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Title: Seasonal stem loss and self-thinning in low marsh *Spartina alterniflora* in a New England tidal marsh

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Abstract: Dense monocultures of the grass *Spartina alterniflora* dominate the low marsh in typical New England tidal marshes. These marshes provide a number of important ecosystem services; thus, it is important to understand the factors that influence *S. alterniflora* productivity. End of season live biomass is often used to estimate *S. alterniflora* productivity, but this measure fails to account for stems lost within the growing season and may lead to a significant underestimate. We explored two possible factors that may influence *S. alterniflora* stem loss within the growing season: 1) density-dependent mortality (self-thinning), and 2) the physical force of moving water via tidal action. At four tidal creeks in the Plum Island Sound estuary, Massachusetts, we found that on average 34% of the *S. alterniflora* stems present in June were lost by August, but this varied from

11-44% among creeks. This stem loss accounted for at least 20% of the estimated annual productivity. We found little evidence that tidal action drives spatial variation in stem loss. Seasonal stem loss was greater in stands with higher early season density, consistent with self-thinning. As self-thinning occurred, density became more similar among creeks, meaning that end of the season density patterns are not reflective of early season stands. Adding a simple measure of early season stem density can improve productivity estimates by incorporating loss due to self-thinning.

Keywords: *Spartina alterniflora*, self-thinning, tidal salt marsh, New England, primary productivity, end of season live biomass

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Introduction

Monocultures of the perennial grass *Spartina alterniflora* Loisel. dominate the intertidal zone or low marsh (*ca.* mean sea level [MSL] to mean high water [MHW]) of tidal salt marshes from Canada to the Gulf of Mexico. This species is also invading intertidal mud flats in the Pacific Northwest, Asia, and other areas of the world, disrupting existing patterns of ecological structure and function (Strong and Ayres 2013; Meng et al. 2020). Coastal marshes provide a number of ecological functions and ecosystem services including wave attenuation (Gedan et al. 2011; Shepard et al. 2011), carbon sequestration (Duarte et al. 2013), habitat for a range of estuarine animals, and nutrient processing, among others (Barbier et al. 2011; McKinley et al. 2020). Many of these functions are directly or indirectly related to the stem density and productivity of salt marsh graminoids (Barbier et al. 2011; Shepard et al. 2011; Duarte et al. 2013), making accurate and efficient assessment of these measures critical. Thus, identifying the factors and interactions that affect low marsh *S. alterniflora* stem density and primary productivity can help quantify ecosystem functions and services provided by these systems.

Low marsh *S. alterniflora* stand structure varies seasonally, and several studies have found that stem density declines during parts of the growing season (Houghton 1985; Cranford et al. 1989; Morris and Haskin 1990; Dai and Wiegert 1996; Logan 2018). Including these lost stems is necessary to accurately assess the productivity of *S. alterniflora* and many methods have been developed to do so, but quantifying stem loss can be difficult and time consuming (Shew et al. 1981; Houghton 1985; Cranford et al. 1989; Hill and Roberts 2017). Because of this difficulty, end of season live (EOSL) biomass has often been used as a conservative proxy for productivity (e.g., Kirwan et al.

2009; Więski and Pennings 2014; Zheng et al. 2018). The degree to which EOSL underestimates actual production is heavily dependent on rates of stem loss and may vary between and even within sites. The causes and spatial patterns of stem loss within a marsh have not been explored.

At a broad scale, the temporal patterns of stem loss in *S. alterniflora* vary with latitude, which may indicate different mechanisms of loss. Unlike warmer regions where the growing season is year round, in northeastern North America cold temperatures and ice scour create a much shorter growing season and cause dieback to the ground surface each winter (Morris et al. 2013). In these areas *S. alterniflora* emerges in late spring, and studies from New York to Nova Scotia have found that shoots are lost over the entire *ca.* April to September growing season, particularly after May/June when peak stem density is reached. (Houghton 1985; Cranford et al. 1989; Logan 2018). Measurements of stem density of other dominant tidal marsh species across the growing season have rarely been reported, but a similar decline in stem density through the summer growing season has been found in *Zizania aquatica*, a dominant annual grass in freshwater tidal marshes in New Jersey (Whigham and Simpson 1977).

