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Scaling the Spatial and Temporal Effects of Wrack Disturbance Across a Saltmarsh Landscape

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Abstract

Disturbance effects are rarely distributed uniformly over space or time. Thus, scaling up the effects of disturbances requires detailed measurements across multiple spatial scales. To characterize disturbance from wrack we used monthly images from an unmanned aerial vehicle (UAV) in a 144,500 m^2 *Spartina alterniflora* saltmarsh on Sapelo Island, Georgia (USA), from March 2020 to December 2022. Prior work as well as the results of our study demonstrated that wrack persisting for ≥ 2 months ("persistent wrack") affects underlying vegetation. During our study, persistent wrack comprised ~ 30% of the average monthly wrack area (161 m^2 or ~ 0.10% of the total *S. alterniflora* marsh) and showed an annual peak between July and September. We quantified the effects of persistent wrack on live *S. alterniflora*, two invertebrate taxa (snails and burrowing marsh crabs), and porewater via field surveys of paired wrack-affected and wrack-free controls. At each monthly sampling point relative to controls, *S. alterniflora* stem density in wrack-affected plots was 41% lower on average and snail density lower by 25%, while crab burrow abundance and porewater parameters remained similar between controls and disturbed plots. Using wrack area from monthly UAV imaging, we scaled-up plot-level effects to marsh-level and found a < 1% change per species in abundance. Thus, our data suggest that even if wrack has strong local effects, the effects can be minor in *S. alterniflora* marshes at a landscape scale. This study demonstrates that field monitoring to quantify the effects of disturbances, coupled with repeat UAV imagery, allows for scaling that better contextualizes the overall impact than either method alone.

Keywords Drones · Wrack · *Spartina alterniflora* · Marsh periwinkles · Crabs · Pulse disturbance

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Introduction

Disturbances can be heterogeneous in their frequency, intensity, and magnitude, which can influence their net effects on ecosystem structure and function (Connell, 1978; Sousa, 1979; Rykiel, 1985). For example, Strydom et al. (2020) found that effects of a marine heatwave on seagrass cover were uneven, with greater losses in areas that experienced greater intensity and duration of high temperatures. Large-scale, one-time studies can capture the heterogeneity of disturbances across space and can facilitate estimation of effects at the landscape scale (entire area considered to be affected or have the potential to be affected by disturbances). However, these studies may miss temporal trends in the disturbance regime that have strong effects on community structure and population dynamics (Connell, 1978). Therefore, considering the patterns of disturbance and the magnitude in an ecosystem across both space and time is key to generating a clearer understanding of disturbance effects.

Disturbance effects on communities and ecosystems are of particular interest in coastal vegetated systems where dominant foundation species provide the primary physical habitat (Wernberg, 2011; Boström et al., 2011; Byers & Grabowski, 2014; Romero et al., 2015; Byers, 2024). Many of these structured coastal habitats are damaged or lost due to increased stressors from natural disturbances such as hurricanes and cold snaps in mangrove forests (Danielson et al., 2017), overgrazing in seagrass meadows (Tomas et al., 2015), and warming in coral reefs (Adjeroud et al., 2002). Coastal saltmarshes are no exception due to their global distribution and wide variation in the drivers, such as hydroperiod, seascape, and climatic region, that structure their ecosystem functioning, like support of nursery habitats or forage areas of nekton (Ziegler et al., 2021). Regional disturbances to saltmarshes along the East Coast of the United States include droughts (Alber et al., 2008) and hurricanes (Guntenspergen et al., 2021; Smith et al., 2024), while local disturbances include winter ice scouring (Reidenbaugh et al., 1983; FitzGerald et al., 2020), wrack deposition (Li & Pennings, 2016), ponding (DeLaune et al., 1994), and vegetation dieback (McFarlin et al., 2015). Although coastal saltmarshes cover a small area of the globe, they provide multiple ecosystem services including nursery habitat for recreational and commercially important nekton (Vinagre et al., 2009), carbon sequestration (Chmura et al., 2003; Mudd et al., 2009; Macreadie et al., 2013) and shoreline protection (McKee & Vervaeke, 2018). Understanding the susceptibility and effects of disturbances on saltmarshes is especially important due to the important services these ecosystems provide (Pennings & Bertness, 2001).

In saltmarsh ecosystems, one of the most common localized disturbances is wrack, which is detrital material that is deposited into the marsh by the tide. In the Southeastern United States, wrack is commonly derived from the dominant marsh cordgrass, *Spartina alterniflora* (as per Bortolus et al., 2019; Reidenbaugh & Banta, 1980). Past studies quantifying wrack effects have used aerial imagery (Alexander, 2008; Reidenbaugh & Banta, 1980), field surveys (Valiela & Rietsma, 1995; Fischer et al., 2000), plot-level quantification (Moffett et al., 2015), and manipulative experiments (Pennings & Richards, 1998; Hanley et al., 2017). These studies generated many new insights but often lacked the spatial and temporal resolution necessary to account for disturbance heterogeneity across the landscape.

Past studies have shown that wrack that is present for only a short period (<2 months; henceforth "ephemeral wrack") has little or no effect on *S. alterniflora* (Reidenbaugh & Banta, 1980; Bertness & Ellison, 1987; Stalter et al., 2006). In contrast, if *S. alterniflora* is covered by wrack for longer periods (≥2 months; hereafter "persistent wrack"), the wrack will smother and kill the underlying vegetation, reducing overall plant biomass and leaving behind an area of bare substrate (Valiela & Rietsma, 1995; Li & Pennings, 2016). In a Rhode Island, USA saltmarsh, it took *S. alterniflora* 7 weeks to be completely killed when covered by wrack (Bertness & Ellison, 1987). Similarly, in a 7-month study of wrack disturbance Stalter et al. (2006) found that at least 2 months of continuous wrack deposition led to *S. alterniflora* death in a South Carolina, USA saltmarsh. Additionally in a Massachusetts, USA saltmarsh, a 12-month study of wrack disturbance at low marsh elevations found that after 2 months of wrack burial, *S. alterniflora* cover in the low marsh was reduced by ~10% and was completely killed within 6 months of initial deposition (Hartmann et al., 1982). Thus, distinguishing ephemeral wrack from persistent wrack, and documenting the spatial extent of persistent wrack should provide a better estimate of the effects of wrack on saltmarsh systems at a landscape scale.

Wrack disturbances are often assessed by measuring the effects on the vegetative community and/or dominant plant species (Bertness & Ellison, 1987; Smith et al., 2021). However, the destruction of the aboveground plant biomass likely cascades to affect the organisms that use the vegetation as food or habitat, given the important relationships between saltmarsh invertebrates and *S. alterniflora* (Bertness & Miller, 1984; Bertness, 1985; McFarlin et al., 2015), and the key role these invertebrates play in the marsh food web (Bertness, 1985; Angelini et al., 2015). Thus, determining how invertebrates are affected by wrack would improve our overall understanding of disturbance in these systems. Due to the predominant effects of wrack on *S. alterniflora* vegetation shown by past studies, it is also important to consider belowground effects from wrack disturbances. *Spartina alterniflora* roots release oxygen into the anoxic sediment leading to increased oxidation and expansion of the oxic zone (Koretsky et al., 2008). This alteration of oxygen within the sediments of the marsh can lead to chemical interactions that can alter pH, redox potential (Eh), and salinity (Moffett & Gorelick, 2016). Thus, disturbances to aboveground leaves and stems have the potential to translate into belowground effects such as changes in root activity, which can affect porewater chemistry. Therefore, studying these effects to sediment biogeochemistry is necessary to understand the total possible effects of wrack deposition on saltmarsh function as it relates to vegetation, invertebrate, and biogeochemical alterations.

