The effects of crab bioturbation on Mid-Atlantic saltmarsh tidal creek extension: Geotechnical and geochemical changes

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**A B S T R A C T**

Understanding saltmarsh response to sea-level rise is critical for management and mitigation of these valuable coastal areas. However, comprehensive field studies of sea-level driven changes to the marsh landscape that consider combined biological, geological, and hydrodynamic interactions are rare. This study analyzes ecophysical feedbacks from crab colonization and bioturbation on geotechnical and geochemical properties of the soil in a Mid-Atlantic Spartina alterniflora saltmarsh. The study area is within a marsh that is experiencing creek extension due to accelerated sea-level rise and increasing periods of marsh inundation. Measurements of redox potential, pH, belowground biomass, and soil strength reveal that intense crab bioturbation by Sesarma reticulatum significantly changes the biogeochemical properties of the soil. Oxidized conditions in the upper 10–15 cm of the marsh induced by burrowing causes enhanced degradation of S. alterniflora belowground biomass (roots and rhizomes, reduction from 1.9 ± 0.6 kg/m² to 1.1 ± 0.4 kg/m²), which reduces the structural integrity of the soil. This process ultimately increases the erosion potential of the sediment in creek head areas (documented by a reduction in shear strength from 10 ± 7 kPa to 2 ± 1 kPa), facilitating creek extension in order to accommodate tidal flows. The pervasiveness of similar tidal creek morphology in southeast Atlantic saltmarshes suggests this process is occurring in other marshes with a moderate tidal range undergoing sea-level rise.

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1. **Introduction**

An understanding of saltmarsh morphodynamics requires knowledge of biological, geological, and hydrodynamic interactions that create changes to the marsh landscape (Mudd et al., 2004, 2009; Nyman et al., 2006; Augustin et al., 2009; Huat et al., 2009; Hughes et al., 2009; Howes et al., 2010; Fagherazzi et al., 2011). For example, sediment deposition in marshes is highly dependent on suspended sediment availability and hydrodynamic conditions; both of which are modulated by presence and type of vegetation (Moeller et al., 1996; Christiansen et al., 2000; Leonard and Croft, 2006; Neumeier, 2007; Temmerman et al., 2007; Augustin et al., 2009). Concomitantly, plant productivity and organic contribution to saltmarsh accretion help maintain marsh elevation in the face of accelerating sea-level rise (SLR; Redfield, 1965; Morris et al., 2002; Nyman et al., 2006; Kirwan and Murray, 2007; Mudd et al., 2010). Saltmarsh response to rising sea levels has been the subject of many studies to date (Reed, 1990; Schwimmer and Pizzuto, 2000; Rybczyk and Cahoon, 2002; Nyman et al., 2006; Wilson and Allison, 2008), yet only recently have geomorphic process studies taken a comprehensive, interdisciplinary approach (Perillo and Iribarne, 2003; Perillo et al., 2005; Escapa et al., 2007). Saltmarsh biota (e.g., vegetation, macrofauna), framework geology, sediment character and availability, and hydrodynamic forcings must be considered as a whole to accurately describe and quantify saltmarsh geomorphology. Moreover, field-based information is needed in order to make valid predictions and provide well-founded parameters for models of marsh evolution with sea-level rise and climate change (van Wijnen and Bakker, 2001; Morris et al., 2002; Kirwan and Temmerman, 2009; Kirwan and Guntenspergen, 2010; Fagherazzi et al., 2011, 2012).

A recent study by Hughes et al. (2009) found that Spartina alterniflora platform marshes of Cape Romain, South Carolina (southeast U.S. Atlantic coast, Fig. 1), are responding to SLR and the consequent increase in tidal prism through expansion of the tidal creek network. Straight, low order tidal creeks have developed along the margins of larger, higher order channels and are lengthening and becoming more complex over time (Fig. 1c and d). Damming of the Santee River in 1939 significantly reduced sediment discharge, thereby decreasing the contribution of inorganic material available for saltmarsh accretion across the delta. In response to this condition as well as possible subsidence, the

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marshes of the Santee delta (including Cape Romain) are experiencing a high level of relative sea-level rise (RSLR, >3.2 mm/yr) and marsh inundation. The observed creek extension is likely a result of the increase in tidal prism and hydraulic duty that must be accommodated (Allen, 1997; Friedrichs and Perry, 2001; Hughes et al., 2009). Drainage density (total creek length divided by marsh area) has increased 23% between 1958 and 2006 through the formation and elongation of these creeks (Fig. 1b).