The causes of stem loss through the growing season are unclear, but multiple possible mechanisms exist. Given the near monoculture of *S. alterniflora* and high density of stems within the low marsh, density dependent mortality (self-thinning) could lead to stem loss over the growing season. Self-thinning has been shown to occur due to intraspecific competition amongst individuals in high-density monocultures in experimental, agroforestry, and natural communities (Yoda et al. 1963; Lonsdale and Watkinson 1982; Ellison 1987; Sletvold 2005; Zeide 2010). While clonal species are less

likely to show patterns of self-thinning due to intraclonal regulation of density, self-thinning may occur when densities are high enough (de Kroon and Kalliola 1995; Makita 1996; Osawa and Kurachi 2004). The possibility of self-thinning as an explanation for stem loss in the dense low marsh *S. alterniflora* monocultures has largely been unexamined. Liu and Pennings (2019) found an inverse relationship between plant height and density in *S. alterniflora* in Georgia that is consistent with self-thinning but did not directly explore the relationship between stem density and stem loss. Self-thinning may be particularly relevant in northeastern North America where shoots emerge from a “barren landscape” in late spring (Morris et al. 2013) creating dense, even-aged stands of stems, similar to the structure of other self-thinning populations.

Another factor that might contribute to seasonal stem loss is the force of moving tidal water. Experimental studies with other salt marsh species have shown that waves and storm surges can break stems and remove them from the system (Rupprecht et al. 2017; Vuik et al. 2018). Stem breakage is tied to water velocity, thus is higher at more exposed locations in the marsh. The strongest storm surges in northeastern North America are in the fall and winter, which doesn't correspond with the period of stem loss in these marshes. However, low marsh *S. alterniflora* along the fringes of tidal creeks is regularly exposed to tidal currents. While the lower velocity of tidal currents may be less likely to break stems, experiments with macroalgae have shown that repeated lower velocity events can lead to eventual breakage (Mach et al. 2007). Regardless of the mechanism for stem mortality, ebbing tides quickly export lost shoots out of the system, masking potential evidence of the mechanism.

If self-thinning is a major factor driving seasonal *S. alterniflora* stem loss, areas with higher initial stem densities would undergo greater loss due to increased competition among individual stems, as has been found for many other species (e.g., Lonsdale and Watkinson 1982; Sletvold 2005). In this case, the variability in density among sites would likely decrease over the season as the densest sites lose more stems. Thus, end of season measurements may not be able to reconstruct patterns in initial density. In addition to greater loss in denser areas, evidence of self-thinning is often seen through a linear negative relationship between plant size and density (Yoda et al. 1963; Lonsdale and Watkinson 1982; Puntieri and Hall 1996; Shibuya et al. 2004; Liu and Pennings 2019).

If tidal action contributes significantly to seasonal *S. alterniflora* stem loss, then stem loss would be expected to be higher in areas exposed to greater tidal energy (Rupprecht et al. 2017). Cranford et al. (1989) found that plots exposed to more regular tidal flow (i.e., lower in the tidal range) experienced greater loss, which could support this idea. Sections of the tidal creeks closer to the source of the incoming tide drain larger areas and have stronger tidal currents (personal observation). Thus, relative position along the tidal creeks could influence rate of stem loss, with areas further downstream showing greater loss. The effects of tidal currents on vegetation are poorly studied and we are unaware of any tests of this pattern.

Identifying the factors that lead to stem loss is critical for understanding the relationship between EOSL biomass and productivity in these systems. If stem loss is similar across space, then productivity estimates could easily be corrected for this loss. If stem loss varies predictably with spatial position, then corrections to EOSL biomass as an

estimate of productivity would need to incorporate these variables. However, if self-thinning is an important mechanism driving stem loss, spatial variation in EOSL biomass may not be correlated with initial density and thus the magnitude of stem loss. In this case, it would not be possible to correct EOSL biomass to incorporate loss without additional information from earlier in the season.

This study focused specifically on factors that could be influencing stem densities, and thus seasonal patterns of production, in low marsh *S. alterniflora*. Our objectives are: 1) to quantify the degree and pattern of seasonal stem loss of *S. alterniflora* across a salt marsh complex in Massachusetts, USA, 2) to explore whether seasonal stem loss is impacted by tidal action or self-thinning, and 3) to determine the extent to which incorporating a simple measure of seasonal stem loss into EOSL biomass can improve productivity estimates based on this proxy.

Methods

Site Description

The study was conducted within the *ca.* 10,000 ha Plum Island Sound estuary in northeastern Massachusetts, which includes the Ipswich, Parker, and Rowley Rivers and is part of the Plum Island Ecosystems LTER (<https://pie-lter.ecosystems.mbl.edu>). Tides are semi-diurnal with a 2.6 m mean tide range; neap-spring averages are *ca.* 2.4 – 3.6 m. The Plum Island Sound salt marshes are typical of New England systems, with distinct patterns of vegetation zonation; the low marsh (*ca.* MSL – MHW), typically one to four meters wide and directly adjacent to the creek bank, is flooded twice daily and characterized by a monoculture of tall-form *S. alterniflora*. The abutting high marsh, *ca.* 80 % of the total

marsh area, is dominated by the less flood-tolerant congener, *Spartina patens*, often mixed with varying amounts of *Distichlis spicata* and interspersed with stands of short-form *S. alterniflora*. Unlike *S. alterniflora* marshes farther south (Morris and Haskin 1990), in this system all stems are killed by cold and low marsh stems are largely removed by ice scour during the winter. New stems emerge in spring, reaching maximum density in early summer (as in Cranford et al. 1989).

