

# Living on the Edge: Increasing Patch Size Enhances the Resilience and Community Development of a Restored Salt Marsh

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**Abstract** Foundation species regulate communities by reducing environmental stress and providing habitat for other species. Successful restoration of biogenic habitats often depends on restoring foundation species at appropriate spatial scales within a suitable range of environmental conditions. An improved understanding of the relationship between restoration scale and environmental conditions has the potential to improve restoration outcomes for many biogenic habitats. Here, we identified and tested whether inundation/exposure stress and spatial scale (patch size) can interactively determine (1) survival and growth of a foundation species, *Spartina alterniflora* and (2) recruitment of supported fauna. We planted *S. alterniflora* and artificial mimics in large and small patches at elevations above and below local mean sea level (LMSL) and monitored plant survivorship and production, as well as faunal recruitment. In the first growing season, *S. alterniflora* plant survivorship and stem densities were

greater above LMSL than below LMSL regardless of patch size, while stem height was greatest in small patches below LMSL. By the third growing season, *S. alterniflora* patch expansion was greater above LMSL than below LMSL, while stem densities were higher in large patches than small patches, regardless of location relative to LMSL. Unlike *S. alterniflora*, which was more productive above LMSL, sessile marine biota recruitment to mimic plants was higher in patches below LMSL than above LMSL. Our results highlight an ecological tradeoff at ~LMSL between foundation species restoration and faunal recruitment. Increasing patch size as inundation increases may offset this tradeoff and enhance resilience of restored marshes to sea-level rise.

**Keywords** Biogenic habitat · Exposure · Foundation species · Recruitment · *Spartina alterniflora*

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## Introduction

Biogenic habitats are composed of one or more foundation species that create locally stable conditions required for the persistence of other species, thus regulating community structure and function (sensu Dayton 1972). Anthropogenic disturbance (e.g., land conversion, pollution, climate change) has resulted in the loss of biogenic habitats, and thus foundation species, at unprecedented rates, with 32% of tropical forests lost since 2000 (Hansen et al. 2013), 30% declines in seagrass (Waycott et al. 2009), and 65–85% declines in shellfish reefs (Zu Ermgassen et al. 2012). The loss of foundation species has shifted faunal community structure, altered nutrient cycling, and increased invasibility of ecosystems (Lirman 1999; Ellison et al. 2005; Hughes et al. 2009; Prev y et al. 2010).

Foundation species promote the colonization and persistence of other organisms via provision of refuge from

environmental stress (e.g., desiccation, high temperatures) and predation (Bruno et al. 2003). For example, red mangroves create structurally complex habitats (e.g., reduced wave energy) suitable for benthic macroinvertebrates and fishes (Ellison and Farnsworth 2001). The typically diverse assemblages of organisms found within biogenic habitats are unlikely to persist without the refugia provided by foundation species (Altieri and Witman 2006; Hewitt et al. 2008). Current trends in biogenic habitat loss have precipitated a shift from conservation alone towards restoration that inherently occurs in degraded or high-stress areas (Prach and Hobbs 2008; Holmgren and Scheffer 2010). When biogenic habitats are degraded or lost, restoration of the foundation species is often critical because natural or spontaneous succession is inhibited by high-stress conditions (Pastorok et al. 1997; Prach and Hobbs 2008; Suding and Hobbs 2009) and may lead to less productive alternative states (Scheffer et al. 2009).

To maximize success and minimize cost, restoration practitioners often elect to maximize spatial coverage within the most suitable conditions (e.g., lowest environmental stress) for the restored foundation species (Hilderbrand et al. 2005; Silliman et al. 2015). A potentially more cost-effective approach may be to focus on areas of elevated stress, where refuge provision will be most beneficial to colonizing organisms and invasive species may be less capable of colonizing. However, stress levels must not exceed physiological tolerances that would prevent the survival and growth of the restored foundation species (Prach and Hobbs 2008; Holmgren and Scheffer 2010). Even small shifts in environmental stress or the scale (e.g., size of the restored patch) of restoration can result in failure or hysteresis (i.e., restoration progresses to a human-caused alternative state rather than to the original non-degraded state) (Lamb 1998; Zedler 2000; Manning et al. 2006; Suding and Hobbs 2009; Kremin and M’Gonigle 2015). Here, we manipulate both stress (tidal inundation) and scale (patch size) in a tidal salt marsh to determine whether increasing the size of the restored patch can increase foundation species resilience to stress, and thus enhance faunal recruitment and improve restoration outcomes.

Tidal salt marshes are dominated by the foundation species, smooth cordgrass, *Spartina alterniflora*, which has a high tolerance for stressful intertidal environments, including tolerance to sediment hypoxia and anoxia associated with prolonged periods of inundation (Adams 1963; Pennings et al. 2005; Gittman and Keller 2013). *S. alterniflora* is commonly used for tidal marsh restoration (Broome et al. 1988; Craft et al. 1999) and provides refuge from abiotic stress and predation by dissipating wave energy, stabilizing sediments, and providing structurally complex habitat (Bruno 2000; Craft et al. 2009). Similar to other coastal biogenic habitats, more than 50% of salt marsh habitat has been lost in the USA alone and losses are likely to continue as sea level rises (Kennish 2001). Previous studies have proposed stress ranges for

productivity, supported faunal recruitment, and overall restoration success of *S. alterniflora* based on position relative to local mean sea level (LMSL), rates of relative sea-level rise (RSLR), and resulting inundation time (Redfield 1972; Broome et al. 1988; Levin et al. 1996; Morris et al. 2002). Morris et al. (2002) predicted that the near-term stability of salt marshes in response to rising sea level will depend on the current elevation of the marsh in relation to local mean sea level (MSL) and the marsh’s depth response curve (Fig. 1, adapted from Morris et al. 2002). If the RSLR rate is high, marshes restored below LMSL could be considered “unstable” and may ultimately deteriorate, despite high rates of primary production (Morris et al. 2002). Additionally, Angelini and Silliman (2012) found *S. alterniflora* patches smaller than one square meter had limited ability to expand and recolonize adjacent habitat, a key component of restoration success.