Here, we used repeated wrack measurements from UAV imagery combined with concurrent fine-scale field measurements to scale up the effects of wrack disturbance to the entire area of the *S. alterniflora* marsh. Our study was focused on a Southeastern US saltmarsh since most historical studies of wrack disturbance effects were performed in higher latitudes of the Mid-Atlantic and Northeastern US. Studies often use small (~0.25 m^2) plot-level manipulations (Pennings & Richards, 1998; Brewer et al., 1998; Hanley et al., 2017) or aerial and UAV imagery (Alexander, 2008; Lynn et al., 2024) to assess the effects of wrack disturbance, but few have combined both approaches to contextualize plot-level data and scale it up to the larger system. The combination of multiple approaches can lead to better estimates when scaling disturbance effects (Mayor et al., 2015).We focused on wrack deposited on *S. alterniflora* only, because this is the dominant plant in southeastern marshes. Our objectives were to: (1) assess the proportion of wrack that persists in the marsh for ≥2 months and how the proportion fluctuates over time, (2) quantify the absolute and relative effects of persistent wrack on marsh biota and porewater chemistry in the field, and (3) scale-up the plot-level data to assess the landscape-level effects of persistent wrack on major saltmarsh biota.

Materials and Methods

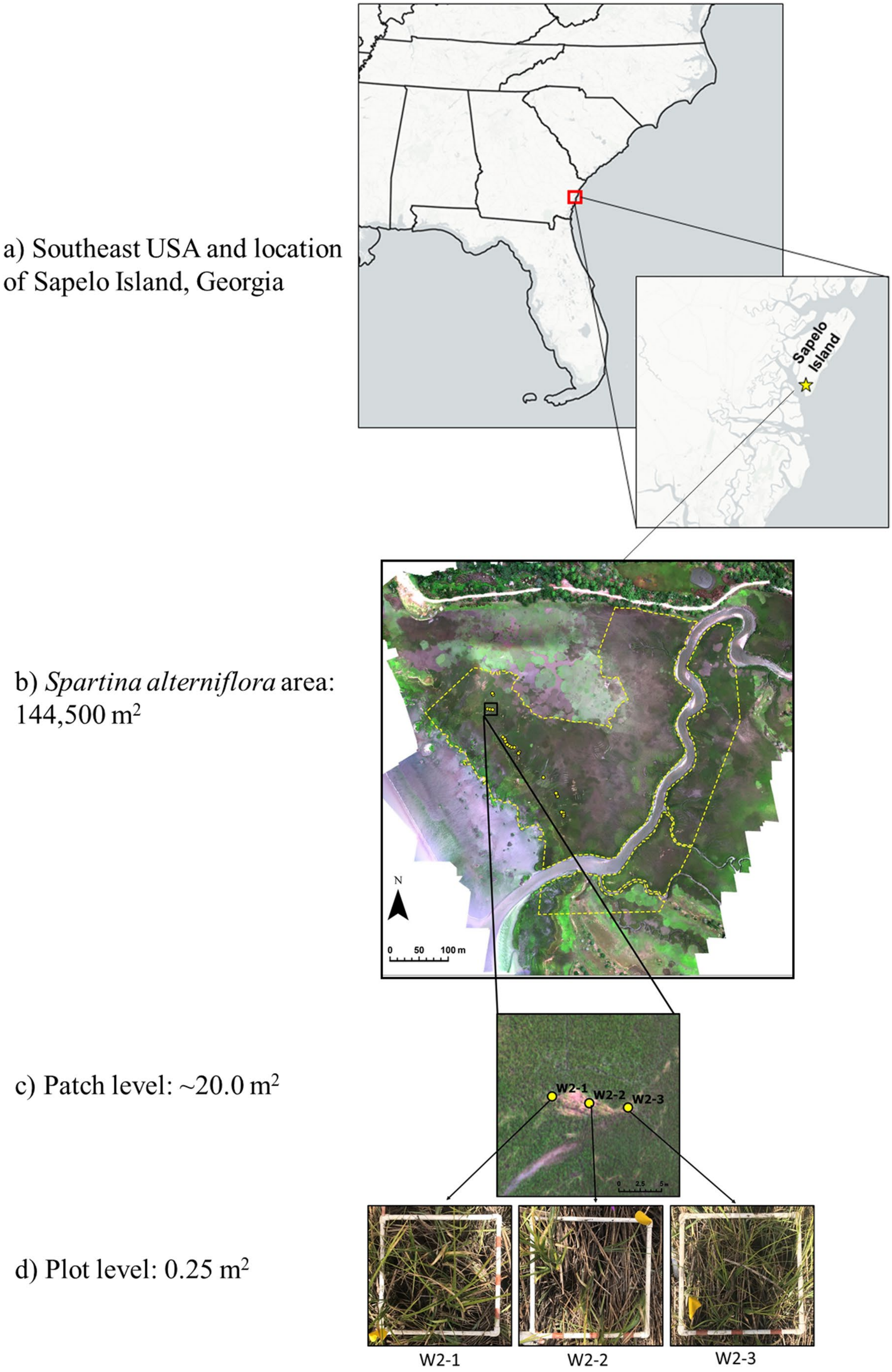
Site Description

We examined wrack patches in Dean Creek saltmarsh on the southern end of Sapelo Island, Georgia, USA (Fig. 1a), within the domain of the Georgia Coastal Ecosystems Long-Term Ecological Research (GCE LTER) site (31.387806°, −81.281861°). Dean Creek marsh experiences semidiurnal tides and is a mesotidal system with a tidal range of 2–3 m. In our system above average high tide events caused by wind, hurricanes, and perigean spring tides can all cause wrack settlement on the marsh platform. The senescence of *Spartina alterniflora* in the fall and winter contributes to the formation of large wrack patches in waterbodies adjacent to saltmarshes and peaks in wrack settlement in winter while strong storms can cause observed peaks in the summer (Lynn et al., 2024). The area of marsh covered by *Spartina alterniflora* comprises 81% of the Dean Creek marsh (or 144,500 m^2 of 177,800 m^2: Fig. 1b, dashed yellow line). The plant community across the remaining area of the site includes *Juncus roemerianus* Scheele, *Batis maritima* Linnaeus, *Sarcocornia* sp. Scott, and *Spartina patens* (Aiton) Muhl. The dominant macroinvertebrate species at the site are the marsh periwinkle snail (*Littoraria irrorata*), marsh fiddler crab (*Minuca pugnax)*, mud crabs (*Panopeus herbstii*, *Panopeus obesus*, *Eurytium limosum*, and *Eurypanopeus depressus*), and the purple marsh crab (*Sesarma reticulatum)*.

Wrack patches in the *S. alterniflora* area of the marsh cover a range of sizes and elevations. Lynn et al. (2024) found that wrack patches were most frequently 1–5 m^2 in area but ranged up to more than 200 m^2. Furthermore, when only considering areas where persistent wrack was observed (i.e., stayed in place for at least 2 consecutive months), wrack was most often deposited in areas with higher elevations (>1.3 m elevation relative to NAVD88) and close to the water's edge (~40–50 m) (Lynn et al., 2024). The *S. alterniflora* area used within this study (Fig. 1) was delineated in Lynn et al., 2024.

