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Effects of common seagrass restoration methods on ecosystem structure in subtropical seagrass meadows

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ABSTRACT

Seagrass meadows near population centers are subject to frequent disturbance from vessel groundings. Common seagrass restoration methods include filling excavations and applying fertilizer to encourage seagrass recruitment. We sampled macrophytes, soil structure, and macroinvertebrate infauna at unrestored and recently restored vessel grounding disturbances to evaluate the effects of these restoration methods on seagrass ecosystem structure. After a year of observations comparing filled sites to both undisturbed reference and unrestored disturbed sites, filled sites had low organic matter content, nutrient pools, and primary producer abundance. Adding a nutrient source increased porewater nutrient pools at disturbed sites and in undisturbed meadows, but not at filled sites. Environmental predictors of infaunal community structure across treatments included soil texture and nutrient pools. At the one year time scale, the restoration methods studied did not result in convergence between restored and unrestored sites. Particularly in filled sites, soil conditions may combine to constrain rapid development of the seagrass community and associated infauna. Our study is important for understanding early recovery trajectories following restoration using these methods.

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1. Introduction

Loss of seagrass resources in coastal ecosystems is accelerating (Waycott et al., 2009), and physical disturbance from storm events, dredging, development, and fishing gear impacts, contributes to this decline (Grech et al., 2012; Orth et al., 2006; Short and Wyllie-Echeverria, 1996). Seagrass soils are critical in supporting key ecosystem functions such as nutrient cycling and benthic remineralization processes (Hemminga and Duarte, 2000; Marba et al., 2006). Physical disturbance to seagrass meadows that disrupts the rhizosphere leads to persistent changes in ecosystem function, including primary production, nutrient cycling, and habitat provision for seagrass-associated organisms (Di Carlo and Kenworthy, 2008; Hammerstrom et al., 2007; Neckles et al., 2005). Disturbance results in alterations to soil structure including loss of organic matter and stored nutrients (Bourque, 2012; Kenworthy et al., 2002). Seagrass ecosystems in locations where boating is popular are subject to frequent and severe physical disturbance when vessels run aground (Dunton and Schonberg, 2002; Kirsch et al., 2005; Sargent et al., 1995; SFNRC, 2008). Accordingly, interest in seagrass restoration has increased in recent decades (Fonseca, 2011; Paling et al., 2009; Treat and Lewis, 2006).

Resource managers attempt to accelerate recovery of disturbed seagrass communities through restoration. Filling grounding excavations, providing a fertilizer source, and transplanting seagrasses are commonly-used restoration techniques (Farrer, 2010; Fonseca et al., 1998; Kirsch et al., 2005; McNeese et al., 2006). Placing soil fill into excavations is intended to prevent erosion and recreate the physical matrix that supports seagrasses and ecosystem functioning (Farrer, 2010; Hall et al., 2012; Hammerstrom et al., 2007; Kirsch et al., 2005). Seagrasses also may be transplanted to accelerate replacement of plant structure and associated functions over natural secondary succession (Lewis, 1987). Because seagrass ecosystems are often nutrient limited (Short, 1987; Fourqurean et al., 1992), applying fertilizer aims to reestablish or augment pools of limiting nutrients. Since the discovery that seabirds will perch on poles emerging from the water and fertilize the seagrasses of south Florida resulting in changes to

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community structure (Fourqurean et al., 1995; Powell et al., 1989), such bird perches have been used as inexpensive low-maintenance fertilizer additions in seagrass restorations in the region (Kenworthy et al., 2000; Farrer, 2010).

