

2014

THE INFLUENCE OF SALT MARSH FUCOID ALGAE (ECADS) ON SEDIMENT DYNAMICS OF NORTHWEST ATLANTIC MARSHES

M. C. Tyrrell

Carol S. Thornber

University of Rhode Island, thornber@uri.edu

See next page for additional authors

Follow this and additional works at: https://digitalcommons.uri.edu/bio_facpubs

**The University of Rhode Island Faculty have made this article openly available.
Please let us know how Open Access to this research benefits you.**

This is a pre-publication author manuscript of the final, published article.

Terms of Use

This article is made available under the terms and conditions applicable towards Open Access Policy Articles, as set forth in our [Terms of Use](#).

Citation/Publisher Attribution

Tyrrell, M.C., C.S. Thornber, J.A. Burkhardt, and M. Congretel. "The Influence of Salt March Furoid Algae (Ecads) on Sediment Dynamics of Northwest Atlantic Marshes." *Estuaries and Coasts*, December 2014. Available: <http://link.springer.com/article/10.1007/s12237-014-9919-x>

This Article is brought to you for free and open access by the Biological Sciences at DigitalCommons@URI. It has been accepted for inclusion in Biological Sciences Faculty Publications by an authorized administrator of DigitalCommons@URI. For more information, please contact digitalcommons@etal.uri.edu.

Authors

M. C. Tyrrell, Carol S. Thornber, J. A. Burkhardt, and M. Congretel

1 THE INFLUENCE OF SALT MARSH FUCOID ALGAE (ECADS) ON SEDIMENT
2 DYNAMICS OF NORTHWEST ATLANTIC MARSHES

3
4
5
6 M.C. Tyrrell^{1*}, C.S. Thornber², J.A. Burkhardt², M. Congretel^{2,3}

7
8 ¹ Cape Cod National Seashore, National Park Service, 99 Marconi Site Road, Wellfleet, MA
9 02667 USA

10 ² Dept. of Biological Sciences, University of Rhode Island, 120 Flagg Road, Kingston RI 02881
11 USA

12 ³ AgroParisTech – UMR SAD-APT – 16 rue Claude Bernard, 75231 Paris cedex 05, France

13
14
15
16 *Author for correspondence (email: Megan_Tyrrell@nps.gov; phone: 508.487.3262 fax:
17 508.487.7153)

18
19
20 *for submission to Estuaries and Coasts*

21

1 Abstract

2 Resilience is currently a key theme within salt marsh ecological studies. Understanding the
3 factors that affect salt marsh accretion and elevation gains are of paramount importance if
4 management of these ecosystems is to be successful under increasing synergistic stresses of
5 storm surge, inundation period, and eutrophication. We present the results of salt marsh furoid
6 algae (ecads) removal experiments on *Spartina alterniflora* abundance, production and
7 decomposition and the sedimentary dynamics of two marshes on Cape Cod, Massachusetts. The
8 presence of the thick layer of marsh fucoids had a significant and positive influence on sediment
9 deposition, accretion, concentration of water column particulates, while it inhibited water flow.
10 Decomposition rates of *Spartina alterniflora* in the field were significantly higher under the
11 furoid macroalgae layer, and, in lab experiments, *S. alterniflora* seedlings added more leaves
12 when the marsh fucoids were present. In contrast, fucoids caused a significant decrease in *S.*
13 *alterniflora* seedlings' survival in the field. We found that marsh fucoids are stable despite not
14 being attached to any substrate, and field surveys revealed a relatively widespread, but not
15 ubiquitous, distribution along outer Cape Cod. Salt marsh furoid algae directly and substantially
16 contribute to salt marsh sediment elevation gain, yet their potential inhibitory effects on
17 colonizing *S. alterniflora* may counteract some of their overall contributions to salt marsh
18 persistence and resilience.

19

20 **Keywords:** ecads, resilience, salt marsh, sedimentation, *Spartina alterniflora*, accretion

21

1 **Introduction**

2 Climate change-driven sea level rise and the increased intensity and frequency of major
3 coastal storms have brought increased attention to the protective function of vegetated
4 ecosystems and their substantial economic and ecological benefits (e.g., Costanza et al. 2008;
5 Borsje et al. 2011; Spalding et al. 2013). Continual provision of these benefits will depend on the
6 ability of salt marsh ecosystems to keep up with accelerated rates of sea level rise through
7 sediment accumulation and elevation increases (e.g., Craft et al. 2009; Langley et al. 2009). The
8 contributions of vascular salt marsh vegetation to sediment retention (Gleason et al. 1979;
9 Stumpf 1983) and elevation gain are well documented (e.g., Richard 1978; Reed and Cahoon
10 1992; Morris et al. 2002), yet the roles of macroalgae that co-occur with marsh plants on
11 sediment processes remain comparatively unknown.

12 Macroalgae in salt marshes range from dense mats of opportunistic species that rapidly
13 respond to nutrient inputs (Boyer and Fong 2005) and may inhibit growth of salt marsh
14 cordgrass, *Spartina alterniflora* (Newton and Thornber 2013), to a persistent layer of densely
15 entangled brown algae whose biomass can exceed that of the aboveground portion of *S.*
16 *alterniflora* (Chock and Mathieson 1983; Roman et al. 1990; Gerard 1999). To the extent that
17 algal biomass, complex structure and year round occurrence may influence the sediment
18 trapping, stabilization and wave buffering function of salt marshes, the latter category of marsh
19 algae merits further investigation.

20 Marsh fucoids, or ecads, are unattached perennial brown macroalgae that have reduced
21 air bladders, profuse lateral branching, and occur in a thick, often contiguous layer on the salt
22 marsh sediment surface (Chock and Mathieson 1976; Mathieson et al. 2006). Initial colonization
23 of a salt marsh by fucoids occurs via algal fragments (Mathieson et al. 2006) and vegetative

1 growth results in the algae becoming entangled among the vascular plants and often partially
2 buried in the sediments. Based on their high biomass, and concentration in the lowest portions of
3 the marsh (Tyrrell et al. 2012), we hypothesized that they may have important roles in sediment
4 accumulation and stabilization at the most dynamic portion of the marsh. Furthermore, we
5 suspected that this potential to enhance sediment deposition and elevation gain may decline with
6 increasing distance from the lowest portion of marshes.

7 Although several studies have assessed whether the interaction between marsh
8 macroalgae and *S. alterniflora* is facilitative or inhibitory, the results have been contradictory
9 (e.g., Brinkhuis 1976; Chapman and Chapman 1999; Gerard 1999; Tyrrell et al. 2012). Tyrrell et
10 al. (2012) reviewed the results from previous studies, finding one study each supporting
11 beneficial effects (Gerard 1999), neutral (Chapman and Chapman 1999) and inhibitory effects
12 (Brinkhuis 1976a); with the new results from their marsh furoid removal experiments showing
13 that standing-dead *S. alterniflora* had significantly higher stem density and biomass when marsh
14 fucoids were removed. Abundance, production, survival and decomposition of *S. alterniflora* all
15 affect its sediment trapping and elevation gain functions (Gleason 1979; Morris et al. 2002), thus
16 the positive or negative effects of marsh fucoids on all of these traits merit further exploration.
17 For example, the potential for new *S. alterniflora* shoots to be inhibited by a thick, densely
18 intertwined layer of furoid algae at the marsh surface, is high.