The study site included four tidal creeks (Sweeney, West, Clubhead, and Nelson) of the Rowley River in Rowley and Ipswich, Massachusetts (Fig. 1; also see Deegan *et al.* 2007). The site is also the focus of an ongoing study of the long-term effects of anthropogenic eutrophication on coastal marshes; two of the four study creeks, Sweeney and Clubhead, were experimentally manipulated with nitrogen fertilizer, and the other two creeks, West and Nelson, serve as references (Deegan et al. 2007; Drake et al. 2009; Deegan et al. 2012). Sweeney was fertilized starting in 2004 and Clubhead starting in 2008. Sampling for this study was done over the 2011 growing season.

Each of the four study creeks branch near their heads; we sampled along both branches at Sweeney and West and along one each at Clubhead and Nelson. At each of the six branches, we established three permanently marked points along the creek bank that supported pure stands of tall form *S. alterniflora*. Starting from the confluence, we spaced the points approximately 50 – 70 m apart, with Position 1 closest to and 70 – 100m above the confluence and Position 3 farthest away, and thus farthest from the incoming tide. Creek widths at Position 1 were *ca.* 10 – 15 m, tapering to *ca.* three to five m at Position 3.

Seasonal Measurements

We measured density and height of *S. alterniflora* at each point (Positions 1, 2, and 3) along each of the six creek branches four times throughout the 2011 growing season (June 14-23, July 11-14, August 17-25, and September 12-15). To obtain stem densities, we placed four 0.25 m² quadrats within 10m of each of the eighteen points at *ca.* the mid-point elevation between the lower and upper edges of the low marsh and counted every *S. alterniflora* stem within each quadrat. We averaged the density among the four quadrats at each point and then used the average as a single data point each month for analysis. We estimated percent *S. alterniflora* stem loss during the 2011 growing season by calculating the difference in June and September density divided by June density.

To sample the distribution of stem heights in each quadrat, we cut all the stems from one quarter of each quadrat at the ground surface. In the lab, we measured the height of each harvested shoot from the bottom of the stem to the end of the longest leaf. To ensure that stem densities were not counted in areas that had been previously cut, we placed the quadrats in slightly different locations each month.

Estimates of EOSL Biomass and Annual Productivity

We estimated EOSL biomass in August 2011 because height and size were greatest at this stage of the growing season. Biomass measures required calculating the specific weight of the stems, so we haphazardly selected 25 *S. alterniflora* stems within five meters of each of the 18 points and cut them at the ground level. In the lab, each stem was rinsed free of sediment, dried at 80°C to constant mass, and weighed. We calculated specific weight as the mass per cm of height. We then calculated EOSL biomass for each point by

multiplying the average height of *S. alterniflora* stems by the specific weight for that point and the stem density.

To get a more accurate estimate of annual productivity that includes the stems that are lost over the summer, we calculated the estimated biomass lost from June to August at each point. Stems were not weighed earlier in the summer of 2011, so we used data on specific weights taken at two of the four creeks every two weeks during the summer in 2004 using the same procedure as in 2011 (RSW unpublished data). For each month (June to July and July to August) we averaged the mean stem heights from the beginning and end of the period and multiplied this by the specific weight from the 2004 data taken at a point in the midpoint of the month (June 30 and July 27) to estimate the per stem mass during this month. We then multiplied per stem mass by the number of stems lost during the month to estimate the total biomass lost during that month. Estimated annual productivity for each point (in g/0.25m²/year) included the EOSL biomass plus the biomass lost in the previous two months.

Relationship Between Plant Size and Density

To see if the patterns in plant growth and density across the growing season were consistent with self-thinning, we compared stem density and average plant height in each creek at each of the sample dates with both variables on a logarithmic scale. We similarly compared density with average stem biomass, using specific weights from 2004 to calculate stem biomass.

Statistical Analysis

We compared differences in stem density among creeks and months using mixed two-factor ANOVA using SPSS 25 (IBM Corporation). If the interaction between creek and month was significant, we followed up with one-factor repeated measures ANOVA for each creek and one-factor ANOVA for each month. Differences among individual creeks and months were assessed using Bonferroni post-hoc comparisons. We also compared productivity using EOSL biomass and our loss-corrected biomass estimate at each creek using paired t-tests.

