spatial estimate and can actually affect 4%–12% of total marsh area (Appendix S2).

In both Virginia (Figure 2A) and Georgia (Figure 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, suggesting that labile carbon may be an important source in this system (Figure 2C). Surprisingly, South Carolina carbon stocks in the recovered zones were 33% higher than in the ungrazed zones. This recovery, which exceeded undisturbed areas, follows a disturbance trajectory outlined by Wu et al. (2021) (Figure 2B), and is most likely driven by the tight coupling between *Spartina* productivity and elevation (FitzGerald & Hughes, 2019). 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 (Figure 3C).

The lowered elevation driven by *Sesarma* fronts creates conditions unfavorable for continued crab colonization, yet favorable for *Spartina* revegetation (Vu & Pennings, 2021). In fact, *Spartina* can reoccupy denuded zones within a single growing season (Wittyngham, unpublished data), suggesting potential for rapid recovery of carbon stocks. However, when considering *Sesarma* disturbance in time to replacement calculations (Equation 3; Smith & Kirwan, 2021), impacts to carbon stocks can persist for decades (Figure 4), despite quick *Spartina* revegetation. Specifically, when using the carbon gain rate from this study (i.e., denuded to recovered transition), the inclusion of grazing caused a 10-fold increase in Georgia's recovery time, while Virginia will never replace its lost carbon (Figure 4B). Interestingly, the sizable carbon stock of the recovered zone in South Carolina (Figure 2B) shortened its replacement time (Figure 4B) when compared with calculations using the South Atlantic-Gulf region CAR (Wang et al., 2019).

The space-for-time substitution approach we used relies on the key assumption that prior to *Sesarma* front formation, carbon stocks in the recovered low marsh were equivalent to the ungrazed high marsh. *Sesarma* fronts are directly responsible for lowering elevation and causing a transition from high to low marsh (Vu et al., 2017; Vu & Pennings, 2021; Wu et al., 2021), supporting this assumption. Nevertheless, if this assumption does not hold (i.e., low marsh carbon stocks were always lower than ungrazed high marsh), then our estimates of carbon stock loss and recovery rates are too high.

Overall, we show that a small invertebrate consumer has substantial, negative effects on carbon stocks, a finding in agreement with some (Persico et al., 2017) and contrary to other (Graversen et al., 2022) previous work on large consumers (Davidson et al., 2017). 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 carbon cycling in blue carbon ecosystems (FitzGerald & Hughes, 2019). Plant–sediment feedbacks that stabilize wetlands under sea-level rise are governed by tidal channel evolution (D'Alpaos et al., 2019), yet observations of channel elongation are often restricted to locations with consumer fronts or other vegetation disturbance (Hughes et al., 2009; Kirwan et al., 2008). Our observation of accelerated front migration rates suggests that the direct (carbon consumption) and indirect (marsh stability) impacts of consumers on carbon cycling will intensify under accelerated sea-level rise. Given *Sesarma*'s significant 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, especially in blue carbon ecosystems.

AUTHOR CONTRIBUTIONS

Serina S. Wittyngham, David Samuel Johnson, and Matthew L. Kirwan designed the study. Serina S. Wittyngham conducted field collections, and Yaping Chen conducted remote sensing analyses. Serina S. Wittyngham analyzed data and wrote the first draft. All authors contributed to drafts and gave approval for publication.

ACKNOWLEDGMENTS

This work was funded by the National Science Foundation (#1654374, 1832221, and 2012670). We thank E. Goetz, A. Nemeth, J. Davis, E. Harper-Smith, J. Krask, and K. Martínez-Soto for field help, B. Rein, M. Watts, A. Wilkinson, and T. Meredith for lab support, and Dr. A. Smith for discussions that improved this work. We also thank Dr. S. Pennings and Dr. CK Ho for providing percent carbon values of *Spartina* from their previous study (Ho & Pennings, 2013), and Dr. E. Smith for advice on site selection in South Carolina.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Wittyngham et al., 2024) are available in the Environmental Data Initiative's EDI Data Portal at https://doi.org/10.6073/pasta/bf80a94af8efe34482e5919ddaf75c06.

ORCID

Serina S. Wittyngham https://orcid.org/0000-0002-1421-9690
David Samuel Johnson https://orcid.org/0000-0002-7898-4893
Yaping Chen https://orcid.org/0000-0003-1372-8861
Matthew L. Kirwan https://orcid.org/0000-0002-0658-3038

REFERENCES

Angelini, C., S. G. van Montfrans, M. J. S. Hensel, Q. He, and B. R. Silliman. 2018. "The Importance of an Underestimated Grazer under Climate Change: How Crab Density, Consumer Competition, and Physical Stress Affect Salt Marsh Resilience." *Oecologia* 187: 205–217.