19 We present results from field and lab experiments where the effect of marsh fucoids on *S.*
20 *alterniflora* survival, growth and decomposition rates were assessed. We also manipulated
21 marsh fucoids in large plots of two New England back barrier marshes and assessed their
22 influence on sediment deposition, accretion/erosion rates, percent fines, total suspended solids
23 and relative water flow. Furthermore, we evaluated contributions of marsh fucoids to sediment

1 organic matter content, which is an important factor in the nutrient poor, sandy sediments that
2 characterize the lower portion of back-barrier marshes where marsh fucoids reach their highest
3 abundance (Tyrrell et al. 2012) and where *S. alterniflora*'s productivity and abundance is most
4 critical for marsh growth and maintenance (Gedan et al. 2011). The interaction between marsh
5 fucoids, sedimentation dynamics and pioneer species such as *S. alterniflora* is likely highly
6 relevant for clarifying the ecogeomorphic feedbacks (*sensu* Kirwan et al. 2010) that contribute to
7 marsh elevation gain and resilience. Specifically, the answer regarding whether marsh fucoids
8 are inhibitory or facilitative of *S. alterniflora*'s growth and survival will likely depend on *S.*
9 *alterniflora*'s life history stage and the physical conditions (e.g. sediment type, drainage,
10 inundation period) of the study site. We discuss our results in terms of ecosystem functioning
11 and resilience in the face of a changing climate.

12

13 **Methods**

14 *Study system*

15 The majority of the salt marshes on outer Cape Cod have a back-barrier (as opposed to
16 riverine) geomorphic setting (Smith 2009). Salt marsh cordgrass, *Spartina alterniflora*, is the
17 most abundant vegetation species in these marshes, with the upper limits of *S. alterniflora*
18 roughly corresponding to the mean high water elevation (Richard 1978). The marsh fucoid
19 surveys, as well as the manipulative field experiments described below, took place in the *S.*
20 *alterniflora* zone. While the focus of this study was to identify the function(s), not the species of
21 the brown algae that composed the marsh fucoids, the marsh fucoids were generally composed of
22 a mixture of *Ascophyllum nodosum* ecads and *Fucus* spp. ecads (Tyrrell et al. 2012). Zero to low
23 ($\sim < 1.0 \text{ g/m}^2$ wet mass) densities of other macroalgal species were present in our study habitats.

1 *Regional distribution and movement tracking*

2 In April and May of 2011, we conducted a survey of seventeen salt marshes on outer
3 Cape Cod (Orleans to Provincetown, MA USA; Fig. 1) to determine the presence or absence of
4 marsh furoids. We conducted timed searches of approximately twenty minutes in the lowest
5 extent of *S. alterniflora* in each marsh. Presence of marsh furoids was determined as
6 encountering a contiguous $>2\text{m}^2$ patch of unattached brown macroalgae.

7 To determine whether marsh furoids were relatively stationary in their natural setting, we
8 used plastic flagging to mark 10 patches ($\sim 2 \times 2 \text{ m}$) each of marsh furoids in West End and
9 Nauset marshes. Using a handheld GPS (Garmin 76CSx), we relocated the flagging from 2
10 weeks to 3 months later.

11 *Marsh furoid removal experiment*

12 In May 2011, we set up a marsh furoid removal experiment in two Cape Cod, MA back
13 barrier salt marsh sites (West End and Hatches Harbor). Edge plots were located approximately
14 1 meter landward of the lower edge of the *S. alterniflora* zone and each were 2 m x 2 m. A total
15 of 10 edge plots were marked at each site. We also created a set of five paired 2 m x 2 m interior
16 plots to examine the effect of marsh furoids with increasing distance from the lowest extent of
17 marsh vegetation. These plots were spaced 5 m apart, moving landward (upslope) from the
18 marsh edge. To obtain an initial biomass estimate of marsh furoids, we measured the canopy
19 thickness (distance from the sediment surface to the top of the marsh furoid layer) at five random
20 locations within each plot. We used a previously established relationship to determine biomass
21 from furoid canopy thickness ($r^2=0.86$, $p<0.0001$; Tyrrell unpubl. data). We cut the marsh
22 furoids along the perimeter of each plot to standardize disturbance at the plot edges and then
23 randomly selected half of the edge plots and half of the interior plots and removed all marsh

1 furoids from them (henceforth called removal plots). We used a two way ANOVA to analyze
2 the effect of site and location (edge/interior) on marsh furoid abundance. For the interior plots
3 only, we examined the effect of distance from the marsh edge as a covariate on marsh furoid
4 abundance; in nearly all cases, this distance was not significant. Mid-way through the
5 experiments, we used real time kinematic GPS to measure the elevations of each plot.

6

7 Sediment deposition above and below marsh furoid canopy

8 To measure whether the thick canopy of marsh furoids intercepted a significant portion
9 of suspended particulates, we measured sediment deposition in polyvinyl chloride (PVC) pipes
10 (5.98 cm inside diameter) that were capped at the lower end. The pipes were driven into the
11 sediment so that the opening was either 2 cm above the sediment surface ('low'), or so that the
12 opening was level with the marsh furoid canopy (or at the same height where the marsh furoids
13 would have been in the removal plots; 'high'). We utilized 'low' rather than flush with the
14 sediment surface to reduce the potential for horizontal sediment transport to be interpreted as
15 deposition. Each marsh edge plot had one low and one high PVC pipe. We put the pipes out in
16 early August 2011 at West End and Hatches Harbor and retrieved them 42 days post deployment.
17 When we returned to the laboratory, we removed sediments from pipes, dried the sediments at
18 60° C for >24 hours, and weighed them.

19 Sediment deposition on traps

20 To assess sediment deposition rates directly on the marsh surface, in May 2011 we placed
21 10 cm x 10 cm pieces of aluminum flashing on the sediment surface and secured them using two
22 lawn staples, on all plots at both sites. Traps were placed directly on the sediment surface, which
23 entailed parting the marsh furoid canopy to expose the marsh surface in control plots. Three

1 traps were placed in each plot, and one trap per plot was removed every six weeks. Upon
2 retrieval, each trap was carefully removed and individually placed in a small plastic bag for
3 transport to the lab. Traps in bags were dried at 60° C for >24 hours. We determined sediment
4 dry mass by weighing the sediment trap within its bag, disposing of the sediment, and
5 reweighing the trap and bag.

6 Physical characteristics of sediment surface

7 We used a putty knife to scrape the top 1.5 cm (~20 cm³) of sediment for analysis of
8 grain size and organic content and placed the samples into individually sealed bags. We took a
9 total of four scrapings in each plot; three of these samples were used for analysis of organic
10 content (average value per plot was used for statistical analyses), and one was used for particle
11 size analysis. We obtained the sediment scraping samples at the end of September from all
12 experimental plots. We dried the samples in their bags at 60° C for >24 hours. The distribution
13 of sediment grain size was measured for each sample, using approximately 20 g of dried
14 sediment that was poured into a standard sieve set (>2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.106 mm
15 and 0.053 mm) and placed on a shaker for five minutes. The weight of each fraction was
16 recorded and used to calculate the percent of the total sediment sample that fell within each size
17 category. We grouped the three smallest sieves into a “fines” category and, data from the three
18 largest sieves were combined to make a “sand” category (Wentworth 1922). Samples for organic
19 content were burned for four hours at 550° C in a muffle oven, placed in a desiccator and
20 immediately weighed upon removal from the desiccator.

