



Sea-level rise thresholds for stability of salt marshes in a riverine versus a marine dominated estuary



Wei Wu ^{a,*}, Patrick Biber ^a, Deepak R. Mishra ^b, Shuvankar Ghosh ^c

^a Division of Coastal Sciences, School of Ocean Science and Engineering, The University of Southern Mississippi, 703 East Beach Dr., Ocean Springs, MS 39564, USA

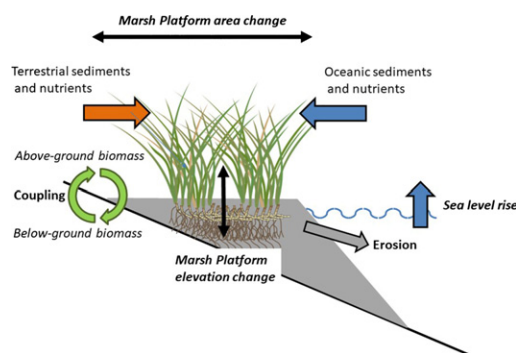
^b Center for Geospatial Research, Department of Geography, University of Georgia, Athens, GA 30602, USA

^c Department of Geospatial Monitoring and Information Technology, French Institute of Pondicherry (IFP), 11, St Louis St, White Town, Puducherry 605001, India

HIGHLIGHTS

- Salt marshes are more resilient to sea-level rise in estuary with larger river input.
- The higher resilience is mainly due to more riverine-borne mineral sediments.
- Sea-level rise thresholds are more sensitive to biomass in a marine dominated estuary.
- Biomass & sediment affect sea-level rise thresholds alike in river-dominated estuary.
- Belowground biomass contributes more to accretion in estuary with limited river input.

GRAPHICAL ABSTRACT



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ABSTRACT

We studied the ecological resilience of salt marshes by deriving sea level rise (SLR) thresholds in two estuaries with contrasting upland hydrological inputs in the north-central Gulf of Mexico: Grand Bay National Estuarine Research Reserve (NERR) with limited upland input, and the Pascagoula River delta drained by the Pascagoula River, the largest undammed river in the continental United States. We applied a mechanistic model to account for vegetation responses and hydrodynamics to predict salt marsh distributions under future SLR scenarios. We further investigated the potential mechanisms that contribute to salt marsh resilience to SLR.

The modeling results show that salt marshes in the riverine dominated estuary are more resilient to SLR than in the marine dominated estuary with SLR thresholds of 10.3 mm/yr and 7.2 mm/yr respectively. This difference of >3 mm/yr is mainly contributed by larger quantities of riverine-borne mineral sediments in the Pascagoula River. In both systems, sediment trapping by the above-ground vegetation appears to contribute more to marsh platform accretion than organic matter from below-ground biomass based on the medians of the accretion rates. However, below-ground biomass could contribute up to 90% of accretion in the marine dominated estuary compared to only 60% of accretion in the riverine dominated estuary. SLR thresholds of salt marshes are more sensitive to vegetation biomass in the marine dominated estuary while biomass and sediment similarly affect SLR thresholds of salt marshes in the riverine dominated estuary.

This research will likely help facilitate more informed decisions on conservation/restoration policies for these two types of systems in the near-term needed to minimize future catastrophic loss of these coastal marsh habitats once SLR thresholds are exceeded.

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* Corresponding author.

E-mail address: wei.wu@usm.edu (W. Wu).

1. Introduction

Coastal human populations and economies in some parts of the world are heavily dependent on the marsh ecosystem for a wide array of goods and services, including fish production, carbon sequestration, habitat for fish, birds and other species, storm surge reduction, flood control, nutrient regulation etc. (Costanza et al., 1997; Engle, 2011). This is especially true along the northern Gulf of Mexico (NGOM) where marsh ecosystem services contribute significantly to the well-being, livelihood, and economic resilience of coastal communities. However, coastal marshes along NGOM are increasingly threatened by multiple natural and anthropogenic stressors, which have been and will continue to be exacerbated by sea level rise (SLR) due to their narrow elevation range within the intertidal zone (Mogensen and Rogers, 2018).

The way coastal marshes respond to SLR shows large spatial variability because it is dependent on multiple factors of both terrestrial and oceanographic origins, such as coastal geomorphology, rate of subsidence, climate, sediment supply, hydrodynamic and ecological conditions, as well as anthropogenic influences, such as extent of engineering modification to the landscape (Donchyts et al., 2016; Fagherazzi et al., 2012; Hagen and van der Pluijm, 2017; Hardy and Wu in revision; Kirwan et al., 2010; Osland et al., 2017; Passeri et al., 2016, 2015a; Raposa et al., 2016; Schuerch et al., 2018; Stagg et al., 2016; Turner, 1997; Twilley et al., 2016). The largest wetland loss in the United States occurred in the southeastern states in the 1970s (Li et al., 2018; Mitsch and Gosselink, 2007). Whether coastal marshes can keep up with future SLR will rely on the complex interactions between geomorphology, physical forcing, and ecological processes that are unique to each estuarine system. Due to the fundamental role of marsh vegetation in coastal wetlands, the survival of these ecosystems is mainly a question of how the vegetation will respond to increased inundation and salinity, particularly in estuaries with limited availability of mineral sediments. The large variability of vegetation responses to inundation leads to the large variability of salt marshes' response to SLR, requiring localized predictions of future landscape structure and function. The marsh vegetation above- and/or below-ground biomass can exhibit either a linear decrease (Janousek et al., 2016; Snedden et al., 2014; Voss et al., 2013; Watson et al., 2014), or a quadratic relationship with inundation (Kirwan and Guntenspergen, 2012; Morris et al., 2002; Schile et al., 2014). The response of vegetation productivity to inundation (van Belzen et al., 2017) is further complicated by salinity and nutrient levels, and localized erosional processes (Aldred et al., 2017; Graham and Mendelsohn, 2014; Janousek et al., 2016; Watson et al., 2015), thereby resulting in potentially complex and location-specific responses by marsh vegetation to future SLR.

Both above- and below-ground biomass can contribute to the accretion of salt marsh platform elevation through different processes (Fig. 1). Above-ground biomass traps mineral sediments from the water column to augment the elevation, while below-ground biomass contributes organic matter to further promote accretion of the salt marsh platform (Kirwan and Guntenspergen, 2012; Morris et al., 2002; Mudd et al., 2010; Neubauer, 2008; Nyman et al., 2006). Above- and below-ground biomass perform different physiological functions, with the above-ground biomass responsible for photosynthesis and carbon assimilation (organic matter production) while the below-ground biomass takes up water and nutrients necessary for vegetation growth. Therefore, the above- and below-ground biomass fractions are coupled through fluxes of water, nutrients, and carbohydrates (Scheiter and Higgins, 2013). This coupling can result in different strategies of biomass allocation between above- vs. below-ground biomass fractions potentially influencing vegetation growth and morphology, which is an important strategy to help plants to adapt to environmental conditions (Guo et al., 2016; Li et al., 2015; Weiner, 2004), and therefore could strongly influence coastal wetlands' resilience to press disturbance such as SLR.

Ecological resilience is defined as the amount of disturbance (SLR rate in this study) that an ecosystem could withstand without changing key structures and functions (Gunderson, 2000; Holling, 1973). The larger the amount of disturbance an ecosystem can withstand, the higher the resilience of the ecosystem. A related concept is that of ecological threshold, which indicates the presence of a state transition and assumes alternate equilibrium states of the ecosystem. Ecological threshold can be defined as the frequency and magnitude of disturbances an ecosystem can sustain before a significant change of key ecological functions results in the switch to the alternate stable state (Groffman et al., 2006; Halpern et al., 2015, 2008). Due to the feedback among inundation, vegetation productivity, and sediment trapping, coastal marshes can adapt to SLR. Previous studies in sediment analysis and numerical modeling show that coastal wetlands can keep up with SLR rates up to 12 mm/yr (Jankowski et al., 2017; Kirwan et al., 2010). However, just like many ecosystems, coastal marshes are subject to regime shifts, which are abrupt state transitions after crossing a threshold due to increasing environmental stress that may be naturally or anthropogenically driven (Scheffer et al., 2001; Foley et al., 2015). Here the ecological threshold is in response to SLR rate, and the state of salt marshes is indicated by total area, with a state transition occurring when marsh is lost and becomes open water.

We aim to study the resilience of salt marshes to SLR in two estuaries with significant contrasting hydrological inputs using SLR rate thresholds. Previous studies show that salt marshes in marine dominated systems are potentially more vulnerable to collapse compared to marshes in fluvial estuaries due to relatively uniform topography and/or lack of sediment sources (Alizad et al., 2018; Kirwan et al., 2010). We examine and discuss underlying processes that may contribute to future landscape dynamics of salt marshes under SLR. Identifying the ecological threshold for marsh habitat stability and the potential mechanisms contributing to collapse will help in understanding the nonlinear response of these ecosystems to different environmental factors, and could potentially be informative for resource managers to evaluate ecological resilience and make proactive plans for conservation and restoration.