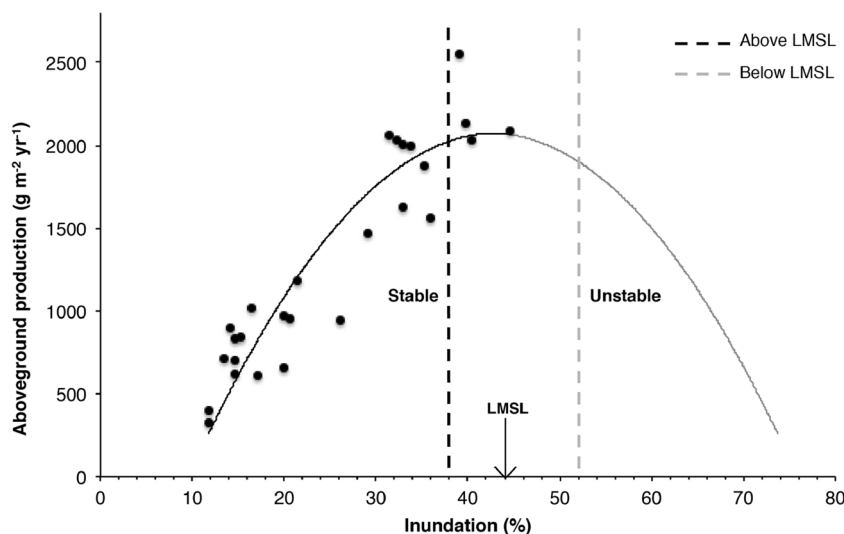
We conducted a manipulative field experiment to determine how patch size and environmental stress (induced by inundation time) affect the following: (1) the survival, growth, expansion rate, and sediment retention of *S. alterniflora* and (2) the recruitment of marine fauna and flora to restored *S. alterniflora* habitat. We selected elevations corresponding to inundation times associated with “stable” (above local mean sea level [LMSL]) and “unstable” (below LMSL) combinations of equilibrium productivity for *S. alterniflora* (Fig. 1, adapted from Morris et al. 2002). Circular patch sizes of slightly less than 1 m<sup>2</sup> (0.5-m radius) and greater than 3 m<sup>2</sup> (1-m radius) were used to further refine the patch sizes defined by Angelini and Silliman (2012).

## Methods

### Study Site

Our study was conducted on Carrot Island, part of the Rachel Carson National Estuarine Research Reserve System in Beaufort, NC (34° 42' 13" N, 76° 37' 29" W). The mean tidal range in the region is 0.92 m and the salinity ranges from 30 to 35 psu (Beaufort, NC - Station ID: 8656483, NOAA 2011–2014). The maximum wave height (m) experienced by our site from 2011 to 2014 was 0.09 ± 0.006 m (wind data obtained from Cape Lookout, NC, Station ID: CLKN7, NOAA 2015a, NOAA Wave Exposure Model [WEMo] 2013). We conducted our study as part of a larger project to stabilize the unvegetated shoreline along the southeastern end of Carrot Island. The project included construction of two sills with a mean base width of 2.5 m (seaward-landward axis) and a mean height of 0.8 m, using loose oyster shell that extended across ~200 m of shoreline, interrupted by a 10-m unprotected gap between the two sills (see Online Resource Fig. 1). The sills were constructed in the first 2 weeks of May 2012 at approximately

**Fig. 1** Relationship between aboveground production and inundation (%), adapted from Morris et al. (2002). Data points are the observed productivity of *S. alterniflora* since 1984 in North Inlet, South Carolina (Morris et al. 2002). The solid black and gray lines represent the “stable” and “unstable” regions of productivity,  $B$ , and percent inundation,  $I$ , respectively. Dashed lines represent the percent inundation for above LMSL (black) and below LMSL (gray) patches we restored in this study



– 0.6 to – 0.8 m NAVD88 and approximately 25 m from the lower edge of existing maritime forest or sand scarp. These sills were intended to attenuate wave energy and prevent further erosion of the shoreline. The experiment occurred directly landward of the oyster sills in an approximately 25-m wide intertidal zone that ranged in elevation from 0.2 to – 0.4 m NAVD88.

### Experimental Design and Setup

To determine the effects of inundation and marsh patch size on the success of marsh restoration, we established experimental patches at an elevation  $0.10 \pm 0.06$  m above local mean sea level (LMSL) ( $0.0 \pm 0.01$  m North American Vertical Datum of 1988 [NAVD88], referred to as “Above” patches herein) and at an elevation  $0.10 \pm 0.06$  m below LMSL ( $-0.2 \pm 0.01$  m NAVD88, referred to as “Below” patches herein). Between June and October of 2012, patches located above LMSL were inundated approximately 38% of the time and patches located below LMSL were inundated approximately 52% of the time. Patch surface elevations and corresponding inundation percentages were determined using a Trimble® Real Time Kinematic (RTK) Global Positioning System (GPS). The RTK base station was located on a published benchmark (865-6539 D). HOBO® water level recorders (one for atmospheric pressure and one for water pressure) were deployed at our study site from June to October 2012. Patch elevations relative to NAVD88 were transformed to LMSL using VDATUM with a transformation error of 0.05 m between NAVD88 and LMSL (NOAA 2015b).

Our patch elevations also represent inundations that correspond to a “stable” (above LMSL) and an “unstable” (below LMSL) combination of equilibrium productivity regimes for *S. alterniflora* (per Morris et al. 2002, Fig. 1). To verify inundation percentages determined for each elevation fell within