21 Relative changes in marsh surface elevation

22 To assess whether the presence of a thick layer of marsh fucoids affected changes in
23 marsh surface elevation, we haphazardly placed five pin flags in each experimental plot. We

1 adjusted the initial height of each flag so that the top of the stake was exactly 20 cm above the
2 sediment surface. Each marking flag was numbered, and the distance between the top of the
3 stake and the sediment surface was measured to the nearest mm after 6, 12 and 18 weeks.
4 Surface accretion was indicated by a decrease in the average distance between the top of the
5 stake and the marsh surface.

6 Total suspended solids concentration

7 Prior to conducting our large experiment in 2011, we created an identical marsh edge plot
8 configuration on August 5 2010 in the West End marsh (plots were in the same area with the
9 same method to establish treatments but were 3 m x 3 m in size) as a pilot experiment. On
10 September 10, 2010, we conducted total suspended solids (TSS) sampling several weeks after
11 establishing four marsh fucoid removal plots and four control (marsh fucoids left in place) on an
12 ebbing tide. We used suction to obtain 1 L water samples 5 cm above the marsh surface. The 5
13 cm height was chosen so that TSS could be determined within the layer of marsh fucoids (in
14 control plots) but slightly above the marsh surface to avoid disturbing it. We also obtained
15 samples ~50 cm above the sediment surface to subtract out TSS concentrations far above the
16 influence of the marsh fucoids. Sample bottles were transported to the laboratory and inverted
17 ten times before being filtered through a glass microfiber (GF/F 0.7 μm pore size) filter using a
18 vacuum filter pump. Each GF/F filter was then dried at 60° C for >24 hours. We divided the
19 final weight of the dried suspended solids by the volume of water filtered (300-500 mL) to assess
20 suspended solid concentrations. For each replicate, we subtracted the weight of each filter taken
21 50 cm above each plot from the weight of the filter taken 5 cm above the sediment surface to
22 obtain a TSS value.

23 Calcium sulfate dissolution

1 In 2011, we measured dissolution of calcium sulfate (*aka* Plaster of Paris) to assess the
2 relative water flow rates (Thompson and Glenn 1994) when marsh fucoids were removed or left
3 intact on all experimental plots. We poured calcium sulfate into disposable drink cups and
4 pierced the bottom of the cups with a lawn staple to create “popsicles” for assessing dissolution
5 rates. Each popsicle was air dried and weighed prior to being brought to the plots. Popsicles
6 were haphazardly placed on the marsh surface (under the marsh fucoids in the control plots) and
7 after two weeks, they were individually bagged and returned to the laboratory. Popsicles were
8 briefly rinsed, dried at 60° C for >24 hours, and weighed again to assess the percentage mass
9 lost. The first set of popsicles was deployed in late June and a second set of popsicles was placed
10 in the field sites in mid-August.

11 *Decomposition of S. alterniflora*

12 We hypothesized that because of their substantial thickness and effect on microclimate,
13 salt marsh fucoids might increase the rate of decomposition of organic material. We used
14 standard window screen (1.2 mm mesh) to make litter bags (20 x 10 cm) for *S. alterniflora*
15 leaves. We weighed approximately 2 g of freshly collected, freshwater rinsed and blotted dry *S.*
16 *alterniflora* (1.832 g +/- 0.039), placed them into each bag, and sewed them closed. We
17 haphazardly placed five litter bags in each marsh edge plot (n=100 total bags) on June 13 and
18 retrieved one 2, 4, 8, 10 and 14 weeks later. Upon returning them to the lab, we gently rinsed
19 bags and carefully removed all remaining vascular plant material from each bag. The plant
20 material was dried at 60° C for 48 hours and weighed.

21 To create a blotted dry vs. oven dried conversion for *S. alterniflora*, we collected 47
22 leaves, and treated them exactly in the same manner as described above (rinse, blot, weigh).
23 Each leaf was then dried at 60° C for 48 hours and re-weighed. The resulting relationship (oven

1 dried= $0.1817 \times \text{blotted dry} + 0.2105$, $R^2 = 0.8725$) was used to convert the initial blotted dry
2 values to equivalent oven dried values. We used these data to determine the k decomposition
3 constant (rate of change in mass over time) from the slope of the regression for each replicate
4 plot. of *S. alterniflora* in each plot (Mews et al. 2006; Conover 2011).

5 *Effect on S. alterniflora seedlings under lab conditions*

6 We obtained seedlings on June 15 and immediately planted them in twenty 18.9 L
7 buckets that were $\frac{3}{4}$ full of sand. The seedlings in the buckets were watered with fresh water
8 every 3 days and also exposed to natural rainfall. A small hole was made in the side of each
9 bucket at the level of the sediment surface to allow excess water to drain. On July 15, when
10 seedlings were approximately 30 cm high (30.4 cm, ± 1.5 SE), we added 850 grams of marsh
11 fucoids to 10 randomly selected buckets and started watering with salt water to approximate field
12 conditions. We temporarily covered the small hole with duct tape and allowed the saltwater to
13 remain for a few minutes before removing the tape and allowing the water to drain out.
14 Saltwater watering took place 3 times a week.

15 On September 26, we measured plant height and number of live and dead leaves. We
16 then harvested each plant, rinsed and dried (60° C, 24 hours) and took separate weights for the
17 above and belowground portions. We obtained three sediment scrapings in each bucket to assess
18 organic content of the sediments between the treatment types using methods described above.
19 We used t-tests to compare treatment effect on: aboveground biomass, belowground biomass and
20 sediment organic content. We examined the effect of various initial covariates (plant height,
21 number live leaves, number of dead leaves) on their respective parameters; for those parameters
22 where the covariate was not statistically significant, we removed it from subsequent analyses and
23 performed t-tests.

1 *Effect on S. alterniflora seedlings under field conditions*

2 On July 11 2011, we placed 40 flower pots (15.5 cm diameter. 17.5 cm deep) in the sand
3 in an unvegetated, highly dynamic section of the West End marsh. We planted a freshly collected
4 (<48 hours since collection) *S. alterniflora* seedling in each pot and recorded plant height and the
5 number of dead and live leaves. Half of the pots (20) were randomly assigned to the marsh
6 fucoid addition treatment, and half of the pots (20) did not receive fucoids ('bare') and served as
7 controls. We constructed small cages of plastic mesh (~900 cm², 15.24 cm high) around each of
8 the plots to keep the marsh fucoids in place. We put approximately 500 g of salt marsh fucoids
9 into the cages and inserted several lawn staples to further secure them. We also put lawn staples
10 into the control plots to standardize sediment disturbance. On September 19, we measured plant
11 height and counted the number of live and dead leaves. The weight of above and belowground
12 portions of biomass were measured separately after the plants were dried at 60° C for 24 hours in
13 the lab. .