2. Methods

We developed a two-dimensional dynamic and mechanistic model (Wu et al., 2017a) that integrates the Marsh Equilibrium Model (MEM, Morris et al., 2002) and a simplified hydrodynamic model (Kirwan and Murray, 2008) to predict salt marsh changes by 2100. Our model simulates erosion, which MEM does not, and is much quicker to run when compared to Hydro-MEM that is used to simulate very

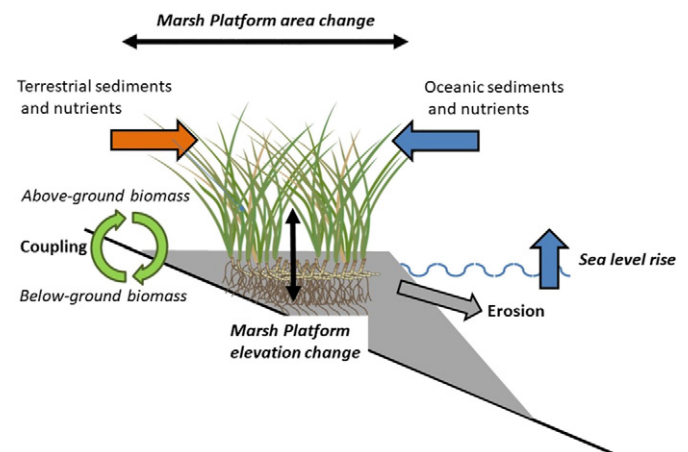


Fig. 1. A conceptual model for the response of salt marshes to sea-level rise (adapted from Wu et al., 2017a) with coupling of above- to below-ground biomass as a potential mechanism important in the vegetation response and influencing the rate of elevation change of marsh platforms.

detailed hydrodynamics in estuaries (Alizad et al., 2016a; Hagen et al., 2013; Passeri et al., 2015b).

2.1. Study area

The study areas are comprised of two adjacent (<20 km apart) estuarine systems with contrasting riverine inputs, located in southeastern Mississippi in the north-central Gulf of Mexico (Fig. 2). The first site is the Grand Bay National Estuarine Research Reserve (NERR) with limited upland input mainly from groundwater flow under pine savannahs with interspersed freshwater wetlands and seepage bogs (Peterson et al., 2007). The second site is the Pascagoula River (PR) delta with plentiful riverine input, drained by the Pascagoula River, the largest undammed river (by volume) in the continental US with an average discharge of 11,520 ft³/s from 1994 to 2007 (<https://waterdata.usgs.gov/nwis>). We purposely selected these two estuarine systems as they represent examples of contrasting end-members on the spectrum of low to high volume hydrological inputs from the adjacent uplands. The two estuaries have identical climate and similar geomorphological properties with erosional shorelines, minimizing potentially confounding influences on marsh vegetation productivity. The climate is subtropical with hot and humid summers and mild winter conditions (Peterson et al., 2007). The terrain is very flat with an average slope of 1.0–1.5°. The study sites are both micro-tidal, shallow estuaries influenced by diurnal astronomical tides with an annual average range of 0.4–0.6 m and an average water depth of 0.6–0.9 m (Christmas, 1973). The salt marshes in Grand Bay are dominated by *Juncus roemerianus* (black needlerush) with a small area of *Spartina alterniflora* (smooth cordgrass) along the low elevation fringe of the marsh habitat. Plant species richness in the Pascagoula River delta is higher than in Grand Bay due to lower salinity, but the two dominant species in the study area are still

J. roemerianus and *S. alterniflora* (Eleuterius, 1972). The Pascagoula watershed and Grand Bay NERR contain about 35% and 15% of the total marsh habitat in coastal Mississippi respectively (MDEQ 2001; Peterson et al., 2007).

2.2. Model description

Our model (see Wu et al., 2017a for detailed description) simulates elevation change from the accretion and erosion of salt marshes and the resulting conversion of salt marshes to estuarine open water. Accretion rate is accounted for by the contribution from mineral sediments in the water column as well as organic matter accumulation from below-ground biomass production. Erosion rate is accounted for by water depth and driven by the rate of SLR. Once the elevation is below mean low water level, salt marshes convert to open water (an ecological state change).

2.3. Model inputs

1) Elevation and Sediments

We used LiDAR-derived elevation data collected by the U.S. Army Corps of Engineers acquired in September to October 2005 available from the NOAA Coastal Services Center (<https://coast.noaa.gov/dataviewer>, last accessed on 25 February 2017). This dataset had a spatial resolution of 2 m and the best vertical accuracy of 7.6 cm in this region and used the datum of NAVD88. Salt marshes in Grand Bay had a median elevation of 0.52 m compared to a median elevation of 0.32 m in the Pascagoula River delta (Fig. 3).

For the sediment concentration in the water column, we used the total suspended solids (TSS) measured by the System-Wide-

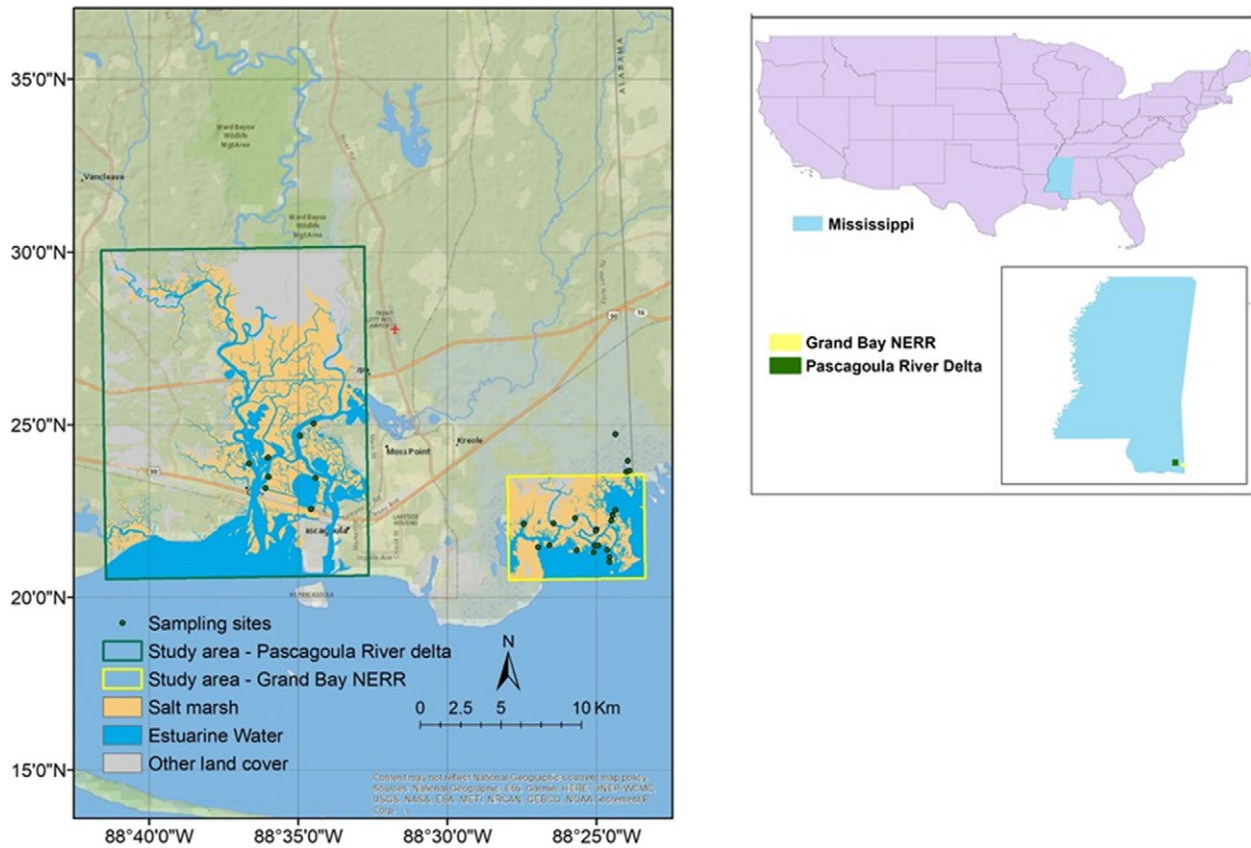


Fig. 2. Study areas: Grand Bay National Estuarine Research Reserve (NERR), a marine dominated estuary, and the Pascagoula River delta, a riverine dominated estuary, both in southeastern Mississippi in the north-central Gulf of Mexico. Boundary of Grand Bay NERR is from the NERR centralized data management office (<https://cdmo.baruch.sc.edu/>). The inset maps of US continental states are from <https://hifld-geoplatfrom.opendata.arcgis.com/search?groupids=e5cf7f3805274fef90100ab704ee2ac1>

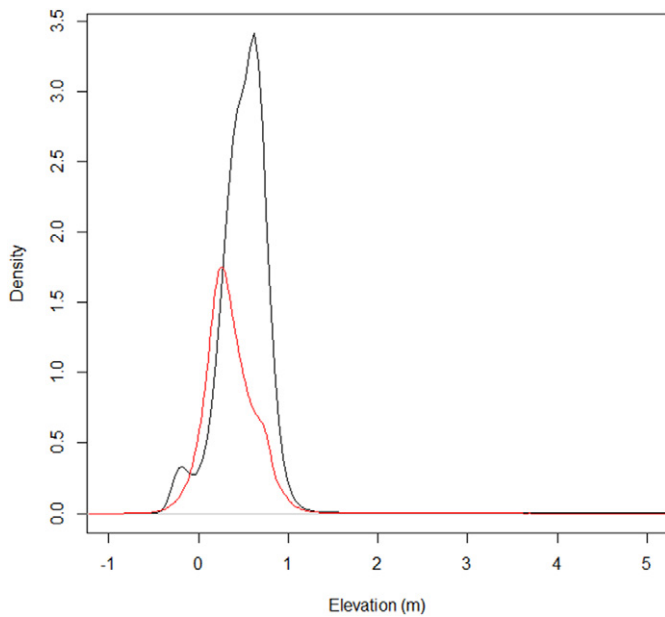


Fig. 3. Probability density plot of elevation for salt marshes in Grand Bay (black) and Pascagoula River delta (red) derived from LiDAR data collected in 2005.

