12-3-2014

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

J. A. Burkhardt
University of Rhode Island

M. Congretel
University of Rhode Island

Citation/Publisher Attribution

Tyrrell, M.C., C.S. Thornber, J.A. Burkhardt, and M. Congretel. "The Influence of Salt March Fucoid 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

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

M.C. Tyrrell[1]*, C.S. Thornber[2], J.A. Burkhardt[2], M. Congretel[2,3]

[1] Cape Cod National Seashore, National Park Service, 99 Marconi Site Road, Wellfleet, MA 02667 USA

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

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

*Author for correspondence (email: Megan_Tyrrell@nps.gov; phone: 508.487.3262 fax: 508.487.7153)

for submission to Estuaries and Coasts

Abstract

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

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

Introduction

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

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

Marsh fucoids, or ecads, are unattached perennial brown macroalgae that have reduced air bladders, profuse lateral branching, and occur in a thick, often contiguous layer on the salt marsh sediment surface (Chock and Mathieson 1976; Mathieson et al. 2006). Initial colonization of a salt marsh by fucoids occurs via algal fragments (Mathieson et al. 2006) and vegetative growth results in the algae becoming entangled among the vascular plants and often partially buried in the sediments. Based on their high biomass, and concentration in the lowest portions of the marsh (Tyrrell et al. 2012), we hypothesized that they may have important roles in sediment accumulation and stabilization at the most dynamic portion of the marsh. Furthermore, we suspected that this potential to enhance sediment deposition and elevation gain may decline with increasing distance from the lowest portion of marshes.

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

We present results from field and lab experiments where the effect of marsh fucoids on *S. alterniflora* survival, growth and decomposition rates were assessed. We also manipulated marsh fucoids in large plots of two New England back barrier marshes and assessed their influence on sediment deposition, accretion/erosion rates, percent fines, total suspended solids and relative water flow. Furthermore, we evaluated contributions of marsh fucoids to sediment organic matter content, which is an important factor in the nutrient poor, sandy sediments that characterize the lower portion of back-barrier marshes where marsh fucoids reach their highest abundance (Tyrrell et al. 2012) and where *S. alterniflora's* productivity and abundance is most critical for marsh growth and maintenance (Gedan et al. 2011). The interaction between marsh fucoids, sedimentation dynamics and pioneer species such as *S. alterniflora* is likely highly relevant for clarifying the ecogeomorphic feedbacks (*sensu* Kirwan et al. 2010) that contribute to marsh elevation gain and resilience. Specifically, the answer regarding whether marsh fucoids are inhibitory or facilitative of *S. alterniflora's* growth and survival will likely depend on *S. alterniflora*'s life history stage and the physical conditions (e.g. sediment type, drainage, inundation period) of the study site. We discuss our results in terms of ecosystem functioning and resilience in the face of a changing climate.

Methods

Study system

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

Regional distribution and movement tracking

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

To determine whether marsh fucoids were relatively stationary in their natural setting, we used plastic flagging to mark 10 patches (~2 x 2 m) each of marsh fucoids in West End and Nauset marshes. Using a handheld GPS (Garmin 76CSx), we relocated the flagging from 2 weeks to 3 months later.

Marsh fucoid removal experiment

In May 2011, we set up a marsh fucoid removal experiment in two Cape Cod, MA back barrier salt marsh sites (West End and Hatches Harbor). Edge plots were located approximately 1 meter landward of the lower edge of the *S. alterniflora* zone and each were 2 m x 2 m. A total of 10 edge plots were marked at each site. We also created a set of five paired 2 m x 2 m interior plots to examine the effect of marsh fucoids with increasing distance from the lowest extent of marsh vegetation. These plots were spaced 5 m apart, moving landward (upslope) from the marsh edge. To obtain an initial biomass estimate of marsh fucoids, we measured the canopy thickness (distance from the sediment surface to the top of the marsh fucoid layer) at five random locations within each plot. We used a previously established relationship to determine biomass from fucoid canopy thickness (r^2=0.86, p<0.0001; Tyrrell unpubl. data). We cut the marsh fucoids along the perimeter of each plot to standardize disturbance at the plot edges and then randomly selected half of the edge plots and half of the interior plots and removed all marsh fucoids from them (henceforth called removal plots). We used a two way ANOVA to analyze the effect of site and location (edge/interior) on marsh fucoid abundance. For the interior plots only, we examined the effect of distance from the marsh edge as a covariate on marsh fucoid abundance; in nearly all cases, this distance was not significant. Mid-way through the experiments, we used real time kinematic GPS to measure the elevations of each plot.