14 *Statistical analysis*

15 Data were examined for heteroscedasticity and normality prior to being subjected to
16 statistics. The sediment grain size percent fines data was square root arcsine transformed prior to
17 analysis. In most cases, a three way fixed factor ANOVA was performed (PVC pipes, percent
18 fines, organic content, relative flow). A three way ANOVA with repeated measures was used
19 for: sediment traps, relative elevation change and decomposition. T-tests were used for TSS and
20 all analyses stemming from the lab and field *S. alterniflora* growth experiments except field
21 survival, which was subjected to a nominal logistic regression. All p values from t-tests were
22 checked with a sequential Holm-Bonferroni correction to ensure significance (Holm 1979);

1 significant p values are indicated with a * in output tables. JMP v 10.0 (SAS Institute) was used
2 to conduct the ANOVAs for all tests.

3

4 **Results**

5 *Regional distribution*

6 Timed searches revealed that marsh furoids were present in six salt marshes and absent in
7 eleven. There was no obvious pattern related to the presence or absence of marsh furoids; they
8 occur on both bay and ocean sides, in riverine and back-barrier marshes, and in locations that
9 have strong anthropogenic influences nearby as well as marshes that are relatively isolated from
10 extensive watershed upland development (e.g. Pamet Harbor at Corn Hill). However, the
11 marshes that had very soft sediments and apparently high organic content did not have salt marsh
12 furoids (e.g. Drummer Cove/Blackfish Creek). In the marsh furoid movement tracking, we
13 found that in every case except one, the flagging was re-located within 3 meters of its original
14 location, which corresponds to the accuracy limit of the handheld GPS.

15

16 *Marsh furoid removal experiment*

17 Although the marsh furoids were severed along the boundary of each plot (and taken
18 away from the removal plots), the stability of the unattached algae was high. The boundaries of
19 the plots remained distinct and encroachment of the marsh furoids into removal plots was rare,
20 thus indicating that the integrity of both treatment types was high throughout the course of the
21 experiment.

22 The estimated biomass of salt marsh furoids was 30% higher at the edge of the marsh
23 platform than in the marsh interior ($p = 0.001$; Table 1, Fig. 2), and 20% higher at Hatches

1 Harbor than West End ($p < 0.0001$), with a non-significant interaction; average height of marsh
2 furoid layer ranged from 6.0 cm (West End interior plots) to 9.6 cm (Hatches Harbor edge pots).
3 In addition, there was no significant difference in initial canopy height between control and
4 removal plots, although there was a significant three way interaction ($F_{1,36} = 4.294$, $p = 0.046$).
5 A separate analyses of covariance indicated that the distance from interior plots to the marsh
6 edge was not correlated with canopy height in interior plots. For all experimental data (post
7 commencement of treatments) except for organic content in the sediment scrapings, the effect of
8 distance to marsh edge was not a significant covariate, so the covariate was removed from final
9 analyses presented here.

10 Sediment deposition above and below marsh furoid canopy

11 Sediment loads in PVC pipes in plots with salt marsh furoids were twice as high as in
12 plots where salt marsh furoids were removed ($p=0.013$; Table 2; Fig. 3). In addition, sediment
13 load was twelve times higher at the sediment surface than at 8cm above (typical average furoid
14 canopy height), regardless if marsh furoids were present or not ($p<0.0001$), and sediment load
15 was nearly five times higher at West End than at Hatches Harbor ($p<0.0001$). The significant site
16 by treatment interaction ($p=0.034$) was primarily driven by very high sediment deposition rates
17 at the West End. Similarly, the significant treatment by pipe height interaction ($p=0.024$)
18 indicated that the presence of salt marsh furoids strongly increased sediment deposition rates at
19 the surface.

20 Sediment deposition on traps

21 Sediment mass on aluminum flashing was twice as high at West End than at Hatches
22 Harbor (Fig. 4; $F_{1,24} = 8.58$, $p = 0.007$). However, we did not find significant differences in

1 sediment mass between any other factors or interactions, including control/removal, edge/interior
2 plots, and length of time in field (Table 3).

3 Physical characteristics of sediment surface

4 There was no difference in sediment grain size between fucoïd control and removal treatments,
5 although edge plots were sandier than interior plots (97.65 +/- 0.53 and 95.50 +/- 1.00% sand,
6 respectively; $F_{1,32} = 11.14$, $p = 0.002$) and West End was sandier than Hatches Harbor (% sand =
7 99.31 +/- 0.69 and 93.85 +/- 6.15% sand, respectively; $F_{1,32} = 127.39$, $p < 0.001$). A significant
8 edge/interior * site interaction ($F_{1,32} = 10.27$, $p = 0.003$) indicated that the difference in edge and
9 interior plots was due to differences at Hatches Harbor, not West End (Table 4a).

10 Control and fucoïd removal plots did not differ significantly in sediment organic content,
11 although interior plots had two to four times higher percent organic content than edge plots (8.8
12 +/- 1.6 vs. 2.5 +/- 0.5%, respectively; $F_{1,32} = 46.08$, $p < 0.0001$), and organic content was at least
13 twice as high at Hatches Harbor than at West End ($F_{1,32} = 63.99$, $p < 0.0001$, Table 4b). In the
14 interior plots, organic content varied significantly with distance from the edge of the marsh ($F_{1,19}$
15 = 10.90, $p = 0.005$; Table 5).

16 Relative changes in marsh surface elevation

17 Marsh accretion in fucoïd removal plots was fifty percent (62% overall edge and interior
18 plots) lower than in control plots (control average = 0.456 +/- SE, removal average = 0.078 +/-
19 SE, $F_{1,32} = 5.47$, $p = 0.026$; Table 6; Fig. 5), as measured by pin flags. Marsh accretion rates
20 varied significantly over time ($F_{2,31} = 9.478$; $p = 0.0006$), with a significant time, site, and
21 location interaction ($F_{2,31} = 4.485$, $p = 0.020$). No differences in marsh accretion rates were found
22 in marsh elevation change in interior vs. edge locations.

23 Total suspended solids concentration

1 There was a statistically significant difference in suspended particulate matter density
2 between control and marsh furoid removal plots (0.125 mg/L and 0.008 mg/L, respectively; $t_3 =$
3 4.01, $p = 0.02$).

4 Calcium sulfate dissolution

5 The initial average mass of the popsicles was 272 +/- 2.3 g. Relative flow rates did not
6 differ between sites, treatments, or marsh locations in early summer (June 2011; Grand mean =
7 57 +/- 0.7% mass loss over 2 weeks; Table 7a). In mid- summer, however, marsh furoid
8 removal plots had higher relative flow rates than control plots (August 2011; 64.3 +/-2.0vs. 60.6
9 +/-1.7%, respectively; $F_{1,32} = 5.33$, $p = 0.028$; Table 7b), and relative flow was significantly
10 higher at the West End marsh than at Hatches Harbor (55.6 +/- 1.2 vs. 69.3 +/- 1.2%,
11 respectively; $F_{1,32} = 68.63$, $p < 0.0001$).

12 Decomposition of *S. alterniflora*

13 *Spartina alterniflora* decayed ~50% faster in plots with marsh fucoids than with those
14 removed (mean $k = 0.18 +/- 0.02$ vs. $0.12 +/- 0.02$; $F_{1,16} = 6.40$, $p = 0.022$; Fig. 6). Decay rates
15 did not vary between sites, with a non-significant treatment by site interaction.

