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W. Judson Kenworthy
Center for Coastal Fisheries and Habitat Reserach, jud.kenworthy@gmail.com

Margaret O. Hall
Florida Fish and Wildlife Conservation Commission

Kamille K. Hammerstrom
Moss Landing Marine Laboratories

Manuel Merello
Florida Fish and Wildlife Conservation Commission

Arthur Schwartzschild
University of Virginia

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Restoration of tropical seagrass beds using wild bird fertilization and sediment regrading

W. Judson Kenworthy[a,*], Margaret O. Hall[b], Kamille K. Hammerstrom[c], Manuel Merello[b], Arthur Schwartzschild[d]

[a] Center for Coastal Fisheries and Habitat Research, NCCOS, NOS, NOAA, 101 Pivers Island Rd., Beaufort, NC 28516 USA
[b] Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, 100 Eighth Ave. SE, St. Petersburg, FL, 33701, USA
[c] Moss Landing Marine Laboratories,8272 Moss Landing Road, Moss Landing, CA, 92626, USA
[d] University of Virginia, Department of Environmental Sciences, Anheuser-Busch Coastal Research Center, PO Box 55, Cheriton, VA 23316, USA

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ABSTRACT

Shallow water seagrass meadows are frequently damaged by recreational and commercial vessels. Severe injury occurs where propeller scarring, hull groundings and mooring anchors uproot entire plants, excavate sediments, and modify the biophysical properties of the substrate. In climax tropical seagrass communities dominated by *Thalassia testudinum* (turtlegrass), natural recovery in these disturbances can take several years to decades, and in some environmental conditions may not occur at all. During the recovery period, important ecological services provided by seagrasses are absent or substantially diminished and injured meadows can degrade further in response to natural disturbances, e.g. strong currents and severe storms. To determine if we could accelerate rehabilitation and prevent further degradation of injured turtlegrass meadows, we evaluated a restoration method called "modified compressed succession" using the fast-growing, opportunistic species *Halodule wrightii* to temporarily substitute ecological services for the slower-growing, climax species *T. testudinum.* In three experiments we showed statistically significant increases in density and coverage rates of *H. wrightii* transplants fertilized by wild bird feces as compared to unfertilized treatments. In one experiment, we further demonstrated that regrading excavated injuries with sediment-filled biodegradable tubes in combination with wild bird fertilization and *H. wrightii* transplants also accelerated seagrass recovery. Specific recommendations are presented for the best practical application of this restoration method in the calcium carbonate-based sediments of south Florida and the wider Caribbean region.

1. Introduction

Worldwide, seagrass ecosystems flourish in shallow coastal environments with unconsolidated substrates (Hemmimga and Duarte, 2000; Green and Short, 2003; Larkum et al., 2006). A large fraction of seagrass biomass, growth and asexual reproduction occur belowground (Kenworthy and Thayer, 1984; Duarte and Chiscano, 1999; Di Carlo and Kenworthy, 2008) where roots and rhizomes anchor the plants, stabilize sediments, absorb nutrients, and enrich the substrate with organic matter (Kenworthy et al., 2014;). Because unconsolidated sediments are essential for most seagrasses, gap-forming disturbances that physically disrupt the substrate can cause acute and chronic modification of seagrass landscapes (Patriquin, 1975; Fonseca and Bell, 1998), sometimes with negative consequences for ecosystem structure and function (Kenworthy et al., 2002; Whitfield et al., 2002, 2004; Uhrin et al., 2011; Bourque et al. 2015).

Motor vessel propeller scars, hull groundings and anchor moorings create gap-forming injuries in seagrass meadows by excavating plants and sediments (Zieman, 1976; Walker et al., 1989; Durako et al., 1992; Hastings et al., 1995; Sargent et al., 1995; Dawes et al., 1997; Dunton and Schonberg, 2002; Whitfield et al., 2002, 2004; Uhrin et al., 2011; Bourque and Fourqurean, 2014). Surveys in Florida reported 70,000 ha of seagrasses damaged by motor vessels (Sargent et al., 1995) and this problem persists in the Florida Keys where ≥300 vessels run aground in seagrass beds annually (Kirsch et al., 2005; Farrer, 2010; Uhrin et al., 2011; Hallac et al., 2012). Whereas natural sediment disturbances from winds and tides cause gaps in seagrass beds that persist in a state of hydrodynamic equilibrium (Patriquin, 1975; Marba et al., 1994; Fonseca and Bell, 1998), vessel excavations often have steep, unstable margins that inhibit seagrass regrowth, making them vulnerable to erosion and expansion (Kenworthy et al., 2002; Whitfield et al., 2002, 2004; Uhrin et al., 2011). Vessel excavations penetrating beneath the

* Corresponding author. Present address: 108 Holly Ln, Beaufort, NC, 28516, USA.
E-mail address: jud.kenworthy@gmail.com (W.J. Kenworthy).

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seagrass rhizome layer destroy clonal integrity, damage meristems and disrupt ecosystem structure and function (Tomlinson, 1974; Dawes et al., 1997; Kenworthy et al., 2002; Di Carlo and Kenworthy, 2008; Bourque and Fourqurean, 2014; Bourque et al., 2015), while sediment berms formed adjacent to the injuries bury seagrass and interfere with regrowth (Fonseca et al., 2004). Organic matter accumulated and sequestered in the sediments (Fourqurean et al., 2012) is reduced or exported from the meadow, leaving substrates coarser-textured and nutrient depleted, and interrupts carbon sequestration (Dawes et al., 1997; Bourque and Fourqurean, 2014).

Decades of seagrass meadow succession and development can be reversed by a single vessel grounding (Whitfield et al., 2002, 2004). In climax *T. testudinum* meadows natural recovery is usually slow (> 3–10 y), and in some vessel excavations may not occur at all (Fonseca et al., 1987; Dawes et al., 1997; Kenworthy et al., 2002; Whitfield et al., 2002, 2004; Fonseca et al., 2004; Hammerstrom et al., 2007; Farrer, 2010; Uhrin et al., 2011; Bourque et al., 2015). In situations where the substrate has been severely disturbed, restoration may be necessary to rehabilitate the injuries and prevent further disturbance and degradation (Kirsch et al., 2005; Farrer, 2010; Bourque and Fourqurean, 2014).

Thalassia testudinum restoration presents difficult challenges (Fonseca et al., 1987; Lewis, 1987; Fonseca et al., 1998; Treat and Lewis, 2006). The deeply buried apical meristems essential for growth, reproduction and meadow expansion are present in low density and difficult to harvest and re-plant. Acquiring sufficient planting stock and avoiding damage to donor beds is labor intensive and expensive (Fonseca et al., 1998; Lewis et al., 2006; Paling et al., 2009). Depending on the site logistics and monitoring plans, seagrass restoration costs are high compared to terrestrial plant restoration (Fonseca, 2006; Treat and Lewis, 2006; Engeman et al., 2008; Paling et al., 2009) and the likelihood of transplant success is demonstrably uncertain (Lewis et al., 2006; Paling et al., 2009; Fonseca 2011; Van Katwijk et al., 2016). Where the goal of seagrass restoration is to re-establish slow growing *T. testudinum* meadows, valuable ecological services will be lost in the interim (Fonseca et al., 2000) and the injuries may further degrade (Whitfield et al., 2002, 2004; Uhrin et al., 2011). The costs in lost services and rehabilitation clearly demonstrate the need for developing practical and reliable methods for restoration of *T. testudinum* meadows.