Sediment deposition above and below marsh fucoid canopy

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

Sediment deposition on traps

To assess sediment deposition rates directly on the marsh surface, in May 2011 we placed 10 cm x 10 cm pieces of aluminum flashing on the sediment surface and secured them using two lawn staples, on all plots at both sites. Traps were placed directly on the sediment surface, which entailed parting the marsh fucoid canopy to expose the marsh surface in control plots. Three traps were placed in each plot, and one trap per plot was removed every six weeks. Upon retrieval, each trap was carefully removed and individually placed in a small plastic bag for transport to the lab. Traps in bags were dried at 60° C for >24 hours. We determined sediment dry mass by weighing the sediment trap within its bag, disposing of the sediment, and reweighing the trap and bag.

Physical characteristics of sediment surface

We used a putty knife to scrape the top 1.5 cm (~20 cm^3) of sediment for analysis of grain size and organic content and placed the samples into individually sealed bags. We took a total of four scrapings in each plot; three of these samples were used for analysis of organic content (average value per plot was used for statistical analyses), and one was used for particle size analysis. We obtained the sediment scraping samples at the end of September from all experimental plots. We dried the samples in their bags at 60° C for >24 hours. The distribution of sediment grain size was measured for each sample, using approximately 20 g of dried sediment that was poured into a standard sieve set (>2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.106 mm and 0.053 mm) and placed on a shaker for five minutes. The weight of each fraction was recorded and used to calculate the percent of the total sediment sample that fell within each size category. We grouped the three smallest sieves into a "fines" category and, data from the three largest sieves were combined to make a "sand" category (Wentworth 1922). Samples for organic content were burned for four hours at 550° C in a muffle oven, placed in a desiccator and immediately weighed upon removal from the desiccator.

Relative changes in marsh surface elevation

To assess whether the presence of a thick layer of marsh fucoids affected changes in marsh surface elevation, we haphazardly placed five pin flags in each experimental plot. We adjusted the initial height of each flag so that the top of the stake was exactly 20 cm above the sediment surface. Each marking flag was numbered, and the distance between the top of the stake and the sediment surface was measured to the nearest mm after 6, 12 and 18 weeks. Surface accretion was indicated by a decrease in the average distance between the top of the stake and the marsh surface.

Total suspended solids concentration

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

Calcium sulfate dissolution

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

Decomposition of S. alterniflora

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

To create a blotted dry vs. oven dried conversion for *S. alterniflora*, we collected 47 leaves, and treated them exactly in the same manner as described above (rinse, blot, weigh). Each leaf was then dried at 60° C for 48 hours and re-weighed. The resulting relationship (oven dried=0.1817*blotted dry + 0.2105, R^2= 0.8725) was used to convert the initial blotted dry values to equivalent oven dried values. We used these data to determine the *k* decomposition constant (rate of change in mass over time) from the slope of the regression for each replicate plot. of *S. alterniflora* in each plot (Mews et al. 2006; Conover 2011).

Effect on S. alterniflora seedlings under lab conditions

We obtained seedlings on June 15 and immediately planted them in twenty 18.9 L buckets that were ¾ full of sand. The seedlings in the buckets were watered with fresh water every 3 days and also exposed to natural rainfall. A small hole was made in the side of each bucket at the level of the sediment surface to allow excess water to drain. On July 15, when seedlings were approximately 30 cm high (30.4 cm, +/- 1.5 SE), we added 850 grams of marsh fucoids to 10 randomly selected buckets and started watering with salt water to approximate field conditions. We temporarily covered the small hole with duct tape and allowed the saltwater to remain for a few minutes before removing the tape and allowing the water to drain out. Saltwater watering took place 3 times a week.

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

Effect on S. alterniflora seedlings under field conditions

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

Statistical analysis

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

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

Results

Regional distribution

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

Marsh fucoid removal experiment

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

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

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

Sediment deposition above and below marsh fucoid canopy

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

Sediment deposition on traps

Sediment mass on aluminum flashing was twice as high at West End than at Hatches Harbor (Fig. 4; $F_{1,24} = 8.58$, $p = 0.007$). However, we did not find significant differences in sediment mass between any other factors or interactions, including control/removal, edge/interior plots, and length of time in field (Table 3).