16

17 Effect on *S. alterniflora* seedlings under lab conditions

18 All *S. alterniflora* characteristics did not differ between treatments at the start of the
19 experiment and all seedlings survived the duration of the laboratory experiment. While the
20 addition of marsh fucoids had a positive effect on number of live *S. alterniflora* leaves after three
21 months (6.90 +/- 0.43 marsh furoid addition vs. 5.40 +/- 0.22 control; $t_{18} = 3.08$, $p = 0.006$);
22 marsh fucoids did not have a significant effect on any other *S. alterniflora* characteristics
23 (number of dead leaves, aboveground biomass, belowground biomass, growth rate). The

1 presence of marsh fucoids significantly enhanced sediment organic content (1.22 marsh fucoid
2 addition, vs. 0.78% controls; $t_{18} = 4.33$, $p < 0.001$).

3

4 Effect on *S. alterniflora* seedlings under field conditions

5 Survival of transplanted *S. alterniflora* seedlings in the field was significantly higher in
6 plots without marsh fucoids (100 vs. 60%, $\chi^2 = 13.11$, $p < 0.001$) as plots with fucoids present.
7 Of the surviving plants, growth rates did not significantly differ between treatments, although
8 there was a trend of increased growth for *S. alterniflora* with marsh fucoids (8.58 cm control vs.
9 13.33 cm marsh fucoid present, $t_{30} = 1.90$, $p = 0.067$). Similarly, neither the aboveground or
10 belowground biomass, nor the final numbers of dead or live leaves varied significantly between
11 treatments.

12

13 **Discussion**

14 The impact of marsh fucoids on sediment dynamics can be substantial, as the thick layer
15 of algae significantly promotes sediment deposition and accretion, dampens water flow at the
16 sediment interface, and is associated with higher concentrations of particulates in the water
17 column above the substrate. Suspended sediment concentrations are an important factor in
18 marsh surface accretion (Reed 1989; Kirwan et al. 2010; Mudd 2011), and we demonstrated that
19 marsh fucoids are positively related to suspended solids concentrations, relative marsh surface
20 elevation, and sediment deposition rates when horizontal advection was eliminated (see the PVC
21 pipes experiment). Considered simultaneously, the several methods we used to assess marsh
22 fucoid effects on sediment dynamics indicate that marsh fucoids have a strong, positive influence
23 on surface accretion and deposition rates. Nevertheless, *S. alterniflora*'s accelerated

1 decomposition rate under marsh fucoids may lead to shallow subsidence and counteract some of
2 the gains in surface elevation and sediment deposition. High resolution marsh surface elevation
3 monitoring (e.g. repeated surveys with ground-based equipment such as RTK, total station or
4 LIDAR) would be needed to assess whether marsh fucoids' enhancement of sediment deposition,
5 relative surface elevation and surface accretion translate to a net gain in marsh surface
6 elevations.

7 In addition to their positive influence on marsh surface sedimentation and deposition
8 rates, marsh fucoids also putatively improve the growing conditions for *S. alterniflora* in sandy
9 soils, as manifested by the significant increase in *S. alterniflora* leaf production in marsh fucoid
10 addition treatments. Organic matter concentration was enhanced by marsh fucoids in lab *S.*
11 *alterniflora* growth experiments, but this treatment effect did not persist in the field based marsh
12 fucoid manipulation plots. This disparity is likely because under controlled lab conditions (vs.
13 field conditions), organic matter and nutrients are not transported out of the experimental arena
14 by tides or other water movement (Newton and Thornber 2013). Lab conditions were less
15 stressful overall (regardless of treatment) than field conditions, and plant growth was greater in
16 the lab. Because field transplanted *S. alterniflora* had relatively low growth rates (0.145 +/-
17 0.018 cm/day) regardless of treatment, we did not expect to see a strong inhibitory impact on
18 field *S. alterniflora* growth. Additionally, initial seedling height was greater for lab than for field
19 experiments (30.40 cm +/- 1.52 SE vs. 17.99 cm +/- 0.74 SE), while the biomass of marsh
20 fucoids did not substantially differ between experiments.

21 The leading edge of back-barrier marshes are dynamic and frequently overwashed,
22 eroded or otherwise influenced by storm activity (Donnelly et al. 2001) and marshes with these
23 characteristics can be less resilient to sea level rise (D'Alapos et al. 2011). High inundation, low

1 nutrient, sandy, dynamic conditions are stressful for marsh plants (Huckle et al. 2000; Kirwan
2 and Guntenspergen 2012). Very sandy sediments do not bind nutrients as well as sediments with
3 higher proportions of silt or other small particle sizes (Murray et al. 2006) and nutrients and
4 organic matter that might be locally contributed due to presence of marsh fucoids will dissipate
5 quickly in well drained, coarse sediments such as our field study sites. *Spartina alterniflora*'s
6 growth in sandy sediments may be inhibited by low nutrient concentrations (Broome et al. 1975),
7 therefore marsh fucoids can be beneficial to *S. alterniflora* in sandy sediments because they can
8 amend low organic matter, nutrient poor sediments. Decomposition rates of *S. alterniflora* were
9 significantly faster when marsh fucoids were present, demonstrating that marsh fucoids, like
10 other macroalgae in marshes, can accelerate nutrient cycling rates (Boyer and Fong 2005;
11 Thomsen et al. 2009). Nevertheless, under stressful, highly dynamic field conditions, survival of
12 transplanted *S. alterniflora* seedlings to a field site where marsh fucoids are naturally absent led
13 to diminished survival for those seedlings with marsh fucoids. In summary, the influence of
14 marsh fucoids on *S. alterniflora* is not uniformly positive, especially when *S. alterniflora* is
15 acting as a pioneer species in an unvegetated, highly dynamic environment.

16 Although we found a significant positive effect of marsh fucoids on a variety of sediment
17 related processes, there were significant differences in several processes between our two sites.
18 Marsh fucoid abundance was significantly higher at Hatches Harbor, and Hatches Harbor
19 sediments had two times higher organic content, greater percent fines, lower dissolution rates of
20 calcium sulfate, and less sediment deposited on the aluminum traps than West End. However, the
21 elevation of the edge plots at Hatches Harbor was approximately 75 cm higher than the
22 corresponding plots at the West End site, and the coefficient of variation for elevation was much
23 lower in Hatches Harbor- meaning the Hatches Harbor site is higher but flat. Furthermore, the

1 interior plots at West End all had slightly higher elevations with distance from the marsh edge,
2 while at Hatches Harbor, the interior plots were at the same elevation (and inundation regime) as
3 the marsh edge plots. Thus, while fucoids likely contributed to sediment processes at this site,
4 the higher elevation and lower inundation period of Hatches Harbor may have also contributed to
5 the significant site effect for relative flow and sediment deposition rates. While physical
6 properties and processes will differ across marshes, we found only one significant site by
7 treatment interaction term, for sediment deposition in PVC pipes (Table 2), indicating that,
8 except in this case, the effect of marsh fucoids was consistent regardless of site to site variation.

