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RESEARCH ARTICLE

Post-storm sediment burial and herbivory of *Vallisneria americana* in the Hudson River estuary: mechanisms of loss and implications for restoration

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This article investigates the mechanics of loss of Hudson River *Vallisneria americana* after the high volume storms at the end of the 2011 growing season, when two severe weather events—Tropical Storm Irene and the remnants of Tropical Storm Lee—struck the Hudson River watershed. In 2012, the distribution of the most common species of submerged aquatic vegetation (SAV), *Vallisneria americana* (wild celery, water celery, or tape grass), in the Hudson River estuary declined by more than 90%, with no appreciable recovery in 2013 and 2014. Because of its important habitat value for aquatic life and for increasing dissolved oxygen, managers and scientists have begun discussing the reasons for the loss, as well as how to assist its recovery through assisted restoration efforts in the estuary. Supported by in situ and in vitro experiments, the article posits the hypothesis that sediment, washed into the river by the storm, buried overwintering tubers of the plant, thus reducing sprouting success. Sprouting was as low as 50% with sediment depth between 2 and 5 cm; sprouting did not occur with sediment depth greater than 10 cm. Field experiments found no support for the hypothesis that herbivory inhibited regrowth of the plant after the storm events. These results suggest that future assisted restoration of *Vallisneria americana* and SAV in general may require attention to system-specific factors.

Key words: estuarine restoration, grazing, Hurricane Irene, plant, submerged aquatic vegetation, wild celery

Implications for Practice

- Relatively small amounts of sediment from storms may cause loss and hamper recovery of *Vallisneria americana*, an important species of submerged aquatic vegetation, suggesting a need for assessing habitat prior to assisted restoration.
- While research has shown that restoration and recovery of *Vallisneria americana* may be impacted by herbivory, this study indicates that protection may not be required in all locations. Site-specific research on herbivory is justified as protection measures would affect cost of restoration.
- Cost of direct restoration of submerged aquatic vegetation should be weighed against indirect methods that decrease sediment input, including agricultural best management practices and riparian restoration.

Introduction

Submerged aquatic vegetation (SAV) provides important ecological services to aquatic ecosystems (Miller 2013). SAV beds increase dissolved oxygen (DO) in rivers (Findlay et al. 2006) and create habitat for fishes (Rozas & Minello 2006), and invertebrates (Strayer & Smith 2001). Not only does SAV provide food, through primary productivity, and the increased density of invertebrates available to fish (Schmidt & Kiviat 1988) and other aquatic life (Heck & Thoman 1984), it is also an indicator of ecosystem health (Findlay et al. 2006) and can control nutrient fluxes between the benthic zone and the water column (Wigand et al. 2002).

Many aquatic ecosystems have experienced large-scale loss of SAV and seagrasses in the last century (Orth et al 2006; Waycott et al. 2009), attributed to diverse causes including extreme weather events such as hurricanes (Rybicki et al. 2001), drought (Harwell & Havens 2003), disease (Short & Wyllie-Echeverria 1996), habitat destruction (Nieder et al. 2004), nutrient loading (Wigand et al. 2000), invasive species competition (Nieder et al. 2004), and herbivory by aquatic wildlife (Crivelli 1983; Hauxwell et al. 2004; Moore et al. 2010). Even when the direct loss of SAV is attributed to a single disturbance event, the lack of regrowth may still be due to other, potentially unrelated

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ecosystem changes (Rybicki et al. 2001). SAV loss translates into loss of fish and other aquatic life, leading to economic loss for fisheries and tourism (Kahn & Kemp 1985).

Vallisneria americana (wild celery, water celery, or tape grass) is a globally common and important rooted dioecious freshwater SAV that grows in thick beds with tape-like leaves. It reproduces sexually through type III pollination and spreads by its capsule-like fruit, containing hundreds of seeds. It also spreads asexually through stolons growing off the main plant, and for the northern ecotype (including the Hudson River estuary (HRE) population), by producing overwintering tubers (McFarland & Shafer 2008). The spread and growth of *V. americana* is influenced by light conditions, sediment composition, flow, competition, climate, salinity, and other water quality parameters (Jarvis & Moore 2008; McFarland & Shafer 2008).

The HRE stretches 240 km from the Federal Dam at Troy, located below the confluence of the upper Hudson and Mohawk rivers, to New York Harbor at New York City, with flow in both directions due to semidiurnal tides of 0.8–1.4 m throughout the system (Fig. 1). *V. americana* comprised most of the SAV community in the HRE (Limburg et al. 1986; Findlay et al. 2006) with all SAV covering 6% of the total estuary and 18% of shallows (<3 m) in the mid-1990s (Nieder et al. 2004). *V. americana* declined from 18 km^2 in the late 1990s to 12 km^2 in the early 2000s in the HRE (Findlay et al. 2014). SAV has been monitored in the river by volunteers every year since 2003, and whole-system inventories based on aerial photography were conducted in 1995–1997, 2002, 2007, and 2014 (Nieder et al. 2004; Findlay et al. 2014; Strayer et al. 2014).

In late August to early September of 2011, precipitation from two major storm events, Tropical Storm Irene (10–45 cm) and the remnants of Tropical Storm Lee (8–20 cm), caused a 70-year high flow event of water entering the estuary at the Federal Dam at Troy, peaking at 5,100 m^3/s, with flows from the major tributaries of Esopus and Rondout Creek reaching 80-year high flow events (Orton et al. 2012). The precipitation and increased discharge introduced 2.7 million metric tons (MT) of sediment into the river, about five times the average annual amount, with only 1 MT observed passing the hydrographic monitoring station at the approximate midpoint of the estuary in the next month (Ralston et al. 2013). Sediment increase led to a 10-fold increase in turbidity (Fig. S1, Supporting Information) as well as an increase in pH of approximately 0.4 units directly after Irene and Lee (HRECOS 2015), falling to 2012 levels after a month. There was also a temporary increase in DO of approximately 2 mg/L and a decrease in water temperature of approximately 5°C after the storm events with levels returning to 2012 levels after 2–4 weeks (HRECOS 2015). The impact of these two storms was widespread along the Eastern Seaboard: in Chesapeake Bay, resuspension and deposition of sediment by Irene and Lee led to more than 4 cm of new sediment in parts of the upper Chesapeake Bay estuary (Palinkas et al. 2014) with a maximum of 10 cm (Cheng et al. 2013). The nearby Connecticut River also experienced similar sediment deposition from Irene and Lee (Yellen et al. 2014). Monitoring sites previously known to have SAV revealed a 90% decrease of *V. americana* the following year (Strayer et al. 2014), with little regrowth for 2013–2014.

Due to its importance to the HRE, the potential assisted restoration of *V. Americana* through planting or seeding has been actively discussed by managers and researchers (Miller 2013). Assisted restoration of SAV has been conducted in multiple rivers, estuaries, and lakes and along coastlines in the United States during the last 40 years (Smart et al. 2005); thousands of acres of SAV, some of it *V. americana*, have been restored in the Chesapeake Bay estuary (Shafer & Bergstrom 2010). Research conducted by multiple institutions have developed successful methods for transplanting and seeding of *V. americana* and other SAV (Orth et al. 2002; Smart et al. 2005; Moore et al. 2010).