Imagery, Wrack Selection, and Wrack Classification and Trends

We collected images using UAV flights to determine the location and size of wrack patches. Between March 2020 and December 2022, we conducted 32 monthly surveys using a DJI Matrice 210 Unmanned Aerial Vehicle (DJI, Shenzhen, China) carrying a MicaSense Altum camera (MicaSense, Seattle, WA, USA). Due to UAV technical issues, we did not collect images in April, November, and December 2020. The UAV was flown during morning low tides, within 1–2 hours of solar noon, and at an altitude of 120 m (resulting in a pixel resolution of 5 cm) to reduce potential effects of sunglint on UAV imagery. Detailed methodology for UAV imagery processing and wrack patch identification can be found in Lynn et al. (2024). Briefly, we used Pix4D Mapper software to process UAV images into orthomosaics, which were georeferenced using ground control points (GCPs) that were installed throughout the study area. Principal Component Analysis was used on the corrected orthomosaics to classify all wrack patches ≥ 1 m^2 in area in each image.


a) Southeast USA and location of Sapelo Island, Georgia
Sapelo Island
b) *Spartina alterniflora* area: 144,500 m²
N
0 50 100 m
c) Patch level: ~20.0 m²
W2-1
W2-2
W2-3
0 2.5 5 m
d) Plot level: 0.25 m²
W2-1
W2-2
W2-3

◀ **Fig. 1** (**a**) Southeast USA, location of Sapelo Island on the Georgia coast (red box), and location of the Dean Creek study site on Sapelo Island (yellow star). (**b**) Unmanned aerial vehicle (UAV) image of Dean Creek marsh. Dashed yellow line outlines the areas dominated by *S. alterniflora* (144,500 m^2), including monitored plots (yellow circles), (**c**) an example of a wrack patch within which (**d**) three replicate 0.25 m^2 plots were monitored. Three control plots were set up adjacent to the wrack patch (not shown)

We identified persistent wrack patches by using the Select by Location tool in ArcGIS Pro (3.0.0) for patches that remained in two consecutive images (i.e., generally across 2 months), whereas those that were only present in one image were considered ephemeral. A wrack patch was considered persistent as long as the polygon had at least 50% overlap with that identified in the previous image. Patches were defined as persistent or ephemeral based on the initial 2 month threshold and these designations did not change throughout the course of the study. As long as 50% overlap remained between UAV imagery from the initial selection to the two month threshold the entire patch was considered persistent. We quantified the area of each wrack patch in ArcGIS Pro based on UAV-derived imagery. We quantified the area of persistent wrack in three ways: in terms of its total area over time, as a proportional percentage of total wrack [i.e., persistent/(ephemeral + persistent)], and as a proportion of the *Spartina alterniflora* marsh area.

Biotic Parameters

From July 2020 to August 2022, we monitored a total of 18 wrack patches for up to 13 months. New patches were onboarded in July 2020, March 2021, June 2021, and January 2022 and only after they had been in place for at least 2 months. Patches, which were chosen to be representative of the distribution of wrack deposits on *S. alterniflora* at this site, ranged in area from 1 to 116 m^2 and were in the low- and mid-marsh area based off of the elevations where the patches were deposited and the mean sea level and tidal range (sensu Morris et al., 2005). Six months were not monitored during this period; these are denoted with an ND (no data) in figures.

To assess responses of biota to persistent wrack, we established 0.25 m^2 haphazardly arranged monitoring plots within the selected wrack patches, described above, at the time of patch onboarding, and marked each with flags so that plots could be revisited at subsequent monthly visits. The number of plots established ranged from 1 to 7 per patch, depending on the extent of the wrack patch area. There was no specific number of plots assigned per patch area due to the variation in patch area between selected patches. In addition, there was no minimum distance between patches selected for monitoring. Three undisturbed 0.25 m^2 control plots were set up and paired to a wrack patch within 5 m in an area with similar vegetation characteristics to that of the wrack patch. Towards the end of the study (at the last two onboarding dates, June 2021 and January 2022), new patches were set up with only one wrack plot and one adjacent control plot without regard to the area of the wrack patch ($n = 5$ patches). In total, we sampled 41 plots in 18 wrack patches (average of 2.3 plots per patch) and 46 control plots in 18 paired control areas.

We stopped monitoring wrack plots once the wrack moved away. If wrack settled on control plots, they were removed from the analysis, which decreased the number of control plots used for that patch. In three instances, patches were re-disturbed by new patches within 1–2 months of losing wrack coverage; in these cases, we began monitoring for disturbance effects again as if the wrack had never left.

We quantified the densities of vegetation and macroinvertebrates through on-the-ground monitoring. *Spartina alterniflora* stem density was quantified by counting all live ramets. We quantified *L. irrorata* densities via visual counts and estimated burrowing crab densities by counting the number of crab burrows within each plot (Warren, 1990; Hubbard, 2008; Angelini et al., 2015). Crab burrows ≥ 0.5 cm in diameter were considered adult crabs while those < 0.5 cm were considered juvenile crabs.

Though previous work (Reidenbaugh & Banta, 1980; Bertness & Ellison, 1987; Stalter et al., 2006) suggests 2 months as the critical time period for wrack to have negative effects, we verified that 2 months was sufficient for wrack to have a negative effect on *S. alterniflora* stem density (and support our definition of persistent wrack), by comparing stem density in control and wrack plots at the initial time of monitoring (i.e., second consecutive month of occurrence). We used a linear mixed-effects model and a Poisson distribution with the glmer() function in the 'lme4' package (Bates et al., 2015) to examine the response of stem density (for each individual plot at the initial sampling date) as a function of a fixed effect of treatment (wrack presence or absence) and random effects of patch (the patch that each plot was located within) and date (one of the four dates when patches were onboarded in the study).

For every monthly sampling, we calculated the absolute effect of wrack on each patch (Δ_P) for each biotic variable per month using the following equation:

$$\Delta_P = \underline{W}_P - \underline{C}_P$$

where $\underline{C}_P$ is the average density of the biotic response variable averaged across control plots within a patch, and $\underline{W}_P$ is the average density of a response variable across all wrack plots in the same patch. We also calculated the percentage difference ($\%\Delta_P$) at the patch-level between wrack and control plots per month as:

$$\%\Delta_P = \frac{W_P - C_P}{C_P} \times 100\%$$

Scaling Up to the Landscape

First, for each biotic variable each month, we averaged all of the patch level differences (Δ_P) to get a marsh wide average change ($\underline{\Delta}_P$). We multiplied the calculated average differences by the monthly persistent wrack area to get total change in the marsh and divided by the total *S. alterniflora* marsh area to yield the total change in each variable if evenly spread over the whole marsh. These marsh-wide changes were calculated by:

$$\underline{\Delta}_{SMA} = \frac{\underline{\Delta}_P \times PWA}{SMA}$$

Here PWA is the monthly persistent wrack area (m^2) measured via UAV imagery, $\underline{\Delta}_P$ is the average difference across patches for our biotic variables (m^{-2}), and SMA is the total *S. alterniflora* marsh area (144,500 m^2).