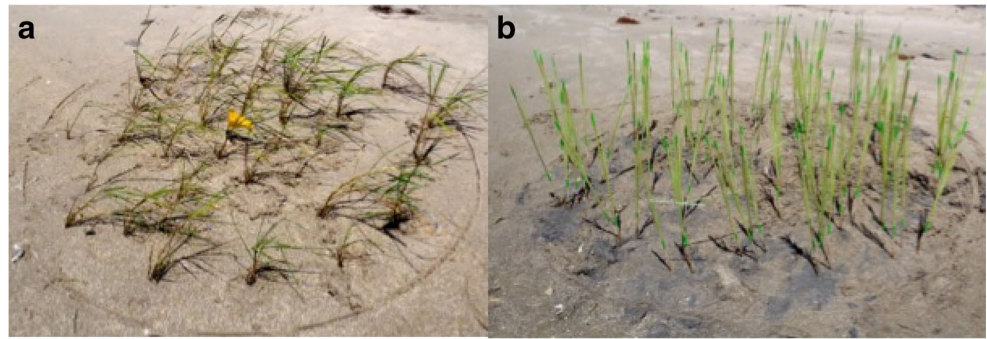
the stable or unstable regions reported by Morris et al. (2002), we obtained the tidal data used in their study (Station ID: 8662245, Oyster landing [N Inlet Estuary], SC, NOAA 2015a), divided the tidal data into 1-cm bins, and calculated percent inundations corresponding to each reported depth,  $D$ , below mean high tide (MHT). We then fit a quadratic relationship between inundation (%),  $I$ , and productivity (aboveground production),  $B$ , ( $R^2 = 0.84$ ):

$$B = -aI^2 + bI - c$$

where coefficients  $a$  and  $b$  were derived from the data and coefficient  $c$  was set to 1364 (per Morris et al. 2002). The derived value of our coefficient  $b$  ( $b = 159$ , Fig. 1) differed slightly from the value of coefficient  $b$  reported by Morris and colleagues ( $b = 155$ ); however, this difference did not affect our ability to define our experimental elevations as within the stable or unstable regions of equilibrium productivity (2002).

At each elevation in the first week of June 2012, we planted *S. alterniflora* culms and artificial mimics (described below) in 0.5-m radius (small) and 1.0-m radius (large) circular patches (Fig. 2a, b). We purchased *S. alterniflora* culms from a local plant nursery, Native Roots Inc., in Clinton, NC. The nursery collects *S. alterniflora* seed from local NC marshes in the fall and rears the seedlings over late winter through early spring in greenhouses. Live culm patch replication was limited to seven replicates per treatment due to space limitations within the site and the number of culms we could purchase from the nursery. Space restrictions within the site limited mimic patch replication to eight replicates of each patch size below LMSL and seven replicates of each patch size above LMSL. Mimics were used to assess faunal recruitment across elevation and patch size independent of variation in live plant morphology and changes in *S. alterniflora* stem density and height through time. Previous work has shown no difference in the composition of fauna that recruits to *S. alterniflora*

**Fig. 2** **a** Large (1-m radius, 96 stems) *S. alterniflora* patch post-planting in June 2012. **b** Large mimic patch post-planting in June 2012



plants and artificial mimics (Sueiro et al. 2011). *S. alterniflora* plants and mimics were planted at the same density (31 stems per  $m^2$ : 24 stems for 0.5-m radius patches and 96 stems for 1-m radius patches). To avoid damaging the roots of *S. alterniflora* culms, stems were planted as grown, either as single stems or grouped as 2 to 5 stems, for a total of either 24 stems for small or 96 stems for large patches. All leaves on *S. alterniflora* stems were trimmed to a height of 30 cm to standardize the initial stem height and reduce drag and subsequent uprooting of plants by waves during the initial planting (Fig. 2a). Each mimic consisted of a 96-cm long (0.5 cm diameter) dowel rod (stem), with five green plastic cut straws (leaves) with a 10 cm by 10 cm vexar base (roots) planted at a depth of 30 cm, resulting in an approximately 66-cm tall stem (Fig. 2b). Because the sediments were sandy and had a low initial organic matter content (OMC, < 10%, R. Gittman unpublished data), both plants and mimics were fertilized during planting with 14-14-14 Osmocote slow-release fertilizer (per Broome et al. 1983). To compare plant growth and faunal recruitment at the restored site to a natural site with similar environmental attributes/characteristics, we also designated 0.5-m radius control patches in a nearby natural fringing *S. alterniflora* marsh (approximately 40 m long and 20 m wide [from upland to subtidal]) at the elevations above ( $N = 7$ ) and below ( $N = 7$ ) LMSL, as described above. All experimental patches (live and mimic) were offset from one another so that no patch was directly seaward or landward of another patch. This offset allowed us to test the effects of inundation on faunal recruitment independent of distance into the live or mimic marsh.

### Marsh Patch Monitoring

We measured stem density within the entire patch monthly from June to October 2012 in the live, mimic, and control patches. Stem densities recorded in late October 2012 were used to determine maximum production of stems per patch (Morris and Haskin 1990). We measured the heights of all *S. alterniflora* stems within live and control plots in late August 2012 to estimate maximum individual *S. alterniflora* plant growth within each patch (Mendelssohn and Seneca

1980; Morris and Haskin 1990). Time constraints associated with tidal fluctuation limited measurements of control patch stem heights to four of the seven control patches, haphazardly selected at each elevation. We also counted the number of *S. alterniflora* stems within a 0.25- $m^2$  quadrat in October 2012 and 2014 for each patch to determine if elevation or patch size affected stem densities (converted to stems  $m^{-2}$ ) over multiple growing seasons. Because aboveground *S. alterniflora* biomass had senesced in all of our patches by November 2012 and ~20 cm of sediment from a winter storm then completely buried four of our patches (two large and two small patches) above LMSL (R. Gittman, personal observations), only patches that produced new *S. alterniflora* stems in 2013 were included in the 2014 stem density census and expansion rate measurements. We calculated the expansion rate ( $m\ year^{-1}$ ) of *S. alterniflora* patches from June 2012 to October 2014 by subtracting the original patch radii (0.5 m for small patches and 1 m for large patches) from the average radii (measurements taken perpendicular and parallel to shore using a transect tape) of each patch measured in October 2014 and then dividing by the number of years (2.4).

To determine changes in the amount of sediment retained by marsh patches across inundation treatments, surface elevation measurements were taken in 2012 and 2014 within restored marsh patches and in adjacent bare areas using the RTK-GPS. The elevation measurements were used to create digital elevation models for the site in 2012 and 2014. Elevation measurements taken in 2012 were subtracted from the 2014 elevation measurements to determine the change in elevation (a proxy for sediment retention) over the study period in surviving *S. alterniflora* patches and bare sediment areas.