We explored two hypotheses about factors related to the loss, lack of recovery, and potential restoration of *V. americana* in the HRE after Irene and Lee. The first hypothesis tested is that failure of *V. americana* tubers to sprout following the storms was caused by excessive sedimentation. Storm-driven sediment burial of tubers and plants has been explored as a factor for loss of *V. americana* in the Chesapeake Bay (Rybicki & Carter 1986; Rybicki et al. 2001). The second hypothesis was that regrowth in subsequent years was reduced by herbivore pressure focused on the few remaining *V. americana* beds. In several aquatic systems in the U.S. where assisted restoration of *V. americana* has been tried, recovery was hampered by grazing (Carter & Rybicki 1985; Hauxwell et al 2004; Moore et al. 2010). To examine our hypotheses, we conducted sediment burial experiments in the lab and field, along with trial plantings in an herbivore exclusion experiment in the field.

Methods

Field and greenhouse experiments on herbivory and sediment burial were conducted during the 2014 growing season and the winter of 2015. Three sediment burial experiments were conducted; two in greenhouse (SDG1 and SDG2) and a field experiment (SDF) in the HRE (Fig. 1). A smaller viability study (SDGV) was also conducted. A summary of all experiments conducted can be found in Table 1 along with an abbreviated code for each experiment given throughout the text. SDG1 and SDGV were conducted in a greenhouse at the Cary Institute of Ecosystem Studies (CIES) in Millbrook, NY. SDG2 was conducted at the State University of New York College of Environmental Science (SUNY-ESF) in Syracuse, NY.

Herbivory and sediment burial field experiments were located in the main stem of the Hudson River outside of Tivoli Bays (river approximately 150 km, coordinates 42°2′27″N, 73°54′38″W) near the eastern shore between Magdalen Island and train tracks, in an area with earlier documented SAV beds according to data collected through aerial surveys (Findlay et al. 2014).

Forty overwintered *Vallisneria americana* tubers were purchased from a commercial nursery on the upper Hudson River, using local genetic stock, for SDG1. Tubers were weighed wet and then buried at 5, 10, 20, and 30 cm, with 10 tubers at each depth. Depths were selected based on prior literature (Rybicki

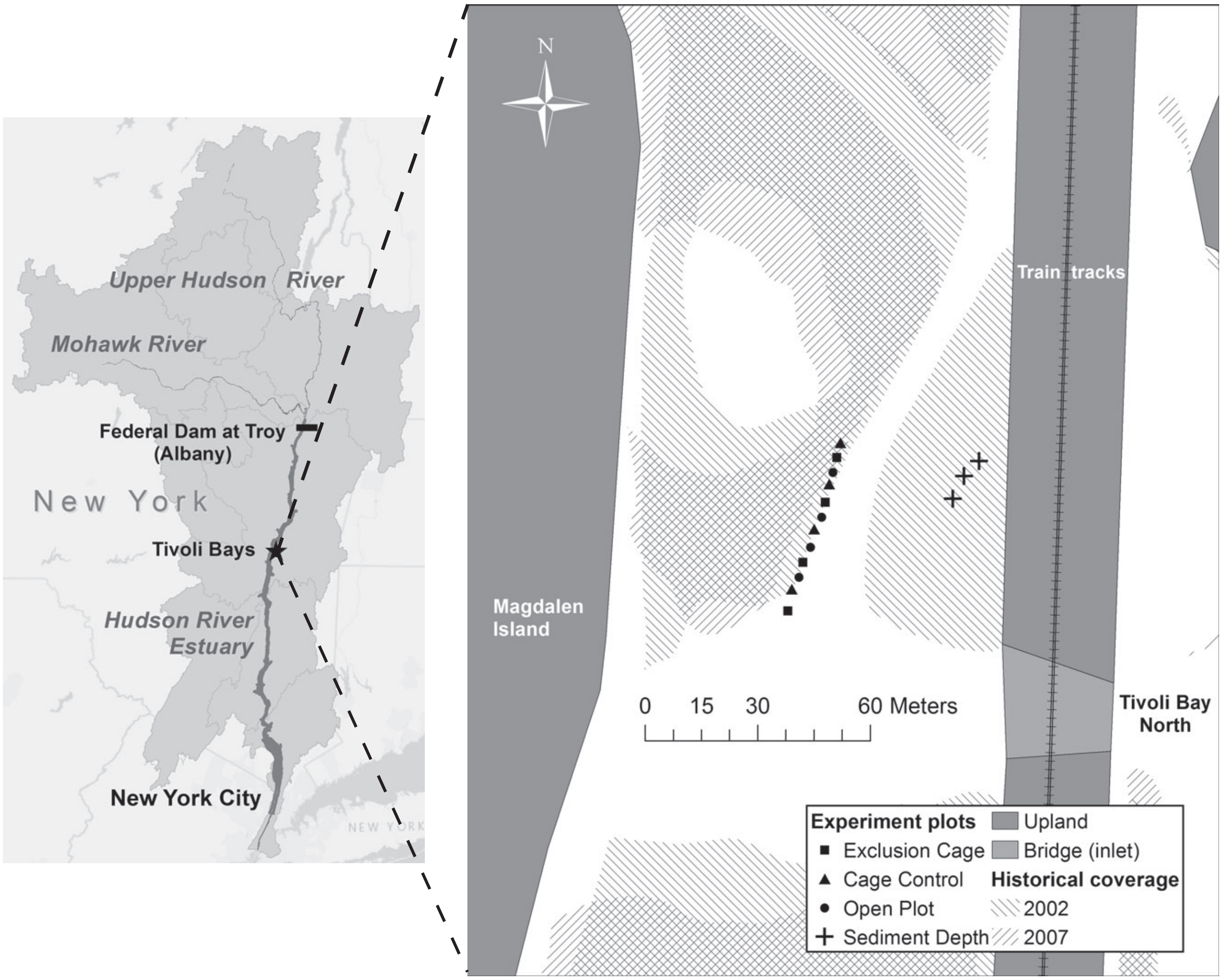

Figure 1. Map of the Hudson River, showing the experiment site at the northern Tivoli Bay. The experiment site map shows the location of herbivory experiment plots and sediment depth experiment plots as well as historical extent of *Vallisneria americana* in 2002 and 2007 (Findlay et al. 2014).

& Carter 1986) and spanned likely post-storm sediment deposition scenarios. Tubers were buried in sediment that had been collected from the Hudson River field site. Polyvinyl chloride (PVC) pipes with a 10 cm diameter were used for pots, and two tubers were put in each pipe with 10 cm of sediment below the planting depth of the tuber. Before planting, the sediment was cleaned of any plant material and then compacted by hand to simulate sediment compaction in the river. Planting was done on 16 May, 2014. All 20 pipes were marked and placed in a 400-L plastic tub in blocks of 4; one for each depth, and each block was adjacent to the next.