Although tidal creek development in saltmarshes is expected under a regime of rising sea-level (observed in Australia, Knighton et al., 1991; United Kingdom, Shi et al., 1995; Bahamas, Allen, 1997; Friedrichs and Perry, 2001; Rankey and Morgan, 2002; Kirwan and Guntenspergen, 2010), feedbacks between biology, hydrodynamics, and sediment dynamics appear to facilitate creek extension in this region. Heads of newly formed creeks exhibit low topography compared to the surrounding marsh platform, are denuded of vegetation (i.e., mudflat), and are heavily populated by herbivorous and burrowing crabs (Fig. 1e; Hughes et al., 2009). Over time, these denuded creek head regions translate with the creeks as they extend into the marsh platform. Vegetated areas of the marsh experience dieback of Spartina alterniflora vegetation and loss in elevation (up to 50 cm), whereas formerly unvegetated areas of the creek head become revegetated and regain elevation as the channel head migrates further inland (Fig. 1d and e). Crab bioturbation and herbivory are strongly associated with plant dieback. Hughes et al. (2009) and more recent results by Vu et al. (2011) found that density of Sesarma reticulatum, a herbivorous crab, and density of crab burrows negatively correlate with S. alterniflora stem density. It is likely that removal of S. alterniflora rooting and modification of saltmarsh sediments (e.g., reworking from burrowing, formation of feeding pellets) affect the cohesion and thus erodibility of the soil, while increased permeability due to burrowing alters the biogeochemistry of the soil (e.g., aeration leading to degradation of organic matter). However these processes are yet to be quantified.

We observe similar tidal creek formation and extension in other southeast U.S. Atlantic saltmarshes (including near Bulls Bay, Beaufort, and Edings Island in South Carolina, and Brunswick, McIntosh, and Savannah in Georgia), indicating the processes occurring in the Santee Delta are not location specific. Moreover, field examination of 21 creeks on Sapelo Island, Georgia (southeast U.S.), confirm that geomorphically similar creeks are heavily populated by Sesarma crabs in denuded creek heads. Further, crab
bioturbation and its effect on vegetation and creek formation has been addressed by recent studies in South American saltmarshes (Perillo and Iribarne, 2003; Minkoff et al., 2006; Escapa et al., 2007). In one case, heavy crab bioturbation caused plant stress and dieback. Subsequent percolation of tidal waters through burrows that were frequently inundated led to undermining of saltmarsh soil and eventual formation of tidal channels (Perillo and Iribarne, 2003). In another study, new creeks developed through subsurface piping created and enlarged from crab and fish bioturbation (Perillo et al., 2005). These findings highlight the need for comprehensive geomorphologic studies that account for biological, geological, and hydrodynamic interactions in saltmarsh settings.

To address this need, this study examines biogeochemical processes and ecophysical feedbacks between bioturbation and tidal creek extension occurring in U.S. southeast Atlantic saltmarshes (Cape Romain, South Carolina; Hughes et al., 2009). This paper primarily examines relationships between rooting (belowground biomass), geotechnical properties (soil strength, bulk density, organic content), and geochemical properties (through measurements of redox potential and pH) in a Spartina alterniflora-dominated saltmarsh. Our findings suggest crab bioturbation is primarily responsible for vegetation dieback near the heads of tidal creeks and the formation of topographic lows, which facilitates rapid headward erosion of creeks.

2. Methods

In situ measurements were taken at a field site in Cape Romain, South Carolina, a Spartina alterniflora dominated backbarrier marsh (tidal range 1.48 m, Fig. 1). Straight, low order tidal creeks have developed along the margins of larger, higher order channels and are currently incising the marsh platform at a rate of \( \sim 2 \text{ m/yr} \) (Hughes et al., 2009). Areas of severe crab bioturbation are associated with creek heads. Relationships between rooting, geotechnical, and geochemical properties were examined at 5 creek heads as described below.

2.1. Creek head core transects

A series of five core transects was taken from the marsh platform into five creek heads in May and September 2010. Historical aerial photographs indicate that these five creeks have been experiencing headward erosion into the marsh platform over the past 50 years and that the present day creek heads transitioned from vegetated marsh within the last decade (Fig. 1d). Each transect consisted of four half-cylinder gouge auger cores (8 cm diameter, 60 cm depth) located: (1) on the marsh platform where healthy short-form Spartina alterniflora dominates; (2) in the transition zone between the vegetated marsh platform and unvegetated creek head (hereafter referred to as the ‘dieback’ area because of noticeable dead stalks of vegetation); (3) in the unvegetated creek head (mudflat); and (4) in the revegetated area where tall-form Spartina alterniflora has recently colonized the creek head mudflat (Fig. 1e). Each core was analyzed for soil oxidation—reduction potential \( (\text{Eh}) \), pH, soil strength, bulk density, bulk organic content, and belowground biomass (procedures outlined below). Care was taken to prevent core compaction upon insertion and extraction; cores exhibiting compaction were discarded.

2.2. Redox potential (Eh) and pH

Soil Eh and pH were determined in the field immediately following extraction of each core using a handheld Hanna Instruments HI91003 oxidation—reduction/pH double electrode probe. A correction factor of 200 mV was applied to calibrate our Ag/AgCl redox electrode readings to a standard hydrogen reference electrode. The probe was inserted 4 cm into the core along the exposed side of the auger and allowed to equilibrate. Measurements were taken at 5 cm intervals to a depth of 15 cm, and every 10 cm thereafter to a depth of 60 cm. Both pH and Eh were recorded for each depth, and the electrode was washed with DI between readings. Due to instrument complications, Eh and pH were not measured at sites SD-8 to SD-11.