To determine if rehabilitation of tropical seagrass meadows could be accelerated, we tested a modification of a restoration approach referred to as “compressed succession” (Derrenbacker and Lewis, 1982; Durako and Moffler, 1984; Lewis, 1987). Compressed succession utilizes a fast-growing species, *Halodule wrightii,* to temporarily substitute ecological services during the relatively slower recovery period of the climax species *T. testudinum*. We modified the original approach by using *H. wrightii* transplants in combination with fertilization and sediment regrading to test whether we could accelerate natural succession. Previous studies of seagrasses growing in phosphorous-limited, calcium carbonate sediments demonstrated that faster *H. wrightii* growth can be attained by adding phosphorus-rich excrement defecated by wild seabirds (Powell et al., 1989; Fourqurean et al., 1995; Herbert and Fourqurean, 2008). Seabirds encouraged to roost on stakes inserted in the sea floor act as a passive fertilizer delivery system (primarily phosphorous), favoring and stimulating faster growing *H. wrightii*. Here, we report the results of three experiments evaluating whether seagrass recovery in climax *T. testudinum* meadows severely disturbed by propeller scarring and larger vessel excavations could be accelerated by application of modified compressed succession.

Initially we examined if fertilization by seabirds would increase survival and growth of *H. wrightii* transplants in unvegetated propeller scars. In two additional experiments we examined a combination of wild bird fertilization and topographical restoration. We hypothesized that re-grading injuries with fine-grained sediments and leveling the topography would physically stabilize excavated injuries and provide a more favorable environment for faster *H. wrightii* recovery and eventually lead to the re-establishment of *T. testudinum*.

2. Methods

2.1. Study site

All three experiments were conducted in the Lignumvitae Key Submerged Land Management Area (LKSLMA) in the middle Florida Keys (24.91 °N, 80.68 °W) (Fig. 1). LKSLMA is comprised of extensive, shallow, calcium carbonate-based seagrass banks dominated by *T. testudinum* typical of south Florida, the tropical western Atlantic and the Caribbean region (Zieman, 1982; Short et al., 1985). Water depths were generally ≤1.5 m (mean high water) and the tidal range was approximately 1m.

2.2. Study plan

In Experiment 1 we evaluated the use of bird roosting stakes to fertilize *H. wrightii* transplants, and tested whether this fertilization technique accelerated rehabilitation of propeller scars. Experiments 2 and 3 were designed to evaluate bird roosting stakes and *H. wrightii* transplants in combination with sediment regrading. We examined recovery of propeller scars (Experiment 2) and a larger vessel excavation (Experiment 3) using a combination of wild bird fertilization*, H. wrightii* transplanting, and a method for re-grading excavations with sediment-filled, biodegradable fabric tubes (hereafter referred to as Sediment Tubes[1]).

2.3. Restoration techniques

2.3.1. Bird roosting stakes

In Experiments 1, 2 and 3, PVC pipe stakes (1.25 cm dia.) capped with 10 cm x 10 cm x 5 cm pressure-treated wooden blocks were designed to encourage seabirds, particularly cormorants (*Phalacrocorax auritus*) and terns (*Sterna spp.)*, to perch and defecate phosphorus-rich feces into the water and sediment (Powell et al., 1989) (Fig. 2). Control stakes (no fertilizer added) in Experiment 1 were fashioned by eliminating the wooden block and cutting the PVC pipe diagonally at the top to discourage roosting birds. Stakes were inserted into the sediment until ≈ 0.25-0.5 m of each stake extended above the water surface at mean high tide.

2.3.2. Sediment tubes

In Experiments 2 and 3, sediment tubes were used to regrade excavated seagrass beds. The tubes (1.0–1.5 m long, 15–20 cm dia.), filled with fine-grained calcium carbonate screening sand (0.63–0.85 mm dia.), were manually deployed into injuries from a shallow draft vessel (Fig. 3).

2.3.3. Seagrass transplanting

We followed the recommended procedures for seagrass bare root transplanting (Fonseca et al., 1998). *Halodule wrightii* shoots with intact roots and rhizomes were collected from a meadow adjacent to Lignumvitae Key, rinsed free of sediment, assembled into planting units and planted the same day. Planting units (hereafter referred to as PU or PUs) were constructed by attaching horizontal rhizomes and shoots to a 25 cm U-shaped metal staple using paper-coated wire twist ties. Each PU had approximately 15–30 shoots and ≥5 rhizome apical meristems. For installation of the PUs into sediment tubes, 5–10 cm slits were cut lengthwise into the top of the sediment tube fabric with a dive knife to create a space for inserting the PUs, and to allow horizontal rhizome growth while the fabric decomposed.

[1] Patented by James F. Anderson, founder of Seagrass Recovery, 5858 Central Ave., St Petersburg, FL 33707.