Each month from June to September 2012, we counted recruited barnacles (*Balanus* spp.), marsh periwinkles (*Littoraria irrorata*), ribbed mussels (*Guekensia demissa*), and oysters (*Crassostrea virginica*) on six live or mimic stems per patch. Given the potential for recruitment of barnacles to the entire surface area of each stem, we divided barnacle counts by the stem heights to standardize densities across stems within a patch. We also measured epiphytic chlorophyll

*a* on the leaves of three mimic stems in September 2012. Epiphytes were gently scraped from a single leaf per mimic stem using a glass slide and filtered. The filter was placed in 10–30 ml of solvent (45% acetone, 45% methanol, 10% water), sonicated, and extracted overnight in a freezer. Chlorophyll *a* concentrations were determined using fluorometry (Parsons et al. 1984). Epiphyte chlorophyll *a* concentrations for three mimic stem plots (two small patches and one large patch below LMSL) not measured because samples were accidentally left out of the freezer overnight.

### Statistical Analyses

We ran two-factor analyses of variance (ANOVAs) with patch size, elevation, and patch\*elevation as the fixed effects for each of the following response variables: *S. alterniflora* stem densities, stem heights, and patch expansion rates. Because control marsh patches were designated within a larger natural marsh, only the effect of inundation (not patch size) was evaluated for control marsh patch stem heights and densities, using a one-way ANOVA. We ran a two-factor ANOVA to compare the elevation change from 2012 to 2014 between restored patches and bare sediment areas as a function of position above and below LMSL. Finally, we ran a one-way ANOVA to compare the total faunal recruitment as of September 2012 (sum of barnacles, periwinkles, oysters, and ribbed mussels per cm of stem) between mimic and live stems across all plots. Two small, live *S. alterniflora* plots (one above LMSL and one below LMSL) had no remaining live stems by September 2012; therefore, faunal recruitment was not recorded for these plots. When necessary, data were transformed (square root and fourth root transformations) to meet the ANOVA assumptions of normality and homogeneity of variance (evaluated using Levene's test). Type II sum of squares were calculated for two-factor ANOVAs of expansion rate, 2014 stem density, and elevation change data to account for the loss of replicates during the experiment, thus resulting in an unbalanced experimental design.

We fit linear mixed effects models using maximum likelihood to determine the effects of patch elevation relative to LMSL, patch size, and sample month (fixed effects) on densities of recruited barnacles and periwinkles, with patches (replicates) nested within months (random effect). Models for barnacle and periwinkle recruitment were fit with a correlation structure that assumes that the farther the residuals of the model are separated in time the lower their correlation (temporal autocorrelation, Zuur et al. 2009), to account for repeated measurements of the patches through time. To determine the effects of patch elevation and patch size (fixed effects) on epiphyte concentrations and on oyster and ribbed mussels densities, we fit linear models using generalized least squares. Because sample sizes were unequal and variances were not homogeneous across elevations, patch sizes, and

months, we used a generalized least square procedure to weight our models with variance corrections. Weighting allowed the variances to differ between treatments for each predictor variables separately and together (Zuur et al. 2009). We used an Akaike Information Criteria (AIC) model selection process to select the most parsimonious model (see Online Resource Table 1). For significant treatment and treatment interactions, Tukey's *post hoc* comparisons were used to determine which levels of each treatment were significantly different from one another. All analyses were run in R 3.2.1 and linear mixed model analyses were run using package nlme (Pinheiro et al. 2015, R Core Development Team 2015).