SDGV was conducted in a separate tub in CIES greenhouses to test if the tubers from the nursery were comparable to those taken directly from the river in terms of their ability to sprout. Fifteen tubers from the commercial plant nursery were planted at 2 cm depth in sediment, and two batches of 15 tubers each, taken from the river near the field experiment site, were planted at 2 and 5 cm, respectively and placed in three pots in a 400-L capacity tub. For both SDGV and SDG1, the tubs were filled with water from the mid-Hudson River and kept aerated; water was refilled when necessary to keep the water level to a point at least 10 cm above the pots. After 2 months, sprouted plants were harvested, and sediment was sieved to recover unsprouted tubers.

SDG2 was conducted in greenhouses at SUNY-ESF for 26 days from 21 January, 2015 to 16 February, 2015. Sixty tubers taken from plants harvested at the end of the herbivory field (HF) experiment in September 2014 were overwintered in cold storage (above freezing) in small batches in plastic bags, together with a mixture of water and sediment. Tubers were planted in plastic pots with a minimum 5 cm sediment depth below tubers and 1, 2, and 5 cm of sediment on top and placed in a 200-L plastic tub in blocks of 3; one of each depth, each block was adjacent to the next. For SDG2, estimates of longest leaf length were taken for each sprouted plant. Temperature was maintained at 18 (±1°C) and light period in the greenhouse was set to 16 hours. Flow was added by a submerged pump (Marineland Maxi-Jet [Spectrum Brands, Middleton, WI, USA]

Table 1. Summary of all experiments performed.

	SDG1—Sediment Depth Greenhouse Experiment 1	*SDGV—Sediment Depth Greenhouse—Viability Study*	*SDG2—Sediment Depth Greenhouse Experiment 2*	*SDF—Sediment Depth Field Experiment*	*HF—Herbivory Field Experiment*
Location	CIES Greenhouse	CIES Greenhouse	SUNY-ESF Greenhouse	HRE outside Tivoli Bay North	HRE outside Tivoli Bay North
Source of plant material	Commercial nursery—Upper Hudson	Commercial nursery—Upper Hudson and HRE outside Tivoli Bay	HRE outside Tivoli Bay (from plants of Upper Hudson stock)	HRE outside Tivoli Bay	Commercial nursery—Upper Hudson
Predictor variable	Depth in sediment	Depth in sediment + plant source	Depth in sediment	Depth in sediment	Herbivore access
Treatments	5, 10, 20, 30 cm	2, 5 cm/nursery versus river	Shallow (1 and 2 cm) versus deep (5 cm)	2, 5, 10 cm	Exclusion cage, cage-control, open plot
Response variable(s)	Sprouting	Sprouting, dry weight	Sprouting, length of leaves	Sprouting, length of leaves, number of rosettes, dry weight	Dry weight, length, and number of leaves
Replicates	10 tubers	15 tubers	20 tubers	10 tubers	32 pots (2 sprouted plants per pot)
Duration	2 months; May–July 2014	2 months; May–July 2014	21 days; January–February 2015	45 days; June–July 2014	82 days; June–September 2014
Main findings	No sprouting	Both nursery and river stock was viable	Significantly higher sprouting at shallow depth	Higher sprouting at shallow depth	No significant difference between treatments

600, 8 W, 160 gallons/hour). Water was refilled to keep the water level at 26 (±5 cm); the water was never completely changed. To avoid desiccation or damage, tubers in the second experiment were not weighed before planting.

DO and temperature readings were taken for each tub SDG1, SDG2, and SDGV using a hand-held DO-meter (YSI) and/or iButtons (Maxim Integrated, San Jose, CA, USA). Pots were monitored every 2–3 days, and date of first observed sprouting was recorded. Six sediment samples taken from the sediment used were dried and then washed to determine organic content using the loss-on-ignition method (Schumacher 2002). Two samples from the same sediment which was used in all sediment experiments were analyzed for texture via sieving and hygrometer, and a separate sample was sieved to determine sand-grain size (Bickelhaupt et al. 1983).

For SDF, 30 unsprouted tubers in good condition were collected from the river near the experiment site, weighed wet and then replanted in individual plastic pots in river sediment with at least 5 cm sediment below the tuber at 2, 5, and 10 cm depth, 10 tubers at each depth. On 16 June, 2014 pots were placed at marked locations in the field under natural conditions (Fig. 1), at a mean low-tide water depth of about 0.4 m with the pots being pushed into the sediment by hand. Each pot was marked by a small flag, and pots were clustered in threes, a few centimeters apart, with one of each depth; 3–4 clusters of pots were in turn arranged around a marker pole (Fig. 1) with about 1 m between clusters, a total of 3 poles with clusters, were installed at about 5 m from each other.

Each pot was monitored for sprouting by feel due to low visibility in the river. This monitoring was conducted on 8 July, 2014 (22 days postplanting) and 21 July, 2014 (35 days). At the end of the experiment, on 31 July, 2014 (45 days), pots were taken out of the river and sprouted plants were measured for length, and the amount of plantlets and tubers or flowers were counted. The plants were then dried and weighed to the nearest 0.01 g. Three sediment samples were taken from the sediment in pots after harvesting, processed, and measured to see if the in-river treatment had changed the organic content of the sediment.

For the HF experiment 12 plots were chosen and laid out in a north–south pattern (upstream–downstream), 4–5 m apart, at a depth of between 0.2 and 0.4 m at mean low tide. The plots were square, with each side measuring approximately 1.2 m (Fig. 2). Plots were designated either as open, exclusion, or cage control. Four replicates of each plot type were constructed, mainly to limit the risk if a plot was damaged. Open plots were marked in each corner with PVC stakes. Exclusion plot cages were made from PVC piping and covered in 2.5 cm metal poultry fencing to a height of 1.2 m with a wire mesh roof. Each side was constructed with a “skirt” of 30 cm poultry fence lying flat against the ground to hinder herbivores burrowing in Moore et al. (2010). Herbivory exclusions resembled those presented for “multiple plant exclosures” in Smart et al. (2005). Cage-control plots were set up just as the exclusion plots but with one side unfenced, facing perpendicular to river flow.

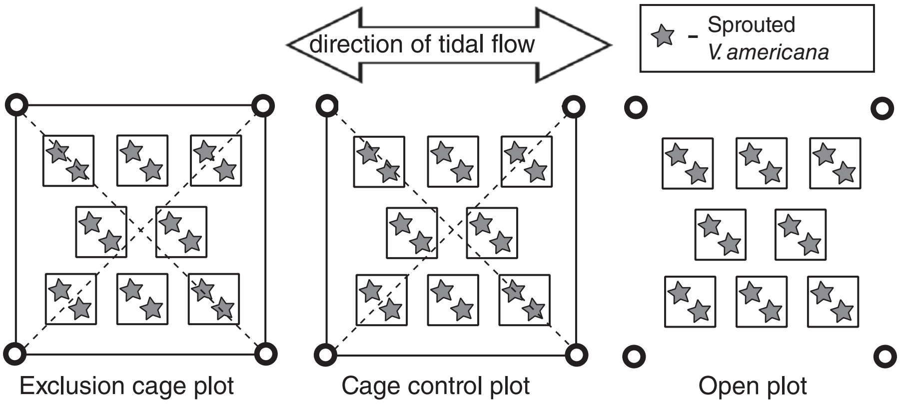

Figure 2. Design of the herbivory plot experiments (HF) with one side open for cage-control plots perpendicular to the direction of tidal flow. Each type of plot had four replicates.