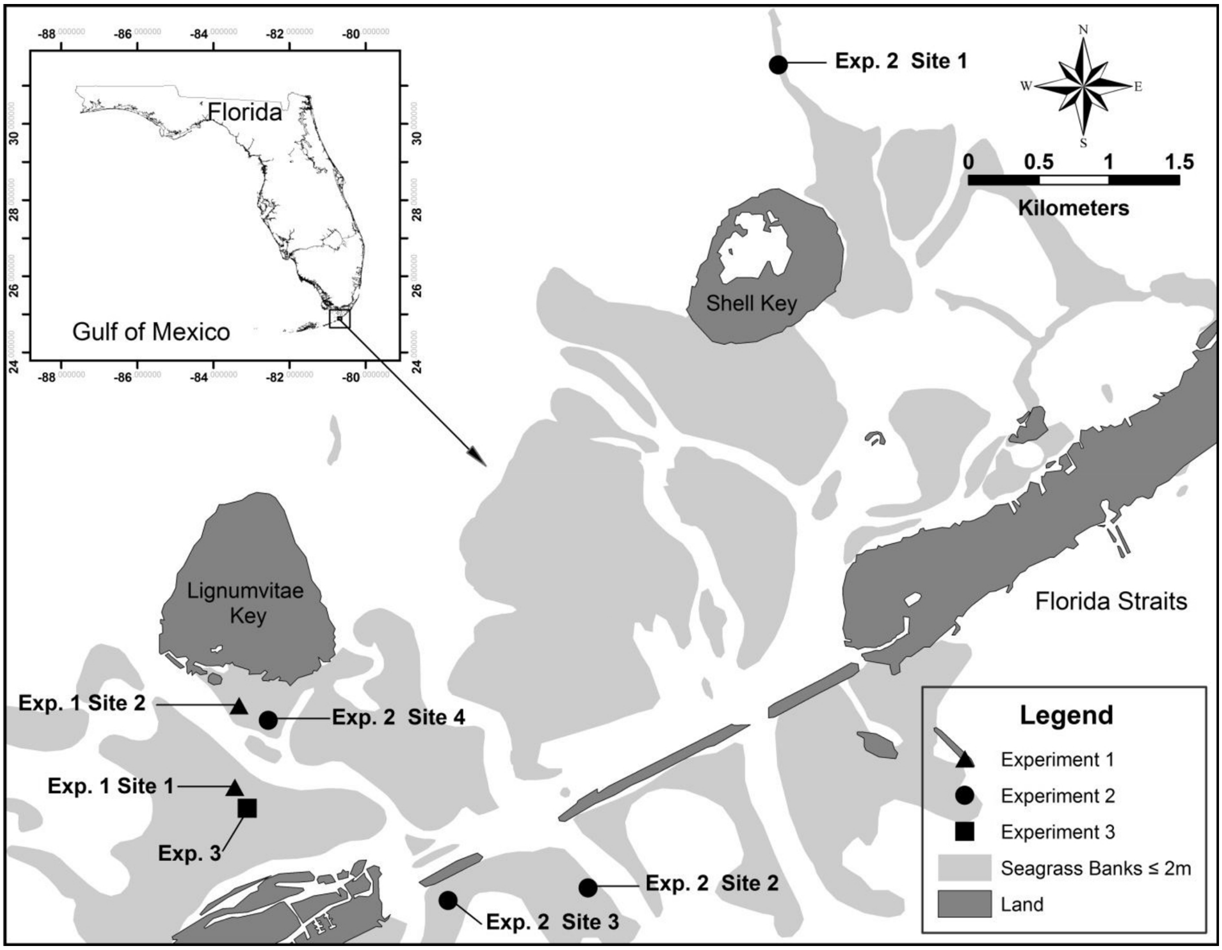

Fig. 1. Map of Florida, USA, showing the location of the study area and the three experiments. Experiment 1 was replicated at two sites and Experiment 2 was replicated at four sites.

2.4. Monitoring

Monitoring included initial assessments of PU survival within 30–80 days of planting (Experiments 1, 2, and 3), measurements of seagrass shoot density using either 0.01, 0.04, or 0.625 m^2 PVC quadrats, depending on density (Experiments 1, 2, and 3), and non-destructive visual estimates of cover (Experiments 2 and 3) in 0.25 m^2 quadrats (Braun-Blanquet, 1932; Fourqurean et al., 2001) (Table 1).

2.5. Experimental design

2.5.1. Experiment 1: bird stake fertilization in propeller scars

Two 80 m long unvegetated propeller scars (Exp. 1; Sites 1 and 2;) (Fig. 1) were selected within *T. testudinum* meadows in the LKSLMA. Maximum water depth over the scars was ≤1.5 m, and vertical relief between the scar bottom and surrounding sediment was ≤ 0.5 m. In July 1994, 20 bird stakes were placed at 4 m intervals along each of the two scars. Ten stakes in each scar were randomly assigned roosting blocks (fertilizer treatments, F), and ten remained free of blocks (non-fertilized treatments, NF). Five of ten roosting stakes (F) and five of ten non-fertilized treatment stakes (NF) in each scar were randomly selected for *H. wrightii* transplants. Initially, none of the original transplants survived and the scars remained unvegetated at the same excavation depths, so we returned in April 1995, ten months later, and replanted the entire experiment using the original planting design with the exception that the site was pre-conditioned with bird roosting stakes for 8 months.

Planting unit survival was surveyed in June 1995 and again in August 1995. By May 1996 many of the PUs had coalesced, making it impossible to identify individual PUs. Thereafter (May 1996 and January 1997), we measured the area covered by *H. wrightii* in each scar using a meter tape to delineate the area covered by seagrass in the scar and calculated the percentage of the entire original scar area occupied by *H. wrightii*. We also counted the number of shoots in 0.01m^2 quadrats placed within 0.5 m on each side of the bird stakes and controls (two quadrats per stake) along the entire length of each scar. To visually document seagrass re-growth into the prop scars at a relatively larger scale, oblique aerial photographs of the sites were taken opportunistically from an aircraft in December 1996, December 1997, September 1998 and January 2000 (Supplementary Fig. 1).

For statistical analyses, shoot counts were transformed (square root of ln + 0.5) and tested for normality and homogeneity of variance. We used *t*-tests to examine whether fertilization affected seagrass shoot density at each individual site in May 1996 and January 1997.

2.5.2. Experiment 2: bird stakes and sediment re-grading in propeller scars

Four locations in LKSLMA were selected (Exp. 2; Sites 1, 2, 3 and 4; Fig. 1). Within each location, four unvegetated propeller scars were chosen with dimensions 30–50 cm wide, 15–20 cm deep and a minimum of 24 m long (16 scars total). Individual scars were divided into 3 m sections and randomly assigned one of four treatments; 1) Control (a section of the scar devoid of any treatment); 2) Sediment Tubes (ST), in which a 3 m section of scar was filled with 2 layers of 4 Sediment Tubes (2 wide and 2 long); 3) Bird stakes + PUs (BS + PUs), and 4) Sediment Tubes + bird stakes + PUs (ST + BS + PUs) for a total of 16 replicates for each treatment. In treatments 3 and 4, bird stakes were placed in the center of the 3 m section, and *H. wrightii* PUs were planted at 50 cm and 100 cm intervals on each side of the bird stake

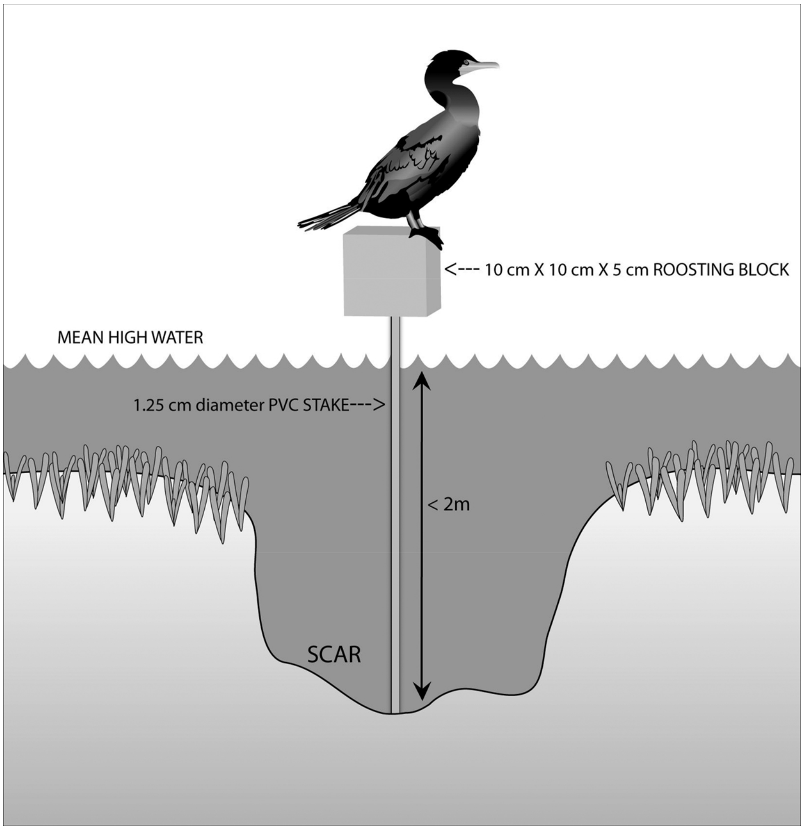

Fig. 2. Diagrammatic illustration and dimensions of a bird roosting stake located in a propeller scar.