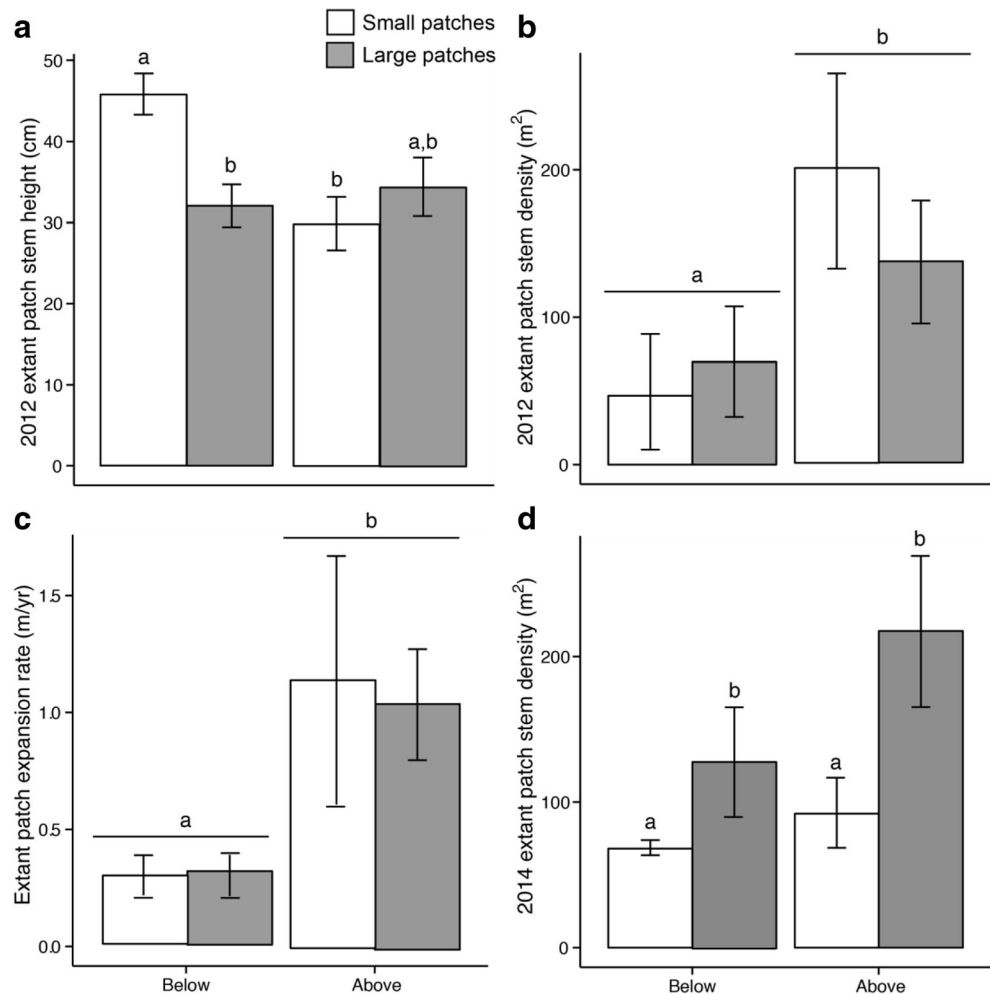
### Results

#### *S. alterniflora* Patch Survival, Growth, Expansion, and Sediment Retention

The mean height of *S. alterniflora* stems in August 2012 was greater in small patches located below LMSL than in large patches located at the same elevation and small patches located above LMSL (Fig. 3a, ANOVA, elevation  $\times$  patch  $F_{1,24} = 9.08$ ,  $DF = 1$ ,  $P = 0.006$ , Tukeys HSD *post hoc* tests  $P < 0.05$ ). This trend in stem height being greater below than above LMSL was also evident in nearby control (natural) marsh patches (below LMSL  $40.4 \pm 3.5$  cm, above LMSL  $20.9 \pm 2.3$  cm,  $F_{1,6} = 21.8$ ,  $P = 0.003$ ). By October of 2012, however, no live *S. alterniflora* stems remained in 43% of the small patches (six out of 14 patches), while only 14% of the large patches (two out of 14 patches) had no remaining live *S. alterniflora* stems. Small patches were twice as likely (four vs. two patches) to lose all live *S. alterniflora* stems below LMSL than above LMSL. Conversely, there was no difference in total patch survival of *S. alterniflora* stems across elevations for large patches (one patch contained no live stems at each elevation). Mean density of *S. alterniflora* stems within patches was greater in patches above LMSL, regardless of patch size (Fig. 3b, elevation  $F_{1,24} = 4.13$ ,  $P = 0.05$ ). This trend in stem density being greater above than below LMSL was also evident in nearby control patches (above LMSL  $345 \pm 27$  stems/m<sup>2</sup>, below LMSL  $153 \pm 49$  stems/m<sup>2</sup>,  $F_{1,12} = 11.7$ ,  $P = 0.005$ ).

By June 2013, live stems remained in only 12 patches: four large patches below and three large patches above LMSL: three small patches below and two small patches above LMSL. Half of the large patches (seven) had no live stems and  $\sim 2/3$  of the small patches (nine) had no live stems. As stated in the methods, two large and two small plots located above LMSL on the east side of our study site were buried by nearly 20 cm of sediment from a landward, eroding bluff during a storm in the winter of 2012/2013, resulting in the loss of these plots (R. Gittman, *personal observations*).

**Fig. 3** *S. alterniflora* patch. **a** Mean stem height (cm) in August 2012. **b** Mean stem density ( $\text{m}^{-2}$ ) in October 2012. **c** Mean linear expansion rate (m/year) from 2012 to 2014. **d** Mean stem density ( $\text{m}^{-2}$ ) in October 2014. White bars are small patches (0.5-m radius) and gray bars are large patches (1-m radius). “Below” and “Above” refer to the position of the patches relative to local mean sea level (LMSL). Bars with different lower case letters (“a” or “b”) are significantly different ( $P < 0.05$ ). Error bars are  $\pm$  SE



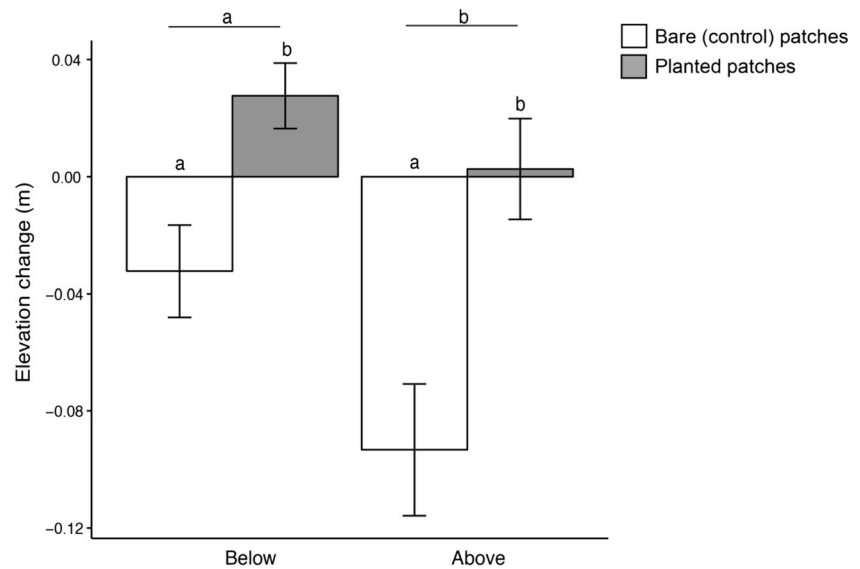
From June 2012 to October of 2014, *S. alterniflora* in extant patches above LMSL expanded more than three times as fast ( $1.1 \pm 0.21 \text{ m year}^{-1}$ ) as *S. alterniflora* in patches below LMSL ( $0.30 \pm 0.06 \text{ m year}^{-1}$ ), regardless of patch size (Fig. 3c, elevation  $F_{1,8} = 17.17$ ,  $P = 0.003$ ). Despite 2012 stem densities and patch expansion rates being driven by elevation relative to LMSL, patch size was a better predictor of stem densities in the remaining patches in October 2014, with larger patches having more stems  $\text{m}^{-2}$  than small patches both above and below LMSL (Fig. 3d, patch  $F_{1,8} = 9.69$ ,  $P = 0.049$ ).

The surface elevation of patches containing planted *S. alterniflora* culms located below LMSL increased by  $0.03 \pm 0.01 \text{ m}$  from 2012 to 2014, while bare sediment patches located at the same position relative to LMSL decreased by  $0.03 \pm 0.02 \text{ m}$  (Fig. 4). The surface elevation of patches containing planted *S. alterniflora* culms located above LMSL did not change ( $0.00 \pm 0.02 \text{ m}$ ) from 2012 to 2014, while bare sediment patches located at the same position relative to LMSL decreased by  $0.09 \pm 0.02 \text{ m}$  (patch type  $F_{1,20} = 21.26$ ,  $P < 0.001$ , elevation  $F_{1,20} = 6.80$ ,  $P = 0.02$ ).