9 While salt marshes have typically been viewed as resilient, their abilities to withstand
10 increasing stressors may be limited (e.g., see review by Gedan et al. 2011). We have
11 demonstrated the vital role of marsh fucoids as contributing to gains in marsh surface relative
12 elevation, surface sediment deposition, and surface accretion; thus, their importance in marsh
13 ecosystem management is apparent. Large-scale removal of salt marsh vegetation can change
14 patterns of water flow and alter sediment accretion rates (e.g. Voss et al. 2013). Some factors
15 that are important in influencing marsh elevation gain and stability, including pasturing livestock
16 (Elschot et al. 2013), organic matter content (Chmura and Hung 2004) and eutrophication
17 (Deegan et al. 2012), are potentially within local to regional level management control. Other
18 factors that strongly influence marsh accretion and resilience, including tidal range/inundation
19 (Morris et al. 2002; D'Alapos et al. 2011), supply of mineral sediments (e.g., Fagherazzi 2013),
20 or elevated CO₂ concentrations (Langley et al. 2009), operate on geographic scales that are too
21 broad for regional level management but nevertheless are also important considerations for
22 enhancing the sea barrier function of marshes. The attenuation of wave energy by coastal
23 wetlands such as salt marshes and mangroves is well documented (e.g., Spalding et al. 2013) and

1 the economic value of the protective functions of vegetated coastal wetlands from extreme storm
2 damage such as hurricanes is substantial (Costanza et al. 2008). Vegetated wetlands are
3 economically and ecologically critical to coastal resilience to climate change damage and
4 impacts (Beatley 2009; Spalding et al. 2013) and the most salient factors contributing to marsh
5 elevation gain are thus of utmost importance for effective management and mitigation strategies.

6 We demonstrated that the presence and abundance of marsh fucoids should be considered
7 among the relevant ecogeomorphic factors to characterize north temperate salt marshes'
8 resilience to climate change stressors. Marsh fucoids, along with *S. alterniflora* and other
9 vascular plants, contribute to sediment deposition and accretion (important for sea level rise)
10 and, by slowing flow, increasing percent fines, suspended particulates, and *S. alterniflora*
11 decomposition rates, function as sediment stabilizing engineers (*sensu* Volkenborn et al. 2009)
12 which is important for resilience to storm related impacts. Due to their high biomass, strong
13 influence on sediment dynamics and *S. alterniflora* abundance, and cascading effects on animal
14 communities through modification of sediment surface microhabitat (Tyrrell et al. 2012), marsh
15 fucoids are analogous to a thicket in terrestrial systems. The complexity that they add to the
16 sediment/vegetation interface contributes to the valuable ecosystem services of salt marshes and
17 merits consideration among the ecogeomorphic feedbacks that contribute to marsh accretion and
18 resilience to climate change impacts.

19

20 **Acknowledgements**

21 Funding for this project was provided by the Friends of Cape Cod National Seashore
22 Nickerson Fellowship and the NPS Atlantic Research and Learning Center. This work is
23 dedicated to the memory of Dr. Michele Dionne, who inspired many colleagues and students to

1 pursue their natural resource conservation passions. We thank Jane Barnes, Maria Downs,
2 Megan Holcomb, Amber Martinez, Kelly Medeiros, and Jessica Stern for their assistance in the
3 lab and/or field. Additional support was provided to C. Thornber by the University of Rhode
4 Island.
5
6

1 **References**

- 2 Beatley, T. 2009. *Planning for coastal resilience: best practices for calamitous times*: Island
3 Press.
- 4 Borsje, B.W., B.K. van Wesenbeeck, F. Dekker, P. Paalvast, T.J. Bouma, M.M. van Katwijk,
5 and M.B. de Vries. 2011. How ecological engineering can serve in coastal protection.
6 *Ecological Engineering* 37: 113-122. doi:10.1016/j.ecoleng.2010.11.027.
- 7 Boyer, K.E., and P. Fong. 2005. Macroalgal-mediated transfers of water column nitrogen to
8 intertidal sediments and salt marsh plants. *Journal of Experimental Marine Biology and*
9 *Ecology* 321: 59-69
- 10 Brinkhuis, B.H. 1976. The ecology of temperature salt marsh fucoïds. Part 1: occurrence and
11 distribution of *Ascophyllum nodosum* ecads. *Marine Biology* 34: 325-338
- 12 Broome, S.W., W.W. Woodhouse, and E.D. Seneca. 1975. The relationship of mineral nutrients
13 to growth of *Spartina alterniflora* in Northern Carolina. II: The effects of N, P, and Fe
14 fertilizers. *Soil Science Society of America Journal* 39: 301-307
- 15 Chapman, A.S., and A.R.O. Chapman. 1999. Effects of cordgrass on saltmarsh fucoïds: Reduced
16 desiccation and light availability, but no changes in biomass. *Journal of Experimental*
17 *Marine Biology and Ecology* 238: 69-91
- 18 Chmura, G.L., and G.A. Hung. 2004. Controls on salt marsh accretion: a test in salt marshes of
19 Eastern Canada. *Estuaries* 27: 70-81
- 20 Chock, J.S., and A. Mathieson. 1976. Ecological studies of the salt marsh ecad *scorpioides*
21 (Hornemann) Hauck of *Ascophyllum nodosum* (L.) Le Jolis. *Journal of Experimental*
22 *Marine Biology and Ecology* 23: 171-190

- 1 Chock, J.S., and A. Mathieson. 1983. Variations of New England estuarine seaweed biomass.
2 *Botanica Marina* 26: 87-97
- 3 Conover, J. 2011. Variability in biomass decay rates and nutrient loss in bloom-forming
4 macroalgal species. Open Access Masters' Theses. Paper 108, University of Rhode Island
5 Kingston, RI.
- 6 Costanza, R., O. Pérez-Maqueo, M.L. Martinez, P. Sutton, S.J. Anderson, and K. Mulder. 2008.
7 The value of coastal wetlands for hurricane protection. *Ambio* 37: 241-248
- 8 Craft, C., J. Clough, J. Ehman, S. Joye, R. Park, S.C. Pennings, H. Guo, and M. Machmuller.
9 2009. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem
10 services. *Frontiers in Ecology and the Environment* 7: 73-78. doi:10.1890/070219.
- 11 D'Alapos, A., S.M. Mudd, and L. Carniello. 2011. Dynamic response of marshes to perturbations
12 in suspended sediment concentrations and rates of relative sea level rise. *Journal of*
13 *Geophysical Research* 116: F04020. doi:10.1029/2011JF002093.
- 14 Deegan, L.A., D.S. Johnson, R.S. Warren, B.J. Peterson, J.W. Fleeger, S. Fagherazzi, and W.M.
15 Wollheim. 2012. Coastal eutrophication as a driver of salt marsh loss. *Nature* 490: 388-
16 392
- 17 Donnelly, J.P., S.S. Bryant, J. Butler, J. Dowling, L. Fan, N. Hausman, P. Newby, B. Shuman, J.
18 Stern, K. Westover, and T.I. Webb. 2001. 700 year sedimentary record of intense
19 hurricane landfalls in southern New England. *Geological Society of America Bulletin*
20 113: 714-727
- 21 Elschot, K., T.J. Bouma, S. Temmerman, and J.P. Baker. 2013. Effects of long-term grazing on
22 sediment deposition and salt marsh accretion rates. *Estuarine, Coastal and Shelf Science*
23 133: 109-115