Fig. 3. Photograph of sediment tubes being deployed into a propeller scar.

inside the scar for a total of 4 PUs. Treatment sections were interspersed by 3 m of untreated scar.

The experiment began in June 2001, and was monitored in September 2001, February 2002, August 2002 and May 2003 for PU survival and Braun-Blanquet visual assessments of seagrass cover within the scar and in the adjacent seagrass bed. The center 2.5 m section of each treatment was surveyed using five 50 cm x 35 cm modified Braun-Blanquet PVC quadrats placed end to end to assess contiguous sections of the treatment. Adjacent seagrass cover (ADJ) was assessed in 50 cm x 35 cm quadrats placed parallel to the scar treatments at a distance of 1 m into the undisturbed seagrass. Two quadrats were assessed per treatment, one on each side, for a total of eight adjacent quadrats per scar. Replicate quadrats were averaged to obtain one value for each treatment in each scar. Quadrats in the adjacent undisturbed seagrass were treated in the same manner. In May 2003 (approximately 2 years after deployment and the final sampling date) we counted the density of *H. wrightii* and *T. testudinum* shoots in each treatment. All counts were standardized to shoots m^{-2} for comparison between treatments.

For statistical analyses, *T. testudinum, H. wrightii* and total seagrass Braun-Blanquet cover data from the final survey date, May 2003, were analyzed. Kruskal-Wallis one-way ANOVA on ranks was conducted on

Table 1
Categorical values for Braun Blanquet visual assessment of seagrass and macroalgae cover.

Category value	Cover description
0	Species or taxa absent
0.1	Species or taxa solitary, with small cover
0.5	Species or taxa with few individuals and small cover
1	Species or taxa with numerous but less than 5% cover
2	Species or taxa with 5–25% cover
3	Species or taxa with 25–50% cover
4	Species or taxa with 50–75% cover
5	Species or taxa with 75–100% taxa

cover data. Wilcoxon signed-ranks tests were used to conduct pairwise comparisons among treatments when the overall ANOVA was significant at the $\alpha = 0.05$ level. *Halodule wrightii* shoot counts were natural log transformed to meet assumptions of normality and variance homogeneity and treatments were compared using one-way ANOVA and a Tukey's studentized range test.

2.5.3. Experiment 3: bird stake fertilization and sediment re-grading in a larger vessel excavation

This experiment was conducted in a large, eroded propeller scar (80 m long, 4.97 m wide and > 0.3 m deep) originally created in 1993 (Fig. 1). Previous efforts to topographically restore the site in 1999 with "ballast rock" fill (3.0 cm dia. limestone rubble) halted erosion and prevented further expansion of the scar (McNeese et al., 2006). However, the concurrent attempt to establish seagrasses by installing bird stakes and *H. wrightii* transplants into the ballast rock were unsuccessful and no natural recruitment of seagrass occurred. Here we designed an experiment to cap the ballast rock with finer-grained calcium carbonate sediment encapsulated in sediment tubes, transplant *H. wrightii*, and fertilize with a density of bird stakes comparable to the spacing used in Experiment 1. Based on the results of Experiments 1 and 2, we hypothesized that the finer-grained sediments placed over the original rock fill along with the additional bird stakes would support *H. wrightii* transplants and initiate seagrass regrowth. We also evaluated whether the thickness of the unconsolidated sediment layer would affect seagrass recovery.

The filled site was divided into thirty individual 3 m by 3 m rectangular plots. Three treatments were randomly assigned to plots as follows: 1) Bird stakes plus *H. wrightii* PUs and a single layer of 40 sediment tubes (S) (n = 10 plots); 2) Bird stakes plus *H. wrightii* PUs and a double layer of 80 sediment tubes (D) (n = 10 plots); and 3) A control treatment that did not receive sediment tubes, additional bird stakes or seagrass PUs on the original rock fill (C) (n = 10 plots).

Treatment plots had nine bird roosting stakes distributed on approximately 1.5 m centers. Four of the nine stakes remained from the first attempt to restore the site (McNeese et al., 2006). The five new stakes in each plot were constructed and installed as described previously to achieve the desired stake spacing and density.

In May 2003, 36 *H. wrightii* PUs were installed on 0.5 m centers in each sediment tube plot. No PUs were installed into the 10 untreated plots because earlier attempts to establish PUs in the ballast rock failed. The experiment was monitored approximately every 90 days until September 2005. Seagrass PU survival was measured during the first monitoring event in September 2003, and missing PUs were replaced in October 2003. Beginning in January 2004, each experimental plot (3 m * 3m) was divided into four equal quadrants, each with four equally sized sub-plots. Within each quadrant we randomly selected one subplot for placement of $0.25 m^2$ Braun-Blanquet quadrats. Seagrass and macroalgal cover were estimated in the quadrats, and species density was quantified by counting shoots in $0.01 m^2$ quadrats placed in a randomly located position within each of the four Braun-Blanquet quadrats. Thus, each plot had four sub-samples for estimating cover and shoot density. Thickness of the unconsolidated sediments was determined at the four positions in each plot during the monitoring events by inserting a measuring stake into the sediment until it reached the ballast rock underneath. In addition, the species composition and number of birds perching on the stakes was recorded at the beginning of each of three sampling events at 5, 8 and 12 months after the initial planting.

Data for *H. wrightii* cover and shoot density were analyzed for the sampling event in September 2005. These data failed to meet the assumption of normality, so we tested for treatment effects using a Kruskal-Wallis one-way ANOVA on ranks ($p = 0.05$). For multiple comparisons we used Tukey's test.

In October 2011 and 2014, approximately eight and 11 years after initiating the experiment, we returned to determine if *T. testudinum* was recolonizing the site. Since all the birdstakes were removed and we could not delineate the original plots, we did not use the original monitoring design. After locating the original four corner points, we divided the entire site into 100 equally sized tessellated hexagons in Arc GIS. In the field, we navigated to the center point of each hexagon using a differential GPS (DGPS). At each point seagrass cover was estimated (Braun-Blanquet visual assessment) and seagrass shoot density was counted in a $0.01 m^2$ quadrat placed in the center of each Braun-Blanquet quadrat. Seagrass cover and shoot density were also assessed in 20 quadrats haphazardly located in the adjacent undisturbed seagrass bed surrounding the original restoration site.

3. Results

3.1. Experiment 1; bird stake fertilization in propeller scars

In June 1995, 78 days after planting, PU survival at Site 1 was 75% in the fertilized/planted treatment and 55% in the non-fertilized/planted treatment. At Site 2, PU survival was 96% in the fertilized/planted treatment and 85% in the non-fertilized/planted treatment. In August 1995, 138 days after planting, survival at Site 1 was 68% for the fertilized PUs and only 18% for the non-fertilized PUs. Survival at Site 2 was 85% and 81% for the fertilized and non-fertilized PUs, respectively. By May 1996, 395 days since planting, many of the PUs had coalesced and spread along the length of the scar, regardless of treatment, and into unplanted areas, so it was impossible to record survival of individual transplants and determine whether the *H. wrightii* originated from the adjacent seagrass bed.