Monitoring-Program in Grand Bay NERR (Wu et al., 2017a) (Sept. 2012 through April 2014 - average of 16.8 mg/L). We applied the average of measured sediment concentrations for the Pascagoula River delta (only available from 1974 to 1975 - average of 52.0 mg/L) obtained from USGS National Water Information System (<https://maps.waterdata.usgs.gov/mapper/index.html>). We expect the sediment concentrations to change over time, for example, due to land use change (Waldron, 2019). However, due to lack of availability of recent data on sediment concentrations, we conducted sensitivity analysis on sediment concentration to evaluate how it would affect SLR thresholds. Sediment bulk density used for both study systems was 0.39 g/cm^3 , as reported in Morris et al. (2016) for Grand Bay.

2) Above- and below-ground biomass

Above- and below-ground biomass are important inputs needed to correctly derive accretion rates of salt marshes in the model. We collected duplicate above-ground biomass samples at 19 randomly selected sites in Grand Bay (7 sites dominated by *J. roemerianus* and 12 sites dominated by *S. alterniflora*) in August–September of 2017, and at 16 randomly selected sites in the Pascagoula River delta (8 sites dominated by *J. roemerianus* and 8 sites dominated by *S. alterniflora*) in October of 2017 using $15 \times 15 \text{ cm}$ quadrats for *J. roemerianus* and $25 \times 25 \text{ cm}$ quadrats for *S. alterniflora*. Green (living) above-ground biomass in salt marshes in the northern Gulf of Mexico peaks between August and October (Eleuterius, 1973; Eleuterius and McDaniel, 1978; Ghosh et al., 2016; Ghosh and Mishra, 2017). All the sampling sites were within 30 m of the coastline as we assume that the marsh fringe represents the most vulnerable location to inundation from SLR. At these sampling sites, we also collected sediment cores ($30 \times 15 \text{ cm}$ diameter) to measure below-ground biomass after removing the above-ground biomass. We transported all samples back to the laboratory on ice and stored the above-ground biomass samples in the refrigerator and below-ground biomass samples in the freezer until they were processed within three months of collection.

In the laboratory, we rinsed the sediments off the below-ground biomass samples using a stacked series of 2 mm-mesh over 1 mm sieves,

after which we manually separated live from dead fractions for both above- and below-ground biomass, before they were oven-dried to constant weight at $75 \text{ }^\circ\text{C}$ (~3 days) and weighed. For above-ground biomass, the separation between live and dead material was based on color, with green leaves/stems considered to be live biomass and brown or yellow leaves/stems considered to be dead biomass. For the below-ground biomass, we submerged the samples in water to separate live from dead fractions. The root/rhizome material floating on the water surface was considered as live biomass and the matter that sank to the bottom was considered to be dead. Hardness and color, with turgid and lighter colored tissues considered to be live (Gross et al., 1991; Schubauer and Hopkinson, 1984), were further used to aid the separation of live from dead material in the below-ground biomass samples.

We used these data to then derive quantitative functions that relate live above- and live below-ground biomass to sampling elevation respectively using the dominant species as a random effect in mixed-effects models. We compared the mixed-effect models to models without random effects based on the Akaike Information Criterion (AIC) (Wu et al., 2017b). We converted the one-year biomass sample measurements from 2017 to long-term averages by dividing the measurement values by a correcting ratio, the ratio of above-ground average summer-fall green biomass in 2017 (single year) to that for 2000–2017 long-term average of above-ground green biomass (GBM) derived from a time series of MODIS imagery (Ghosh et al., 2016). The remote sensing driven biomass model was calibrated using a dataset match-up between GBM measurements at 69 sampling locations and the corresponding 8-day Level 1B atmospherically corrected 500-m MODIS surface reflectance composites (MOD09A1). Visible Atmospheric Resistant Index (VARI) produced the best results when compared with several other vegetation indices with a percent normalized root mean squared error (%NRMSE) of 17%.

2.4. Model calibration and evaluation

We calibrated the model for each study site by comparing the simulated accretion rates with the measured ones, using the feldspar marker horizon technique in Grand Bay NERR (Wu et al., 2017a) and sediment core radioisotope analysis in the Pascagoula River delta (Wu et al., 2015). The timescale for surface marker horizons is months to years while it is 20–50+ years for analysis of radionuclides (Breithaupt et al., 2018). Though the timescales of the two techniques differ, the accretion data measured using the same technique at the two estuaries are not available. Spatial distribution maps of salt marshes were available for 1988 (Shirley and Battaglia, 2006) and 2007 in Grand Bay, and 1996 and 2007 in the Pascagoula River delta from the National Wetland Inventory (NWI) datasets. We used the earlier 1988 or 1996 maps as the initial wetland map in the model and 2007 maps as reference maps for model evaluation. We used a kappa index, which accounts for persistence of landscapes (Wu et al., 2015; van Vliet et al., 2011), with four metrics to evaluate model performance: (1) hits (change simulated correctly), (2) correct rejection (persistent simulated correctly), (3) misses (change simulated as persistence), and (4) false alarms (persistence simulated as change) (Wu et al., 2017a; Pontius et al., 2011). We also calculated “figure of merit”, i.e. the ratio of hits to the sum of hits, misses, and false alarms to quantify how well the model simulated land cover change (Pontius et al., 2011). As we focused on simulating the conversion from salt marshes to water, we did not have wrong hits (change simulated as change but in a wrong land/water type). Further details on the calibration and evaluation of the model for Grand Bay NERR can be found in Wu et al., 2017a.

2.5. Derivation of SLR thresholds

We ran the calibrated model under 33 different scenarios of increasing annual SLR rates from 4 mm/yr (current SLR rate) to 20 mm/yr (extremely high SLR rate), with a step increment of 0.5 mm/yr. Based on

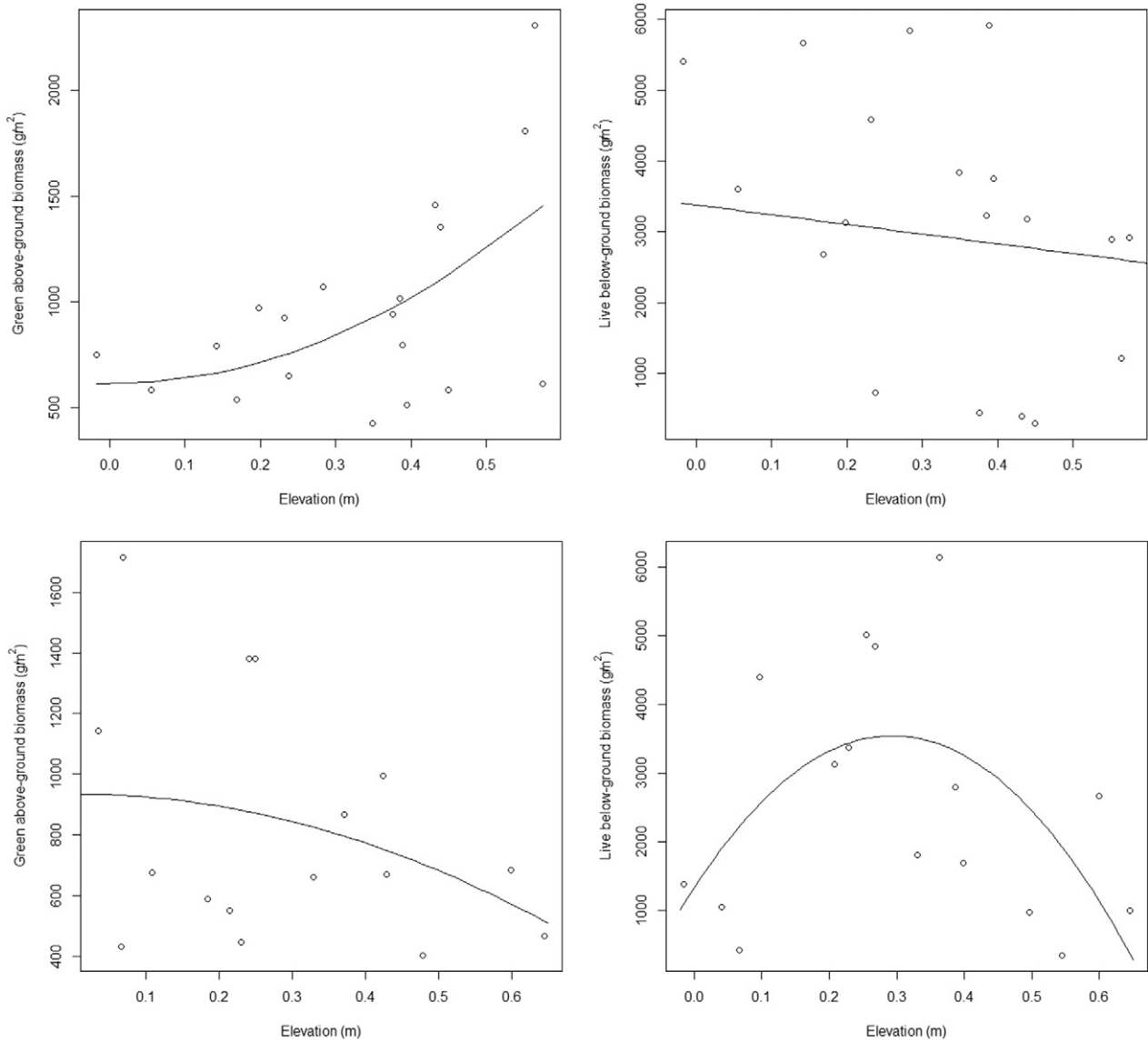


Fig. 4. Measured live above-ground (left panels) and live below-ground biomass (right panels) vs. elevation (scatter points) and best-fit functions (lines) in the Grand Bay (upper panel) and the Pascagoula River delta (lower panel).