Birt, A. G., and R. N. Coulson. 2015. "Southern Pine Beetle Herbivory in the Southern United States: Moving from External Disturbance to Internal Process." In *Simulation Modeling of Forest Landscape Disturbances*, edited by A. Perera, B. Sturtevant, and L. Buse. Cham: Springer. https://doi.org/10.1007/978-3-319-19809-5_7.

Chen, Y., and M. L. Kirwan. 2022. "A Phenology- and Trend-Based Approach for Accurate Mapping of Sea-Level Driven Coastal Forest Restreat." *Sensing of Environment* 281: 113229.

Coverdale, T. C., A. H. Altieri, and M. D. Bertness. 2012. "Belowground Herbivory Increases Vulnerability of New England Salt Marshes to Die-Off." *Ecology* 93: 2085–94.

Coverdale, T. C., C. P. Brisson, E. W. Young, S. F. Yin, J. P. Donnelly, and M. D. Bertness. 2014. "Indirect Human Impacts Reverse Centuries of Carbon Sequestration and Salt Marsh Accretion." *PLoS One* 9: e93296. https://doi.org/10.1371/journal.pone.0093296.

Craft, C. B., E. D. Seneca, and S. W. Broome. 1991. "Loss on Ignition and Kjeldahl Digestion for Estimating Organic Carbon and Total Nitrogen in Estuarine Marsh Soils: Calibration with Dry Combustion." *Estuaries* 14: 175–79.

Crotty, S. M., C. Ortals, T. M. Pettengill, L. Shi, M. Olabarrieta, M. A. Joyce, A. H. Altieri, et al. 2020. "Sea-Level Rise and the Emergence of a Keystone Grazer Alter the Geomorphic Evolution and Ecology of Southeast US Salt Marshes." *Proceedings of the National Academy of Sciences of the United States of America* 117: 17891–902.

D'Alpaos, A., S. Lanzoni, A. Rinaldo, and M. Marani. 2019. "Salt-Marsh Ecogeomorphological Dynamics and Hydrodynamic Circulation." In *Coastal Wetlands: An Integrated Ecosystem Approach*, edited by G. M. E. Perillo, E. Wolanski, D. R. Cahoon, and C. S. Hopkinson. Amsterdam, Netherlands: Elsevier. https://doi.org/10.1016/B978-0-444-63893-9.00005-8.

Davidson, K. E., M. S. Fowler, M. W. Skov, S. H. Doerr, N. Beaumont, and J. N. Griffin. 2017. "Livestock Grazing Alters Multiple Ecosystem Properties and Services in Salt Marshes: A Meta-Analysis." *Journal of Applied Ecology* 54: 1395–1405.

Farron, S. J., Z. J. Hughes, D. M. FitzGerald, and K. B. Strom. 2020. "The Impacts of Bioturbation by Common Marsh Crabs on Sediment Erodibility: A Laboratory Flume Investigation." *Estuarine, Coastal and Shelf Science* 238: e106710.

FitzGerald, D. M., and Z. Hughes. 2019. "Marsh Processes and Their Response to Climate Change and Sea-Level Rise." *Annual Review of Earth and Planetary Sciences* 47: 481–517.

Graversen, A. E. L., G. T. Banta, P. Masque, and D. Krause-Jensen. 2022. "Carbon Sequestration Is Not Inhibited by Livestock Grazing in Danish Salt Marshes." *Limnology and Oceanography* 67: 519–535.

He, Q., H. Li, C. Xu, Q. Sun, M. D. Bertness, C. Fang, B. Li, and B. R. Silliman. 2020. "Consumer Regulation of the Carbon Cycle in Coastal Wetland Ecosystems." *Philosophical Transactions of the Royal Society B* 375: 20190451.

He, Q., and B. R. Silliman. 2016. "Consumer Control as a Common Driver of Coastal Vegetation Worldwide." *Ecological Monographs* 86: 278–294.

Ho, C., and S. C. Pennings. 2013. "Preference and Performance in Plant-Herbivore Interactions across Latitude – A Study in U.S. Atlantic Salt Marshes." *PLoS One* 8: e59829.

Holdredge, C., M. D. Bertness, and A. H. Altieri. 2009. "Role of Crab Herbivory in Die-off of New England Salt Marshes." *Conservation Biology* 23: 672–79.

Howard, J., A. Sutton-Grier, D. Herr, J. Kleypas, E. Landis, E. Mcleod, E. Pidgeon, and S. Simpson. 2017. "Clarifying the Role of Coastal and Marine Systems in Climate Mitigation." *Frontiers in Ecology and the Environment* 15: 42–50.

Hughes, Z. J., D. M. FitzGerald, C. A. Wilson, S. C. Pennings, K. Więski, and A. Mahadevan. 2009. "Rapid Headward Erosion of Marsh Creeks in Response to Relative Sea Level Rise." *Geophysical Research Letters* 36: L03602.