In May 1996 there were significantly greater numbers of *H. wrightii* shoots in the fertilized treatment compared to the non-fertilized treatment at both Site 1 ($t = 3.1270$, $p = 0.0029$, $df = 18$) and Site 2 ($t = 3.5837$, $p = 0.0024$, $df = 10$) (Fig. 4). There continued to be significantly greater numbers of *H. wrightii* shoots in the fertilized treatments compared to the unfertilized treatments at both sites in January 1997 (Site 1; $t = 2.9570$, $p = 0.0042$, $df = 18$ and Site 2; $t = 4.8589$, $p = 0.0001$, $df = 14$) (Fig. 4).

In May 1996, when the *H. wrightii* transplants began coalescing and it wasn't possible to distinguish cover between the original treatments, we measured the percent of each scar covered by seagrass. Percent cover of *H. wrightii* in the scars at Sites 1 and 2 were 22 and 40%, respectively (Fig. 5). By January 1997, 639 days since planting, *H. wrightii* cover in the scars increased to 43% at Site 1 and 56% at Site 2 (Fig. 5). *Halodule wrightii* continued to grow and expand rapidly, colonizing unplanted portions of the scars, and by January 2000 the scar at Site 1 had become completely covered with *H. wrightii* (Supplementary Fig. 1d).

3.2. Experiment 2: bird stakes and sediment regrading in propeller scars

Thalassia testudinum cover increased steadily in all the treatments throughout the course of the monitoring period, but was still less than half of the ambient cover in the adjacent seagrass meadow after

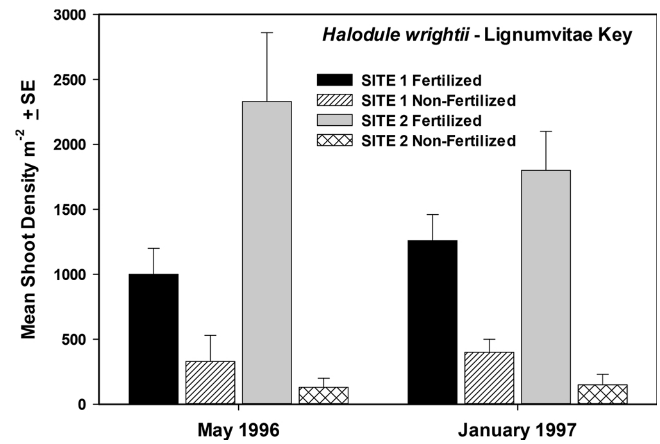

Fig. 4. Results of Experiment 1 showing mean *Halodule wrightii* shoot density (± SE) at sites 1 and 2 in fertilized and non-fertilized treatments on two sampling dates, May 1996 and January 1997.

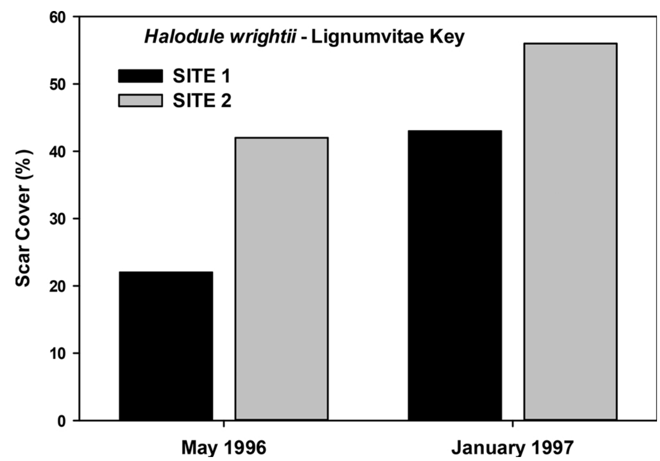

Fig. 5. Results of Experiment 1 showing the percent coverage of *Halodule wrightii* in each scar at sites 1 and 2 on two sampling dates, May 1996 and January 1997.

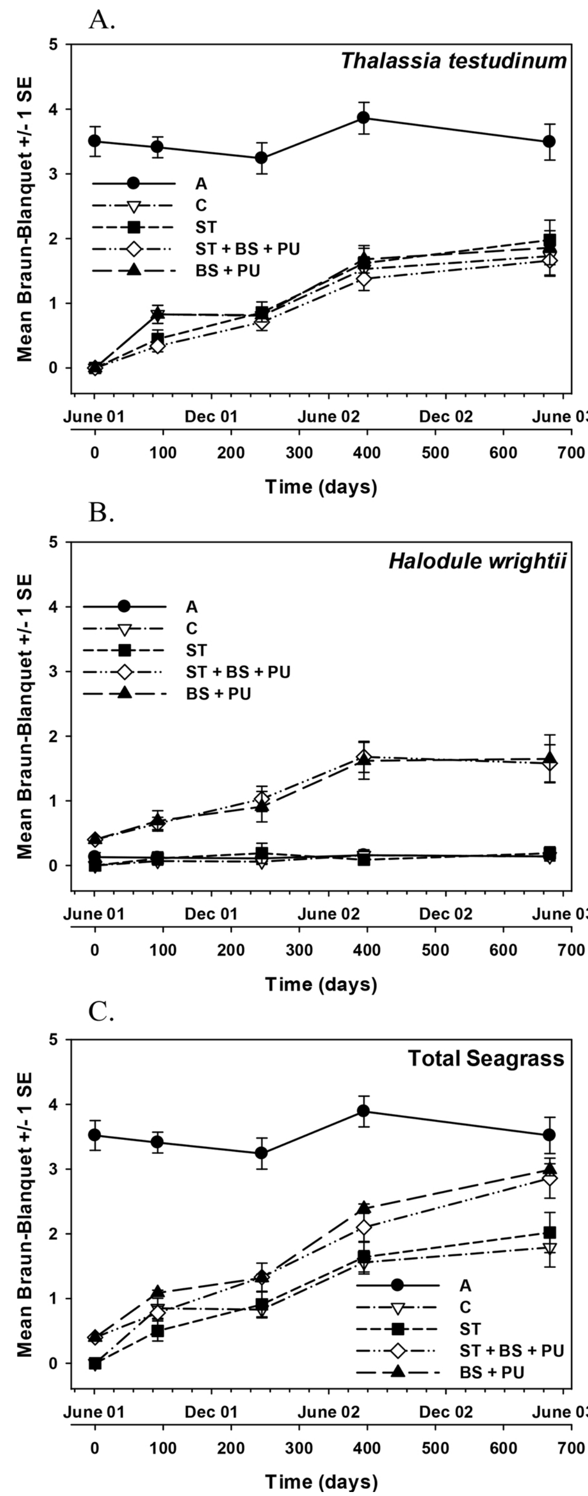

Fig. 6. Results of experiment 2 showing mean (± SE) Braun Blanquet cover for *Thalassia testudinum* (A), *Halodule wrightii* (B) and total seagrass (C) for five treatments as a function of time (days). Treatments are; A = adjacent seagrass bed, C = control, ST = bird stakes, ST + BS + PU = sediment tubes + bird stakes + *Halodule wrightii* planting units, and BS + PU = bird stakes + *Halodule wrightii* planting units.