Further, we calculated the marsh-wide percentage change of each biotic variable due to wrack at the scale of the whole *S. alterniflora* marsh (*SMA*) by multiplying the average monthly difference ($\underline{\Delta}_P$) by the monthly PWA and dividing by the estimated total marsh abundance of that species, which was calculated as its average density in the control plots over the course of the study multiplied by the total *S. alterniflora* marsh area (144,500 m^2). The resulting proportion was converted to a percentage by multiplying by 100%.

Porewater Variables

Soil porewater was collected at the patch level from a 10 cm depth. Passive porewater sippers were deployed in October 2020 with a glass scintillation vial filled with Milli-Q water (18.2 MΩ), fitted with an open-top cap and 50 mm Nitex mesh, and placed upside down in each collection window (Hughes et al., 2012; Paludan & Morris, 1999). This method relies on diffusive exchange between the vial and surrounding porewater and samples must be collected every 1–2 months. Because of longer sampling intervals we later switched to direct suction approaches using either Porex filter tubes installed in marsh soils (30–70 µm, Porex Technologies) or chemically resistant tubing with perforations (0.24 cm) at one end (Ledford et al., 2020, 2021; Neubauer, 2013). Upon collection, porewater samples were capped, placed on ice, and transported to the UGA Marine Institute for processing. Salinity was measured with a handheld refractometer. pH levels and redox potential were measured with a benchtop dual channel pH/ISE meter (Fisherbrand™ Accumet™ XL250, accuracy ± 0.002 pH units) and a calibrated pH combination electrode (Fisherbrand™ accuTupH™) or Redox potential electrode (Mettler Toledo™ InLab™ Redox ORP Electrode). Redox potential readings (mV) were recorded relative to a reference electrode in a 3.5 M potassium chloride solution, and values were subsequently corrected to the standard hydrogen electrode. Δ_P and $\%\Delta_P$ were calculated for porewater in the same way as for biotic variables above, except there are no plot-level samples so the calculations of the difference are between the sole wrack and control sample in the paired patches. All calculations and analyses described in the Materials and Methods section were performed in R (4.3.2; R Core Team, 2023).

Results

Wrack Classification and Trends

Over the three years of our UAV measurements, persistent wrack area varied each month from a low of 0 m^2 to a high of 835 m^2, while the area of ephemeral wrack varied from 69 m^2 to 1559 m^2 (Fig. 2; Table 1). Notably, the percentage of persistent wrack varied from month to month, ranging from 0% (e.g., Sept. 2020) to more than 80% of the total wrack (e.g., July 2020), with an overall average of 24% over the study period. We found evidence of a seasonal pattern in persistent wrack, with an annual peak between July and August followed by a decrease between September and December (Fig. 2b). However, this pattern was not apparent in the total wrack due to the high interannual variability in ephemeral wrack (Figs. 2c and d). Both ephemeral and persistent wrack at any given time covered only a small percentage of the area dominated by *S. alterniflora* (Table 1). When summed over the entire study period, persistent wrack area affected 6,408 m^2, or 4.4% of the study area (purple area in Fig. 3).

Biotic Parameters

Our assessment of *S. alterniflora* stem density at the initial monitoring point (2 months after initial wrack deposition) showed that wrack plots had 88 fewer stems m^{-2} ($t(30) = -7.1$, $SE = 12.47$); wrack-covered plots had on average 123 ± 30 stems m^{-2} (mean ± SE) as compared with 210 ± 36 stems m^{-2} in control plots (Fig. 4). This difference represents a nearly 40% decline in stems in wrack-affected plots (Fig. 4). A Chi-square test of the effect of treatment on stem density showed that stems differed significantly between wrack and control plots ($X^2(1, N{=}30) = 50.01$, $p < 0.001$).

Spartina alterniflora stem density and *L. irrorata* snail density were reduced in the wrack disturbed plots compared

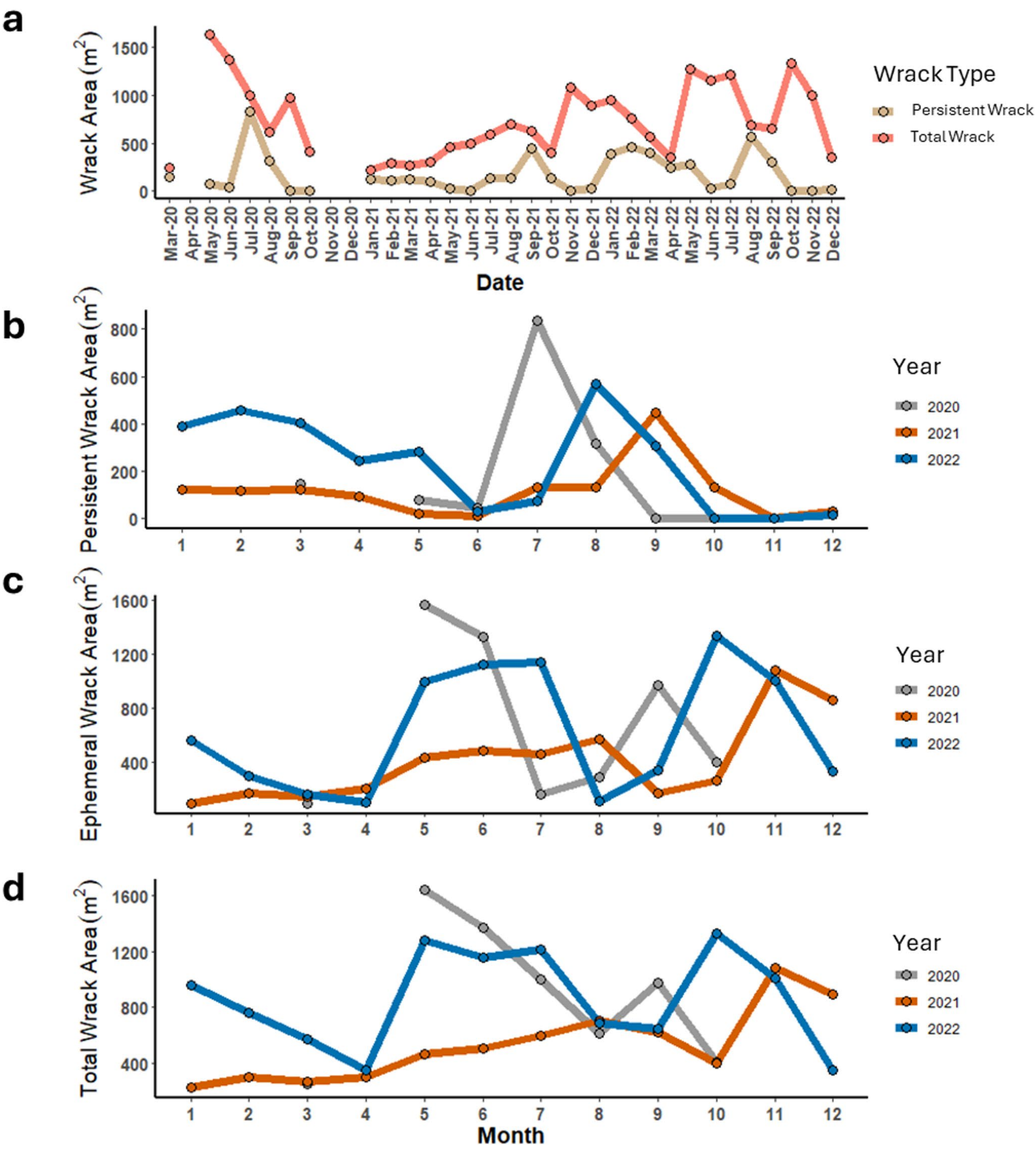


Fig. 2 (**a**) Monthly persistent and total wrack area over the 32-month period of UAV imagery collection. Monthly (**b**) persistent, (**c**) ephemeral, and (**d**) total wrack area (m^2) separated into each of the three years of the study period. Absence of points means no image was collected that month