We explored the potential causes of the observed seasonal changes in density using variables expected to relate to self-thinning (initial stem density) or tidal flow (using position along the creek as a proxy). Points nearer the mouth of the creeks (Position 1) were exposed to faster moving water than points farther upstream. To determine the factors most influencing patterns of stem loss we used hierarchical mixed effects models using the *lme4* package in R 4.0.3 (Bates et al. 2015) with the total stems lost between June and September at each point as the dependent variable. We used absolute stem loss rather than percent stem loss to avoid the necessity of using generalized linear mixed models with a binomial distribution. To assess the importance of each variable we used variance partitioning following the methodology from the Centre for Multilevel Modelling at the University of Bristol (Steele 2020). We assessed the proportion of the total variance explained by Creek using a model with only the random effect Creek at the group level included using the formula $(\text{random variance} / (\text{random} + \text{residual variance}))$. For all the following models we explored the effect of adding creek fertilization to the model, but it never improved models beyond having Creek as a random effect; thus, effects of fertilization are included in the Creek variable in all reported models. To assess the

influence of the fixed effects we created three separate mixed models, each containing Creek as a random effect at the group level. 1) Position Model – containing the variables potentially related to tidal action as fixed effects at the point level (position along stream as two dummy variables – which means that coefficients are comparing the given position to Position 3, the farthest upstream position), 2) Density Model – containing initial density as a fixed effect at the point level, 3) Full Model – containing all fixed effects (see Table 2). We measured the contribution of each variable both by estimating the 95% confidence intervals for each coefficient using the Wald statistic (Bates et al. 2015) as well as by calculating the variance explained by the fixed effects in each model. Following Steele (2020), we calculated the proportion of variance explained by the fixed effects by combining the random and residual variance for each model and comparing this combined variance between the null model and each fixed effects model as follows: (variance of null model – variance of fixed effects model)/variance of null model.

We similarly explored the relationship between EOSL biomass and estimated productivity using the same procedures. To assess how much of the variance in productivity can be explained by EOSL biomass measurements and the extent to which adding Position or Density variables can help better explain patterns in productivity, we created three fixed effects models for productivity: 1) Biomass only – which only included Creek as a random effect and EOSL biomass as a fixed effect, 2) Biomass + Position – which included position along stream and EOSL biomass, and 3) Biomass + Density – which included initial density and EOSL biomass (see Table 3).

Linear mixed effects models assume that the residuals and the coefficients of the random variables are identically distributed and independent (Schielzeth et al. 2020). We

analyzed patterns of residuals using scale-location plots and quantile-quantile plots (Bates et al. 2015). While some models showed small departures from assumptions, simulations have shown that linear mixed effects models are robust to violations of these assumptions (Schielzeth et al. 2020).

Results

Average stem density generally declined over the growing season (Fig. 2a) with a mean loss of 34.2% of the initial stem density by September. The amount of loss varied greatly among creeks (range 11-44%). The mixed ANOVA model showed a significant interaction between month and creek ($F_{9,42}=4.45$, $p<0.001$), so we performed separate analyses for each creek and month. Stem density differed among months for all creeks except Clubhead (Table 1). In June, density varied strongly among creeks, but this pattern became less pronounced through the summer and by September there were no differences in density among creeks (Table 1).

Mean stem heights increased from June to August and then declined slightly in September (Fig. 2b). Using stem density and height to estimate biomass, stem loss accounts for a mean of 20.8% (range 9-25%) of the estimated annual productivity (Fig. 3). For all four creeks, including this estimate of loss increased the productivity estimate ($T>5.5$, $p<0.03$).

There was a consistent negative relationship between stem height and stem density in creeks with higher starting density (Sweeney and West; Fig. 4). Creeks with lower initial density (Clubhead and Nelson; Fig. 4) did not show a large initial loss of density; Nelson showed increasing density loss between July and August as stems got taller and larger, as

would be expected with self-thinning. The overall pattern was the same when comparing stem mass with stem density (not shown).

Stem loss varied significantly among creeks. When included as the only variable, Creek was able to explain 66% of the variation in stem loss (*Creek only Model* in Table 2). However, much of this variation may be due to differences in June stem density among creeks. Initial density explains 82% of the total variation (both within and among creeks) even when Creek is included as a random variable (*Density Model* in Table 2). Thus, at least some of the creek level variation is due to differences in stem density. Adding the position variables to either the *Creek model* or the *Density Model* only slightly increased the explained variance (Table 2). In the *Full Model* points farthest downstream (Position 1) had lower loss than those farthest upstream, contrary to the expected pattern if tidal action were a major factor driving stem loss.

Creek played a much smaller role in the estimated productivity—explaining only 19.5% of the variance in the absence of other variables (Table 3). EOSL biomass by itself explained 60% of the variance in productivity. Adding position variables slightly reduced the explained variance (*Biomass + Position* model), while the combination of EOSL biomass and Initial Density explained almost 85% of the total variance.