2.3. Soil shear strength

Soil shear strength was determined in the field both in situ and within extracted cores using a handheld Seiken shear vane that has four interchangeable vanes and four torsional springs that range from 2 to 50 CN m. This instrument records the failure of cohesive sediment under torsional stress, which can be useful to compare the relative integrity of the root matrix and the cohesiveness of the soil, as determined in other saltmarsh studies (Escapa et al., 2007; Wilson and Allison, 2008; Howes et al., 2010; Turner, 2011). Shear vane measurements have been found to correlate well with sediment erosion threshold measurements, showing similar spatial variation and response to factors such rooting, microalgae and compaction (Chen et al., 2012). Soil shear stress from a torsional vane can also provide insight into soil cohesiveness with depth (a critical advantage for determining weak layers in the subsurface). For in situ measurements a 4 cm vane was used, inserted vertically into the marsh surface. Readings were taken at 10 cm intervals from 5 to 95 cm. For measurements in extracted core samples, a 3 cm vane was inserted into the center of the core along the exposed side of the auger. Readings were taken at 10 cm intervals down-core, beginning at a depth of 5 cm to the end of the core. In situ measurements provide soil shear strength readings along the horizontal \( x-y \) axis, and measurements from the extracted core samples provide soil shear strength readings between the horizontal and vertical plane \( (x-z \text{ axis}) \).

2.4. Below-ground biomass and geotechnical properties

Following redox and shear vane measurements, cores were sectioned into 10 cm intervals to a depth of 60 cm and each section was returned to the lab for belowground biomass, bulk density, and organic content analysis. Samples were washed with a 500 micron sieve to remove mud (predominant grain size in this area) and other inorganic content (such as shells or large sized particles). Organic material trapped in the sieve (consisting of roots, rhizomes, and detritus of Spartina alterniflora) was removed, dried, and weighed. No distinction was made between live and dead belowground biomass. Material that washed through the sieve (<500 µm) and larger inorganic particles (i.e., shells, sand) were collected, dried, and weighed. Bulk density (dry weight per volume) was determined by combining the organic belowground biomass and inorganic dry mass of the samples and dividing by the calculated sample volume (cylinder dimensions: 8 cm diameter, 10 cm height). Bulk organic content of the soil was determined by recombining the organic and inorganic fractions after drying and performing standard loss on ignition (550 °C for 14 h). Biomass, bulk density, and bulk organic content were not quantified at sites SD-26 to SD-29 (sampled in September 2010) due to expected seasonal differences in the belowground biomass.

3. Results

3.1. Eh and pH

Measurements of Eh and pH at depth along the creek head transects ranged from −201 to +617 mV and 4.6 to 7.3, respectively
These results were highly variable depending upon core location (marsh, dieback, creek head, revegetated zone) and depth, but in general, the upper ~10–15 cm of the soil was more oxidized and had a lower pH than at depth (Fig. 2). Below the surface (>20 cm), Eh and pH were relatively stable (averaging ~−150 mV and 6.9, respectively; Fig. 2). In the surficial sediment, Eh and pH varied greatly along transects from the marsh platform across the creek heads into revegetated areas (Fig. 3 and Table 1). Although the absolute values of Eh varied, there seemed to be a distinct trend throughout the five transects in surficial soils (hereafter considered the uppermost 10 cm due to sampling intervals): moderately reduced conditions in the marsh platform sediments (38 ± 126 mV), oxidized soil in the dieback area (averaging 461 ± 145 mV), followed by weakly reducing conditions in the creek head (averaging 182 ± 158 mV; Fig. 3). In the revegetated area where tall-form *Spartina alterniflora* had recolonized the former creek head, the Eh was, on average, more oxidized than in the vegetated marsh platform where short-form *S. alterniflora* dominated (averaging 370 ± 205 mV). Similar trends have been found in previous studies concerning creek bank versus marsh platform soil conditions (i.e., Howes et al., 1981; DeLaune et al., 1983) in which the values are dictated by drainage conditions, waterlogging and the location of the water table at low tide (better drainage and more oxidized soil conditions in the revegetated zone allows the growth of tall-form *S. alterniflora*). Measurements of pH were negatively correlated with redox potential ($R^2 = 0.74$) and displayed a similarly distinctive trend along the transect lines (Fig. 5, Table 1). There was a marked decrease in pH between the surficial sediments of the marsh platform and those in the dieback zone (averages = 6.5 ± 0.2 and
5.6 ± 0.5, respectively), followed by a return to platform levels in the creek head and revegetated zones (averaging 6.4, Table 1).