Plots were maintained, cleaned, and repaired once a week. Water depth of each cage was measured and corrected for tidal influence. Eight peat-pots containing sprouted *V. americana*, obtained from the same commercial nursery as above, with two plants in each pot were planted in each plot about 30 cm apart (Fig. 2), for a total of 96 pots. The peat-pot was made of compacted peat and gravel with no external casing. Plants had approximately 8 cm leaf length when planted. Planting and installation of cages were done on 27 June, 2014 and pots were harvested in three rounds, three pots per plot was collected on 31 July, 2014, two on 28 August, 2014, and the remainder (in most cases 3) on 17 September, 2014.

Plants, along with connected runners outside the pot, were only harvested if the pot could be found. After harvest, the lengths of the three longest leaves were measured, amount of plantlets and leaves were counted, and plants were divided into aboveground and belowground biomass. Any tubers or flowers were counted. In the third harvest, any new tubers present were weighed wet. Plants were dried for a minimum of 24 hours at 60°C and weighed.

Statistical analysis of all experiments (Table 1) was performed in Minitab17 (Minitab Inc., State College, PA, USA) after checking that all assumptions required for each test were met. A Pearson's chi-square test was conducted on the results of SDF with sediment depth as predictor variable and sprouting success as response variable. A two-sided t test was conducted to compare preplanting wet-weight of tubers in SDF to sprouting success. No statistical analysis was conducted for SDG1 due to complete lack of sprouting. A Pearson's chi-square test of association was conducted on the results of SDG2 with depth in sediment as predictor variable (1 and 2 cm depth grouped as "shallow," vs. 5 cm as "deep") and sprouting success as response variable, to test if sprouting success was associated with depth in sediment. Two-sided T tests were conducted on SDG2 plants with depth in sediment as predictor variable for both tests and first day of sprouting (only for sprouted plants) and longest leaf length as response variables. The assumption of equal variance was tested using Levene's method.

For the HF experiment, nine separate one-way analysis of variance (ANOVA) tests were conducted with the three treatments (open, exclusion, and cage-control) being the predictor variable in each case and leaf length, number of leaves, and dry weight being the response variables. Each set of response variables was analyzed separately for each of the three harvest date with the mean of all pots from one plot harvested at that date considered the replicate. One-way ANOVA was also conducted for number of tubers produced in the third harvest. Post hoc analysis was conducted pairwise on the treatments for each harvest date using the Tukey's method. The assumption of equal variance was tested using Levene's method.

Results

Mean organic content of the sediment used in SDG1, SDG2, SDGV, and SDF was 2.94% (SD = 0.24) and sediment was found to be loam (36.7% sand, 45.3% silt, and 18.0% clay). Sediment grain sizes were mostly fine (61% < 0.105 mm; Table S1). Temperature and DO readings from all experiments can be found in Table S2.

No tubers sprouted in SDG1 during the full experiment. The sediment was sieved after 2 months of observation but no tubers were recovered. Sprouting was recorded after 11 days in SDGV with 13 and 10 of the original tubers sprouting from 2 cm depth for the nursery and "wild" tubers respectively. Only 3 of 15 tubers sprouted from the 5 cm depth (Table 2).

In SDG2, two pots were removed after 5 February, 2015 due to sediment being disturbed by the submerged pump. Statistics are therefore presented on all pots up to 5 February, 2015 and on the reduced set through 16 February, 2015. One plant was further dislodged after sprouting and is therefore included in sprouting success statistics but not leaf length. Depth in sediment and sprouting success at 5 February, 2015 was significantly ($p = 0.004$, Pearson's $\chi^2 = 8.352$) associated, with about 70% more sprouting success in shallow (1 and 2 cm) depth versus deep (5 cm) depth (Fig. 3). For 16 February, 2015, tubers in shallow sediment were 31% more successful at sprouting, but depth and sprouting success was not significantly associated ($p = 0.061$, Pearson's $\chi^2 = 3.506$). The mean longest leaf length by 5 February, 2015 was 2.42 cm for shallow and 0.94 cm for

Table 2. Results from the SDGV with tubers from Hudson River near the experiment site and from the commercial nursery buried at 2 and 5 cm depth in sediment from the river.

Source	*Depth in Sediment (cm)*	*Number of Planted Tubers*	*Total Dry Weight of Sprouted Plants*	*Total Number of Rosettes*	*Total Number of Separate Plants*
Nursery	2	15	2.37	13	2
River	2	15	2.2	10	5
River	5	15	1.41	3	1

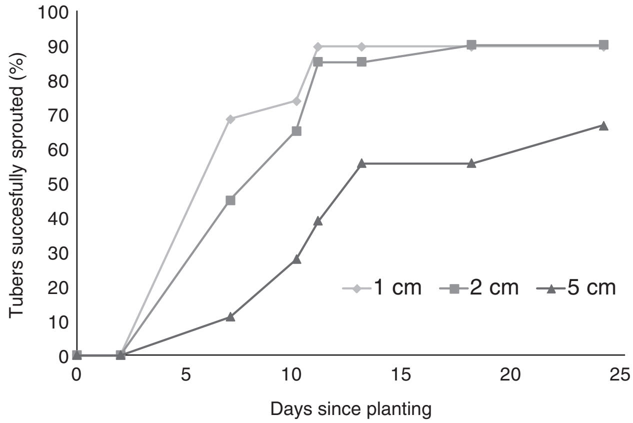

Figure 3. Percent of tubers successfully sprouted for each sediment depth by date since planting for the second greenhouse experiment (SDG2).

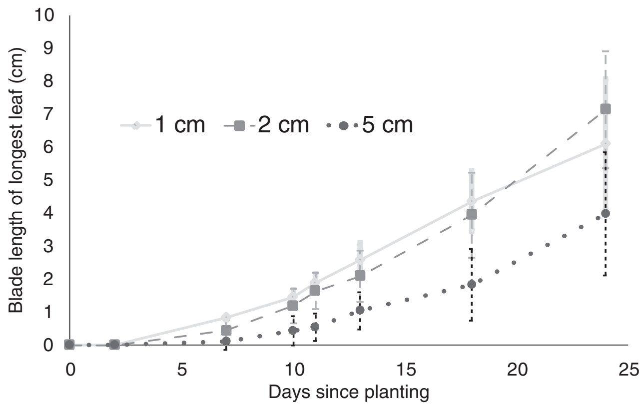

Figure 4. Mean longest leaf length by sediment depth and date since planting for the second greenhouse experiment (SDG2). Error bars for each date represent the ±95% confidence interval.

deep, a difference of about 60% ($p = 0.001$, $T_{58} = -3.50$). Mean longest leaf length observed on 16 February, 2015 was 6.64 cm for shallow depth and 4.00 cm for deep depth (Fig. 4), a difference of about 40% ($p = 0.020$, $T_{56} = -0.240$). Twelve plants at deep depth, and 35 plants at shallow depth sprouted; the mean first observed day of sprouting was 9 days for shallow depth and 14 days for deep depth ($p < 0.021$, $T_{12} = 2.65$). In SDG2, tubers planted at 1 and 2 cm had a greater chance of sprouting than those at 5 cm, sprouted earlier, and produced longer leaves in the same amount of time.