Discussion

We found that *S. alterniflora* stem loss occurred during the growing season in most areas of the low marsh, confirming patterns found in *S. alterniflora* at other sites across northeastern North America (Houghton 1985; Cranford et al. 1989; Logan 2018). On average, more than a third of the stems present in June were lost by August. There was

considerable spatial variation among points both in maximum stem density (67-129 stems/0.25m²) and in the percentage of stems lost (10-60%).

Our results are consistent with self-thinning as a mechanism for stem loss. June density had a strong positive relationship to the amount of stem loss, explaining more than three-quarters of the variation in stem loss in our study. Creeks with higher June densities showed loss of stems while those with lower starting densities had little initial loss, as found in previous studies of self-thinning (Lonsdale and Watkinson 1982). Only Clubhead did not correspond to the expected pattern of self-thinning as it experienced little stem loss even as plants grew over the summer. In addition, the relationships between plant size and density are largely consistent with the pattern of self-thinning (Fig. 4). Similar negative relationships between plant size and density have been presented as evidence of self-thinning in monocultures of forbs such as *Digitalis purpurea* (Sletvold 2005) and *Galium aparine* (Puntieri and Hall 1996), and in densely growing clonal species including the bamboo *Sasa kurilensis* (Makita 1996) and the large-statured grass *Gynerium sagittatum* (de Kroon and Kalliola 1995). Liu and Pennings (2019) found a very consistent inverse relationship between *S. alterniflora* stem density and stem height across sites and years in a Georgia salt marsh but did not explore patterns of loss during the growing season. To our knowledge, the current study is the first to show higher loss of *S. alterniflora* stems over the growing season in areas with higher density. Given that our site had a similar pattern of *S. alterniflora* stem loss during the limited growing season as sites along the northeastern North America coast (Houghton 1985; Cranford et al. 1989; Logan 2018), we expect a similar pattern of self-thinning occurs in these *S. alterniflora* stands throughout this region.

We found little evidence that tidal flow was a primary driver of spatial variation in

stem loss in these protected tidal creeks. In fact, we found that stem loss was highest at points farther from the mouth of the streams where current velocity would be less intense. Previous research has shown that plots at lower elevation (thus exposed to more frequent tidal inundation) had greater stem loss over the growing season (Cranford et al. 1989). In this study we did not explore the effect of elevation within the tidal range, as all plots were close to the middle of the *S. alterniflora* belt. In other species, experimental studies have shown that stems can be lost due to wave and storm action, but that this is strongly dependent on flow velocity and varies by species (Rupprecht et al. 2017). Thus, stem loss due to water action may be concentrated on more exposed parts of the marsh. More direct measures of tidal action, such as flow velocity, may better elucidate potential patterns that we did not see in our study.

Two-thirds of the variation in stem loss could be explained at the creek level. It is not completely clear what factors lead to this creek level variation. Model results indicate that much of this creek level variation in stem loss may be explained by creek level variation in June density. Stem density can be impacted by exposure to wave action and storm surges, with higher densities developing in areas with increased exposure (Silinski et al. 2018; Schulze et al. 2019). However, this is not consistent with patterns of density found in our study—sites more closely connected to the ocean (Nelson and then Clubhead) had the lowest initial density. Other factors that vary among creeks may also influence stem loss—either directly, or by impacting maximum stem density. Since two of the creeks had been experimentally fertilized with nitrogen (for 3-7 years prior to this sampling), it is possible that nitrogen availability plays a role. However, there was no consistent pattern of density or stem loss due to fertilization. While Clubhead (3 years of fertilization) had

significantly lower stem loss than any other creek and had a relatively low June density, Sweeney (7 years of fertilization) had June density and stem loss that was intermediate between the unfertilized creeks—and much higher than Clubhead. Further research and a spatially broader sampling design would be needed to better understand creek level variation in density and stem loss, which was beyond the scope of this current study. Some recent studies have found slight differences in density among sites, but have not explored causes of site level variation (Hill and Roberts 2017; Liu and Pennings 2019). Importantly, our study suggests that as self-thinning occurred, density became much more similar among creeks. This means that density patterns in August or September are not a good reflection of patterns earlier in the season.

Many previous investigations have shown that using EOSL biomass underestimates *S. alterniflora* productivity in salt marshes due to stem and leaf loss (Shew et al. 1981; Houghton 1985; Cranford et al. 1989; Hill and Roberts 2017). Nevertheless, due to the time and effort required to measure productivity throughout the growing season, EOSL biomass continues to be used as an estimate of productivity (e.g., Visser et al. 2006; Kirwan et al. 2009; Zheng et al. 2018). Unlike some previous studies, our simple measure of stem loss did not include leaf turnover, meaning that even our corrected estimates of productivity are underestimates. For example, a study on *S. alterniflora* productivity in South Carolina found that including leaf turnover increased productivity estimates by 20-38% (Morris and Haskin 1990). In our study including stem but not leaf loss, we found an increase in estimates of 9-25%.