### 3.2. Belowground biomass and inorganic dry weight

Belowground biomass was most variable within the upper 10 cm of the soil due to the differences in extent of live rooting amongst the environments (Figs. 2 and 3). If one considers the average belowground biomass of the whole core (0–60 cm), no noticeable differences were observed among sites (Fig. 2). However, in the surficial sediments belowground biomass decreased up to 60% from the marsh platform into the creek head (average dry weights decreased from 9.3 ± 3.3 g to 3.8 ± 1.5 g), and exhibited a slight increase in revegetated zones (4.6 ± 1.5 g; Fig. 3 and Table 1). This corresponds to a belowground standing stock of 1850 ± 650 g/m² in the upper 10 cm of the marsh, which decreases to 1084 ± 366 g/m² in the dieback area and 764 ± 302 g/m² in the creek head. Growth of tall-form *Spartina alterniflora* in the revegetated areas caused belowground standing stocks to rebound to 931 ± 306 g/m² (Table 1). The inorganic dry weight fraction of surficial samples also decreased significantly (by 52%) from the marsh to the dieback (from 75.1 ± 5.3 g to 35.8 ± 15.9 g), and then rebounded in the creek head and revegetated zone (56.5 ± 13.2 g and 77.2 ± 15.4 g, respectively; Fig. 3). This was due to large void space (honeycombing) of the soil in the dieback region resulting from dense crab burrows.

The ratio of organic to inorganic material can be calculated and compared along the creek head transects. Smaller organic:inorganic ratios were found in the surficial soil layers of the creek head and revegetated areas, compared to healthy marsh and dieback areas, as a result of the degradation of the belowground biomass (Table 1). In the dieback area, however, the inorganic

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**Fig. 3.** Comparison of surficial sediment properties (0–10 cm) in different environments proximal to creek heads: a) average dry weight of belowground biomass, b) average dry weight of inorganic sediment, c) average shear strength, d) average redox potential, Eh.

**Fig. 4.** Relationship between mass of belowground biomass and inorganic sediment. While no apparent trends are observed between belowground biomass and inorganic dry mass for the whole cores (a), surface sediment can be loosely grouped by creek head environment (b).
siltation contribution was also greatly reduced (due to the honeycomb of burrows), so the organic:inorganic ratio was larger compared to other zones (Table 1). No apparent trends were observed between belowground biomass and inorganic dry mass for the whole cores, however surface sediment could be loosely grouped into the different environments (marsh, dieback, denuded creek head, revegetated) by these parameters (Fig. 4).

3.3. Bulk density and bulk organic content

Bulk density in the surficial soil layers also varied significantly in the different environments (Table 1). Bulk density in the dieback regions was 47% lower than that on the marsh platform, again attributed to the large void space resulting from dense crab burrows. Bulk density trends further reflected variations in void volume as it then increases to near-marsh platform levels in the less densely burrowed revegetated zone (Table 1). However, while belowground biomass decreased significantly from the marsh platform into the dieback area, bulk organic content determined from loss on ignition did not reflect this variation and was relatively similar between the zones (Table 1). This suggests a transition from large particulate organic carbon (in the form of plant roots and rhizomes) to another form dissolved in the fine soils (Benner et al., 1991; and references therein).

Table 1

<table>
<thead>
<tr>
<th>Belowground biomass (kg m⁻²)</th>
<th>Inorganic sediment (kg m⁻²)</th>
<th>Bulk density (g/cm³)</th>
<th>Bulk organic content (%)</th>
<th>Organic:Inorganic pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Marsh 1.9 ± 0.7</td>
<td>14.9 ± 1.1</td>
<td>0.17 ± 0.02</td>
<td>23.3 ± 2.8</td>
<td>0.12 ± 0.03</td>
</tr>
<tr>
<td>Dieback 1.1 ± 0.4</td>
<td>7.1 ± 3.2</td>
<td>0.08 ± 0.04</td>
<td>24.9 ± 2.4</td>
<td>0.16 ± 0.03</td>
</tr>
<tr>
<td>Creek head 0.8 ± 0.3</td>
<td>11.2 ± 2.6</td>
<td>0.12 ± 0.03</td>
<td>20.5 ± 1.6</td>
<td>0.07 ± 0.02</td>
</tr>
<tr>
<td>Revegetated 0.9 ± 0.3</td>
<td>15.3 ± 3.1</td>
<td>0.16 ± 0.03</td>
<td>19.8 ± 2.2</td>
<td>0.06 ± 0.06</td>
</tr>
</tbody>
</table>

3.4. Soil shear strength

Values of shear strength reflect the integrity of the root matrix and cohesion of the soil. Therefore, shear strength measurements reflect belowground biomass results (i.e., root density) in addition to compaction with depth (Figs. 2 and 3). Shear strength was most variable in the upper 10 cm (ranging from 1.2 to 17 kPa). Although the absolute values of strength varied, there was a distinct trend throughout the five transects (Fig. 3). Highly variable but on average greater shear strengths in the marsh platform sediments reflect the presence of live Spartina roots and rhizomes (10 ± 7 kPa). Significantly lower shear strengths were observed in the dieback area (averaging 5 ± 3 kPa), unvegetated creek head (averaging 2 ± 1 kPa), and revegetated zone (averaging 3 ± 1 kPa). In the unvegetated area where tall-form S. alterniflora had re-colonized the former creek head, the shear strength remained low, likely because plants had not had sufficient time to fully re-root the weakened soil. Immediately below the active root zone, shear strength decreased to ~4 kPa for all creek head zones (Fig. 2). Below this level shear strength gradually increased to ~8 kPa at a depth of 1 m (likely due to compaction as found in other shear strength studies, e.g., Howes et al., 2010).