Sprouting in SDF was detected after 23 days. No additional sprouting was found in the next observation or during harvest. The area used for the sediment burial experiment had been recorded as an SAV bed in previous years but at the time of planting no *Vallisneria americana* sprouting was observed. However, by the time of the first observation there was dense *V. americana* growth in the area. Sprouting was weakly associated with burial depth ($p = 0.082$, Pearson's $\chi^2 = 5.000$), with 40% of plants sprouted at 2 cm depth, 20% sprouted at 5 cm and none at 10 cm. Total and mean dry weight of the plants sprouting at 2 cm were higher compared to those at 5 cm (Table 3). Mean numbers of leaves and rosettes were also higher at 2 cm than 5 cm. The preplanting wet-weight did not differ significantly ($p = 0.345$, $T_{28} = 0.96$) between tubers that did sprout (2.5 g, $n = 6$) and those that failed to sprout (2.1 g, $n = 24$).

Pots in the river and in the greenhouse were sieved after the experiments but no unsprouted tubers were found. It was also observed during harvesting of tubers for the field experiment in June 2014 that most tubers found naturally in the river were at a sediment depth of approximately 0–3 cm. Mean organic content (three samples) of sediment from river pots after harvest was 3.81% (SD = 0.09), about 1% higher than when buried.

In the HF experiment, 84 plants were harvested out of 96 total planted; plants were not harvested if the peat-pot could not be found. Five plants from cage-control plots, four plants from exclusion plot, and three plants from open plots were not recovered. Exclusion and cage-control plots appeared to accumulate more sediment on top of the pots than open plots.

In the first harvest, leaf lengths ($p = 0.010$, $F_{11} = 8.10$), number of leaves ($p = 0.019$, $F_{11} = 6.32$) and plant dry mass ($p = 0.017$, $F_{11} = 6.68$) differed significantly between open and exclusion plots (Fig. 5), No significant differences were observed between exclusion and cage-control plots. Plants in exclusion plots had, on average, longer leaves but weighed less and had fewer leaves. Mean leaf length was the only factor that differed significantly ($p = 0.001$, $F_{11} = 17.63$) between open plots and exclusion plots in the second harvest, but did not differ significantly between cage-control plots and exclusion plots. There were no significant differences observed across plot types in the third harvest. In the third harvest, 20 out of 24 plants had produced tubers, as compared to 1 plant in the second harvest and none in the first. Number of tubers did not differ significantly ($p = 0.465$, $F_{11} = 0.86$) between the three plot treatments. Relative north–south position of plots showed no significant correlation with plant growth.

Table 3. Data on the SDF comparing multiple indicators of growth and health for each sediment depth.

Depth in Sediment (cm)	*Number of Planted Tubers*	*Number of Sprouted Plants*	*Mean Dry Weight of Sprouted Plants (g)*	*Mean Number of Leaves*	*Mean Number of Rosettes*
2	10	4	0.59	20.5	5
5	10	2	0.31	11	3
10	10	0	—	—	—

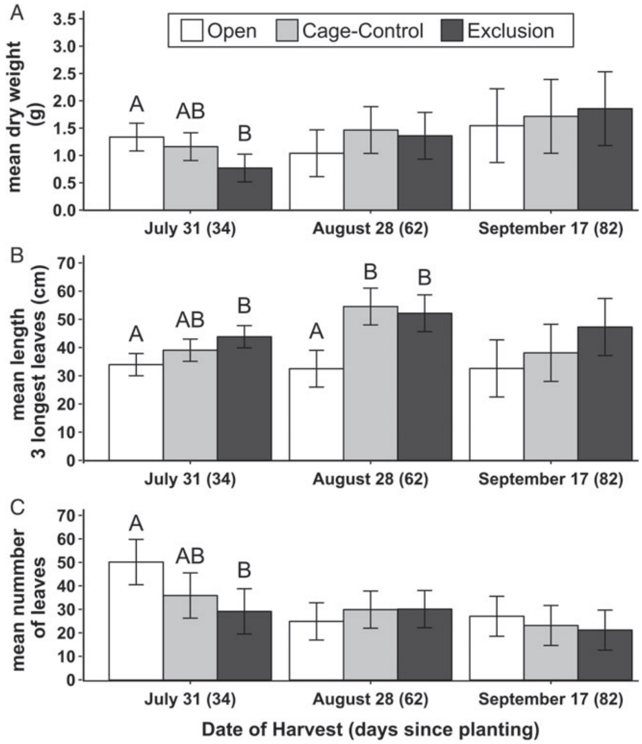

Figure 5. Statistical results of the herbivory field experiment (HF): mean dry weight (A), mean length of three longest leaves (B), and number of leaves (C) per pot and date. Error bars represent the ±95% confidence interval. Significant differences between treatments at same harvest date are denoted with different letter (A and B) as per one-way ANOVA post hoc analysis via Tukey's test noted above bars; if no letter is noted, there is no significant difference between treatments.

Discussion

Of our two hypotheses—that sediment burial and/or herbivory played key roles in the lack of *Vallisneria* recovery—we found significant negative effects of burial depth but no benefit from herbivore exclusion. In sediment depth experiments (SDGV, SDF, and SDG2), overlying sediment affected tuber sprouting, with decreases in successful sprouting of 30–100% between 2 and 5 cm burial depth and no sprouting success at 10 cm or deeper. The difference in absolute sprouting between SDF and SDG2, could be explained by different temperature in sediment or quality of the tubers. Overall, our sediment burial experiments show that increased depth in sediment will decrease and delay sprouting for *V. americana* tubers in the HRE. Delayed sprouting, as shown in SDG2, is a disadvantage for *V. americana* as it shortens the growing season, leaving insufficient time to create flowers and produce seed (Titus & Hoover 1993; Hauxwell et al. 2004).