More importantly, because differential self-thinning driven by variation in early season density seems to be a primary driver of stem loss in this system, measurements

taken late in the growing season are not able to fully explain the spatial variation in productivity across the salt marsh. EOSL biomass only explained 60% of the variation in productivity, and Position within creek did not improve models at all. Previous work has suggested that weekly measurements are best for assessing productivity (Cranford et al. 1989) but this may be impractical in many studies. We found that adding a simple measure of early season stem density can greatly improve estimates of total productivity by allowing for the incorporation of loss due to self-thinning. This may serve as a good compromise between accuracy and effort.

Considerable research has focused on understanding the factors influencing aboveground productivity in salt marshes (e.g., Silliman and Zieman 2001; Visser et al. 2006; Steever et al. 1976) and on methods for incorporating biomass lost during the growing season (Cranford et al. 1989; Morris and Haskin 1990; Hill and Roberts 2017). However, the causes and patterns of that loss have received much less attention. In particular, despite a long history of study in terrestrial systems, self-thinning has only recently been considered as a mechanism for *S. alterniflora* stem loss (Liu and Pennings 2019). Other factors, such as herbivory, could also lead to stem loss and merit future study, although we observed no evidence of herbivory over the growing season.

We acknowledge that our simple methods of assessing productivity and loss of biomass and productivity do not fully capture leaf loss or variation in plant allometry. Nevertheless, we clearly show that stem loss is higher in areas with the highest density and that the relationship between plant size and density over the growing season is consistent with self-thinning. While there is some evidence that self-thinning may be occurring in *S. alterniflora* farther south (Liu and Pennings 2019), we expect our results to be most

relevant in areas with a more restricted growing season and complete dieback to the surface over the winter. Recognizing the role of self-thinning underscores the importance of understanding factors that influence stem density in *S. alterniflora* marshes and of incorporating early season density measurements into productivity estimates. Such efforts are particularly important given the role of salt marsh productivity in driving a number of critical ecosystem services, including wave attenuation and carbon sequestration (Shepard et al. 2011; Duarte et al. 2013).

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Table 1. ANOVA results comparing stem density over time for each creek (top – using repeated measures ANOVA) and comparing density among creeks in each month (bottom). Months or creeks with letters in common in the same row are not significantly different from each other following Bonferroni post-hoc comparisons.

	<i>Sum of Squares</i>	<i>DF</i>	<i>F</i>	<i>p</i>	Jun	Jul	Aug	Sep
Sweeney (SW)	4589.2	1.8, 15*	18.3	0.001	A	AB	B	B
West (WE)	8685.6	3, 15	35.4	0.000	A	AB	BC	C
Clubhead (CL)	117.7	3, 6	3.6	0.085				
Nelson (NE)	1119.6	3, 6	13.6	0.004				
					WE	SW	CL	NE
June	4662.6	3	12.8	0.000	A	AB	B	B
July	1208.3	3	3.8	0.035				
August	727.9	3	4.1	0.028	A	AB	B	AB
September	353.7	3	1.9	0.175				

*Model results with the Greenhouse-Geisser correction for lack of sphericity.

Table 2. Mixed Model results showing the effect of creek, initial density, and proximity to the confluence on total loss of *S. alterniflora* stem density between June and September 2011. Model coefficients are followed by 95% confidence intervals (in parentheses) as estimated by the Wald statistic (Bates et al. 2015). Coefficients for Position 1 and 2 are relative to Position 3. Coefficients in bold indicate variables for which the confidence interval does not include zero.

	<i>Full Model</i>	<i>Density Model</i>	<i>Position Model</i>	<i>Creek only Model</i>
Intercept	-46.9 (-69.4, -24.3)	-49.5 (-72.4, -26.5)	32.0 (12.2, 51.7)	31.2 (17.5, 44.9)
Position 1	-8.7 (-17.0, -0.3)	Na	-6.5 (-21.1, 8.0)	Na
Position 2	-2.7 (-11.1, 5.6)	Na	-0.3 (-14.9, 14.2)	Na
Initial Density	0.91 (0.67, 1.15)	0.89 (0.65, 1.14)	Na	Na
Random Effect (Creek) Variance	18.0	14.3	290.2	293.2
Residual Variance	54.3	64.4	165.7	153.7
% variance by fixed effects	83.8%	82.4%	-2.0%	-
% variance by random effect	-	-	-	65.6%

Table 3. Mixed Model results showing the effect of proximity to the confluence, initial density, creek, and August standing biomass measures on the overall productivity of the creeks between June 2011 and August 2011. Model coefficients are followed by 95% confidence intervals (in parentheses) as estimated by the Wald statistic (Bates et al. 2015). Coefficients for Position 1 and 2 are relative to Position 3. Coefficients in bold indicate variables for which the confidence interval does not include zero.