the model predictions, we then calculated total area of salt marsh in 2050 and 2100, and derived SLR thresholds. To identify the actual thresholds, we fitted a sigmoidal regression curve to the data pairs of marsh area against SLR rate and used the inflection point on the fitted sigmoid curve as the threshold (Osland et al., 2013; Wu et al., 2017a). The analysis was done using the 4-parameter function package “drc” available in R (<https://cran.r-project.org/web/packages/drc/drc.pdf>, last accessed on July 11, 2018). In general, the higher the SLR thresholds for the conversion from marsh to open water, the higher the resilience of salt marshes to future SLR.

2.6. Model sensitivity analysis on biomass and sediment functions

To better understand the sensitivity of the plant biomass and sediment related functions on the modeled response of salt marshes to SLR, we reran the model scenarios with 25%, 50% increase and 25%, 50% decrease (chosen based on standard deviation of measured biomass in the result section) compared to the baseline values of live above-ground biomass (AB), live below-ground biomass (BB), total live biomass (AB + BB), and suspended sediment concentration in the water column. All simulations were run to 2100 predicting remaining salt

Table 1
The best selected models for live above- and below-ground biomass in Grand Bay and Pascagoula River delta.

Location	Biomass	Best function form	Intercept	Slope for elevation	Slope for elevation ²	Random effect of species included?
Grand Bay	Above-ground	Quadratic	609.7		2560.8	No
	Below-ground	Linear	3378.3	-1365.8		Yes
Pascagoula River delta	Above-ground	Quadratic	935.8		-1009.0	Yes
	Below-ground	Quadratic	1326.4	15,071.0	-25,565.3	No

Table 2
Metrics to show how the model simulates wetland change between 1988/1996 to 2007.

	Grand Bay	Pascagoula River delta
Accretion rate (mm/yr)	2.8 simulated vs. 2.0 in Raposa et al., 2016	4.1 simulated vs. 6.5 in Wu et al., 2015
Overall Kappa accounting change from initial 1988 map*	0.54	0.43
Kappa for amount of change	0.78	0.79
Kappa for location of change	0.69	0.54
Hit (ha)	143.4	320.4
Correct rejection (ha)	3293.7	10,002.8
Misses (ha)	152.7	300.0
False alarm (ha)	55.0	384.5
Figure of merit (%)	41	32

* product of Kappa for amount and location of change.

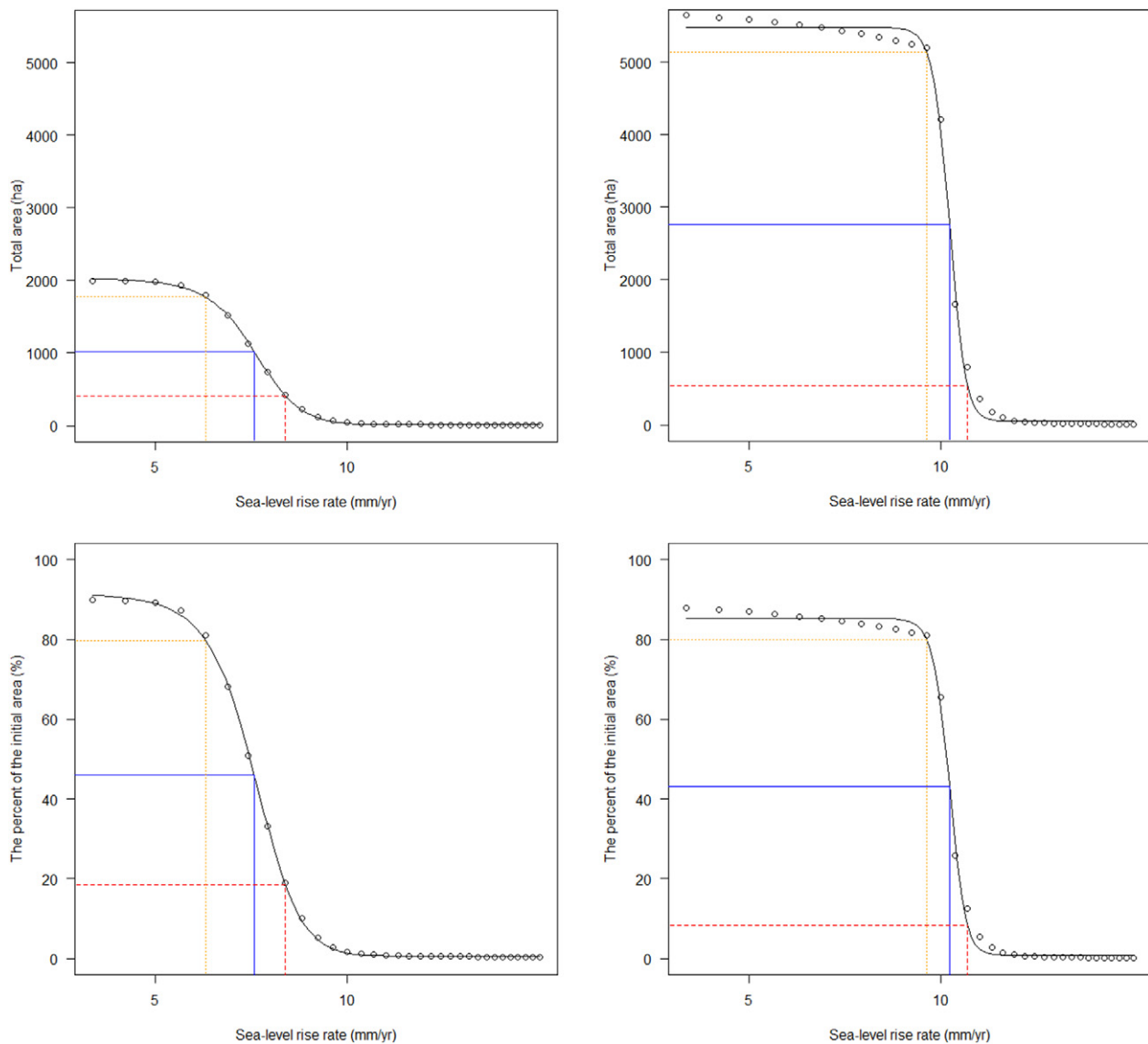


Fig. 5. Predicted salt marsh areas (ha - top panels) and relative to the initial area (% - bottom panels) in 2100 under increasing SLR rates in Grand Bay (left) and the Pascagoula River delta (right). The SLR threshold is denoted using blue lines, the beginning of the transition zone is denoted using orange lines, and the ending of the transition zone is denoted using red lines.

marsh area (ha) over time under the previous range of SLR rates (4 mm/yr to 20 mm/yr). We then compared the new SLR thresholds under these different scenarios of biomass and sediment concentrations to that under no change of biomass or sediment concentrations as described previously.

3. Results

The SLR thresholds for salt marsh survival in the Pascagoula River delta are larger than those in Grand Bay for both 2050 and 2100 based on total area, indicating that salt marshes in the Pascagoula River delta are potentially more resilient to SLR than those in Grand Bay.

1) Above- and below-ground biomass

The measured 2017 seasonal peak green above-ground biomass and live below-ground biomass for salt marshes in the Pascagoula River delta were 816.4 ± 397.2 g/m² (mean \pm sd) and 2562.4 ± 1784.1 g/m² respectively. These values are 14% and 18% lower than those measured in Grand Bay, where the green above-ground biomass was 951.5 ± 484.8 g/m² and live below-ground biomass was $3140.5 \pm$

Table 3
SLR thresholds and ranges of maximum rates of change (= transition zones with lower and upper boundary indicated) for 2100.

Location	Lower boundary (mm/yr)	Corresponding Area (ha)	SLR threshold (mm/yr)	Corresponding Area (ha)	Upper boundary (mm/yr)	Corresponding Area (ha)
Grand Bay	6.0	1770.4	7.2	1022.2	8.0	412.0
Pascagoula River delta	9.5	5140.3	10.3	2766.8	11.0	538.4

1861.9 g/m². The mean live below- to above-ground biomass ratio in the Pascagoula River delta was 3.4, which is smaller than 4.1 for Grand Bay. Based on the AIC from mixed-effects modeling (random effect is species), the response of both live above- and below-ground biomass to elevation showed similar quadratic functions in the Pascagoula River delta, whereas in Grand Bay, different functions (quadratic function for live above- and linear function for live below-ground) best predict biomass (Fig. 4, Table 1).