Physical characteristics of sediment surface

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

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

Relative changes in marsh surface elevation

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

Total suspended solids concentration

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

<u>*Calcium sulfate dissolution*</u>

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

<u>*Decomposition of S. alterniflora*</u>

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

<u>*Effect on S. alterniflora seedlings under lab conditions*</u>

All *S. alterniflora* characteristics did not differ between treatments at the start of the experiment and all seedlings survived the duration of the laboratory experiment. While the addition of marsh fucoids had a positive effect on number of live *S. alterniflora* leaves after three months (6.90 <u>+/-</u> 0.43 marsh fucoid addition vs. 5.40 <u>+/-</u> 0.22 control; $t_{18} = 3.08$, $p = 0.006$); marsh fucoids did not have a significant effect on any other *S. alterniflora* characteristics (number of dead leaves, aboveground biomass, belowground biomass, growth rate). The presence of marsh fucoids significantly enhanced sediment organic content (1.22 marsh fucoid addition, vs. 0.78% controls; $t_{18} = 4.33$, $p < 0.001$).

Effect on S. alterniflora seedlings under field conditions

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

Discussion

The impact of marsh fucoids on sediment dynamics can be substantial, as the thick layer of algae significantly promotes sediment deposition and accretion, dampens water flow at the sediment interface, and is associated with higher concentrations of particulates in the water column above the substrate. Suspended sediment concentrations are an important factor in marsh surface accretion (Reed 1989; Kirwan et al. 2010; Mudd 2011), and we demonstrated that marsh fucoids are positively related to suspended solids concentrations, relative marsh surface elevation, and sediment deposition rates when horizontal advection was eliminated (see the PVC pipes experiment). Considered simultaneously, the several methods we used to assess marsh fucoid effects on sediment dynamics indicate that marsh fucoids have a strong, positive influence on surface accretion and deposition rates. Nevertheless, *S. alterniflora*'s accelerated decomposition rate under marsh fucoids may lead to shallow subsidence and counteract some of the gains in surface elevation and sediment deposition. High resolution marsh surface elevation monitoring (e.g. repeated surveys with ground-based equipment such as RTK, total station or LIDAR) would be needed to assess whether marsh fucoids' enhancement of sediment deposition, relative surface elevation and surface accretion translate to a net gain in marsh surface elevations.

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

The leading edge of back-barrier marshes are dynamic and frequently overwashed, eroded or otherwise influenced by storm activity (Donnelly et al. 2001) and marshes with these characteristics can be less resilient to sea level rise (D'Alapos et al. 2011). High inundation, low nutrient, sandy, dynamic conditions are stressful for marsh plants (Huckle et al. 2000; Kirwan and Guntenspergen 2012). Very sandy sediments do not bind nutrients as well as sediments with higher proportions of silt or other small particle sizes (Murray et al. 2006) and nutrients and organic matter that might be locally contributed due to presence of marsh fucoids will dissipate quickly in well drained, coarse sediments such as our field study sites. *Spartina alterniflora*'s growth in sandy sediments may be inhibited by low nutrient concentrations (Broome et al. 1975), therefore marsh fucoids can be beneficial to *S. alterniflora* in sandy sediments because they can amend low organic matter, nutrient poor sediments. Decomposition rates of *S. alterniflora* were significantly faster when marsh fucoids were present, demonstrating that marsh fucoids, like other macroalgae in marshes, can accelerate nutrient cycling rates (Boyer and Fong 2005; Thomsen et al. 2009). Nevertheless, under stressful, highly dynamic field conditions, survival of transplanted *S. alterniflora* seedlings to a field site where marsh fucoids are naturally absent led to diminished survival for those seedlings with marsh fucoids. In summary, the influence of marsh fucoids on *S. alterniflora* is not uniformly positive, especially when *S. alterniflora* is acting as a pioneer species in an unvegetated, highly dynamic environment.