The hypothesis that sediment burial caused loss of *V. americana* is based on the large amount of sediment that was washed into the river during the storm events in 2011, and that if tubers are buried too deep, they may lack sufficient energy to send up shoots through the sediment. The 1.7 MT of sediment that remained in the upper portion of the estuary 1-month post-storm (Ralston et al. 2013) would be enough, when deposited, to increase new sediment cover by a depth of 3 cm if spread evenly across the entire riverbed from the dam at Troy to Poughkeepsie. The actual amount deposited in SAV beds may have been greater in SAV beds due to their sediment-trapping propensity (Gacia et al. 1999; Findlay et al. 2006). The tubers obtained for our experiments were found mostly in the top 2 cm layer of the sediment (J. Hamberg 2014, State University of New York, College of Environmental Science and Forestry (SUNY-ESF), personal observation). Three centimeters added to this depth—a total of up to 5 cm between tubers and surface—may have reduced and potentially slowed sprouting in the season after Irene and in turn affected the available stock to produce tubers for coming seasons.

Burial by sediment of already sprouted seagrasses, including members of the same family, Hydrocharitaceae, as *V. Americana*, has been studied by Cabaço et al. (2008) who show that *Thalassia testudinum* experienced 50% mortality at 5 cm sediment depth while other seagrass species showed a threshold of 50% mortality at 2–19.5 cm. Other studies of seed burial of aquatic plants show emergence dropping drastically in the first 2.5 to 5 cm burial depth (Dugdale et al. 2001).

We found that sprouting of *V. americana* was constrained to significantly shallower sediment burial depths than was found in experiments in the Potomac River, where sprouting success began to decrease at 10 cm sediment depth (Rybicki & Carter 1986) in both sandy and silty clay soils. Jarvis and Moore (2008) found that *V. americana* seed showed no effect of sediment burial on germination success between 0.2 and 10 cm and that seed germinated most successfully in well oxygenated (8 mg/L) sediments that were less than 3% organic matter and greater than 40% sand. We did not monitor sediment DO, but we note that most of the sediment yielded by the 2011 storms consisted of very fine-grained particles (G.R. Wall, U.S. Geological Survey, Troy, NY, personal communication) and our sediment sample was fine texture with high silt-clay content. The difference in sprouting between our experiment and the one by Rybicki and Carter (1986) may potentially be due to differing genetic stock (Lloyd et al. 2011), differences in the condition of tubers, or their growing conditions.

In contrast to sediment burial, herbivory did not appear to be a factor inhibiting *Vallisneria* recovery in the HRE. This stands in contrast to the demonstrated need for herbivory protection in many parts of Chesapeake Bay and the Potomac River, which had limited success in establishments of new SAV without netting to protect the young plants (Carter & Rybicki 1985; Moore et al. 2010). Blue crab, *Callinectes sapidus*, has been implicated in destruction of *V. americana* in Chesapeake Bay as the crab clips the plants (K. Moore 2014, Virginia Institute of Marine Science (VIMS), personal communication). Waterfowl consume SAV, including overwintering tubers (Sponberg & Lodge 2005). Common carp (*Cyprinus carpio*), a long-time invasive species in the HRE, as well as muskrat (*Ondatra zibethicus*) have been shown to destroy SAV in other systems (McFarland & Shafer 2008), including in wetlands connected to the HRE (Connors et al. 2000). In Florida, even with herbivory protection at time of planting, Hauxwell et al. (2004) found that when the fencing was removed, grazers, in this case manatees (*Trichechus manatus*), consumed all established *V. americana* in weeks.

The results from our HF experiment in the HRE provided no evidence that herbivory impeded *V. americana* regrowth in the area. There was no significant improvement in plant health (length, blades, weight) for protected plants over the growing season. This may be due to the Hudson River having a low density of herbivores. Chesapeake Bay has a large commercial fishery of blue crab (Chesapeake Bay Foundation 2008), whereas a much smaller fishery in the Hudson River (Hudson River Fisheries Unit 2015) suggests lower densities of blue crab in the river. Animals reliant on SAV may have decreased or changed migration patterns, as has happened in other systems with both waterfowl (Hansson et al. 2010) and with fish (Winemiller & Jepsen 1998). Another hypothesis is that herbivore populations in the HRE were also directly affected by the storms. Such changes in aquatic life communities have been recorded after hurricanes (Piazza & La Peyre 2009). Our results from the herbivory experiment show the usefulness of conducting site-specific studies of the potential need for herbivory protection, to avoid costly large-scale investments.

Other potential factors explaining the loss of *Vallisneria* could be lowered light availability, scouring, or a simultaneous event unrelated to the storm such as disease or pollution. In our herbivory experiment, we observed that tubers were set at the end of the season between late August 2014 and mid-September 2014, similar to other observations (McFarland & Shafer 2008). This timing corresponds to when Lee and Irene would have caused extreme turbidity in the river (Ralston et al. 2013), which may have led to lower light availability for plants entering the reproductive stage and created smaller tubers that would have had a more difficult time sprouting when buried. As each stage negatively reinforces the next, the second year's crop may not have had enough energy reserves to reestablish quickly (Titus & Hoover 1993). As the growing season in the HRE occurs during the hurricane season on the Atlantic seaboard (NOAA/NWS 2014), most hurricanes affecting the HRE would cause both light-extinction and sediment burial issues for SAV.

Storms and associated precipitation could also increase river pH and decrease temperature to unsuitable levels for *V. americana* (Titus & Hoover 1993; Greening et al. 2006). pH and temperature decreases in HRE were, however, short, relatively minor, and happened at a late stage in the growing season (HRECOS 2015).

In the HRE, the increased flow due to the storm events may have reduced reseeding, if flowers and fruit were washed out of the system. Sediment resuspension and transport during storm flows from Irene and Lee in the HRE (Ralston et al. 2013) may also have contributed to decreasing tuber and seed viability for the next season. Scouring would have caused patchy loss depending on the physical setting of individual SAV beds, but the loss of SAV in 2012 was system-wide. Scouring and resuspension from storms can damage SAV, either by removing the substrate in which the plants are rooted and the seeds or tubers are buried, or by destroying the plant itself (Greening et al. 2006; McFarland & Shafer 2008). Storm waves and storm surges can also cause direct damage to SAV (James et al. 2008). Sediment resuspension and movement could shift the microbial communities and sediment nutrient levels, which could affect SAV (Sloth et al. 1996).

One of the more important outcomes of the HF experiment was that plants from nursery stock could survive, grow, spread, and produce tubers when planted at a suitable location and depth in the HRE. The peat-pot method used in the herbivory experiment has been shown to be costly in similar planting comparisons of seagrasses (Busch et al. 2010) and comparative cost studies need to be made with direct planting of tubers and different seeding methods. The apparent lack of a need for herbivory protection should reduce costs for any future restoration efforts in the HRE, compared to ecosystems with significant grazing pressure.

"Tuber banks" have been discussed as a source for *V. americana* recovery after disturbance (Harwell & Havens 2003), but from our experiment, tubers that do not sprout will apparently deteriorate to a point where we could not find them, resulting in a tuber bank that could only last one growing season. Reestablishment after a storm event that removes, or creates, lasting negative conditions for tubers may therefore necessitate sources such as seed banks, surviving *V. americana* beds in the river, and from other nearby populations through hydrochory or zoochory (Rybicki et al. 2001; McFarland & Shafer 2008).