### Flora and Fauna Recruitment to Experimental Patches

Multiple taxa, including marsh periwinkles, barnacles, ribbed mussels, oysters, and epiphytes, recruited to *S. alterniflora* mimics. The position of mimics relative to LMSL strongly influenced the density of recruited organisms. Barnacles were observed at three times higher densities (across months) on mimics located below LMSL than above LMSL, with barnacle densities on mimics below LMSL decreasing in August and then densities increasing at both elevations in September 2012 (Fig. 5, elevation  $\times$  month  $F_{3,76} = 16.68$ ,  $P < 0.0001$ , Tukey's HSD *post hoc* tests  $P < 0.05$ ). In contrast, marsh periwinkles were twice as dense on mimics located above LMSL than below LMSL, with no difference in periwinkle densities between months (Fig. 6a, elevation  $F_{1,76} = 15.34$ ,  $P = 0.0002$ ). In patches below LMSL, higher densities of marsh periwinkles were found in small marsh patches when compared to large marsh patches (Fig. 6a, patch  $F_{1,76} = 5.26$ ,  $P = 0.02$ ). The concentration of epiphytes on mimics located below LMSL was three times higher than the concentration of

**Fig. 4** Mean change in elevation (m) from 2012 to 2014 in bare (control) patches (white bars) and planted *S. alterniflora* patches (gray bars)



epiphytes on mimics above LMSL in September 2012 (Fig. 6b, elevation  $F_{1,23} = 156.02$ ,  $P < 0.0001$ ). Oysters and ribbed mussels were completely absent from mimics located above LMSL in 2012; however, densities of  $0.7 \pm 0.2$  per stem were observed for each bivalve species on mimics below LMSL in September 2012 (Fig. 6c [oysters], elevation  $F_{1,26} = 17.95$ ,  $P = 0.0003$ , and Fig. 6d [ribbed mussels], elevation  $F_{1,26} = 12.18$ ,  $P = 0.002$ ). Oyster and mussel recruitment was limited to within the first 10 cm of the mimic stem extending from the sediment in plots located below LMSL. Although faunal recruitment (barnacles, periwinkle, oysters, and ribbed mussels) to *S. alterniflora* culms was much lower than to mimics ( $F_{1,54} = 41.45$  DF = 1,  $P < 0.0001$ ), the patterns of recruitment across inundation and patch size were similar.

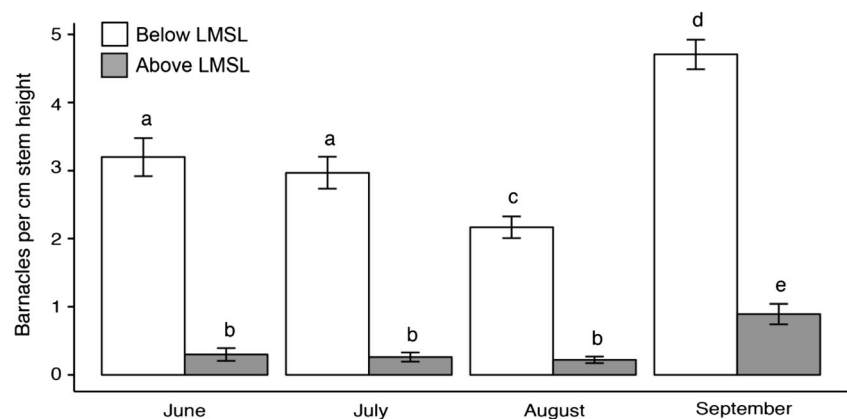
## Discussion

Restoration of foundation species has become a primary strategy for protecting and promoting the recovery of threatened species, as well as enhancing ecosystem functions and

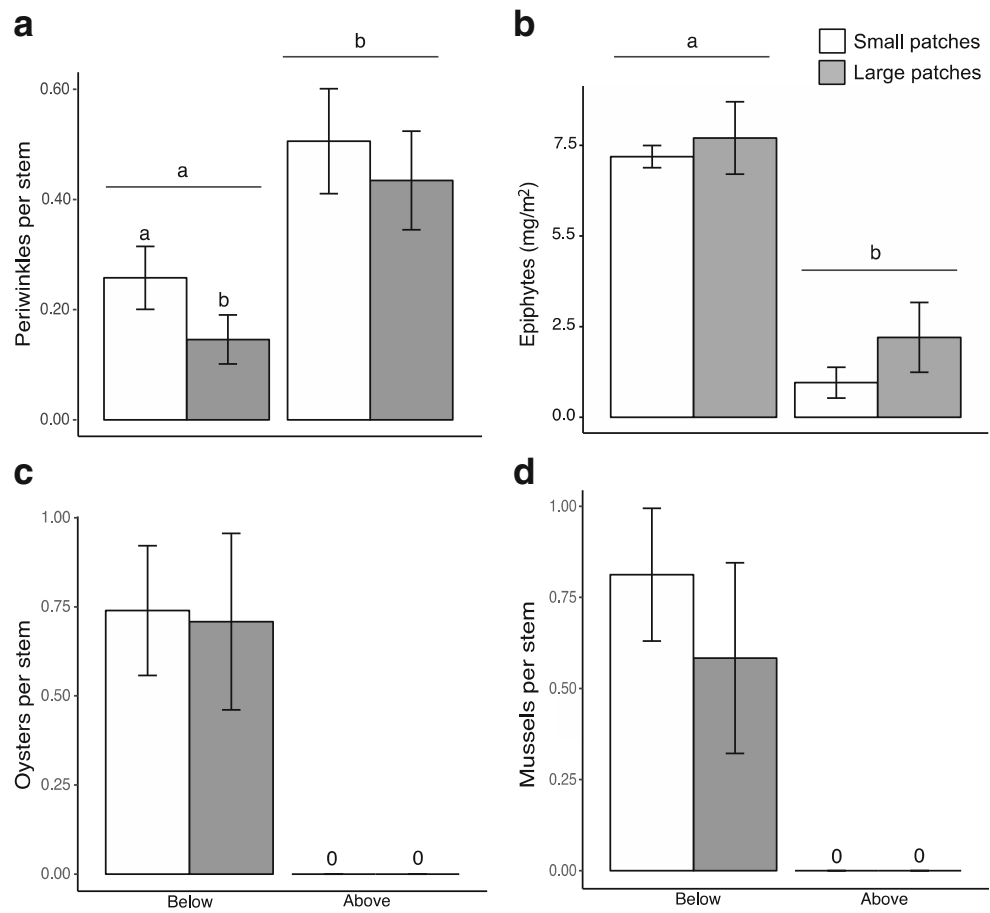
services (Halpern et al. 2007; Coiffait-Gombault et al. 2012; Gedan et al. 2014). Environmental stress and patch size have previously been shown to play a role in the outcome of foundation species restoration (Suding and Hobbs 2009; Fodrie et al. 2014). The results of our experiment suggest that inundation induces a tradeoff between the development of the foundation species, *S. alterniflora*, and recruitment and development of the supported faunal community. Consistent with previous studies by Broome et al. (1988), *S. alterniflora* growth (stem densities in 2012, Fig. 3b) and expansion (2012–2014, Fig. 3c) during the initial growing seasons was more successful above LMSL than below LMSL. These results are also consistent with the stable (above LMSL) and unstable (below LMSL) equilibrium productivities of *S. alterniflora* observed and predicted by Morris et al. 2002, with higher primary production above LMSL (near the peak of the production curve, Fig. 1) than below.