Although we found a significant positive effect of marsh fucoids on a variety of sediment related processes, there were significant differences in several processes between our two sites. Marsh fucoid abundance was significantly higher at Hatches Harbor, and Hatches Harbor sediments had two times higher organic content, greater percent fines, lower dissolution rates of calcium sulfate, and less sediment deposited on the aluminum traps than West End. However, the elevation of the edge plots at Hatches Harbor was approximately 75 cm higher than the corresponding plots at the West End site, and the coefficient of variation for elevation was much lower in Hatches Harbor- meaning the Hatches Harbor site is higher but flat. Furthermore, the interior plots at West End all had slightly higher elevations with distance from the marsh edge, while at Hatches Harbor, the interior plots were at the same elevation (and inundation regime) as the marsh edge plots. Thus, while fucoids likely contributed to sediment processes at this site, the higher elevation and lower inundation period of Hatches Harbor may have also contributed to the significant site effect for relative flow and sediment deposition rates. While physical properties and processes will differ across marshes, we found only one significant site by treatment interaction term, for sediment deposition in PVC pipes (Table 2), indicating that, except in this case, the effect of marsh fucoids was consistent regardless of site to site variation.

While salt marshes have typically been viewed as resilient, their abilities to withstand increasing stressors may be limited (e.g., see review by Gedan et al. 2011). We have demonstrated the vital role of marsh fucoids as contributing to gains in marsh surface relative elevation, surface sediment deposition, and surface accretion; thus, their importance in marsh ecosystem management is apparent. Large-scale removal of salt marsh vegetation can change patterns of water flow and alter sediment accretion rates (e.g. Voss et al. 2013). Some factors that are important in influencing marsh elevation gain and stability, including pasturing livestock (Elschot et al. 2013), organic matter content (Chmura and Hung 2004) and eutrophication (Deegan et al. 2012), are potentially within local to regional level management control. Other factors that strongly influence marsh accretion and resilience, including tidal range/inundation (Morris et al. 2002; D'Alapos et al. 2011), supply of mineral sediments (e.g., Fagherazzi 2013), or elevated CO_2 concentrations (Langley et al. 2009), operate on geographic scales that are too broad for regional level management but nevertheless are also important considerations for enhancing the sea barrier function of marshes. The attenuation of wave energy by coastal wetlands such as salt marshes and mangroves is well documented (e.g., Spalding et al. 2013) and the economic value of the protective functions of vegetated coastal wetlands from extreme storm damage such as hurricanes is substantial (Costanza et al. 2008). Vegetated wetlands are economically and ecologically critical to coastal resilience to climate change damage and impacts (Beatley 2009; Spalding et al. 2013) and the most salient factors contributing to marsh elevation gain are thus of utmost importance for effective management and mitigation strategies.

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

Acknowledgements

Funding for this project was provided by the Friends of Cape Cod National Seashore Nickerson Fellowship and the NPS Atlantic Research and Learning Center. This work is dedicated to the memory of Dr. Michele Dionne, who inspired many colleagues and students to pursue their natural resource conservation passions. We thank Jane Barnes, Maria Downs, Megan Holcomb, Amber Martinez, Kelly Medeiros, and Jessica Stern for their assistance in the lab and/or field. Additional support was provided to C. Thornber by the University of Rhode Island.

References

Beatley, T. 2009. *Planning for coastal resilience: best practices for calamitous times*: Island Press.

Borsje, B.W., B.K. van Wesenbeeck, F. Dekker, P. Paalvast, T.J. Bouma, M.M. van Katwijk, and M.B. de Vries. 2011. How ecological engineering can serve in coastal protection. Ecological Engineering 37: 113-122. doi:10.1016/j.ecoleng.2010.11.027.

Boyer, K.E., and P. Fong. 2005. Macroalgal-mediated transfers of water column nitrogen to intertidal sediments and salt marsh plants. Journal of Experimental Marine Biology and Ecology 321: 59-69

Brinkhuis, B.H. 1976. The ecology of temperature salt marsh fucoids. Part 1: occurrence and distribution of *Ascophyllum nodosum* ecads. Marine Biology 34: 325-338

Broome, S.W., W.W. Woodhouse, and E.D. Seneca. 1975. The relationship of mineral nutrients to growth of *Spartina alterniflora* in Northern Carolina. II: The effects of N, P, and Fe fertilizers. Soil Science Society of America Journal 39: 301-307

Chapman, A.S., and A.R.O. Chapman. 1999. Effects of cordgrass on saltmarsh fucoids: Reduced desiccation and light availability, but no changes in biomass. Journal of Experimental Marine Biology and Ecology 238: 69-91

Chmura, G.L., and G.A. Hung. 2004. Controls on salt marsh accretion: a test in salt marshes of Eastern Canada. Estuaries 27: 70-81

Chock, J.S., and A. Mathieson. 1976. Ecological studies of the salt marsh ecad *scorpioides* (Hornemann) Hauck of *Ascophyllum nodosum* (L.) Le Jolis. Journal of Experimental Marine Biology and Ecology 23: 171-190

Chock, J.S., and A. Mathieson. 1983. Variations of New England estuarine seaweed biomass. Botanica Marina 26: 87-97

Conover, J. 2011. Variability in biomass decay rates and nutrient loss in bloom-forming macroalgal species. Open Access Masters' Theses. Paper 108, University of Rhode Island Kingston, RI.