	<i>Biomass Only Model</i>	<i>Biomass + Position Model</i>	<i>Biomass + Initial Density Model</i>	<i>Creek Only Model</i>
Intercept	174.7 (57.0, 292.4)	183.3 (61.2, 305.4)	11.5 (-99.3, 122.3)	521.7 (466.4, 577.0)
Position 1	Na	-30.1 (-81.5, 21.4)	Na	Na
Position 2	Na	-23.3 (-74.1, 27.6)	Na	Na
Initial Density	Na	Na	2.2 (1.2, 3.1)	Na
End-of-season Biomass	0.83 (0.56, 1.09)	0.85 (0.57, 1.12)	0.76 (0.55, 0.96)	Na
Random Effect (Creek) Variance	1386.9	1355.0	40.6	1616.4
Residual Variance	1927.9	2015.0	1240.0	6651.7
% variance by fixed effects	59.9%	59.2%	84.5%	-
% variance by random effect	-	-	-	19.5%

Figure Captions

Fig. 1. Location map of the study area within the Plum Island Sound salt marsh system. Sampling was conducted along the four labeled creeks: Sweeney, West, Clubhead, and Nelson. Stars indicate the sampling locations with each star representing three points spaced 50-70m apart along the creek edge.

Fig. 2. Mean stem density (a) and stem height (b) of low marsh *S. alterniflora* in Sweeney and Clubhead (fertilized) and West and Nelson (reference) creeks from June through September 2011. Error bars represent ± 1 SE.

Fig. 3. Comparison of *S. alterniflora* productivity as estimated by EOSL Biomass and EOSL Biomass corrected for loss of stems during the growing season. Error bars represent ± 1 SE. Significance of paired t-tests between productivity measures are indicated as follows: * <0.05 and >0.01 , ** <0.01 and >0.001 ; *** <0.001 .

Fig. 4. Relationship between *S. alterniflora* stem height and density over the growing season. Open points indicate June, gray points July and black points August. Both height and density are plotted on a log scale. September numbers are not included because overall height and biomass were decreasing.