Because shear strength measurements were taken both in situ and in the extracted cores, it is possible to analyze soil strength in two different dimensions, along the x–y plane (in situ) and x–z plane (extracted core). In general, these measurements were found to be similar (Fig. 2). At depth, shear strength measured in the x–z plane appeared to be lower than strength in the x–y plane (Fig. 2), although this excludes measurements taken in the revegetated zone where results are almost exactly the same. The only significant difference was seen in the surficial marsh samples, where shear strength in the x–y plane was greater than strength in the x–z plane in the upper 20 cm. This could indicate differential strength associated with live rooting, suggesting that live S. alterniflora roots can withstand greater stress in the vertical dimension compared to horizontal. This seems reasonable considering the vascular bundles and elaborate aerenchyma system that provide the support of Spartina roots and rhizomes are aligned vertically (Maricle and Lee, 2002).

3.5. Correlation of geotechnical properties

Fig. 5 displays correlations between the geotechnical and geochemical properties measured in this study (pH, Eh, belowground biomass, shear strength). It is evident that variation of geotechnical and geochemical properties was only occurring in the surface sediments (0–10 cm) of marsh, dieback, creek head, and revegetated zones (Fig. 2, Table 1). Therefore it is not surprising that no correlations were found when looking at samples from entire cores (to 60 cm depth; Fig. 5). In samples from surficial sediments, strong correlations were found between Eh and pH, and shear strength and belowground biomass; a weak correlation was found between belowground biomass and Eh (Fig. 5).

4. Discussion

Results from our study indicate that rapid headward erosion of newly formed, low order creeks in the Santee Delta (formed by relative sea-level rise; Hughes et al., 2009) is likely facilitated by the geotechnical and geochemical changes associated with crab activity (particularly that of Sesarma reticulatum). Average redox potential (Eh), pH, belowground biomass, inorganic weight, bulk density, and shear strength were all distinctly different in surface sediments of heavily bioturbated zones adjacent to creek heads (locations where visible Spartina alterniflora dieback occurred) compared to more moderately bioturbated marsh platforms and unvegetated mudflats in the creek head. These measurements reveal that intense crab bioturbation and the formation of inter-connected burrows by Sesarma sp. significantly changes the properties of the soil, which affects the geomorphic evolution of the saltmarsh platform.

4.1. Effect of crab bioturbation on plant production and belowground biomass

Different crab species have preferential distribution in saltmarshes; results by Teal (1958) and more recently by Vu et al. (2011) found that fiddler crabs (Uca sp) predominantly inhabit the marsh platform with stunted Spartina alterniflora, whereas creek edges with tall-form S. alterniflora were dominated by Sesarma and Eurytium sp., distribution depending mostly on substrate preference, salinity tolerance, and predation and competition as opposed to food source. In the saltmarshes of the Santee Delta, Vu
et al. (2011) found that burrow density was much greater in dieback regions surrounding creek heads compared to other areas of the marsh, and *Sesarma reticulatum*, a herbivorous crab, was the most common species found in the dieback region. *Sesarma* sp. prefers peaty substrates and digs burrows that are larger than those of *Uca* (2.5–4 cm openings compared to 0.5–2 cm; Bertness et al., 2009). The burrow morphology of *S. reticulatum* is complex, with numerous horizontal interconnecting branches ~10–15 cm beneath the marsh surface, whereas the burrows of fiddler crabs are simple vertical structures that are not inter-connected (Crichton, 1960; Allen and Curren, 1974; Seiple and Salmon, 1982; Bertness et al., 2009). If crab burrows are connected, subsurface tidal flows may increase (Xin et al., 2009). The inter-connected burrows of *Sesarma* in the study area facilitate flooding and drainage of the marsh; water percolates through the elaborate burrow passages before flowing onto the marsh platform at

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**Fig. 5.** Correlations between geotechnical and geochemical properties measured: a) pH and Eh, b) pH and belowground biomass, c) belowground biomass and Eh, d) belowground biomass and shear strength. Only pH and Eh have a statistically significant relationship for whole core samples. Surficial sediment samples also display a significant correlation between shear strength and belowground biomass, and a weak correlation between belowground biomass and Eh.
flooding stages of the tide, and likewise passes through burrow structures into incipient channels of tidal creeks at ebbing stages of the tide (authors personal observations). This has major implications for soil oxygenation conditions and macrophyte primary production.