to control plots (Δ_P) during the study period. Between July 2020 and August 2022, wrack disturbed plots had an average of 127 ± 5 (SE) stems m^{-2} per month, whereas control plots had 211 ± 2 stems m^{-2} (Figs. 5a and S1A): a 41% decrease (%Δ_P) (Fig. 5b) between treatments. During this same period, wrack disturbed plots had an average of 75 ± 7 snails m^{-2}, whereas control plots had 100 ± 4 snails m^{-2} (Fig. S1B): a 25% decrease (%Δ_P) (Fig. 5b). Adult crab burrow densities were similar in the wrack (135 ± 8 burrows m^{-2}: Fig. S1C) and control (115 ± 4 burrows m^{-2}: Fig. S1C) plots

Table 1 The average, minimum, and maximum area (mean ± SE) of persistent, ephemeral, and total wrack and the calculated average percentage of the *S. alterniflora* marsh area (144,500 m^2) that was covered by each wrack type at any given time across our study duration

Persistent Wrack	Average Area (m^2)	Minimum Area (m^2)	Maximum Area (m^2)	% Spartina alterniflora Area Covered
	176 ± 200	0	835	0.12 ± 0.14
Ephemeral Wrack	544 ± 443	69	1559	0.35 ± 0.27
Total Wrack	719 ± 397	99	1559	0.50 ± 0.27

(Fig. 5a). Adult crab burrow densities also exhibited high within-month variability (Fig. 5a and b). Like adults, juvenile crab burrow densities exhibited similar temporal patterns between wrack disturbed plots (189 ± 20 burrows m^{-2}) and control plots (246 ± 13 burrows m^{-2}) (Fig. 5a and b).

Scaling Up to the Landscape

Scaling these observations to the entire area of persistent wrack shows the small effect wrack had on marsh biota. *Spartina alterniflora* showed an average loss per month of –0.13 ± 0.04 (SE) stems m^{-2} over the entire study period (Δ_{SMA}) with a maximum loss of –0.58 stems m^{-2} in July 2020. The stem losses over the entire study period account for an average of 0.05% (~ 18,400 stems) of the total number of estimated stems (31,288,660 stems) in the *S. alterniflora* marsh area (Fig. 5c). When scaled, the average monthly decrease in abundance of *L. irrorata* snails was − 0.10 ± 0.03 snails m^{-2}, with a maximum decrease of −0.40 snails m^{-2} in July 2020. These numbers are both < 0.01% of the total estimated number of snails (15,447,489 snails) across the *S. alterniflora* marsh area (Fig. 5c). Crab burrow densities both increased and decreased under wrack (Fig. 5c). When averaged across months and scaled up, crab burrow densities decreased by −0.003 ± 0.01 burrows m^{-2}, which represents an average of < 0.01% change of the total estimated marsh-wide crab burrow abundance (15,982,135 burrows: Fig. 5c). Juvenile crab burrow densities showed similar patterns to that of adults, with an average decrease of −0.14 ± 0.10 juvenile crab burrows m^{-2}, which again represent an average of < 0.01% of the total (34,287,147 burrows: Fig. 5c).

Porewater Variables

Wrack effects on porewater chemistry were generally weak and inconsistent through the study. Porewater salinity was generally higher in wrack patches during the first two months of monitoring (October 2020 only had one wrack and control patch pair) but similar between wrack and control patches in the spring and summer (Fig. 6). Seasonal patterns in pH and redox were not obvious. Rather, redox was generally lower, and pH was generally higher in wrack patches, though neither was consistent throughout the study.

Discussion

Our approach places the relative effects of wrack, usually examined at small spatial scales and over short periods of time (< 1 year), into a larger scale landscape context. We found that the average monthly area covered by wrack was 719 m^2 ± 397 (SE) over the course of the study, or 0.5% of the *Spartina alterniflora* marsh area of 144,500 m^2. An average of 24% of the wrack was considered persistent (> 2 months), which amounted to only 0.12% of the marsh area. Although the persistent wrack affected marsh biota at the location of the patch, these effects were minimal when considered at the whole marsh scale.

Wrack has been studied as a disturbance in many New England saltmarshes; however past studies did not classify wrack as ephemeral or persistent as we did, occurred at higher latitudes, and did not use the same field methods in combination with UAV imagery. However, comparing those past findings to ours helps contextualize the larger scale impacts of wrack. In particular, the upper intertidal limit of *S. alterniflora* is higher at low versus high latitudes (McKee & Patrick, 1988) so comparisons across latitude based on "the *Spartina alterniflora* zone" may be invalid. Given those caveats, our findings are in line with those of Valiela and Rietsma (1995), who found that wrack cover in a Massachusetts marsh affected 0.7% of the area of the low marsh zone, which is dominated by *S. alterniflora*, as compared to 6.9% of the high marsh zone dominated by *S. patens*. They also found that only 30% of the wrack patches caused damage to underlying vegetation, which is relevant in terms of our focus on persistent wrack and its landscape-scale effects. Bertness and Ellison (1987) found that wrack covered 6% of a *S. patens*-dominated high marsh in Rhode Island, peaking at 30% cover in June. Additionally, past work has found that when wrack incurs damage to high marsh species, such as *S. patens* and *Juncus spp.*, they take longer to recover compared to *S. alterniflora* (Bertness & Ellison, 1987; Brinson & Christian, 1999). Thus, marshes dominated by high marsh plant species are predicted to have higher losses of vegetation and longer lasting effects due to wrack settlement compared to *S. alterniflora* dominated marshes.

Multiple factors can contribute to the location in a marsh where wrack settles and the area of wrack that is deposited. Working in *S. alterniflora* dominated areas of Georgia marshes, Li and Pennings (2016) found that wrack was rare in mid-marsh plots (< 5% of plots affected) compared to creekbank plots. Since we focused only on areas of the marsh