Fig. 1

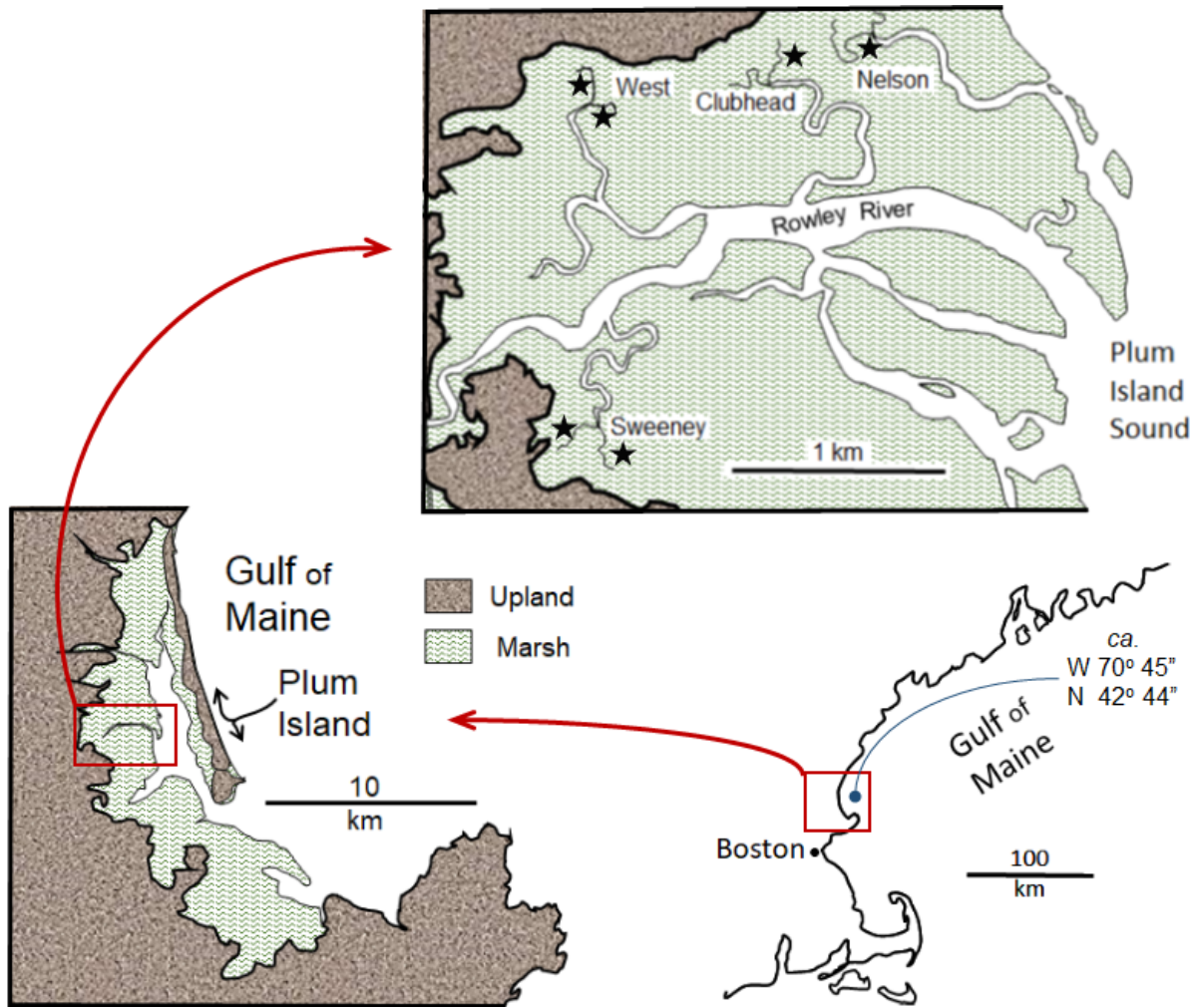


Fig. 2

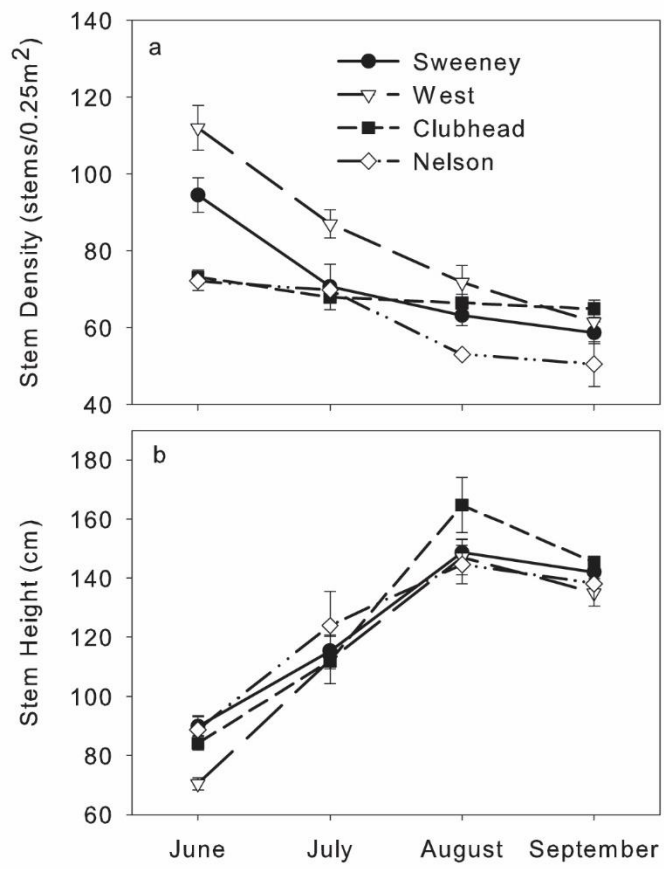


Fig. 3

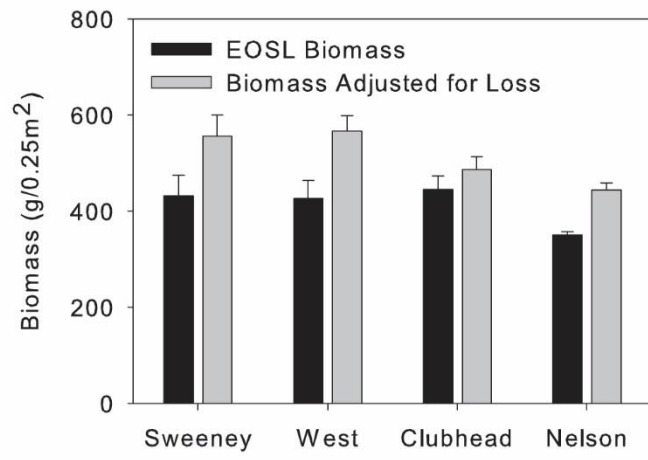


Fig. 4