However, our results also show that increasing *S. alterniflora* patch size (simply from 0.5 to 1-m patch radius) may increase restoration success (initial culm survivorship and subsequent stem production), particularly at higher levels

**Fig. 5** Mean recruitment of barnacles scaled to mimic height (per cm) from June to September 2012 in patches located below (white bars) and above (gray bars) LMSL



**Fig. 6** **a** Mean recruitment of marsh periwinkles (per stem) pooled across months (June to September 2012); and September 2012 recruitment of **b** epiphytes ( $\text{mg}/\text{m}^2$ ); **c** oysters per stem; and **d** ribbed mussels per stem to small (white bars) and large (gray bars) mimic patches located below and above LMSL



of environmental stress (i.e., increased inundation), enhancing the resilience of restored *S. alterniflora*. Specifically, small *S. alterniflora* patches were 1.5 times more likely to have no remaining live stems than large patches at the end of the first growing season both above and below LMSL. Additionally, small patches were twice as likely to lose all *S. alterniflora* stems below LMSL than above LMSL, while only a single large patch both above and below LMSL had no stems remaining by October 2012, indicating that large patch restoration was more successful than small patches restoration, particularly below LMSL. It should be noted that at least in the first growing season, individual plants grew taller below LMSL when in smaller patches, suggesting that more stress-tolerant individuals may have allocated more resources (if only temporarily) to extant stem growth than to rhizome and clonal expansion, potentially as a result of reduced competition for sediment nutrients with conspecifics (Fig. 3a, Pennings and Callaway 1992).

Despite *S. alterniflora* stem densities being driven by position relative to LMSL in the first growing season, patch size became the primary driver of stem densities by year three, with large patches outperforming small patches above and below LMSL, which is consistent with the relative recovery rates of large and small remnant *S. alterniflora* patches

observed by Angelini and Silliman 2012. Plants in large patches likely benefited from positive interactions among a larger number of *S. alterniflora* plants, such as increased wave attenuation by more total stems and oxygenation via clonal rhizome expansion, than small patches (Halpern et al. 2007; Möller et al. 2014; Silliman et al. 2015). This is particularly notable as sessile faunal recruitment was greater below LMSL than above LMSL (Figs. 3, 4, and 5, consistent with findings of Levin et al. 1996), indicating a potential tradeoff in primary and secondary production first observed by Teal (1962). So while significant interactions between patch size and inundation for any one variable measured were rare, collectively, these results lead us to conclude that increasing patch size, particularly at elevations below LMSL, will enhance both *S. alterniflora* resilience to environmental stress and the development of the supported faunal community.

Similar to the response of *S. alterniflora* plants, periwinkle recruitment was twice as high in mimic patches located above LMSL than in mimic patches located below LMSL (Fig. 6a). Predation by blue crabs and other predators has been shown to reduce the abundance of marsh periwinkles along the marsh edge, with predation risk decreasing as distance into the marsh and elevation increases (Vaughn and Fisher 1988; Lewis and Eby 2002). Mimics in patches below LMSL were completely



submerged at high tide, resulting in limited vertical refuge for periwinkles (Vaughn and Fisher 1988), while the top portion of mimics in the patches above LMSL remained exposed at high tide. Higher densities of periwinkles on mimics in small patches than large patches below LMSL may have resulted from higher rates of predation (e.g., blue crabs) in larger patches than in small patches. Hovel and Lipcius (2001) found similar results in seagrass patches, with juvenile blue crab survivorship being higher in small patches than large patches, potentially as a result of more adult blue crabs foraging in large patches than small patches.

In contrast to the generally negative response of *S. alterniflora* and marsh periwinkles to increased inundation, recruitment of sessile marine fauna was higher on average on mimics and live stems in patches below LMSL than on mimics in patches above LMSL (Fig. 5 and Fig. 6b–d). Barnacles (*Balanus* spp.) were the most abundant sessile invertebrate recruiting to our mimic patches, with recruitment densities being more than three times higher in patches below LMSL than patches above LMSL. This recruitment pattern is consistent with previously described peak recruitment occurring between 0.6 and 0.9 m below mean low water (MLW), or between 0.9 and 1.2 m lower in elevation than our patches below LMSL (McDougall 1943). Reduced settlement time and increased desiccation stress above LMSL likely limit the upper distribution of barnacles in our study region. The decline in barnacle density from June to August in all patches was likely a result of a combination of desiccation, predation, and competition for space, with the increase in September likely resulting from a second peak in barnacle settlement (McDougall 1943).

Recent experimental restoration of oysters has also revealed that an elevation/inundation “optimum” exists for intertidal oyster reef growth and production (oyster density) below LMSL (Fodrie et al. 2014; Ridge et al. 2015). Previous studies have also shown that ribbed mussel densities decrease as elevation increases above LMSL, but this relationship was confounded with distance into the marsh (Bertness and Grosholz 1985; Stiven and Gardner 1992). Our study provides evidence for mussel recruitment into the marsh interior being limited by decreasing inundation of the marsh, independent of the increasing probability of encountering marsh stems as one moves from the marsh edge to the marsh interior (Figs. 1 and 6d). Chlorophyll *a* concentration (proxy for epiphyte biomass) followed a similar pattern to sessile fauna and was also likely driven by both settlement and post-settlement processes (e.g., desiccation stress) (Fig. 6b, Jones 1980).