700 days (Fig. 6a). *Halodule wrightii* cover increased only in the treatments with both PUs and bird stakes, and reached an asymptote approximately 400 days after planting (Fig. 6b). We saw no *H. wrightii* recruitment or vegetative growth into the control or sediment tube treatments, not surprising given the very low abundance of *H. wrightii* in the adjacent, undisturbed bed at the start of the experiment. Total seagrass cover also increased over time, with the largest increase in treatments with *H. wrightii* PUs and bird stakes (Fig. 6c).

The ANOVAs revealed significant treatment effects on *T. testudinum*, *H. wrightii*, and total seagrass cover in May 2003 ($p = 0.0004$, $p < 0.0001$, and $p = 0.0018$, respectively, Table 2). Pairwise comparisons for *T. testudinum* cover on the final survey date showed that the only significant differences were between the adjacent seagrass bed and the treatments inside the scars. There were no differences in *T. testudinum* cover among treatments. In contrast, *H. wrightii* cover in ST + BS + PU and BS + PU treatments were similar, but cover in both of these treatments was significantly higher than the other two treatments (C and ST) and the adjacent seagrass beds ($p < 0.0001$) (Fig. 6c, Table 2). By May 2003 total seagrass cover in both bird stake treatments with PUs had reached a level nearly equivalent to cover in the adjacent seagrass bed, primarily as a result of the growth of *H. wrightii* ($p < 0.0018$, Table 2, Fig. 6c). The BS + PU treatment was similar to both the ST + BS + PU treatment and the adjacent seagrass bed (A), which were significantly greater than sediment tubes alone (ST) and the controls (C).

Short-shoot counts of *H. wrightii* ranged from $4.0\,m^{-2}$ in the adjacent seagrass bed to $1130\,m^{-2}$ in the ST + BS + PU treatment (Fig. 7). One-way ANOVA for *H. wrightii* shoot density revealed differences among treatments ($p < 0.0001$, Table 2). Pairwise comparisons of the shoot density data revealed that the two bird stake treatments with PUs (ST + BS + PU and BS + PU) had significantly higher *H. wrightii* shoot densities than the other three treatments (ST, C, and A),

Table 2
Statistical analysis of results for experiment 2 including both the main effects and the pairwise comparisons between the five treatments. Treatments are; ADJ = adjacent seagrass bed, C = control, ST = sediment tubes, BS = bird stakes, PU = Planting Unit. Significant treatment effects are indicated by different letters in the pairwise comparisons ($p < 0.05$).

Main Effects Results			Pairwise Comparisons				
Variable	Test	p-value	ADJ	C	ST	ST + BS + PU	BS + PU
T. testudinum cover	Kruskal-Wallis	0.0004	A	B	B	B	B
H. wrightii cover	Kruskal-Wallis	< 0.0001	A	A	A	B	B
Total seagrass cover	Kruskal-Wallis	0.0018	A	B	B	A	A
H. wrightii shoot density	ANOVA	< 0.0001	A	A	A	B	B

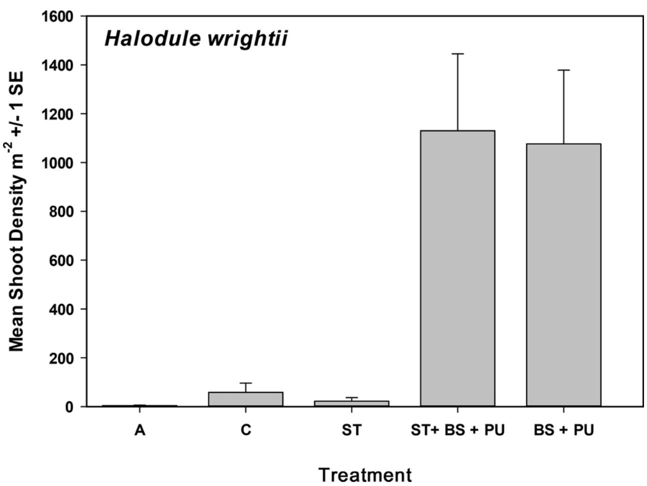

Fig. 7. *Halodule wrightii* shoot density (± SE) for each treatment in May 2003.

which were not significantly different from each other (Fig. 7; Table 2).

The sediment tube fabric began to decompose within three months of deployment and we did not find any fabric during the May 2003 survey. Despite this, most of the calcium carbonate sediment introduced in the tubes remained in the scars throughout the study, leveling the topography between the scars and the adjacent seagrass beds.

3.3. Experiment 3: bird stake fertilization and sediment regrading in a larger vessel excavation

At the first monitoring event in September 2003, *H. wrightii* PU survival was 26.2% in the single tube and 29% in the double tube treatments. Based on this low survival, we replaced all of the missing PUs in both treatments in October 2003. Following replanting, *H. wrightii* growth was rapid, and by January 2004 we could not distinguish individual PUs to estimate survival. *Halodule wrightii* cover and shoot density in the plots without tubes remained low throughout the experiment, as they had in the prior attempt to restore the site (Fig. 8). In the two sediment tube treatments, both *H. wrightii* shoot density and cover increased between January and May 2004, with cover values reaching their highest levels in both treatments in September 2004 (Fig. 8a, b). Shoot density reached the highest value in the double tube treatment in May 2004, followed by a steady decline for both tube treatments until September 2005. Shoot density ranged from 0 to 305 m^{-2} in the plots without sediment tubes, and from 1300–6800 shoots m^{-2} in the two tube treatments.

Results in September 2005 revealed significant treatment effects on *H. wrightii* cover ($p < 0.002$) and shoot density (ANOVA on ranks,