- 1 Fagherazzi, S. 2013. The ephemeral life of a salt marsh. *Geology* 41: 943-944
- 2 Gedan, K.B., A.H. Altieri, and M.D. Bertness. 2011. Uncertain future of New England salt
3 marshes. *Marine Ecology Progress Series* 434: 229-237
- 4 Gerard, V.A. 1999. Positive interactions between cordgrass, *Spartina alterniflora*, and the brown
5 alga, *Ascophyllum nodosum* ecad scorpioides in a mid-Atlantic coast salt marsh. *Journal*
6 *of Experimental Marine Biology and Ecology* 239: 157-164
- 7 Gleason, M.L., D.A. Elmer, N.C. Pien, and J.S. Fisher. 1979. Effects of stem density upon
8 sediment retention by salt marsh cordgrass, *Spartina alterniflora* Loisel. *Estuaries* 2: 271-
9 273
- 10 Holm, S. 1979. A simple sequential rejective method procedure. *Scandinavian Journal of*
11 *Statistics* 6: 65-70
- 12 Huckle, J.M., J.A. Potter, and R.H. Marrs. 2000. Influence of environmental factors on the
13 growth and interactions between salt marsh plants: effects of salinity, sediment, and
14 waterlogging. *Journal of Ecology* 88: 492-505
- 15 Kirwan, M.L., and G.R. Guntenspergen. 2012. Feedbacks between inundation, root production,
16 and shoot growth in a rapidly submerging brackish marsh. *Journal of Ecology* 100: 764-
17 770. doi:10.1111/j.1365-2745.2012.01957.x.
- 18 Kirwan, M.L., G.R. Guntenspergen, A. D'Alapous, J.T. Morris, S.M. Mudd, and S. Temmerman.
19 2010. Limits on the adaptability of coastal marshes to rising sea level. *Geophysical*
20 *Research Letters* 37: L23401. doi:10.1029/2010GL045489.
- 21 Langley, J.A., K.L. McKee, D.R. Cahoon, J.A. Cherry, and J.P. Megonigal. 2009. Elevated CO2
22 stimulates marsh elevation gain, counterbalancing sea level rise. *Proceedings of the*
23 *National Academy of Sciences, USA*. doi:10.1073/pnas.0807695106.

- 1 Mathieson, A., C.J. Dawes, A.L. Wallace, and A.S. Klein. 2006. Distribution, morphology, and
2 genetic affinities of dwarf embedded *Fucus* populations from the Northwest Atlantic
3 Ocean. *Botanica Marina* 49: 283-303
- 4 Mews, M., M. Zimmer, and D.E. Jelinski. 2006. Species-specific decomposition rates of beach-
5 cast wrack in Barkley Sound, British Columbia, Canada. *Marine Ecology Progress Series*
6 328: 155-164
- 7 Morris, J.T., P.V. Sundareshwar, C.T. Nietch, B. Kjerfve, and D.R. Cahoon. 2002. Responses of
8 coastal wetlands to rising sea level. *Ecology* 83: 2869-2877
- 9 Mudd, S.M. 2011. The life and death of salt marshes in response to anthropogenic disturbance of
10 sediment supply. *Geology* 39: 511-512
- 11 Murray, L.G., S.M. Mudge, A. Newton, and J.D. Icelly. 2006. The effects of benthic sediments
12 on dissolved nutrient concentrations and fluxes. *Biogeochemistry* 81: 159-178
- 13 Newton, C., and C.S. Thornber. 2013. Ecological impacts of macroalgal blooms on salt marsh
14 communities. *Estuaries and Coasts* 36: 365-376
- 15 Reed, D.J. 1989. Patterns of sediment deposition in subsiding coastal salt marshes, Terrebonne
16 Bay, Louisiana: the role of winter storms. *Estuaries* 12: 222-227
- 17 Reed, D.J., and D.R. Cahoon. 1992. The relationship between marsh surface topography,
18 hydroperiod, and growth of *Spartina alterniflora* in a deteriorating Louisiana salt marsh.
19 *Journal of Coastal Research* 8: 77-87
- 20 Richard, G.A. 1978. Seasonal and environmental variations in sediment accretion in a Long
21 Island salt marsh. *Estuaries* 1: 29-35

- 1 Roman, C.T., K.W. Able, M.A. Lazzari, and K.L. Heck. 1990. Primary productivity of
2 angiosperm and macroalgae dominated habitats in a New England salt marsh: a
3 comparative analysis. *Estuarine, Coastal and Shelf Science* 30: 35-45
- 4 Smith, S.M. 2009. Multi-decadal changes in salt marshes of Cape Cod, Massachussetts: a
5 photographic analysis of vegetation loss, species shifts, and geomorphic change.
6 *Northeastern Naturalist* 16: 183-208
- 7 Smith, S.M. 2014. Salt marsh vegetation at Cape Cod National Seashore: status and trends. In
8 *Natural Resources Technical Report, Cape Cod National Seashore. Wellfleet, MA.*
- 9 Spalding, M.D., S. Ruffo, C. Lacambra, I. Meliane, L. Zeitlin Hale, C.C. Shepard, and M.W.
10 Beck. 2013. The role of ecosystems in coastal protection: adapting to climate change and
11 coastal hazards. *Ocean and Coastal Management*. doi:10.1016/j.ocecoaman.2013.09.007.
- 12 Stumpf, R.P. 1983. The process of sedimentation on the surface of a salt marsh. *Estuarine,*
13 *Coastal and Shelf Science* 17: 495-508
- 14 Thompson, T.L., and E.P. Glenn. 1994. Plaster standards to measure water motion. *Limnology*
15 *and Oceanography* 39: 1768-1779
- 16 Thomsen, M.S., K.J. McGlathery, A. Schwarzschild, and B.R. Silliman. 2009. Distribution and
17 ecological role of the non-native macroalga *Gracilaria vermiculophylla* in Virginia salt
18 marshes. *Biological Invasions* 11: 2303-2316
- 19 Tyrrell, M.C., M. Dionne, and S.A. Eberhardt. 2012. Salt marsh furoid algae: overlooked
20 ecosystem engineers of north temperate salt marshes. *Estuaries and Coasts* 35: 754-762
- 21 Volkenborn, N., D.M. Robertson, and K. Reise. 2009. Sediment destabilizing and stabilizing bio-
22 engineers on tidal flats: cascading effects of experimental exclusion. *Helgoland Marine*
23 *Research* 63: 27-35

1 Voss, C.M., R.R. Christian, and J.T. Morris. 2013. Marsh macrophyte responses to inundation
2 anticipate impacts of sea-level rise and indicate ongoing drowning of North Carolina
3 marshes. *Marine Biology* 160: 181-194. doi: 10.1007/s00227-012-2076-5.

4 Wentworth, C.K. 1922. A Scale of Grade and Class Terms for Clastic Sediments. *The Journal of*
5 *Geology*. 30(5): 377-392.