Previous studies have shown that moderate crab bioturbation may be beneficial to saltmarsh primary productivity; in particular, burrowing by fiddler crabs, *Uca* sp., benefits growth of *Spartina alterniflora* (Montague, 1982; Bertness, 1985). *S. alterniflora* has the ability to oxidize the sediment surrounding its roots by passive diffusion, however under waterlogged conditions plant growth is limited by a decrease in oxygen release, which lowers the redox potential of the soil and increases accumulation of toxins such as sulfides (Howes et al., 1981; Delaune et al., 1983). Burrow structures may increase the surface area of the marsh for oxygen exchange from both the atmosphere and tidal waters (20–60% or more; Montague, 1982; Koo et al., 2005; Xin et al., 2009; Thomas and Blum, 2010), which may reduce the concentration of sulfides and increase the uptake of nitrogen, fueling plant production (Howes et al., 1981; Delaune et al., 1983; Bradley and Morris, 1990). However, crab bioturbation may also affect the remineralization of organic material in the soil, both aerobically (Bertness, 1985; Koo et al. 2005; Thomas and Blum, 2010) and anaerobically (Kostka et al., 2002; Gribsholt et al., 2003), which could hinder preservation of belowground plant material.

In our study, belowground biomass decreased significantly (41%) from the marsh platform into the dieback area where *Sesarma* burrow densities were greatest, redox conditions were oxygenated, and pH was lowest (Figs. 2 and 3; Table 1). This suggests that *Sesarma* crab bioturbation causes the aerobic remineralization of belowground organic material. Bulk organic content of the soil (determined from loss on ignition) did not decrease in parallel, which indicates a possible transition from large particulate organic carbon (in the form of plant roots and rhizomes) to another form dispersed in the fine soils (Table 1). For example, other studies have shown that during the decomposition of *Spartina alterniflora*, substantial quantities of dissolved organic matter are produced (Benner et al., 1991; and references within). However, differentiation of particulate and dissolved organic matter was not measured in this study.

Aeration of saltmarsh soils can have negative effects on soil conditions, as well. Oxygenation can result in formation of severely acidic conditions (pH<2) from the oxidation of pyrite (FeS2, common in reduced soil) to ferric hydroxide (Fe(OH)3) and sulfuric acid (H2SO4; Reddy and Delaune, 2008). Measurements of lower pH (~5.5 compared to ~6.5) were found in dieback zones, indicating acidification of saltmarsh soil from aeration could be a factor in the *Spartina alterniflora* dieback. Further research is needed to evaluate these geochemical effects.

Although evidence presented here attributes the loss in belowground biomass to oxygenation and remineralization of the organic material, it cannot be discounted that the herbivore *Sesarma reticulatum* may be foraging on the roots and rhizomes of this plant, or that the physical act of burrowing damages them. These crabs preferentially feed on the surface at high tide and at night, picking small pieces of plant material from the substrate and consuming leaf material from the culms (Seiple and Salmon, 1982). Although crab herbivory by *Sesarma* has been cited as responsible for recent vegetation dieback in certain marshes (i.e., New England, Holdredge et al., 2008; Smith, 2009), these studies primarily focused on changes in aboveground biomass. Belowground foraging or damage to roots has not been studied in this crab species. Moreover, Holdredge et al. (2008) found that changes in predator population dynamics (e.g., decrease in predation of *Sesarma* crabs on Cape Cod compared to Narragansett Bay) reduced top-down control on *Sesarma* populations and thus increased dieback occurrence. This suggests that population dynamics of key species can have a drastic effect on geomorphic changes in saltmarshes.

### 4.2. Effect of crab bioturbation on soil stability

Many studies have shown enhancement of soil erosion results from macrofaunal habitation and bioturbation whereby cohesive fine-grained sediment (mud and silt) is disaggregated and repackaged into particles that are more easily transported (Rhoads, 1974; Blanchard et al., 1997; Austen et al., 1999; Paterson et al., 2000; de Deckere et al., 2001). Blanchard et al. (1997) found that the critical erosion threshold from flume measurements on surficial mudflat soils is highly dependent on sediment cohesiveness and bioturbating infauna lower this threshold. Further, experimental reduction in the density of infauna (de Deckere et al., 2001) created a 300% increase in sediment stability on intertidal mudflats in the Humber estuary (UK). From these and other studies, it is generally accepted that bioturbators have a destabilizing effect and enhance the erodibility of intertidal sediments.

Our study shows weakening of vegetated marsh soil that is highly correlated with crab bioturbation and loss of belowground biomass (Figs. 3 and 5). There was a 50% decrease in shear strength in areas with high *Sesarma* sp. crab density, which was likely due to the loss in the belowground biomass of *Spartina* plants. The roots and rhizomes of these plants bind the soil and create a stronger, more cohesive substrate (van Erdt, 1986), and loss of these structures (decomposition from oxygenation of the soil or crab foraging) causes instability of the soil. Escapa et al. (2007) similarly found that crab bioturbation (by *Chasmagnathus granulatus*) severely weakened saltmarsh soil. The resulting unconsolidated substrate may be more easily eroded under normal tidal flow conditions, and translates to lower critical erosion thresholds (Blanchard et al., 1997; Chen et al., 2012), although direct measurements of this parameter were not undertaken in this study.