2) Model calibration and evaluation

For calibration purposes, the model simulated wetland changes from 1988 to 2007 (19 years) in Grand Bay and from 1996 to 2007 (11 years) in the Pascagoula River delta. The overall kappa values, which account for the initial salt marsh area and persistence by 2007 are 0.54 and 0.43 for Grand Bay and Pascagoula River delta respectively (Table 2). The model simulates amount of change similarly for both estuarine systems (similar Kappa for amount of change), and it simulates the location of change more accurately in Grand Bay (0.69) than in the Pascagoula River delta (0.54) (Table 2). Figure of merit is higher in Grand Bay (0.41) than in the Pascagoula River delta (0.32), showing overall better performance of the model in Grand Bay than in the Pascagoula River delta. The model could correctly simulate 48% of the reference change between 1988 and 2007 in Grand Bay, and 52% of the reference change (both number and location of change) between 1996 and 2007 in the Pascagoula River delta. Simulating half of the reference change is considered to be reasonable for a land use/land cover model (Wu et al., 2015). The simulated average accretion rate was ~3.0 mm/yr under the current SLR rate in Grand Bay (1986–2007), which was larger than the short-term accretion rate measurements of 2.0 mm/yr using the feldspar marker horizon method (Raposa et al., 2016). The simulated average accretion rate was ~4.0 mm/yr under the current SLR rate in the Pascagoula River delta (1996–2007), which was less than the long-term accretion rate of 6.5 mm/yr inferred from radioisotope analysis (Wu et al., 2015).

3) Model predictions for derivation of SLR thresholds

The SLR threshold for stability of salt marshes is 7.2 mm/yr in Grand Bay, based on the 33 simulated scenarios by 2100. The area of maximum rate of change (Osland et al., 2014), referred to hereafter as the “transition zone” from salt marsh to open water, lies between SLR rates of 6.0 and 8.0 mm/yr (Fig. 5, Table 3). In contrast, in the Pascagoula River delta, the SLR threshold for stability of salt marshes is 10.3 mm/yr, with the transition zone occurring between SLR rates of 9.5 and 11.0 mm/yr (Fig. 5, Table 3). The transition zone, when rapid loss of marsh to open water occurs, is steeper for the Pascagoula River delta than that for Grand Bay, mainly due to the larger values of the SLR rates needed before the marshes enter the transition zone (Fig. 5). For either system, the salt marsh area at the lower boundary of the transition zone is about 80% of the initial total area (2220.3 ha for Grand Bay and 6426.1 ha for Pascagoula River delta), and the marsh area at the SLR threshold is about 45% of the initial total area (Fig. 5, Table 3). The SLR threshold in Grand Bay (7.2 mm/yr) is near the upper boundary of very likely future SLR under a very conservative Representative Concentration Pathway 3 (RCP 3) climate change scenario (~7 mm/yr, Horton

et al., 2014). The SLR threshold in the Pascagoula River delta (10.3 mm/yr) is within the likely range of SLR under the more aggressive RCP 8.5 climate change scenario (Horton et al., 2014). Once these thresholds are exceeded, the area of marsh declines rapidly converting the landscape to an open water estuarine system (Fig. 6).

Although the SLR thresholds for marsh collapse occurring by 2050 are larger than those for 2100, the values of total marsh areas remaining at the thresholds are very similar for both time points in each estuary. In particular, the total area of marsh remaining at the threshold appears to be remarkably consistent at ~1020 ha in Grand Bay and 2800 ha in the Pascagoula River delta no matter which target year is used (Table 4), potentially signaling some underlying tipping point of marsh resiliency as a function of system-specific landscape configuration. The total marsh area and area loss relative to the total could provide reliable indications or (early) warning signals toward the vulnerability of salt marshes under different rates of SLR.

4) Model sensitivity analysis

A change in total biomass (increase or decrease) was found to have a larger impact on the SLR thresholds compared to a change in the sediment concentration in Grand Bay, while biomass and sediment concentration played a similar role in the Pascagoula River delta simulation (Fig. 7, Table 5.1). In addition, change of above-ground biomass has a larger impact on SLR thresholds than below-ground biomass for both systems. However, SLR thresholds in the Pascagoula River delta are more sensitive to above-ground biomass and less sensitive to below-ground biomass than in Grand Bay (Fig. 7, Table 5.2).

4. Discussion

In order to increase confidence in the model's ability to accurately predict future scenarios, we compared our results to the predictions derived from a different model based on first principles (Morris et al., 2016). The SLR threshold for Grand Bay was 7.5 mm/yr in Morris et al. (2016) model with k_1 (density of pure organic matter) of 0.056, k_2 (density of pure mineral matter) of 1.267 g cm⁻³, and 40 cm of water at high tide, which is almost identical to our modeled prediction of 7.2 mm/yr. The SLR threshold for the Pascagoula River delta using the model developed by Morris et al. (2016) is 10.6 mm/yr, which is also very close (within 0.3 mm) to our modeled prediction of 10.3 mm/yr. Furthermore, our predicted SLR thresholds for these two systems align well with the derivation of SLR thresholds at similar sediment concentrations by Kirwan et al. (2010).

The main factor influencing future marsh stability with accelerated SLR will be the capacity of the marsh platform to accrete and maintain pace with increasing SLR rates (Neubauer, 2008; van Belzen et al., 2017; Lalimi et al., 2018; Elsey-Quirk et al., 2019). As such, the accretion due to both inorganic mineral sediment deposition and in-situ organic matter production, largely in the form of below-ground biomass organic matter sequestration, are both critical components to understand and model accurately. Our model results showed that the largest accretion rates occurring across all 33 SLR scenarios we simulated differed between the two systems. In Grand Bay, the largest accretion rate is about 5.0 mm/yr, which is less than the SLR threshold of 7.2 mm/yr for this system (Fig. 8), suggesting it may be compromised in accretion capacity due to the higher mean platform elevation (~0.2 m - see Fig. 3).

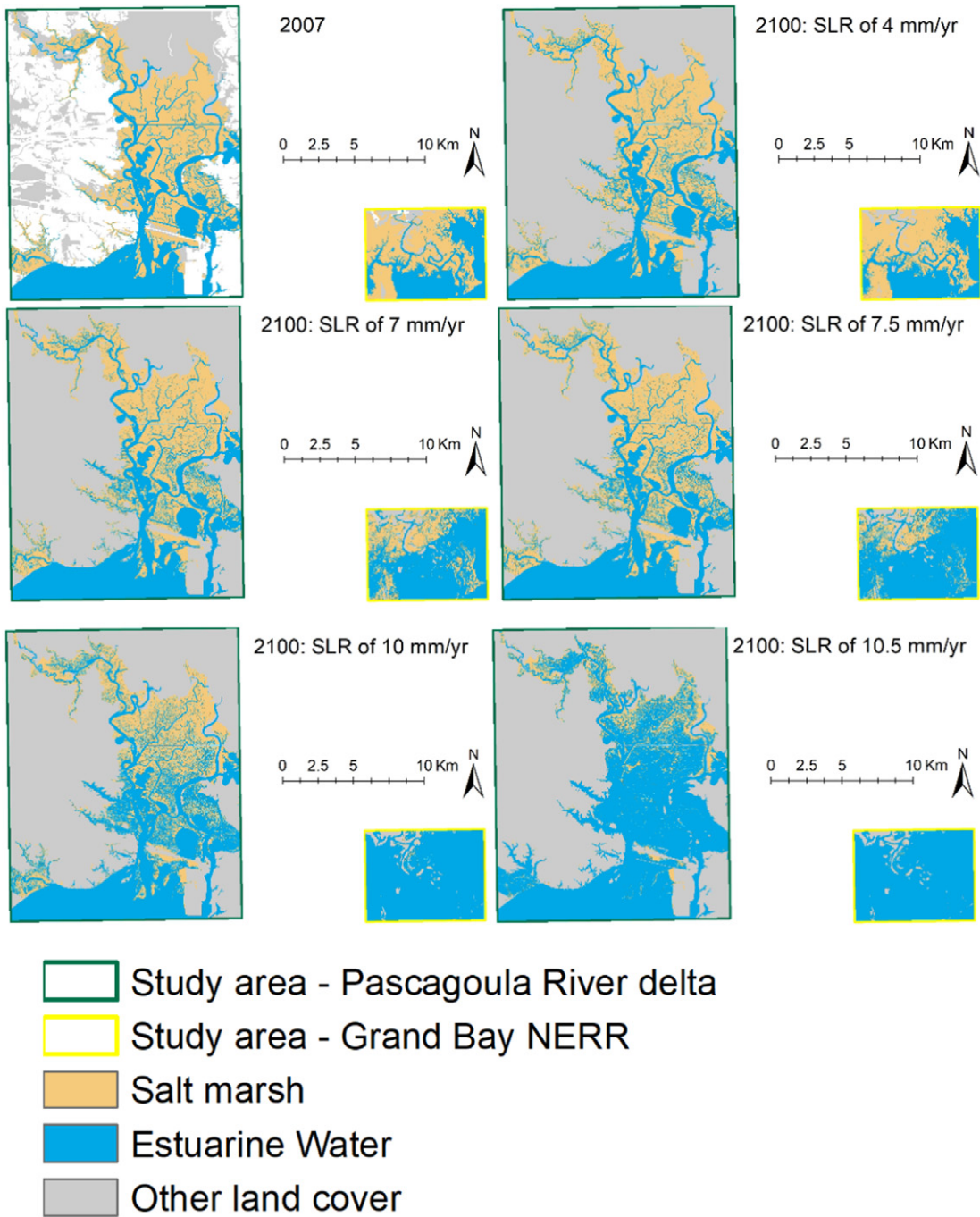


Fig. 6. Salt marsh distribution in 2007 and 2100 under different scenarios of increasing SLR rates for Grand Bay and the Pascagoula River delta. Marsh collapse in Grand Bay occurs around 7 mm/yr, while the threshold is exceeded in the Pascagoula River delta around 10 mm/yr rates of SLR.