Hurricane Floyd caused a similar loss of light availability as Irene and Lee in the HRE in 1999, although about 2 weeks later in the season, and while only introducing a little more than a tenth of the load of inorganic and organic particles (Strayer et al. 2014). Although no systematic SAV inventories were made in 1999 or 2000, SAV extent was observed to be close to the same in 2002 as it was in 1997 (Nieder et al. 2004).

Large-scale storms can have serious, long-lasting effects on rivers (Strayer et al. 2014). It is important to understand how hurricanes may affect SAV in the long term, with climate change predicted to increase the strength of hurricanes and amount of precipitation over the U.S. Northeast (IPCC 2013). Because not much can be done to stop hurricanes, it is important to focus on how to increase the resilience of the river to decrease loss and increase the rate of recovery. Rybicki et al. (2001) identified storms as being the reason for loss of SAV in the Potomac, but slow regrowth is posited to be due to degraded water quality from high nutrients and turbidity. Water quality has improved in the Hudson River in the past decades due to better wastewater management (Miller 2013). Agricultural best management practices (BMPs) and riparian restoration could reduce sediment loading, which could improve light penetration after a disturbance event. This could create a positive feedback with more *V. americana* improving water quality (Findlay et al. 2006). Much of the sediment introduced into the river by Irene and Lee came from the Catskills area and the Mohawk River (Ralston et al. 2013). With increasing implementation of BMPs, the new sediment introduced from agricultural land and deforested areas should decrease (Allan 2004).

Prerestoration habitat monitoring to evaluate site vulnerability, and monitoring during and after assisted restoration to evaluate SAV reestablishment on the site, would increase our understanding of sediment effects of storms on SAV and restoration success. This may be even more important because of the anticipated increase in storm strength due to climate change. Future restoration efforts of SAV should consider that benefits may be temporary if future storms create sufficient damage. The HRE has a history of environmental concern (Limburg et al. 1986) and there is support among local stakeholders for general environmental restoration in the area (Connelly et al. 2002). On the one hand, if the persistence of restored SAV is low, assisted restoration through seeding or planting, even without need for herbivory protection in the HRE, could pose annual costs in the millions of dollars (Hamberg 2015). On the other, if restoration is not done, and changes in land management practices are not implemented fast enough, multiple recurring storm events could overwhelm any natural recovery and potentially extirpate the stock of *V. americana*, and possibly SAV in general, which would diminish fish spawning and water quality, something that has occurred in other systems (Rybicki et al. 2001). Assisted restoration can bring back SAV faster than natural regrowth (Smart et al 2005; Busch et al. 2010) and limit any effects on important fish species in the river. Future restoration efforts should weigh the financial cost of direct assisted restoration against—or if possible be combined with—other options for improving the resilience of the river, as well as against the potential economic and ecological cost to the HRE, its population, and the people that rely on it, of rivers without *V. americana* and the ecosystem services it provides.

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LITERATURE CITED

Allan JD (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology, Evolution, and Systematics 35:257–284

Bickelhaupt DH, Davey CB, White EH (1983) Laboratory methods for forest tree nursery soil analysis. State University of New York, College of Environmental Science and Forestry, Syracuse, NY miscellaneous publication

Busch KE, Golden RR, Parham TA, Karrh LP, Lewandowski MJ, Naylor MD (2010) Large-scale *Zostera marina* (eelgrass) restoration in Chesapeake Bay, Maryland, U.S.A. Part I. A comparison of techniques and associated costs. Restoration Ecology 18:490–500

Cabaço S, Santos R, Duarte CM (2008) The impact of sediment burial and erosion on seagrasses: a review. Estuarine, Coastal and Shelf Science 79:354–366

Carter V, Rybicki NB (1985) The effects of grazers and light penetration on the survival of transplants of *Vallisneria americana* Michs in the tidal Potomac River, Maryland. Aquatic Botany 23:197–213

Cheng P, Li M, Li Y (2013) Generation of an estuarine sediment plume by a tropical storm. Journal of Geophysical Research: Oceans 118:856–868

Chesapeake Bay Foundation (2008) Bad water and the decline of blue crabs in the Chesapeake Bay. https://www.conservationgateway.org/Documents/CBF-BadWatersReport.pdf (accessed Jan 18 2015)

Connelly NA, Knuth BA, Kay DL (2002) Public support for ecosystem restoration in the Hudson River Valley, U.S.A. Environmental Management 29:467–476

Connors LM, Kiviat E, Groffman PM, Ostfeld RS (2000) Muskrat (*Ondatra zibethicus*) disturbance to vegetation and potential net nitrogen mineralization and nitrification rates in a freshwater tidal marsh. The American Midland Naturalist 143:53–63

Crivelli AJ (1983) The destruction of aquatic vegetation by carp. Hydrobiologia 106:37–41

Dugdale TM, de Winton MD, Clayton JS (2001) Burial limits to the emergence of aquatic plant propagules. New Zealand Journal of Marine and Freshwater Research 35:147–153

Findlay SEG, Strayer DL, Bain M, Nieder WC (2006) Ecology of Hudson River submerged aquatic vegetation. Final Report to the New York State Department of Environmental Conservation

Findlay SEG, Strayer DL, Smith SD, Curri N (2014) Magnitude and patterns of change in submerged aquatic vegetation of the tidal freshwater Hudson River. Estuaries and Coasts 37:1233–1242

Gacia E, Granata TC, Duarte CM (1999) An approach to measurement of particle flux and sediment retention within seagrass (*Posidonia oceanica*) meadows. Aquatic Botany 65:255–268

Greening H, Doering P, Corbett C (2006) Hurricane impacts on coastal ecosystems. Estuaries and Coasts 29:877–879

Hamberg, LJ (2015) Factors of loss and restoration of *Vallisneria americana* in the Hudson River estuary. MSc thesis. State University of New York, College of Environmental Science and Forestry, Syracuse, NY

Hansson LA, Nicolle A, Brönmark C, Hargeby A, Lindström Å, Andersson G (2010) Waterfowl, macrophytes, and the clear water state of shallow lakes. Hydrobiologia 646:101–109

Harwell MC, Havens KE (2003) Experimental studies on the recovery potential of submerged aquatic vegetation after flooding and desiccation in a large subtropical lake. Aquatic Botany 77:135–151

Hauxwell J, Frazer TK, Osenberg CW (2004) Grazing by manatees excludes both new and established wild celery transplants: implications for restoration in Kings Bay, FL, U.S.A. Journal of Aquatic Plant Management 42:49–53

Heck KL, Thoman TA (1984) The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. Estuaries 7:70–92

HRECOS (Hudson River Environmental Conditions Observing Data) (2015) Historical data. http://www.hrecos.org/index.php?option=com_content&view=article&id=143&Itemid=54 (accessed 1 Apr 2015)

Hudson River Fisheries Unit (2015) Blue crabs of the Hudson River. http://www.dec.ny.gov/animals/37185.html (accessed 18 Jan 2015)