Kirwan, M. L., A. B. Murray, and W. S. Boyd. 2008. "Temporary Vegetation Disturbance as an Explanation for Permanent Loss of Tidal Wetlands." *Geophysical Research Letters* 35: L05403.

Lauzon-Guay, J., and R. E. Scheibling. 2007. "Seasonal Variation in Movement, Aggregation and Destructive Grazing of the Green Sea Urchin (*Strongylocentrotus droebachiensis*) in Relation to Wave Action and Sea Temperature." *Marine Biology* 151: 2109–18.

Mcleod, E., G. L. Chmura, S. Bouillon, R. Salm, M. Björk, C. M. Duarte, C. E. Lovelock, W. H. Schlesinger, and B. R. Silliman. 2011. "A Blueprint for Blue Carbon: Toward an Improved Understanding of the Role of Vegetated Coastal Habitats in Sequestering CO_2." *Frontiers in Ecology and the Environment* 9: 552–560.

Morris, J. T., P. V. Sundareshwar, C. T. Nietch, B. Kjerfve, and D. R. Cahoon. 2002. "Responses of Coastal Wetlands to Rising Sea Level." *Ecology* 83: 2869–77.

Persico, E. P., S. J. Sharp, and C. Angelini. 2017. "Feral Hog Disturbance Alters Carbon Dynamics in Southeastern US Salt Marshes." *Marine Ecology Progress Series* 580: 57–68.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Ren, L., K. Jensen, P. Porada, and P. Mueller. 2022. "Biota-Mediated Carbon Cycling – A Synthesis of Biotic-Interaction Controls on Blue Carbon." *Ecology Letters* 25: 521–540.

Schultz, R. A., S. C. Anisfeld, and T. D. Hill. 2016. "Submergence and Herbivory as Divergent Causes of Marsh Loss in Long Island Sound." *Estuaries and Coasts: Journal of the Estuarine Research Federation* 39: 1367–75.

Silliman, B. R., M. W. McCoy, C. Angelini, R. D. Holt, J. N. Griffin, and J. van de Koppel. 2013. "Consumer Fronts, Global Change, and Runaway Collapse in Ecosystems." *Annual Review of Ecology, Evolution, and Systematics* 44: 503–538.

Smith, A. J., and M. L. Kirwan. 2021. "Sea Level-Driven Marsh Migration Results in Rapid Net Loss of Carbon." *Geophysical Research Letters* 48: e2021GL092420.

Vu, H. D., and S. C. Pennings. 2021. "Directional Movement of Consumer Fronts Associated with Creek Heads in Salt Marshes." *Ecology* 102: e03447.

Vu, H. D., K. Więski, and S. C. Pennings. 2017. "Ecosystem Engineers Drive Creek Formation in Salt Marshes." *Ecology* 98: 162–174.

Wang, F., X. Lu, C. J. Sanders, and J. Tang. 2019. "Tidal Wetland Resilience to Sea Level Rise Increases Their Carbon Sequestration Capacity in United States." *Nature Communications* 10: 5434. https://doi.org/10.1038/s41467-019-13294-z.

Williams, B. L., and D. S. Johnson. 2021. "Role of Ecological Interactions in Saltmarsh Geomorphic Processes." *Marine Ecology Progress Series* 658: 149–161.

Wilson, C. A., Z. J. Hughes, and D. M. FitzGerald. 2012. "The Effects of Crab Bioturbation on Mid-Atlantic Saltmarsh Tidal

Creek Extension: Geotechnical and Geochemical Changes." *Estuarine, Coastal and Shelf Science* 106: 33–44.

Wittyngham, S. S., D. S. Johnson, Y. Chen, and M. L. Kirwan. 2024. "A Grazing Crab Drives Saltmarsh Carbon Storage and Recovery in VA, SC, and GA ver. 3." Environmental Data Initiative. https://doi.org/10.6073/pasta/bf80a94af8efe34482e5919ddaf75c06.

Wu, F., S. C. Pennings, C. Ortals, J. Ruiz, W. R. Farrell, S. M. McNichol, C. Angelini, A. C. Spivak, M. Alber, and C. Tong. 2021. "Disturbance Is Complicated: Headward-Eroding Saltmarsh Creeks Produce Multiple Responses and Recovery Trajectories." *Limnology and Oceanography* 67: S86–S100. https://doi.org/10.1002/lno.1.1867.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Wittyngham, Serina S., David Samuel Johnson, Yaping Chen, and Matthew L. Kirwan. 2024. "A Grazing Crab Drives Saltmarsh Carbon Storage And Recovery." *Ecology* 105(9): e4385. https://doi.org/10.1002/ecy.4385