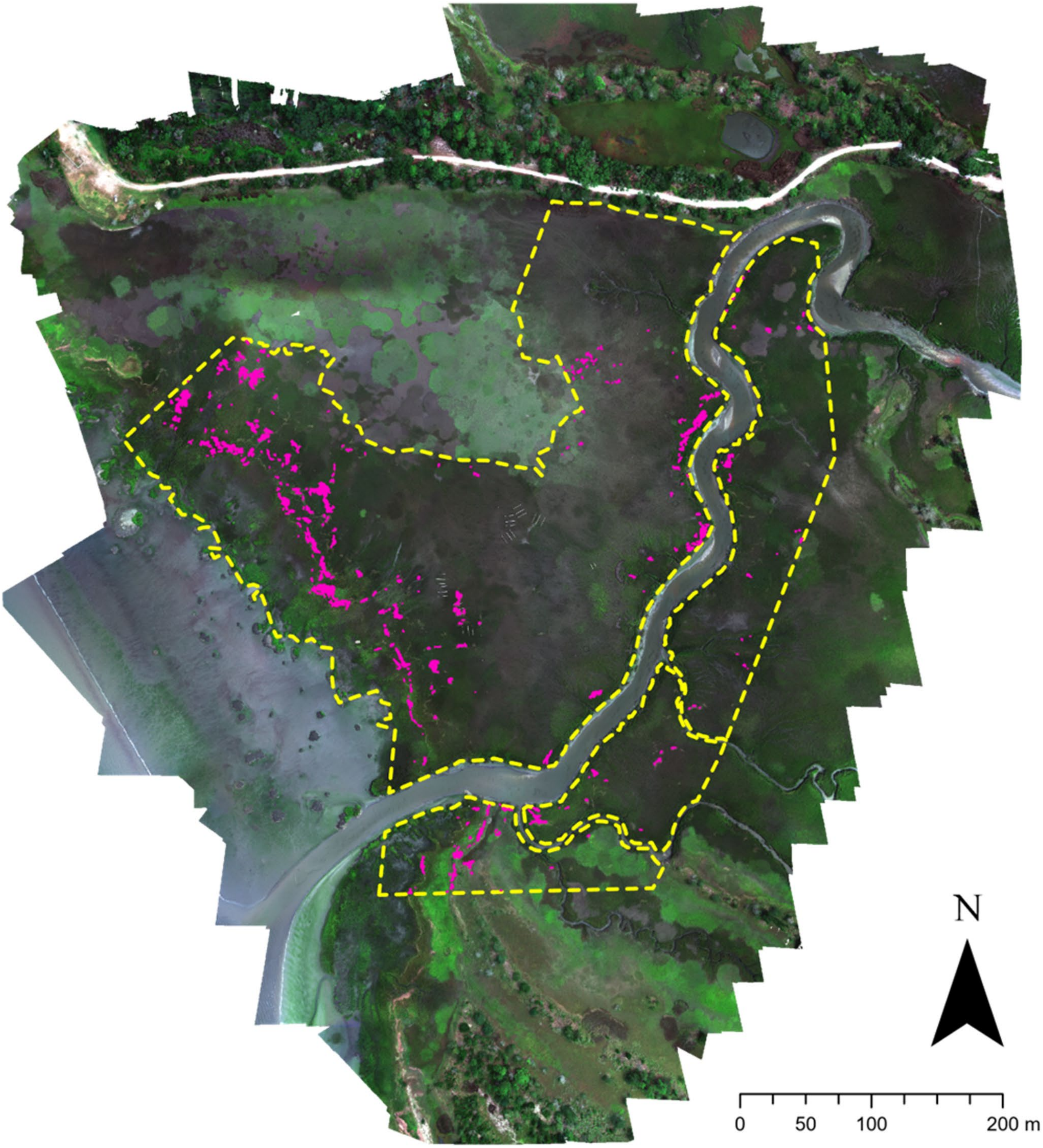


Fig. 3 The distribution of persistent wrack (purple patches) observed across the *S. alterniflora* marsh (dashed yellow line) from March 2020 – December 2022

dominated by *S. alterniflora*, we cannot formally compare our results with high-marsh vegetation areas that are dominated by other plant species in Georgia. However, wrack is often deposited within the *S. alterniflora* zone (Fig. 3), and wrack tends to most frequently be deposited at the higher high water line (~ 1 m elevation relative to NAVD88) and near tidal creeks and shorelines (~40–50 m) (Lynn et al., 2024). Other studies, however, have found that wrack can be common (as high as 70% cover) at high elevations in Georgia marshes where it is trapped at the base of tall, high-marsh vegetation

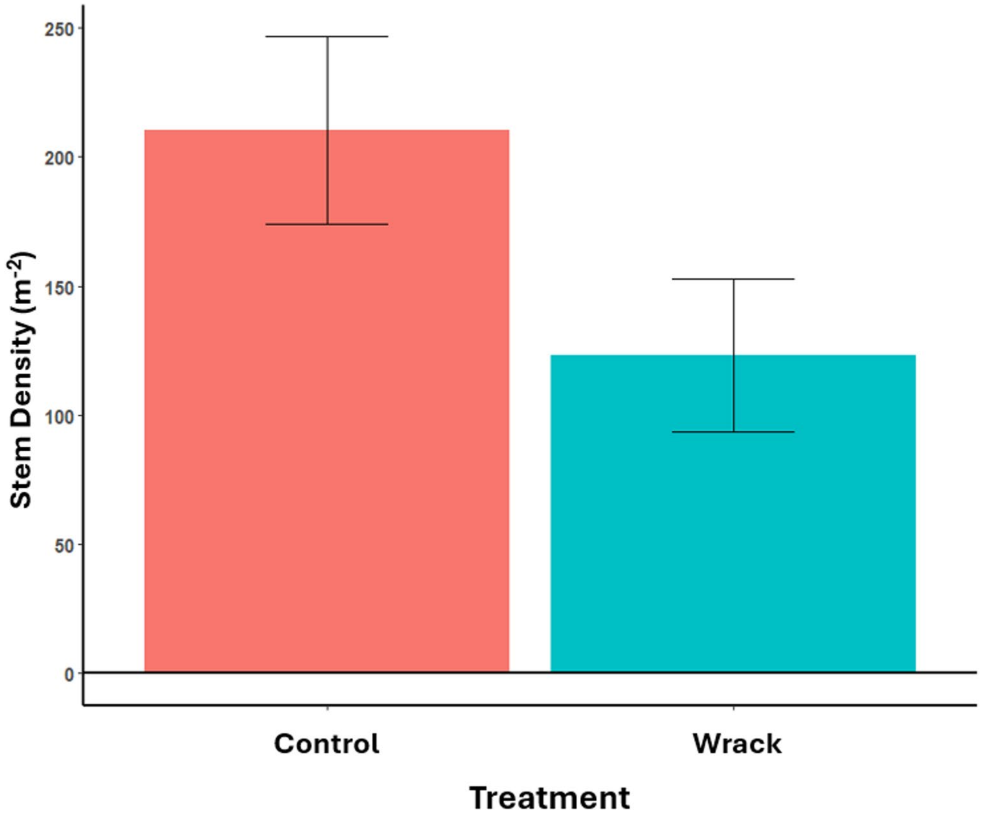


Fig. 4 Average patch-level (m^2) *Spartina alterniflora* stem densities for wrack and control plots during the initial monitoring survey (approximately 2 months after initial wrack deposition). Bars are standard errors