Costanza, R., O. Pérez-Maqueo, M.L. Martinez, P. Sutton, S.J. Anderson, and K. Mulder. 2008. The value of coastal wetlands for hurricane protection. Ambio 37: 241-248

Craft, C., J. Clough, J. Ehman, S. Joye, R. Park, S.C. Pennings, H. Guo, and M. Machmuller. 2009. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. Frontiers in Ecology and the Environment 7: 73-78. doi:10.1890/070219.

D'Alapos, A., S.M. Mudd, and L. Carniello. 2011. Dynamic response of marshes to perturbations in suspended sediment concentrations and rates of relative sea level rise. Journal of Geophysical Research 116: F04020. doi:10.1029/2011JF002093.

Deegan, L.A., D.S. Johnson, R.S. Warren, B.J. Peterson, J.W. Fleeger, S. Fagherazzi, and W.M. Wollheim. 2012. Coastal eutrophication as a driver of salt marsh loss. Nature 490: 388-392

Donnelly, J.P., S.S. Bryant, J. Butler, J. Dowling, L. Fan, N. Hausman, P. Newby, B. Shuman, J. Stern, K. Westover, and T.I. Webb. 2001. 700 year sedimentary record of intense hurricane landfalls in southern New England. Geological Society of America Bulletin 113: 714-727

Elschot, K., T.J. Bouma, S. Temmerman, and J.P. Baker. 2013. Effects of long-term grazing on sediment deposition and salt marsh accretion rates. Estuarine, Coastal and Shelf Science 133: 109-115

Fagherazzi, S. 2013. The ephemeral life of a salt marsh. Geology 41: 943-944

Gedan, K.B., A.H. Altieri, and M.D. Bertness. 2011. Uncertain future of New England salt marshes. Marine Ecology Progress Series 434: 229-237

Gerard, V.A. 1999. Positive interactions between cordgrass, *Spartina alterniflora*, and the brown alga, *Ascophyllum nodosum* ecad scorpioides in a mid-Atlantic coast salt marsh. Journal of Experimental Marine Biology and Ecology 239: 157-164

Gleason, M.L., D.A. Elmer, N.C. Pien, and J.S. Fisher. 1979. Effects of stem density upon sediment retention by salt marsh cordgrass, *Spartina alterniflora* Loisel. Estuaries 2: 271-273

Holm, S. 1979. A simple sequential rejective method procedure. Scandinavian Journal of Statistics 6: 65-70

Huckle, J.M., J.A. Potter, and R.H. Marrs. 2000. Influence of environmental factors on the grwoth and interactions between salt marsh plants: effects of salinity, sediment, and waterlogging. Journal of Ecology 88: 492-505

Kirwan, M.L., and G.R. Guntenspergen. 2012. Feedbacks between inundation, root production, and shoot growth in a rapidly submerging brackish marsh. Journal of Ecology 100: 764-770. doi:10.1111/j.1365-2745.2012.01957.x.

Kirwan, M.L., G.R. Guntenspergen, A. D'Alapos, J.T. Morris, S.M. Mudd, and S. Temmerman. 2010. Limits on the adaptability of coastal marshes to rising sea level. Geophysical Research Letters 37: L23401. doi:10.1029/2010GL045489.

Langley, J.A., K.L. McKee, D.R. Cahoon, J.A. Cherry, and J.P. Megonigal. 2009. Elevated CO2 stimulates marsh elevation gain, counterbalancing sea level rise. Proceedings of the National Academy of Sciences, USA. doi:10.1073/pnas.0807695106.