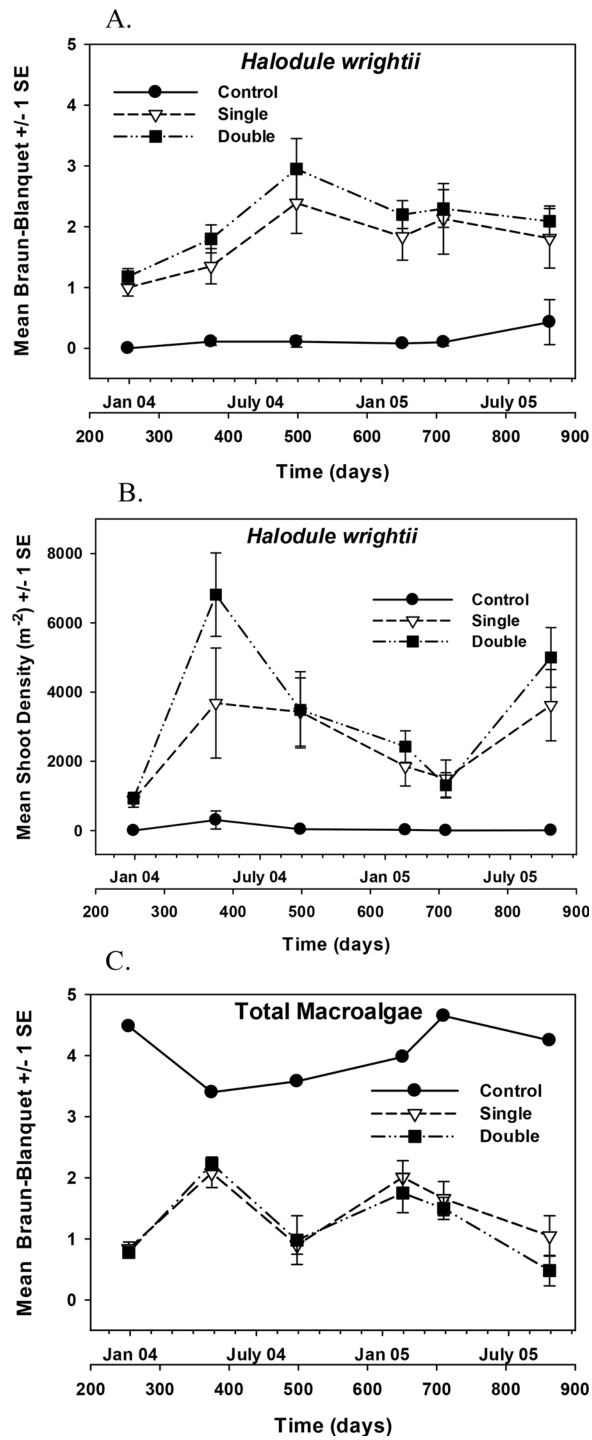

Fig. 8. Results of experiment 3 showing mean (± SE) Braun Blanquet cover for *Halodule wrightii* cover (A), *Halodule wrightii* shoot density (B) and total macroalgae (C) for three treatments as a function of time (days). Treatments are control, single layer of sediment tubes and double layer of sediment tubes.

$p < 0.001$, Table 3). Pairwise comparisons indicated there were no differences in cover and shoot density between the single and double layer tube treatments, but both were significantly higher than the untreated plots.

Total macroalgal cover was always higher in the plots without tubes than either of the sediment tube treatments (Fig. 8c, Table 3). Between January 2004 and May 2004, macroalgal cover more than doubled in the sediment tubes coincidental with more than a quadrupling of *H. wrightii* density. These high macroalgal cover values prompted concern

Table 3
Statistical analysis of results for experiment 3 for the September 2005 sampling event including both the main effects and the pairwise comparisons between the three treatments. Treatments are; Control = no sediment tubes, Double = double layer of sediment tubes, and Single = single layer of sediment tubes. Significant treatment effects are indicated by different letters in the pairwise comparisons ($p < 0.05$).

Main Effects Results			Pairwise Comparisons		
Variable	Test	p-value	Control	Double	Single
H. wrightii cover	Kruskal-Wallis	< 0.002	A	B	B
Macroalgae cover	Kruskal-Wallis	< 0.001	A	B	B
H. wrightii shoot count	Tukeys Test ANOVA	< 0.001	A	B	B

for nutrient over-enrichment, so in September 2004 we removed the five newest bird stakes installed in each sediment tube treatment, leaving only the original four stakes. Thereafter, macroalgal cover fluctuated, and by September 2005 macroalgal cover was similar to the initial monitoring event in January 2004.

We returned to the site in May 2009, removed all the remaining bird stakes and observed very little *T. testudinum* at the site. In October 2011 *H. wrightii* densities in the filled scar decreased from ≈ 4000 shoots m^{-2} recorded in September 2005 to 840 shoots m^{-2} in 2011 (Fig. 9). This decline continued, and by 2014 densities were slightly less than 193 shoots m^{-2}.

In 2011 *T. testudinum* shoot densities were 96 m^{-2} and increased to 122 m^{-2} in 2014, or 33% of the density in the adjacent undisturbed seagrass bed (367 shoots m^{-2}) (Fig. 9). No *H. wrightii* was observed in the adjacent undisturbed *T. testudinum* meadow in either 2011 or 2014.

At all monitoring dates during Experiment 3 the stakes were occupied by terns (*Sterna hirundo*) and cormorants (*Phalacrocorax auritus*). Total bird occupancy ranged between 17% and 69% of the stakes during the entire experiment. Sediment depths changed very little. In April 2005 there was < 1.0 cm of sediment in the controls while 7.5 cm remained on the single layer of tubes, and 16 cm on the double layer.

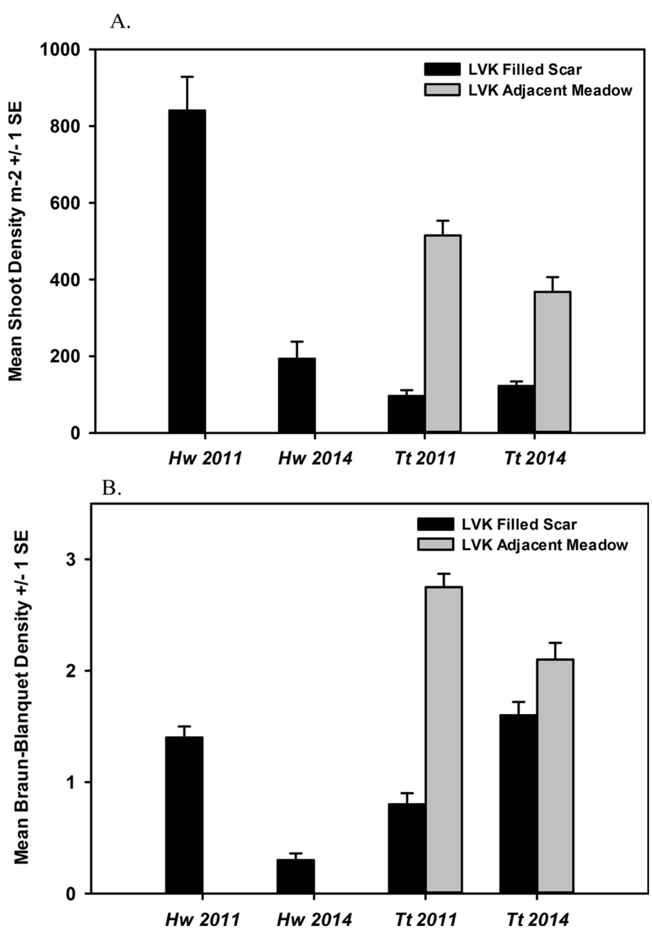

Fig. 9. Shoot density (± SE) (top panel) and Braun Blanquet density (bottom panel) for *Halodule wrightii (Hw)* and *Thalassia testudinum (Tt)* in experiment 3 in October 2011 and October 2014. Data are for shoot densities of *T. testudinum* and *H. wrightii* in the filled scar and *T. testudinum* in the adjacent undisturbed seagrass meadow. There was no *H. wrightii* observed in the adjacent undisturbed seagrass meadow.