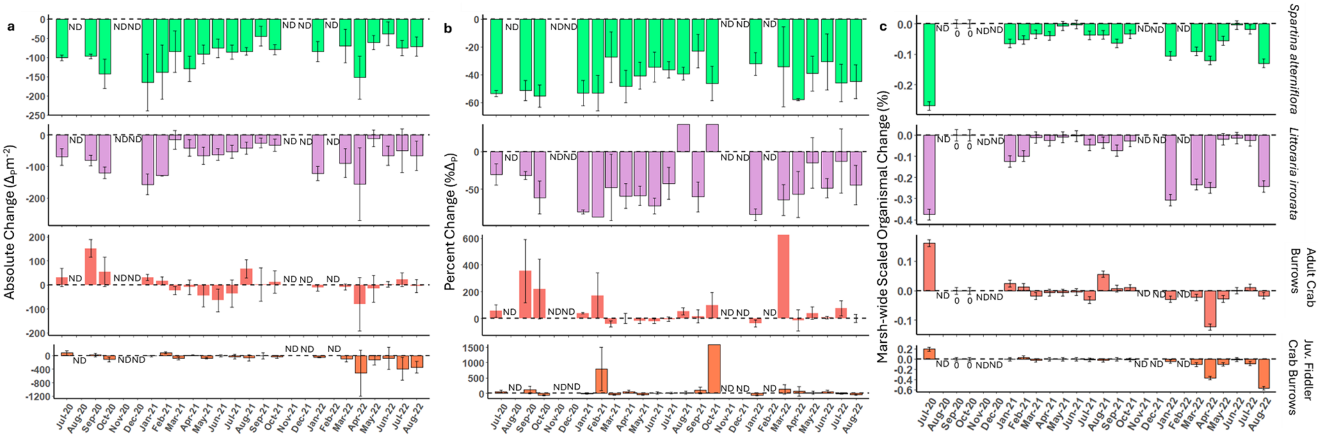


Fig. 5 Calculated patch-level estimates of (**a**) absolute density changes (Δ_P) between wrack disturbed and control areas monthly for *Spartina alterniflora* stems, *Littoraria irrorata* snails, adult crab burrows, and juvenile crab burrows on each sampling date, (**b**) percentage change (%Δ_P) for each variable, and (**c**) the marsh-wide percentage change of each biotic variable per month due to wrack at the scale of the whole *S. alterniflora* marsh. This latter variable was calculated as the average patch-level difference across the marsh (panel a) multiplied by the persistent wrack area and divided by the total estimated marsh-wide abundance of each biotic variable and multiplied by 100. Bars are standard errors. For all panels, values above zero (dashed black line) represent increases in a variable in the wrack disturbed areas, while values below represent decreases in a variable in the wrack disturbed area compared to controls. ND's indicate months with no data and 0's represent months with no persistent wrack

(Pennings & Richards, 1998). Wrack has also been shown to accumulate at the high marsh border after high energy storm events such as hurricanes (Smith et al., 2020) and along built structures such as docks (Alexander, 2008). A storm event occurred in November 2021 in this study area and the increase in persistent wrack in the following months (Fig. 2) may be associated with the storm event. Thus, the area affected by wrack would potentially increase if one considered other vegetation types, severe weather events, and areas around built structures all of which would be useful in future studies.

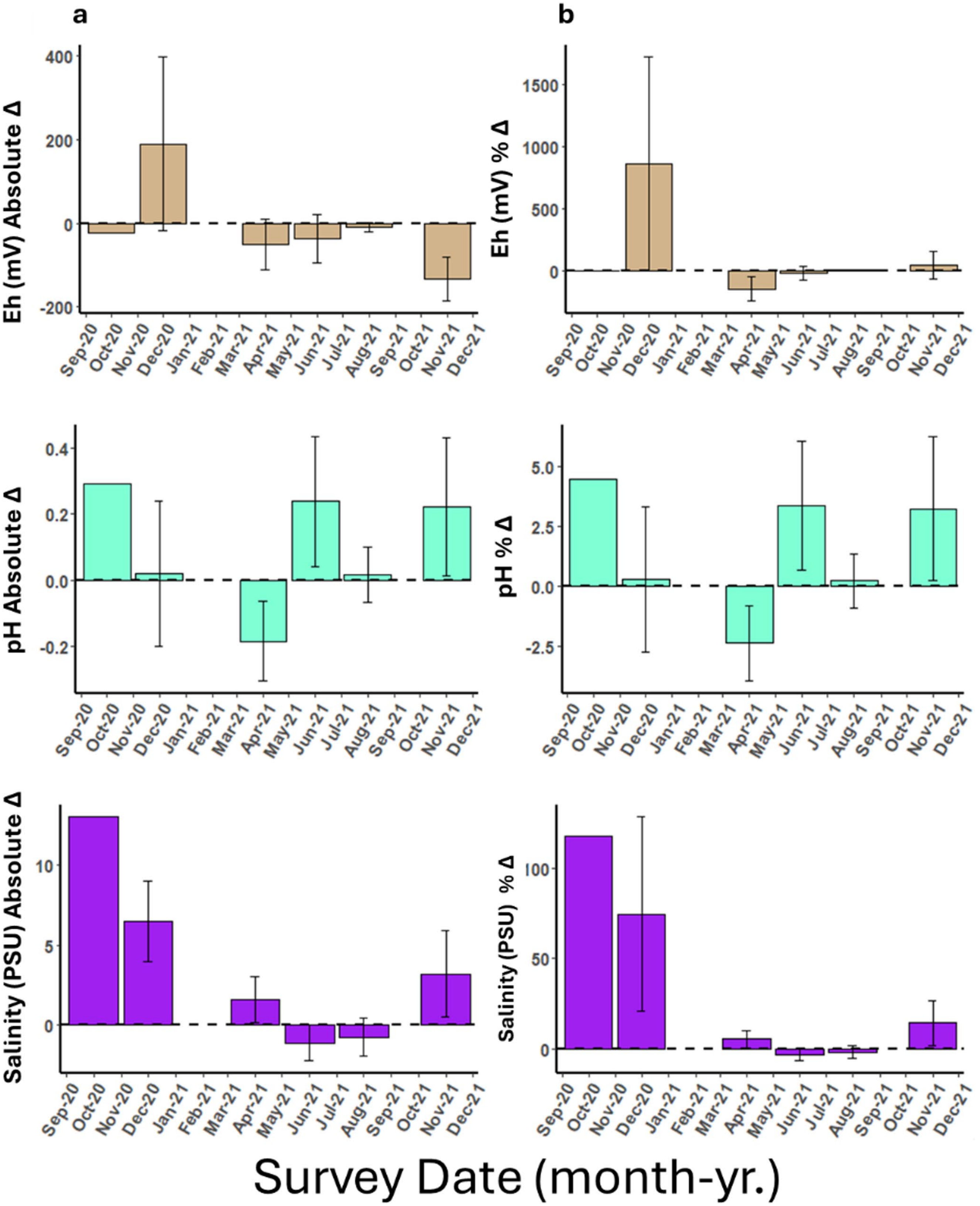


Fig. 6 (**a**) Calculated absolute difference (Δ_P) for redox potential, pH, and salinity of porewater between wrack disturbed and control patches. (**b**) Calculated percentage difference (% Δ_P) for redox potential, pH, and salinity of porewater between wrack disturbed and control patches during the monitoring period of the study. Bars are standard errors. For all panels, values above zero (dashed black line) represent increases within the wrack disturbed areas and values below represent decreases within the wrack disturbed area compared to undisturbed controls. No standard error bars are present for October 2020 due to only having one wrack patch sampled for porewater on this date

Despite these differences in methodology of wrack characterization, we hypothesize that wrack percent cover is higher overall in New England (higher latitudes) versus Southeastern (lower latitudes) saltmarshes along the Atlantic Coast of the United States. In New England saltmarshes, plants have a sharply constrained growing season, senesce synchronously in the fall, and plant stems are likely to be physically broken lose from their roots by snow and ice; these factors lead to a large, synchronous pulse of wrack production early in the growing season (Pennings & Bertness, 2001; Hardwick-Witman, 1985, 1986). In contrast, there was no evident seasonality in the total wrack accumulation in our study. Plants at lower latitudes have an extended growing season, do not senesce synchronously in the fall (Turner, 1976), and in the absence of physical disturbance from snow and ice, most stems decompose while standing in place (Newell et al., 1998). These factors lead to gradual and limited production of wrack over the course of the year (Pennings & Bertness, 2001). With the advent of modern UAV technology, rigorously testing this latitudinal hypothesis would be straightforward. If it is supported, it suggests that the various ecological processes initiated by wrack disturbance, such as secondary succession (Bertness & Ellison, 1987) and the promotion of fugitive species (Bertness et al., 1992), are also more important in structuring marsh communities at high versus low latitude sites.