In contrast, in the Pascagoula River delta the largest accretion rate is about 10.5 mm/yr and this is very close to the SLR threshold of ~10 mm/yr (Fig. 8) in this system. A higher elevation salt marsh platform means that it takes longer for the vegetation to become inundated by a given local SLR rate. When we ran the model to 2300 for the Grand

Bay NERR, the SLR threshold became 5.1 mm/yr, close to the maximum accretion rate of 5.0 mm/yr in 2300. This cross-system comparison shows that salt marshes may have unique system-specific responses to accelerated SLR and may not always need to accrete sediments at the same rate as the SLR rate in order to maintain wetland elevation

Table 4
SLR thresholds in 2050 vs. 2100 and the corresponding marsh area (ha) at these SLR thresholds.

Location	SLR thresholds (mm/yr)		Values of total area			
	2050	2100	1988/1996	2007	2050 (threshold)	2100 (threshold)
Grand Bay	10.8	7.2	2220.3	1917.6	1019.7	1022.2
Pascagoula Delta	12.4	10.3	6426.1	5692.2	2958.0	2762.7

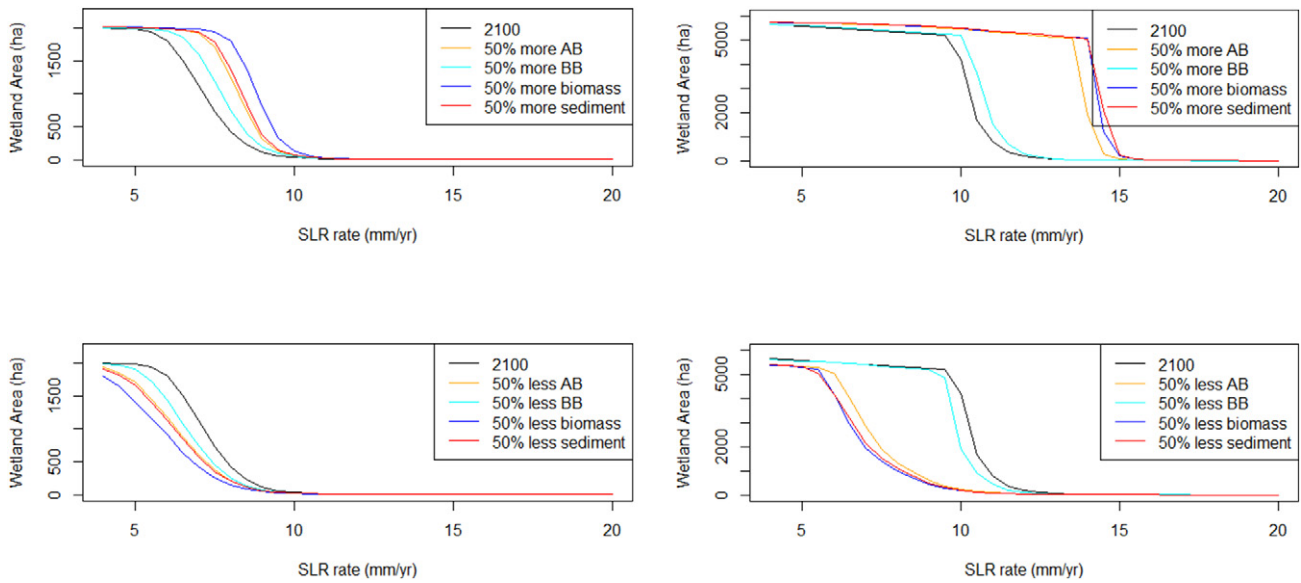


Fig. 7. Predicted salt marsh areas in 2100 vs. increasing SLR scenarios under current, 50% more, and 50% less of above-ground biomass (AB), below-ground biomass (BB), both above- and below-ground biomass (biomass), and mineral sediments (sediment) in Grand Bay (left panels) and the Pascagoula River delta (right panels). Results for 25% change are not shown.

by a given year. Therefore, the target time to reach marsh collapse at a given SLR threshold may vary from system to system depending on local elevation and accretionary processes. This suggests that management thresholds and actions will need to be derived locally for given salt marsh systems.

Overall marsh platform accretion is a function of both contributions from allocthonous mineral sediments and autocthonous organic matter production. In both systems, future autocthonous below-ground biomass contributes a smaller proportion to accretion rates than does allocthonous mineral sediment settling and trapping by above-ground biomass based on the medians of accretion rates, despite the large below-ground to above-ground biomass ratios (Grand Bay = 4.1, Pascagoula River delta = 3.4). However, in Grand Bay, the potential below-ground organic contribution can be up to 90% of the accretion rate during the present day rate of SLR at 4 mm/yr, whereas in the Pascagoula River delta, it can contribute up to 60% of the accretion rate at the present day (Fig. 9). Further, the proportion of below-ground contribution to accretion rates in Grand Bay is larger than that in the Pascagoula River delta in the present day as well as in the future. Under future conditions, the median contribution of autocthonous below-ground biomass production to overall accretion decreases and lies between 30 and 40% in Grand Bay, but only between 10 and 30% for the Pascagoula River delta (Fig. 9). The proportion continues to decrease with increasing SLR rate before the SLR threshold is reached for each system, suggesting

that inundation decreases the ability of the vegetation to effectively sequester biomass (but see Rogers et al., 2019), and causes an increasing reliance on allocthonously derived sediments to augment marsh platform accretion (Elsey-Quirk et al., 2019).

In mineral rich estuaries, large amounts of available dissolved inorganic nutrients may promote increased above-ground productivity over below-ground productivity as vegetation does not require as much below-ground biomass to obtain necessary nutrients and water (Deegan et al., 2012). In contrast, in mineral poor estuaries, below-ground biomass needs to expand widely to reach sufficient nutrients needed to support vegetation growth. The different strategies that salt marsh vegetation adopts in these contrasting hydro-chemical environments influence the potential coupling strength between above- and below-ground biomass and this may have an important and hitherto underappreciated influence on coastal wetland resilience to SLR. In each system, the live above- and below-ground biomass changes in opposite directions, potentially as a response to this trade-off in sediment and nutrient availability. The ratio of below- to above-ground biomass decreased with SLR rate before the SLR thresholds were reached in the Pascagoula River delta, whereas the opposite was the case in Grand Bay, potentially showing different biomass allocation strategies in marsh vegetation in estuaries with different upland inputs (Fig. 10).

Two main theories exist to explain the pattern of biomass partitioning: optimal partitioning (Bloom et al., 1985) and allometric

Table 5.1

SLR thresholds for 2100 under different scenarios of biomass and sediment concentrations (the numbers for scenarios represent the proportion of base scenario for a particular variable).

Scenarios	SLR (mm/yr)		Percent change compared to base scenario (%)	
	Grand Bay	Pascagoula Delta	Grand Bay	Pascagoula Delta
Base	7.2	10.3		
Biomass_50	5.7	6.7	-20.83	-34.95
Biomass_75	6.4	8.4	-11.11	-18.45
Biomass_125	8	12.3	11.11	19.42
Biomass_150	8.8	14.3	22.22	38.83
Sediment_50	6.2	6.7	-13.89	-34.95
Sediment_75	6.6	8.4	-8.33	-18.45
Sediment_125	7.7	12.3	6.94	19.42
Sediment_150	8.4	14.4	16.67	39.81

Table 5.2

SLR thresholds for 2100 under different scenarios of above- (AB) and below-ground biomass (BB) (unit: mm/yr, and the numbers for scenarios represent the proportion of base scenario for a particular variable).