4. Discussion

The experiments demonstrated the feasibility of accelerating restoration of injured *T. testudinum* meadows by transplanting and fertilizing a fast-growing opportunistic seagrass, *H. wrightii.* Initially, survival was poor in Experiments 1 and 3. However, after replanting, *H. wrightii* grew rapidly and began expanding and coalescing in the disturbances. Within one to two years, *H. wrightii* in fertilized treatments increased in areal coverage and reached shoot densities similar to the highest densities reported in an earlier bird stake fertilization experiment (Fourqurean et al., 1995). Compared to previously measured rates of *T. testudinum* recovery in untreated propeller scars (Kenworthy et al., 2002), the results of the present study indicate that *H. wrightii* growth in planted and fertilized treatments was three to five times faster and significantly accelerated seagrass recovery in the excavations. The rapid growth of *H. wrightii* in the fertilized treatments of all three experiments compressed the rate of succession in a sub-tropical seagrass community and ensured the substitution of ecological services and physical stability during the slower pace of *T. testudinum* recovery. Some *T. testudinum* recolonized the propeller scars in Experiment 2, but the total seagrass cover during the two year monitoring period was largely the result of high densities of transplanted *H. wrightii* responding to the fertilization. After removal of the fertilizer treatment in Experiment 3, longer-term monitoring indicated that densities of *H. wrightii* declined and regrowth of *T. testudinum,* the injured and dominant species in the undisturbed adjacent meadow, was proceeding.

We tested the application of compressed succession in combination with topographic restoration in propeller scars in Experiment 2 and a much larger excavation in Experiment 3. Normally, undisturbed *T. testudinum* meadows trap and stabilize fine-grained sediments and organic matter which provide unconsolidated substrate and nutrients required for the development and maintenance of a seagrass meadow (Zieman, 1982; Williams, 1990). This important physical-chemical process occurs very slowly in naturally developing *T. testudinum* beds (Zieman, 1982), and even more slowly in meadows recovering from severe physical disturbance by vessel excavations (Kenworthy et al., 2002; Di Carlo and Kenworthy, 2008; Uhrin et al., 2011; Bourque and Fourqurean, 2014; Bourque et al., 2015). The natural process of filling and regrading may be delayed for years or even decades, leaving the vessel injures exposed to further degradation from scouring and expansion (Williams, 1988; Whitfield et al., 2002, 2004; Di Carlo and Kenworthy, 2008; Uhrin et al., 2011). Both Experiments 2 and 3 demonstrated that re-grading injuries with biodegradable fabric tubes filled with fine-grained calcium carbonate sediment provided a satisfactory physical substrate for the growth of both *H. wrightii* and *T. testudinum* (Figs. 7, 8, and 9). However, the results of Experiment 2 demonstrated that fertilizing with bird stakes and planting *H. wrightii* yielded the highest density and recovery rates of seagrass and it was evident that sediment tubes were not a necessary pre-requisite for recovery of relatively smaller propeller scars.

In contrast, the larger excavation in Experiment 3 failed to recover after re-grading with ballast rock and installing bird stakes (McNeese et al., 2006). But, after capping the coarse-textured ballast rock with sediment tubes, increasing bird stake density, and planting *H. wrightii,* seagrass recovery proceeded (Fig. 9). Initial survival of transplants was low, but after replanting *H. wrightii* grew rapidly and increased in cover and density on the both the single and double layers of tubes, while the

ballast rock treatment supported primarily macroalgae. Removing all of the bird stakes from Experiment 3 in 2009 reduced the delivery of nutrients and *H. wrightii* densities declined while *T. testudinum* started to recolonize. Removing the fertilizer treatment relaxed the compressed succession, but a reservoir of nutrients remained in the sediment (Herbert and Fourqurean, 2008) that could be utilized by the slower-growing climax species during the longer recovery process (Fig. 9).

5. Summary and recommendations

Initial recovery of vessel injuries in shallow water *T. testudinum* meadows was accelerated by transplanting a fast-growing pioneer species (*H. wrightii)* and fertilizing with bird roosting stakes. This method of "modified compressed succession" passively delivers phosphorous, the limiting nutrient for seagrasses growing in carbonate sediments (Short et al., 1985; Fourqurean et al., 1995), and will most likely succeed in environments where seagrasses are phosphorus limited. Our study was restricted to environments where it was scientifically demonstrated that carbonate sediments were the primary source of phosphorus limitation. However, this method could also be successful in locations where water column phosphorus concentrations are limiting seagrasses. Future experimental studies should address the use of this method in locations where it is known that phosphorus availability in the water column is limiting seagrasses. The results of these studies would help to either broaden or constrain the scope of application for this restoration method.

Our study also addressed sub-tropical seagrass recovery in different sized disturbances. Whereas relatively shallow and narrow propeller scars can be restored without filling (also see Hammerstrom et al., 2007), recovery of larger and deeper excavated disturbances is much slower and may never occur without sediment regrading (Uhrin et al., 2011). We know from ecological studies (Zieman, 1982) and prior restoration experiments (McNeese et al., 2006; Hammerstrom et al., 2007) that the texture and thickness of unconsolidated sediments are important for seagrass growth and the recovery of injured meadows. For best results, particle size of the fill material should achieve a balance between a size large enough to resist erosion yet still be able to support seagrass growth and ecosystem structure and function (Bourque and Fourqurean, 2014; Bourque et al., 2015). Filling the lower portion of a deep excavation with coarse-textured material (e.g., McNeese et al., 2006) and capping the fill with finer-grained sediments encapsulated in biodegradable fabric tubes is a means of stabilizing larger and deeper injuries while retaining the fine-grained characteristics of the surface sediments. Filling a disturbance will increase the cost of restoration (see supplemental Table 1), but it also provides a more optimum substrate for planting and fertilizing, as well as sediment stabilization. These conditions will improve the likelihood of faster seagrass recovery while preventing further expansion of the disturbances, especially in high energy environments where disturbance gaps are more likely to erode and may never recover (Uhrin et al., 2011). When installing sediment tubes we recommend waiting 3–5 months before planting seagrass to; 1) allow the fabric to deteriorate enough for the seagrass rhizome and roots to penetrate, and 2) allow nutrients to accumulate when using tubes in conjunction with bird stakes. In the short term ($\leq$1year) there may be some delays in recovery of sediment structure and function associated with topographic restoration (Bourque and Fourqurean, 2014), but in the long-term, prevention of further deterioration and recovery of the seagrass will compensate for the delays.

The initial goal of modified compressed succession is to temporarily stimulate the opportunistic pioneer species, but restoration practitioners must be careful not to over-fertilize a site. Excess phosphorous could create a sustained disturbance by stimulating an overabundance of *H. wrightii* and/or macroalgae and potentially slow *T. testudinum* recovery (Herbert and Fourqurean, 2008). Our results indicate that these two over-fertilization responses can happen relatively quickly and suggest that the restoration sites should be frequently monitored to ensure detection of any detrimental response. Results indicated that modified compressed succession can be attained in $\approx$ 12 to 18 months to gain the full benefit of the fertilizer after which time the bird stakes can be removed and recycled for use in other projects. Within this time frame, monitoring of the site should take place at a minimum of every three months to determine if the bird stakes should be removed. This step will relax the nutrient inputs, avoid the over-growth of macroalgae and allow for the slower-growing climax species *T. testudinum* to recolonize the site and complete the succession.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecoleng.2017.12.008.

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