We found that persistent wrack reduced the stem density of *S. alterniflora* by ~40% at the plot scale. This finding aligns with Valiela and Rietsma (1995), who found a reduction in *S. alterniflora* stem densities of 82% under wrack packages that damaged vegetation. However, when scaled up, wrack affected only 0.01%–0.03% of the low marsh area in Great Sippewissett Marsh, MA. Similarly, we estimated a marsh-wide monthly average reduction of *S. alterniflora* of 0.13%. Thus, although effects of wrack can be acute immediately underneath persistent wrack, the effects of wrack disturbance on marsh habitat structure overall are limited due to its small spatial coverage at the landscape level.

The decrease in the density of snails was likely due to emigration out of wrack plots once the preferred grazing and living substrate of the snails, *S. alterniflora*, declined. This shift in snail densities was expected given the strong relationship between *L. irrorata* and *S. alterniflora* aboveground structure (Haines & Montague, 1979). Because wrack seemingly does not kill snails (we did not find any dead snails in the plots), the shift in snail density at the plot-level does not indicate a total loss or gain at the marsh scale but instead, most likely, reflects a redistribution of individuals across the marsh.

Crab burrows, which were used as our proxy for crab abundance, showed high spatial variation across the wrack disturbed and control areas (Fig. 5). This effect was surprising, because other studies have shown that crabs benefit from the structure provided by plant stems when burrowing in soft sediment (Bertness & Miller, 1984; Bertness, 1985) and from the protective effect of the vegetation canopy when burrowing in high marsh areas (Nomann & Pennings, 1998). It may be that the effects on vegetation that we found were not severe enough to affect crabs. Moreover, the lack of physical disturbance to the soil may have allowed crab burrows to persist during the study period. Changes in crab density could in theory be masked if crab burrows stay intact after crabs have migrated away from disturbed areas. However, unmaintained crab burrows would be expected to fill in overtime (2–4 months; Bertness & Miller, 1984).

Wrack effects on aboveground plant properties did not translate into belowground responses in porewater chemistry. It is possible, however, that belowground responses were muted because roots and rhizomes of different *S. alterniflora* individuals are intertwined, and patches of persistent wrack were small. *Spartina alterniflora* is clonal and roots and rhizomes extend laterally and down into soils. The implication being that roots and rhizomes from healthy plants may be able to buffer highly localized effects of dead plants on porewater chemistry. Such buffering effects would likely decrease with increasing size of persistent wrack patches and area of dead vegetation. Similarly lateral porewater movement and mixing may have been strong enough to mute potential plant dieback effects under small, persistent wrack patches. An alternate hypothesis is that short-term dieback of aboveground shoots and leaves may not mean that belowground roots and rhizomes are also dead: at more temperate latitudes, aboveground plant tissues die back seasonally and resprout from roots and rhizomes that survive overwinter. Better understanding how disturbance effects on aboveground communities propagate belowground may be useful in assessing mechanisms of ecosystem resilience to disturbance in coastal marshes.

This study highlights the utility of applying a joint approach of UAV imagery and field measurements to facilitate more informed calculations of the effects of coastal disturbance. Given the heterogeneity in wrack patch size, duration, and frequency, UAV imagery provides a practical way to measure and track these properties at large scale (Lynn et al., 2024). Although effects immediately underneath persistent wrack can be strong at the local level, in areas directly affected by wrack, scaling on-the-ground data to the landscape better contextualizes the overall effects of wrack disturbance. In addition, the potential seasonal trend in persistent wrack highlights the importance of accounting for seasonal and annual variability. While in our study the landscape-level effects did not have significant effects on ecosystem services of Dean Creek marsh, more work should be done to study the effects of large and long-lasting wrack settlement along built structures like docks, seawalls, and causeways. Due to the reduction in vegetation and possible reduction in accretion these areas have the potential to lose elevation capital and drowning, but further work needs to be done to test this mechanism. The coupling of both methods can be applied to a variety of locations and ecosystems and may provide a cost-effective monitoring strategy. For instance, UAV or satellite-imagery has been used to track and monitor the destruction of marsh habitat by invasive feral hogs and provides detailed information on where to target on-the-ground sampling to assess landscape-scale impacts (Hensel et al., 2021; Harris et al., 2024). In addition, the employment of UAVs in the field can allow for rapid surveying of landscapes after unexpected or rare disturbance events. By initially quantifying the scale of a disturbance using UAV imagery field crews can more efficiently plan their monitoring program and target specific areas of interest based on imagery that may be missed or overlooked from on-the-ground monitoring alone. As disturbances in coastal systems increase due to climate change (Craft et al., 2009; Crotty et al., 2020), studies that expand the scope of field monitoring to include remote sensing tools can readily quantify the extent of large-scale disturbances, thereby placing their impacts measured at small scales into landscape-scale perspective. Moving towards the incorporation of UAV technologies into coastal monitoring programs would not only provide the benefits listed above but would allow for more advancements in landscape-scale studies that would more accurately account for landscape features and patterns that are not easily visible from on-the-ground monitoring. Through the incorporation of UAVs and other remote sensing systems in field monitoring of the same habitats cross-site and cross-latitude comparisons can more easily be made from geographic information systems in addition to field-based comparisons alone. This change has the potential to greatly expand our current knowledge base of landscape effects of disturbances through advancing monitoring protocols and other coastal changes such as phenological shifts in plants (O'Connell & Alber, 2016) or movement of intertidal saltmarsh creeks (Dutt et al., 2024). The combination of the two has great potential to advance our insights into ecosystem-level phenomena and how to best quantify the patterns observed.

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Authors' Contributions All relevant authors and institutions approve of this manuscript for publication. MA, SCP, DM, AS and JEB conceived of the study idea; MP, SZ, and JEB conceived of the presented analytical approaches of the data; MP performed the calculations and wrote the manuscript; TL processed UAV imagery and generated maps; SR, SD, and CB processed porewater samples; and MP, JG, and SW performed field monitoring. All authors contributed to the editing and review of the manuscript.

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Data Availability The datasets used for and produced during this study are still in use as part of other ongoing research studies and are not yet available at this time.

Declarations

Ethics approval and consent to participate This study was performed within the jurisdiction of the Georgia Department of Natural Resources, Sapelo Island National Estuarine Research Reserve, and Georgia Coastal Ecosystems Long Term Ecological Research project. All necessary permissions were received prior to the implementation of this study and kept up-to-date throughout. This study did not require the collection of any plants or animals.

Consent for publication Not applicable.

Competing interests The authors declare that they have no competing interests.

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