Scenarios	SLR thresholds (mm/yr)		Percent change compared to base scenario (%)	
	Grand Bay	Pascagoula delta	Grand Bay	Pascagoula delta
Base	7.2	10.3		
AB_50	6.2	7.1	-13.89	-31.07
AB_75	6.7	8.7	-6.94	-15.53
AB_125	7.7	12.1	6.94	17.48
AB_150	8.3	13.9	15.28	34.95
BB_50	6.6	9.9	-8.33	-3.88
BB_75	6.9	10.1	-4.17	-1.94
BB_125	7.4	10.5	2.78	1.94
BB_150	7.7	10.7	6.94	3.88

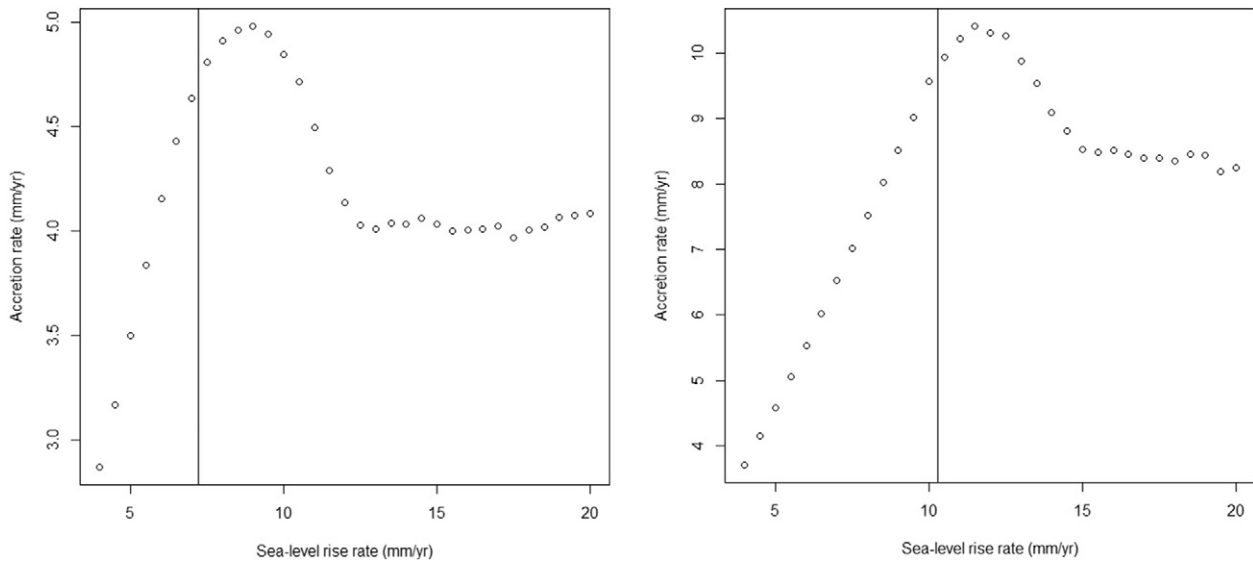


Fig. 8. Accretion rate of salt marshes under different scenarios of increasing SLR rates in Grand Bay (left panel) and the Pascagoula River delta (right panel). The vertical lines denote SLR thresholds derived in Fig. 5.

partitioning (Yang and Luo, 2011). In optimal partitioning theory, plants allocate biomass to the organ that helps to capture the most limiting resource (McCarthy and Enquist, 2007). While in allometric partitioning theory, biomass is allocated based on the constraints of body size and is not sensitive to local environmental conditions (Enquist and Niklas, 2002). Both theories can be combined to investigate biomass partitioning not accounted for by allometric constraints across broad environmental gradients (McCarthy and Enquist, 2007). Optimal partitioning theory seems to explain above- and below-ground allocation in the Grand Bay NERR and Pascagoula River delta under SLR due to the theory's implied trade-off, as found in our study (Fig. 10). In the Grand Bay NERR, below-ground biomass increases at the expense of above-ground biomass to capture limited nutrients as sea level rises. In contrast, in the Pascagoula River delta, biomass partitioning favors above-ground biomass for the vegetation when inundation becomes more frequent under SLR, suggesting potentially higher nutrient availability in this riverine dominated estuary.

We further investigated this interaction between above- and below-ground biomass productivity across the two systems, and whether a stronger coupling response between the above- and below-ground biomass fractions has the potential to delay the threshold to higher rates of SLR, i.e. the increase of resilience of salt marshes to SLR. Previous studies in grasslands showed that strong coupling between below- and above-ground biomass fractions maximized vegetation productivity, whereas, intermediate coupling maximized the persistence of grasslands prone to fire disturbance (Scheiter and Higgins, 2013). Similar coupling mechanisms have rarely been studied in coastal marshes resulting in a gap in our understanding of potential resilience of these ecosystems to future SLR scenarios. Although there is no formal way to quantify coupling between above- and below-ground biomass, coupling mainly represents the strength of the relationship between the two fractions. The strongest coupling can be viewed as the growth of new root biomass being exclusively determined by new shoot biomass (Scheiter and Higgins, 2007), consistent with the interpretation of $R^2 = 1$ for a regression function between live belowground biomass and live aboveground biomass. Therefore, we applied R^2 to quantify the strength of above- and below-ground biomass coupling. From the field observations on biomass, R^2 and adjusted R^2 in the quadratic equation used to predict below-ground biomass as a function of above-ground biomass was 0.24 and 0.12 in the Pascagoula River delta versus 0.079 and 0.025 in the Grand Bay NERR. Therefore, based on these R^2 values, the strength of the coupling is stronger in the Pascagoula River delta than in Grand Bay.

In order to conduct an initial test of this hypothesis that stronger coupling of above- and below-ground biomass contributes to the resilience of salt marshes to future SLR, we switched the biomass functions (see Fig. 4) by applying the biomass coupling from the Pascagoula River delta to Grand Bay and vice versa, and then compared the resulting changes to the SLR thresholds when the estuary-specific biomass coupling function is used. As both average above- and below-ground biomass is higher in Grand Bay than in Pascagoula Delta, we expect the SLR threshold becomes smaller in Grand Bay using the biomass coupling function from the Pascagoula Delta. However, we found the SLR threshold increased from 7.1 mm/yr to 7.7 mm/yr, when the Pascagoula River delta's biomass coupling function was used for Grand Bay (Table 6). When the biomass coupling relation of Grand Bay was used for the Pascagoula River delta, the SLR threshold decreased from 10.3 to 8.8 mm/yr (Table 6). This suggests that the vegetation in the Pascagoula River delta exemplifies a stronger biomass coupling relationship and a morphological growth strategy where above-ground biomass is increased at the expense of below-ground biomass. In contrast, in Grand Bay, the biomass coupling is weaker under a condition where vegetation uses a growth strategy of increasing below-ground biomass at the expense of above-ground biomass. This also suggests that there may be vegetation coupling responses that are specific to local environmental conditions and need to be analyzed accurately in order to be able to predict future resilience when running long-term SLR scenarios. The current modeling effort suggests that stronger coupling contributes to larger marsh accretion. Future mechanistic experiments to explain the coupling hypothesis will need to involve the measurement of a suite of abiotic factors such as soil salinity in addition to biomass to test this response further.

Translocation between below-ground and above-ground biomass can contribute to the strength of coupling between these two compartments, and may help interpret marsh accretion processes (Connor and Chmura, 2000) and the resilience of salt marshes to future SLR. Along the northeastern Atlantic coast, seasonal patterns of below- and above-ground biomass switch showed translocation from live below-ground biomass to aerial tissues at the beginning of the growing season, followed by a translocation of photosynthates to below-ground biomass after the standing stock peak to better store energy in below-ground biomass over winter (Connor and Chmura, 2000; Gallagher and Howarth, 1987; Gross et al., 1991). Biomass translocation seems to become more complex with reduced seasonal variability in the southern end of the distribution of salt marshes, like in Louisiana (Darby and