IPCC (International Panel on Climate Change) (2013) Climate change 2013: the physical science basis. Pages 1535. In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Contribution of Working Group I to the Fifth Assessment Report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, NY

James TR, Chimney MJ, Sharfstein B, Engstrom DR, Schottler SP, East T, Jin KR (2008) Hurricane effects on a shallow lake ecosystem, Lake Okeechobee, Florida (U.S.A). Fundamental and Applied Limnology 172:273–287

Jarvis JC, Moore KA (2008) Influence of environmental factors on *Vallisneria americana* seed germination. Aquatic Botany 88:283–294

Kahn JR, Kemp WM (1985) Economic losses associated with the degradation of an ecosystem: the case of submerged aquatic vegetation in Chesapeake Bay. Journal of Environmental Economics and Management 12:246–263

Limburg KE, Moran MA, McDowell WH (1986) The Hudson River ecosystem. Springer-Verlag, New York

Lloyd MW, Burnett RK, Engelhardt KAM, Neel MC (2011) The structure of population genetic diversity in *Vallisneria americana* in the Chesapeake Bay: implications for restoration. Conservation Genetics 12:1269–1285

McFarland DG, Shafer DJ (2008) Factors influencing reproduction in American wild celery: a synthesis. Journal of Aquatic Plant Management 46:129–144

Miller DE (2013) Hudson River estuary habitat restoration plan. New York State Department of Environmental Conservation, Hudson River Estuary Program, New York

Moore KA, Shields EC, Jarvis JC (2010) The role of habitat and herbivory on the restoration of tidal freshwater submerged aquatic vegetation populations. Restoration Ecology 18:596–604

Nieder WC, Barnaba E, Findlay SEG, Hoskins S, Holochuck N, Blair EA (2004) Distribution and abundance of submerged aquatic vegetation and *Trapa natans* in the Hudson River estuary. Journal of Coastal Research Special Issue 45:150–161

NOAA/NWS (National Oceanographic and Atmospheric Administration/National Weather Service) (2014) Tropical cyclone climatology. http://www.nhc.noaa.gov/climo/ (accessed 8 Dec 2014)

Orth RJ, Batiuk RA, Bergstrom PW, Moore KA (2002) A perspective on two decades of policies and regulations influencing the protection and restoration of submerged aquatic vegetation in Chesapeake Bay, U.S.A. Bulletin of Marine Science 71:1391–1403

Orth RJ, Carruthers TJ, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, et al. (2006) A global crisis for seagrass ecosystems. Bioscience 56:987–996

Orton P, Georgas N, Blumberg A, Pullen J (2012) Detailed modeling of recent severe storm tides in estuaries of the New York City region. Journal of Geophysical Research 117:1–17

Palinkas CM, Halka JP, Li M, Sanford LP, Cheng P (2014) Sediment deposition from tropical storms in the upper Chesapeake Bay: field observations and model simulations. Continental Shelf Research 86:6–16

Piazza BP, La Peyre MK (2009) The effect of Hurricane Katrina on nekton communities in the tidal freshwater marshes of Breton Sound, Louisiana, U.S.A. Estuarine, Coastal and Shelf Science 83:97–104

Ralston DK, Warner JC, Geyer WR, Wall WR (2013) Sediment transport due to extreme events: the Hudson River estuary after tropical storms Irene and Lee. Geophysical Research Letters 40:5451–5455

Rozas LP, Minello TJ (2006) Nekton use of *Vallisneria americana* Michx. (Wild celery) beds and adjacent habitats in Coastal Louisiana. Estuaries and Coasts 29:297–310

Rybicki NB, Carter V (1986) Effect of sediment depth and sediment type on the survival of *Vallisneria americana* Michx grown from tubers. Aquatic Botany 24:233–240

Rybicki NB, McFarland DG, Ruhl HA, Reel JT, Barko JW (2001) Investigations of the availability and survival of submersed aquatic vegetation propagules in the tidal Potomac River. Estuaries 24:407–424

Schmidt RE, Kiviat E (1988) Communities of larval and juvenile fish associated with water-chestnut, water milfoil and water-celery in the Tivoli Bays of the Hudson River. Report to the Hudson River Foundation, New York

Schumacher BA (2002) Methods for the determination of total organic carbon (TOC) in soils and sediments. U.S. Environmental Protection Agency, Washington D.C.

Shafer D, Bergstrom P (2010) An introduction to a special issue on large-scale submerged aquatic vegetation restoration research in the Chesapeake Bay: 2003–2008. Restoration Ecology 18:481–489

Short FT, Wyllie-Echeverria S (1996) Natural and human-induced disturbances of seagrass. Environmental Conservation 23:17–27

Sloth NP, Riemann B, Nielsen LP, Blackburn T (1996) Resilience of pelagic and benthic microbial communities to sediment resuspension in a coastal ecosystem, Knebel Vig, Denmark. Estuarine, Coastal and Shelf Science 42:405–415

Smart RM, Dick GO, Snow JR (2005) Update to the propagation and establishment of aquatic plants handbook (No. ERDC/EL-TR-05-4). Engineer Research and Development Center, Environmental Laboratory, Vicksburg, MS

Sponberg AF, Lodge DE (2005) Seasonal belowground herbivory and a density refuge from waterfowl herbivory for *Vallisneria americana*. Ecology 86:2127–2134

Strayer DL, Smith LC (2001) The zoobenthos of the freshwater tidal Hudson River and its response to the zebra mussel (*Dreissena polymorpha*) invasion. Archiv für Hydrobiologie, Supplement 139:1–52

Strayer DL, Cole JJ, Findlay SEG, Fischer DT, Gephart JA, Malcolm HM, Pace ML, Rosi-Marshall EJ (2014) Decadal-scale change in a large-river ecosystem. BioScience 64:496–510

Titus JE, Hoover DT (1993) Reproduction in two submersed macrophytes declines progressively at low pH. Freshwater Biology 30:63–72

Waycott M, Duarte CM, Carruthers TJ, Orth RJ, Dennison WC, Olyarnik S, et al. (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences U.S.A. 106:12377–12381

Wigand C, Wehr J, Limburg KE, Gorham B, Longergan S, Findlay SEG (2000) Effect of *Vallisneria americana* (L.) on community structure and ecosystem function in Lake mesocosms. Hydrobiologia 418:137–146

Winemiller KO, Jepsen DB (1998) Effects of seasonality and fish movement on tropical river food webs. Journal of Fish Biology 53:267–296

Yellen B, Woodruff JD, Kratz LN, Mabee SB, Morrison J, Martini AM (2014) Source, conveyance and fate of suspended sediments following Hurricane Irene, New England, U.S.A. Geomorphology 226:124–134

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. A comparison of temperature, dissolved oxygen, pH, and turbidity in the Hudson River estuary in the growing season of 2011 and 2012.
Table S1. Grain-size distribution of sand in sediment used for all sediment in depth experiments.
Table S2. Median and quartile of dissolved oxygen (in mL/L) and water temperature (in °C) for all experiments measured with iButtons, DO meter, and from HRECOS data (2015).

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