The mismatch between peak *S. alterniflora* survivorship and expansion and peak sessile invertebrate and epiphyte initial recruitment has potential consequences for the trajectory of marsh community development. Increased inundation of the marsh is associated with higher abundances of mobile fish and crustaceans (nekton, Kneib 1997; Minello et al. 2003) and

is also expected to increase production of commercially valuable crustaceans, such as penaeid shrimp (Roth et al. 2008). Marsh resident fauna, such as periwinkles, barnacles, oysters, and mussels, as well as epiphytic and benthic microalgae, serve as forage resources for nekton and are sources of energy being transferred via “trophic relays” between the marsh and higher trophic levels found in adjacent estuarine waters (Marinucci 1982; Currin et al. 1995; Kneib 2000). Thus, marsh restoration projects with a goal of maximizing the ecosystem service of habitat provision should target a range of elevations that provide an optimal inundation for both the survival and growth of salt marsh plants and the recruitment of marine biota.

Restoring *S. alterniflora* in large (at least 3 m<sup>2</sup>), dense (Silliman et al. 2015) patches may increase marsh plant survivorship and growth under suboptimal inundation regimes (e.g., elevations below LMSL, future, higher relative sea levels). These findings are of particular importance for informing marsh restoration efforts in estuaries like those found in North Carolina, where *S. alterniflora* regularly occurs and is also regularly restored at or just below LMSL, despite suboptimal inundation regimes. For example, *S. alterniflora* occurs from –0.4 to 0.4 m NAVD88 (corresponding to elevations both well above and well below LMSL) in natural and restored fringing marshes along the central North Carolina coast (Gittman et al. 2014, 2016; Davis et al. 2015). Furthermore, *S. alterniflora* is often planted below LMSL along eroding shorelines landward of a constructed, offshore breakwater or sill designed to reduce wave energy and promote sediment accretion (see Gittman et al. 2016; Currin et al. 2008). As sea level rises, “optimal” habitat for *S. alterniflora* marshes will become “suboptimal,” increasing the need for refined restoration strategies that will promote the recovery and persistence of salt marsh habitats.

However, if erosion rates or relative SLR rates are greater than the rates at which *S. alterniflora* marsh can either keep up through biomass accumulation and sediment accretion or transgression to higher elevations via clonal expansion and seed dispersal, then increasing patch size will only result in temporary improvements to restoration success. If erosion rates or relative SLR rates are high, then restoring *S. alterniflora* in large patches above LMSL may allow for higher marsh plant survivorship and more rapid restored marsh patch expansion than planting the entire site, while still allowing for delayed faunal recruitment as the patches expand into lower elevations. Therefore, site-specific sediment erosion and accretion rates, wave energy, and the local rate of SLR must also be considered when selecting sites to restore *S. alterniflora*.

With climate change resulting in accelerating rates of SLR, identifying the optimal location for the restoration of coastal foundation species, such as mangroves, bivalves, seagrasses, and marsh plants, which accrete sediment is a critical objective

(Craft et al. 2009). We did not observe losses in elevation in our *S. alterniflora* patches and even saw an average increase of 30 mm in elevation (15 mm year<sup>-1</sup>) in the patches below LMSL (Fig. 4). Given that the current RSLR is approximately ~ 3 mm year<sup>-1</sup> and land subsidence is minimal (~ 1 mm year<sup>-1</sup>) at our study site (Kemp et al. 2011; Theuerkauf et al. 2015), results from our study suggest that marshes restored below LMSL, in conjunction with intertidal oyster sills that enhance sediment accretion rates (Rodriguez et al. 2014), may keep pace with current rates of SLR. Additionally, a recent meta-analysis by Kirwan and colleagues, which analyzed rates of accretion and elevation change from marshes on the Gulf and Atlantic coasts of North America and Europe, only considered a marsh to be in the process of submerging (i.e., not keeping up with RSLR) if its elevation or accretion deficit was greater than 0.5 mm year<sup>-1</sup> (2016). The mean rate of elevation change was 6.9 mm year<sup>-1</sup> for low-elevation marshes and less than 5% (2 of 41) of the marshes in their dataset were determined to be submerging (Kirwan et al. 2016). Our annual increase in surface elevation was higher than mean rate of change reported by Kirwan and colleagues at 15 mm year<sup>-1</sup>, with the higher rate of change likely a result of the sediment trapping capabilities of the seaward oyster sill constructed immediately prior to the start of the project (Davis et al. 2015; Gittman et al. 2014, 2016). We do acknowledge that these rates of elevation increase will likely slow as the oyster sill reaches equilibrium with LMSL (Rodriguez et al. 2014). Other recent models suggest that marshes will be able to adapt to SLR via feedbacks between inundation and sediment accretion, assuming adequate suspended sediment supply (Rogers et al. 2012; Schile et al. 2014). Kirwan and colleagues concluded that marshes would generally survive relative SLR rates of 10–50 mm year<sup>-1</sup> during the twenty-first century, depending on tidal range and suspended sediment availability, as long as lateral losses to seaward erosion are not so great as to result in lateral collapse of the marsh. Additional research is needed to further evaluate the success of using intertidal oyster reef restoration to reduce both vertical and lateral marsh loss under potentially accelerating rates of SLR.

E. O. Wilson's prediction that the twenty-first century would be "era of restoration in ecology" (1992) appears prescient with the rapid expansion of the restoration ecology sub-discipline in the last two decades and the increasing desire of governments and other organizations to fund restoration projects (Suding 2011). Emergence of the concept of foundation species restoration being critical to the recovery of ecosystems in dynamic, high-stress environments represents both a guiding framework and challenge in restoration ecology (Halpern et al. 2007). We provide a mechanism (increasing the restoration patch size) for offsetting stress on a coastal foundation species to enhance recovery of the supported community. Salt marsh restoration often consists of planting individual culms

in evenly spaced rows, not in dense aggregations, which has shown to be more effective (Silliman et al. 2015). Building on previous research, our results suggest that planting marsh not only in dense, but large patches, instead of small, spaced out patches will likely increase restoration success.

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