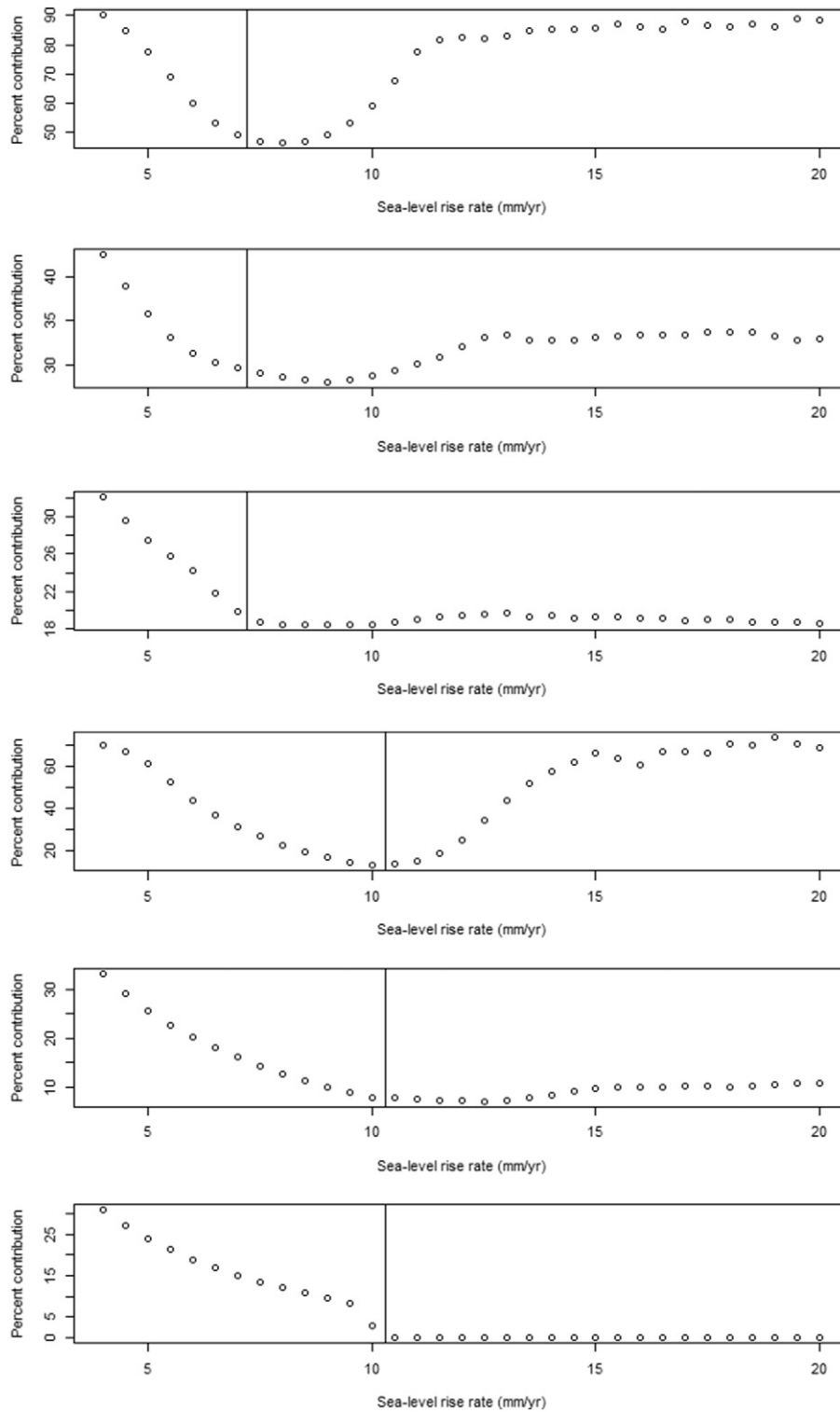


Fig. 9. Percent contribution by below-ground organic matter to accretion rate in Grand Bay (top three panels) and the Pascagoula River delta (bottom three panels) under increasing SLR rates. The three panels show the 97.5%, 50%, and 2.5% quantiles for each system (Note different scales of the Y-axis). The vertical lines show SLR thresholds derived in Fig. 5.

Turner, 2008). One possible explanation for the simulated stronger above- and below-ground biomass coupling in the Pascagoula River delta is lower salinity (less stress), which is not accounted for in the current model. If that is the case, then higher salinity due to SLR may reduce coupling in the future, which may lead to less resilient salt marshes than predicted by the current model simulations.

In addition, the accuracy of LiDAR-derived elevation may have contributed to the uncertainty of our model predictions. Studies have

shown that LiDAR-derived elevation may be biased toward higher values in dense vegetation areas like salt marshes (Alizad et al., 2016b, 2018; Medeiros et al., 2015; Rogers et al., 2016). We did not correct the LiDAR elevation as we applied right-after-hurricane elevation when much of the vegetation zone was converted to bare land or water. In addition, we focused on the lower elevation area with shorter vegetation where potential bias of elevation tends to be smaller, and we did not have highly precise in-situ measurements of elevation of salt

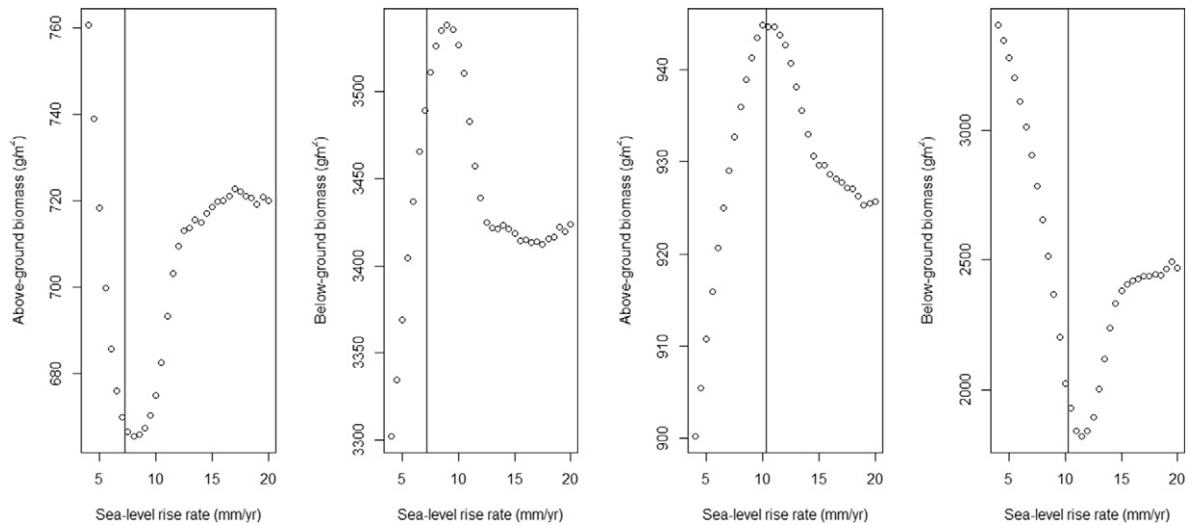


Fig. 10. Live above- and below-ground biomass responses under increasing SLR rates in Grand Bay (left two panels) and the Pascagoula River delta (right two panels). The vertical lines show SLR thresholds derived in Fig. 5.

marsh platforms to derive the location-specific correction equation needed for these two estuary systems. Therefore, our derived SLR thresholds are likely to be an optimistic estimate (i.e. overestimate) of resilience of salt marshes to SLR without this additional correction to the elevation surface. We applied the correction to the Grand Bay NERR derived by Alizad et al. (2018) and found the predicted SLR threshold becomes 1 mm/yr less, which is smaller than the difference of SLR thresholds between the two contrasting estuarine systems. Therefore, our conclusion on resilience of salt marshes to SLR in the riverine vs. marine dominated estuaries will not likely change when appropriate LiDAR elevation corrections are performed in the Pascagoula River delta.

Other natural and anthropogenic factors will also influence how salt marshes respond to future SLR. Marsh primary productivity will potentially increase for some time as atmospheric CO₂ concentration increases, particularly for C₃ plants (Curtis et al., 1989; Cherry et al., 2009; Langley et al., 2009), however the plants may simultaneously become limited by possible lengthy and more frequent drought events under climate change scenarios (Wuebbles et al., 2017). Upland land-use land-cover changes with population increase (Hauer et al., 2016) will also likely change upland hydrodynamics and sediment delivery to the downstream estuarine systems (Hovenga et al., 2016). Localized development within the coastal zone may also alter marsh responses, for instance the western distributary of the Pascagoula River has experienced little anthropogenic modification, whereas the adjacent eastern distributary is bordered by a large shipyard and has experienced more intense anthropogenic disturbance and is regularly dredged to allow for commercial shipping traffic (Waldron, 2019). The lack of spatial data on mineral sediment contributions to the marsh makes this assessment difficult to conduct and this is a data gap that needs to be addressed to help refine the analysis of salt marsh resilience in each system. Though suspended sediment concentration is a valid indicator

for sediment availability (Weston, 2014), the coarse representation of sediment dynamics in the current model without sediment transport processes or the ability to simulate tidal creek widening could lead to overestimates of salt marsh resilience to SLR. High-resolution remote sensing data and updated measurements of suspended sediment concentration will need to be used in future studies to model the sediment dynamics in the estuary and creeks around the marsh sites. Overall, more research on contrasting marine dominated vs. riverine dominated estuaries is needed to generalize the intriguing findings from this research.

5. Conclusion

We derived and examined the SLR thresholds in two estuaries with contrasting upland inputs. We also analyzed the mechanisms that contribute to potential resilience of salt marshes to future SLR, including availability of sediment in the water column and the relation between live below- and above-ground biomass. We found that salt marshes in the riverine dominated estuary (Pascagoula River delta) are more resilient to SLR than in the marine dominated estuary (Grand Bay NERR), mainly contributed by larger quantities of riverine-borne mineral sediments in the Pascagoula River, but also possibly due to different resource allocation strategies between above- and below-ground biomass. In both systems, the above-ground biomass production is found to contribute more to the accretion rate based on the medians despite the often larger below-ground biomass pool. Below-ground biomass contributes up to 90% of accretion in the marine dominated estuary compared to up to 60% of accretion in the riverine dominated estuary. SLR thresholds are more sensitive to above-ground biomass in the riverine dominated estuary than in the marine dominated estuary while they are more sensitive to below-ground biomass in the marine dominated estuary than in the riverine dominated estuary. Whereas the change in biomass has a larger impact on the SLR thresholds than does change in sediment concentration in the marine dominated estuary, change in either biomass or sediment concentration has a comparable impact on the SLR thresholds in the riverine dominated estuary.

This research provides potentially relevant indicators and information that resource managers can use to make more-informed decisions on conservation and restoration policies in the near-term to minimize future catastrophic loss of coastal marsh habitats once SLR thresholds are exceeded.

Table 6
SLR thresholds (mm/yr) under two different biomass coupling scenarios.

Location	Using the current bay biomass	Using the other bay biomass
Grand Bay	7.15 (6.0–8.0)	7.74 (7.0–8.5)
Pascagoula River delta	10.31 (9.5–11.0)	8.79 (8.0–9.5)

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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