Mathieson, A., C.J. Dawes, A.L. Wallace, and A.S. Klein. 2006. Distribution, morphology, and genetic affinities of dwarf embedded *Fucus* populations from the Northwest Atlantic Ocean. Botanica Marina 49: 283-303

Mews, M., M. Zimmer, and D.E. Jelinski. 2006. Species-specific decomposition rates of beach-cast wrack in Barkley Sound, British Columbia, Canada. Marine Ecology Progress Series 328: 155-164

Morris, J.T., P.V. Sundareshwar, C.T. Nietch, B. Kjerfve, and D.R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. Ecology 83: 2869-2877

Mudd, S.M. 2011. The life and death of salt marshes in response to anthropogenic disturbance of sediment supply. Geology 39: 511-512

Murray, L.G., S.M. Mudge, A. Newton, and J.D. Icely. 2006. The effects of benthic sediments on dissolved nutrient concentrations and fluxes. Biogeochemistry 81: 159-178

Newton, C., and C.S. Thornber. 2013. Ecological impacts of macroalgal blooms on salt marsh communities. Estuaries and Coasts 36: 365-376

Reed, D.J. 1989. Patterns of sediment deposition in subsiding coastal salt marshes, Terrebonee Bay, Louisiana: the role of winter storms. Estuaries 12: 222-227

Reed, D.J., and D.R. Cahoon. 1992. The relationship between marsh surface topography, hydroperiod, and growth of *Spartina alterniflora* in a deteriorating Louisiana salt marsh. Journal of Coastal Research 8: 77-87

Richard, G.A. 1978. Seasonal and environmental variations in sediment accretion in a Long Island salt marsh. Estuaries 1: 29-35

Roman, C.T., K.W. Able, M.A. Lazzari, and K.L. Heck. 1990. Primary productivity of angiosperm and macroalgae dominated habitats in a New England salt marsh: a comparative analysis. Estuarine, Coastal and Shelf Science 30: 35-45

Smith, S.M. 2009. Multi-decadal changes in salt marshes of Cape Cod, Massachussetts: a photographic analysis of vegetation loss, species shifts, and geomorphic change. Northeastern Naturalist 16: 183-208

Smith, S.M. 2014. Salt marsh vegetation at Cape Cod National Seashore: status and trends. In Natural Resources Technical Report, Cape Cod National Seashore. Wellfleet, MA.

Spalding, M.D., S. Ruffo, C. Lacambra, I. Meliane, L. Zeitlin Hale, C.C. Shepard, and M.W. Beck. 2013. The role of ecosystems in coastal protection: adapting to climate change and coastal hazards. Ocean and Coastal Management. doi:10.1016/jocecoaman.2013.09.007.

Stumpf, R.P. 1983. The process of sedimentation on the surface of a salt marsh. Estuarine, Coastal and Shelf Science 17: 495-508

Thompson, T.L., and E.P. Glenn. 1994. Plaster standards to measure water motion. Limnology and Oceanography 39: 1768-1779

Thomsen, M.S., K.J. McGlathery, A. Schwarzschild, and B.R. Silliman. 2009. Distribution and ecological role of the non-native macroalga *Gracilaria vermiculophylla* in Virginia salt marshes. Biological Invasions 11: 2303-2316

Tyrrell, M.C., M. Dionne, and S.A. Eberhardt. 2012. Salt marsh fucoid algae: overlooked ecosystem engineers of north temperate salt marshes. Estuaries and Coasts 35: 754-762

Volkenborn, N., D.M. Robertson, and K. Reise. 2009. Sediment destabilizing and stabilizing bio-engineers on tidal flats: cascading effects of experimental exclusion. Helgoland Marine Research 63: 27-35

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

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

Figure Legends

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

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

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

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

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

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

Tables

Table 1 Three way fixed factor ANOVA analyzing effects of site, location (edge/interior) and treatment (pre-fucoid removal) on marsh fucoid 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 * Control/Removal	1	7.140	4.294	0.046*
Error	36	68.817		

Table 2 Three way fixed factor ANOVA for sediment deposition in PVC pipes above and below the marsh fucoid 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		

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

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

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

Table 4a Three way fixed factor ANOVA analyzing differences in sediment grain size (percent 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		

Table 4b Three way fixed factor ANOVA assessing differences in percent organic matter 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		

Table 5 ANCOVA examining the effect of distance from marsh edge as a covariate for organic 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*

Table 6 Three way repeated measures ANOVA for sediment erosion/accumulation on the marsh 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

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

Table 7a Three way fixed factor ANOVA of relative flow (measured using dissolution of Plaster 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		

Table 7b Three way fixed factor ANOVA of relative flow (measured using dissolution of Plaster 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		