The loss of surficial inorganic material in heavily burrowed creek head areas (Fig. 3) further supports the notion that crab bioturbation affects the removal of sediment in these areas. Moreover, there is a defined loss in elevation (>50 cm) that occurs in creek head areas and focusing of tidal flows has been observed (Hughes et al., 2009). Extensive burrowing also increases the total surface area that might be exposed to flows capable of erosion. The question arises whether the loss in inorganic sediment is through destabilization of cohesive sediment and physical suspension (erosion caused by active burrowing), or repackaging of cohesive mud by crabs into more easily transported fecal, feeding, and/or excavation pellets. A recent study by Gutierrez et al. (2006) found that material collected in burrow mimics inserted into the marsh had a higher percent total and labile carbon content than sediment excavated by crabs, suggesting that crab-excavated material is not transported as bedload. They also report that more material by weight was excavated by crabs than collected in burrow mimics, suggesting a net export of material. As most burrowing activity of *Sesarma* occurs when the marsh is inundated (up to high tide; Seiple and Salmon, 1982), the potential for suspension of destabilized or excavated sediment by tidal flow is high. In addition, percolation of water through burrows has been observed during ebb tides when water level drops below bankfull conditions, thus the potential for destabilized sediment to erode under these conditions is also high. This study highlights the need of further investigation to determine how sediment is eroded in heavily bioturbated regions, and the outcome of this sediment (i.e.,
whether material excavated by crabs is suspended and subsequently exported through creeks or redistributed onto the adjacent marsh surface).

4.3. Tidal creek ecophysical processes: bioturbation impacts on geomorphology

Although recent research has shown that crab bioturbation affects the production and degradation of organic material in saltmarshes (Kostka et al., 2002; Gribsholt et al., 2003; Koo et al., 2005; Thomas and Blum, 2010), our study highlights the resultant geomorphologic impact on the marsh platform. Biotic (macrophyte, macrofauna), sediment, and hydrodynamic interactions act in concert to facilitate creek headward erosion. We propose a conceptual model to summarize the mechanisms responsible for rapid creek extension (Fig. 6). Aboveground Spartina alterniflora plants are consumed proximal to the heads of tidal creeks by the herbivorous crab, Sesarma reticulatum (Vu, personal comment), and there is extensive degradation of belowground biomass in the upper 10–20 cm of the soil, which includes the roots and rhizomes that bind the soil. Sesarma habitation and bioturbation does not benefit primary production, but instead increases breakdown of subsurface peat and Spartina roots and rhizomes, which destabilizes the sediment (Fig. 6b). The impact of the crab bioturbation is fourfold: (1) crabs destabilize soil by burrowing and repackaging sediment into more easily eroded pellets; (2) oxygenation of the soil leads to degradation of stabilizing belowground biomass and possible acidification of the soil; (3) physical erosion of material.

![Fig. 6. Conceptual model of bioturbation facilitated creek incision. Red symbol in aerial photographs at left represents fixed location and cross sectional line as creeks incise platform from 1987 to 2006. Dark brown subsurface color at right indicates fibrous, peaty soil. a) Cross section of marsh platform proximal to creek head, vegetated by Spartina alterniflora and moderately bioturbated by Uca sp. crab. b) Severe bioturbation and herbivory of creek edge by Sesarma reticulatum and oxygenation of subsurface from interconnected burrows contributes to loss in belowground biomass and weakening of remaining sediment. c) Subsequent loss in elevation from deflation and erosion leads to focusing of tidal flows and allows creek extension into area. d) Former creek head area is revegetated with tall-form S. alterniflora as creek becomes channelized and continues to incise marsh platform. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)]
and remineralization of subsurface organics leads to loss in elevation at creek heads and focusing of tidal flows from the marsh platform, and finally; (4) decreased aboveground biomass (from stress or foraging: Hughes et al., 2009) reduces baffling of tidal flows, allowing higher current velocities (Temmerman et al., 2007). These mechanisms occurring in creek heads enhance the ability of tidal waters to erode soil where bioturbation is prolific, facilitating rapid creek extension in the Santee delta saltmarshes (Fig. 6c). As creeks extend into the marsh platform, former creek head mudflats become more channelized and transition from erosional to depositional environments, revegetating with tall-form S. alterniflora (Fig. 6d).