6

1 **Figure Legends**

2 **Fig. 1** Map of locations in outer Cape Cod salt marshes where timed searches for marsh furoids
3 were conducted in April- May 2011; checks indicate presence of salt marsh furoids (6 sites), X's
4 indicate absence of marsh furoids (11 sites). The two sites at the north-western edge of Cape
5 Cod, Hatches Harbor and West End, were used for all manipulative experiments in this study

6
7 **Fig. 2** Thickness (in cm) of the marsh furoids in interior and edge plots at Hatches Harbor and
8 West End marshes prior to initiating the removal treatment. Marsh furoids are significantly
9 more abundant in edge vs. interior plots and more abundant at Hatches than at West End (Table
10 1). Data are means +/- 1 standard error

11

12 **Fig. 3** Sediment deposition in PVC pipes situated above and below marsh furoid layer, for
13 control and marsh furoid removal plots at: A. Hatches Harbor, B. West End. Data are means +/-
14 1 standard error

15

16 **Fig. 4** Sediment deposition on aluminum flashing traps placed in the field in May 2011, for
17 control and marsh furoid removal plots at: A. Hatches Harbor, B. West End. Data are means +/-
18 1 standard error

19

20 **Fig. 5** Erosion (negative values) or accretion (positive values) of marsh surface in marsh edge
21 control and furoid removal plots, as measured using sediment flags (in cm), at West End marsh.
22 Data are means +/- 1 standard error

23

1 **Fig. 6** Decomposition rates of *S. alterniflora* in litter bags during the summer of 2011, in marsh
2 control and removal plots, at: A. Hatches Harbor, B. West End. Data are means +/-1 standard
3 error
4
5

1 **Tables**

2 **Table 1** Three way fixed factor ANOVA analyzing effects of site, location (edge/interior) and
 3 treatment (pre-furoid removal) on marsh furoid abundance

Source	df	SS	F	P
Site	1	24.180	14.540	0.0006
Edge/Interior	1	40.602	24.415	<0.0001*
Site * Edge/Interior	1	1.640	0.986	0.328
Control/Removal	1	3.660	2.201	0.148
Site * Control/Removal	1	1.26	0.758	0.390
Edge/Interior * Control/Removal	1	3.54	2.129	0.154
Site * Edge/Interior *	1	7.140	4.294	0.046*
Control/Removal				
Error	36	68.817		

4

5 **Table 2** Three way fixed factor ANOVA for sediment deposition in PVC pipes above and below
 6 the marsh furoid layer

Source	df	SS	F	P
Site	1	7645.225	20.671	<0.0001*
PVC height	1	11923.209	32.237	<0.0001*
Site * PVC height	1	4999.696	13.518	0.0009*
Control/Removal	1	2537.649	6.861	0.0134*
Site * Control/Removal	1	1806.336	4.884	0.0344*
PVC height * Control/Removal	1	2079.361	5.622	0.0239*
Site * PVC height * Control/Removal	1	1442.401	3.900	0.0570
Error	32	44,269.384		

7

8

1 **Table 3** Three way repeated measures ANOVA assessing differences in sediment mass on
 2 aluminum traps

3 Between subjects (denominator df = 24)

Source	df	F	P
Site	1	8.576	0.0074*
Control/Removal	1	0.192	0.6654
Site * Control/Removal	1	1.966	0.1737
Edge/Interior	1	1.151	0.2939
Site * Edge/Interior	1	0.459	0.5045
Control/Removal * Edge/Interior	1	0.051	0.8230
Site * Control/Removal * Edge/Interior	1	2.493	0.1274

4

5 Within Subjects (denominator df = 23)

Source	df	F	P
Time	2	0.080	0.9238
Time * Site	2	0.895	0.4224
Time * Control/Removal	2	0.256	0.7759
Time * Site * Control/Removal	2	1.683	0.2079
Time * Edge/Interior	2	0.002	0.9979
Time * Site * Edge/Interior	2	0.851	0.4400
Time * Control/Removal * Edge/Interior	2	1.821	0.1845
Time * Site * Control/Removal * Edge/Interior	2	0.286	0.7543

6

7

1 **Table 4a** Three way fixed factor ANOVA analyzing differences in sediment grain size (percent
 2 fines) between sites, control/removal, and edge/interior plots

Source	df	SS	F	P
Site	1	0.260	127.387	<0.0001*
Control/Removal	1	0.002	0.999	0.325
Site * Control/Removal	1	0.0001	0.058	0.811
Edge/Interior	1	0.023	11.137	0.002*
Site * Edge/Interior	1	0.021	10.272	0.003*
Control/Removal * Edge/Interior	1	0.003	1.465	0.235
Site * Control/Removal * Edge/Interior	1	0.001	0.703	0.408
Error	32	0.065		

3

4 **Table 4b** Three way fixed factor ANOVA assessing differences in percent organic matter
 5 between sites, control/removal, and edge/interior plots

Source	df	SS	F	P
Site	1	553.879	63.989	<0.0001*
Control/Removal	1	22.505	2.600	0.117
Site * Control/Removal	1	4.945	0.271	0.455
Edge/Interior	1	398.859	46.080	<0.0001*
Site * Edge/Interior	1	185.017	21.375	<0.0001*
Control/Removal * Edge/Interior	1	1.840	0.213	0.650
Site * Control/Removal * Edge/Interior	1	0.091	0.010	0.919
Error	32	276.987		

6

7

1 **Table 5** ANCOVA examining the effect of distance from marsh edge as a covariate for organic
 2 content within the interior plots

Source	df	SS	F	P
Site	1	689.569	77.849	<0.0001*
Control/Removal	1	18.606	2.100	0.168
Site*Control/Removal	1	1.848	0.209	0.654
Distance from edge (interior plots only)	1	96.507	10.895	0.005*

3
 4
 5

6 **Table 6** Three way repeated measures ANOVA for sediment erosion/accumulation on the marsh
 7 surface, as measured using pin flags. Between subjects (denominator df = 32)

Source	df	F	P
Site	1	1.363	0.252
Control/Removal	1	5.470	0.026*
Site * Control/Removal	1	3.220	0.082
Edge/Interior	1	0.283	0.598
Site Name* Edge/Interior	1	0.174	0.680
Edge/Interior * Control/Removal	1	2.025	0.164
Site * Edge/Interior * Control/Removal	1	1.363	0.252

8
 9 Within subjects (denominator df = 31)

Source	df	F	P
Time	2	9.478	0.0006*
Time * Site	2	2.230	0.124
Time * Control/Removal	2	0.060	0.942
Time * Site * Control/Removal	2	1.316	0.283
Time * Edge/Interior	2	1.435	0.254
Time * Site* Edge/Interior	2	4.485	0.020*
Time * Control/Removal * Edge/Interior	2	0.378	0.688
Time * Site * Control/Removal * Edge/Interior	2	0.033	0.722

10
 11

1 **Table 7a** Three way fixed factor ANOVA of relative flow (measured using dissolution of Plaster
 2 of Paris) for June 2011 deployment

Source	df	SS	F	P
Site	1	14.052	0.645	0.428
Edge/Interior	1	6.259	0.287	0.595
Site * Edge/Interior	1	7.134	0.328	0.571
Control/Removal	1	40.523	1.860	0.182
Site * Control/Removal	1	0.046	0.002	0.964
Edge/Interior * Control/Removal	1	2.259	0.104	0.750
Site * Edge/Interior * Control/ Removal	1	16.933	0.777	0.384
Error	32	697.069		

3

4 **Table 7b** Three way fixed factor ANOVA of relative flow (measured using dissolution of Plaster
 5 of Paris) for August 2011 deployment

Source	df	SS	F	P
Site	1	1866.558	68.630	<0.0001*
Edge/Interior	1	13.624	0.501	0.484
Site * Edge/Interior	1	3.699	0.136	0.715
Control/ Removal	1	144.832	5.325	0.028*
Site * Control/ Removal	1	11.087	0.408	0.528
Edge/Interior * Control/ Removal	1	12.881	0.474	0.496
Site * Edge/Interior * Control/ Removal	1	3.108	0.114	0.738
Error	32	870.318		

6