The influence of crab bioturbation on saltmarsh geomorphology is not unique to Cape Romain. Geomorphically similar creeks are found in other southeast U.S. Atlantic saltmarshes, and rapid erosion is also occurring at heavily bioturbated creek heads with Sesarma on Sapelo Island, Georgia (Vu and Pennings, pers. comm.). In addition, heavily bioturbated areas close to incising tidal creeks were described by May (2002) on the Delmarva Peninsula. The study identifies “transition” areas of low-density vegetation with “a mixture of dead and dying plants,” distinct “erosional holes in the marsh surface” greater than 5 cm diameter and a decrease in belowground biomass in the creek head areas where these holes exist. Although no direct link was drawn between crab activity and creek incision, the erosional holes described by May (2002) are likely burrows, with the crabs causing stress and death of the vegetation, as in our study. Other ecophysical studies globally have connected crab activity to creek incision. Perillo and Iribarne (2003) linked the formation of new tidal creeks to crab bioturbation in a Salicornia dominated marsh of the Bahia Blanca Estuary of Argentina. On upper reaches of the marsh, undermining and collapse of densely-burrowed saltmarsh sediment is common, forming new channels. On the lower marsh, Chasmagnathus granulatus burrow holes are permanently inundated and erosion occurs as groundwater flows undermine the soil. Escapa et al. (2007) suggested that creek formation and erosion in a similar area in Argentina (Sarcocornia dominated, Chasmagnathus bioturbated) was likely influenced by the change in geotechnical properties of the soil. Modeled interactions between plants and crabs suggest that landscape modifications from these interactions may facilitate the development of tidal creeks (Minkoff et al., 2006). Thus, it can be concluded from this and other studies that tidal flow through disturbed, bioturbated saltmarsh soil is capable of erosion and formation of creeks in many locales.

Although crab interactions with vegetation may enhance creek erosion, it is unlikely to be the driving mechanism. Primary creeks form on saltmarsh platforms where slight topographic gradients focus tidal flow (Chapman, 1960; Perillo et al., 1996; Perillo and Iribarne, 2003; and references therein). Hughes et al. (2009) established that creek network expansion in our study area is a response to SLR and the consequent increase in tidal prism. Moreover, the formation and extension of primary creeks has been observed as a response to SLR in many areas unimpacted by severe bioturbation (Knighton et al., 1991; Shi et al., 1995; Rankey and Morgan, 2002). In addition, numerical models support the paradigm that water surface elevation gradients drive creek network development (Rinaldo et al., 1999; Fagherazzi et al., 2012) and headward erosion can occur at creek heads where the hydrodynamic shear stress exceeds a threshold value (D’Alpaos et al., 2005).

Thus, hydrodynamic forcings (tidal range, rate of relative sea-level rise) modulated by vegetation effects (dominant vegetation type, rooting, adaptation to stress) are more likely to be driving specific rates of creek extension at a particular location. However, feedbacks associated with crab bioturbation are still important and should not be ignored.

Degradation of belowground saltmarsh material, loss in elevation, and erosion is associated with Sesarma crab bioturbation in Cape Romain (and potentially may be occurring in many southeast U.S. saltmarshes), however it is possible that enhanced tidal creek incision may be beneficial for the sustainability of these wetlands. With extension of tidal creeks, larger tidal volumes can be accommodated (Shi et al., 1995; Marani et al., 2003). Moreover, sediments sourced from eroding marsh areas (in this case from creek incision) may provide material for accretion of the surrounding marsh platform, aiding marsh elevation relative to sea-level (Reed, 1995; Morris et al., 2002; Wilson and Allison, 2008). Further, it is generally accepted that marsh areas proximal to creeks experience higher sediment accretion (Stumpf, 1983; Christiansen et al., 2000; LeMay, 2007; Temmerman et al., 2007). It is also possible, however, that this ongoing tidal creek extension may be an initial indication of overall marsh degradation and disintegration: under high rates of sea-level rise, models predict marsh platforms are unable to maintain elevation and eventually submerge (Kirwan and Guntenspergen, 2010), and several studies indicate a recent acceleration in the rate of sea-level rise (Church and White, 2006; Jevrejeva et al., 2008; Kolker et al., 2010). While our study indicates that biological and physical feedbacks impact tidal creek extension, further research focusing on interactions between biota and geomorphology is needed to determine long-term saltmarsh platform response to sea-level rise.

5. Conclusions

Intense crab bioturbation and the formation of inter-connected burrows in the soil, particularly by Sesarma reticulatum, is significantly changing the geochemical and geotechnical properties of saltmarsh soil in the Santee Delta, South Carolina, ultimately impacting the geomorphology of the marsh platform and facilitating tidal creek incision. We observed major alterations of redox potential, belowground biomass, inorganic weight, bulk density, and shear strength in surface sediments of heavily bioturbated zones of creek heads. Dieback of Spartina alterniflora, decomposition of belowground biomass, and destabilization by burrowing crabs weakens the soil. This leads to the formation of a depression, which focuses tidal flows. Destabilization of the soil and formation of a depression enhances the erosion potential of the creeks. The pervasiveness of similar tidal creek morphology in southeast U.S. Atlantic saltmarshes suggests this mechanism is occurring in other marshes with a moderate tidal range undergoing sea-level rise, and this process in general has implications for creek network development, ecogeomorphology, and saltmarsh sustainability.

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