For restoration to be successful, ecological attributes of the system such as structure, composition, and function must be reestablished (Fonseca et al., 1996a; Higgs, 1997; Hobbs and Norton, 1996). Once restoration has been implemented, rapid assessments of plant communities are typically used to monitor restoration success (Farrer, 2010; Fonseca et al., 1998; Kirsch et al., 2005; Uhrin et al., 2011). Few studies have assessed ecosystem structure following seagrass restoration for any aspects other than aboveground plant communities (Fonseca et al., 1996a; McNeese et al., 2006; Hammerstrom et al., 2007; Hall et al., 2012; but see Evans and Short, 2005; Di Carlo and Kenworthy, 2008). Analysis of seagrass associated fauna at restoration sites has included studies of infauna (Bell et al., 1993; Sheridan, 2004a,b; Sheridan et al., 2003) and epibenthic fish and invertebrates (Fonseca et al., 1990, 1996b), but only at sites where transplanting was conducted. We are unaware of studies of seagrass infauna community response to restoration activities involving methods other than seagrass transplanting, such as filling excavations or fertilizing restoration sites.

Recent work has shown that soil structure is substantially altered by some restoration practices, especially placing coarse-grained, erosion-resistant fill into fine-grained seagrass ecosystems (McNeese et al., 2006). Filling excavations achieves the objective of stabilizing sites prone to erosion and providing the physical matrix needed to support macrophyte recolonization, but seagrasses and nutrient pools in the soils may be slow to recover.

We sampled macrophyte and infauna communities and soil properties at seagrass restoration sites quarterly for one year following restoration using the filling and nutrient addition methods, alone and in combination, in order to better understand the effects of common restoration actions on seagrass ecosystem structure. We hypothesized that a) restoration actions including fill placement and fertilizer delivery via bird stakes alter primary producer and infauna abundance and soil properties; and b) sites that had been restored either though filling or fertilization more rapidly converged on pre-disturbance conditions than did unrestored sites. Our response variables included structural attributes essential to habitat quality, nutrient storage, ecosystem metabolism, and the structure of the benthic faunal community.

2. Methods

2.1. Study system

This study was conducted on Cutter Bank (25.36715°, −80.26899° in southern Biscayne Bay, a shallow (<3 m) subtropical estuary located at the southeastern tip of the Florida peninsula, USA. Seagrass communities in southern Biscayne Bay are dominated by dense *Thalassia testudinum* meadows typical of oligotrophic tropical seagrass communities throughout the western Atlantic and Caribbean (Zieman, 1982). *Syringodium filiforme*, *Halodule wrightii*, and calcareous green macroalgae are also found throughout this area in lower abundance and with patchy distribution (Bourque and Fourqurean, 2013). A dissolved inorganic nitrogen gradient decreases from west to east in the bay, influenced by freshwater input from canals along the western shoreline (Caccia and Boyer, 2005), and phosphorus limitation of seagrass abundance and productivity is commonly observed in south Florida (Fourqurean and Zieman, 2002). The limited available information on infauna in seagrass soils of this area (McLaughlin et al., 1983; Roessler, 1971) suggests that these communities are typical of those found in subtropical seagrass meadows. Many shallow seagrass shoals (<1 m) in Biscayne Bay, including Cutter Bank, are heavily impacted by vessel groundings, where seagrass has been removed and soil excavated in discrete areas (Bourque, 2012).

2.2. Experimental design

We evaluated ecosystem structure through seagrass community, soil, and infaunal invertebrate community parameters at eighteen individual sites at Cutter Bank. Sites were an average of 34 m^2 in size and 0.4 m in depth, and the maximum distance between sites was approximately 60 m. A factorial design was employed, with soil condition, fertilization, and time as factors. Soil condition treatments included unrestored vessel grounding injuries ("disturbed" sites), restored grounding injuries that were returned to grade with carbonate sand fill from local south Florida quarries ("filled" sites"), and vegetated plots in the undisturbed seagrass meadow ("reference" sites). At each filled site, eleven to 37 cubic meters of sand was placed into excavations as loose fill using a barge-mounted clamshell bucket. The soil condition factor was crossed with a fertilization factor by installing bird roosting stakes into a subset of sites within each three soil condition treatments, henceforth denoted as "disturbed+", "filled+", and "reference+" sites. At each fertilized site, between five and 28 bird roosting stakes were installed on 2-m centers so that the roosting block was approximately 30 cm above the surface of the water at high tide. Three sites were included in each soil condition × fertilization treatment. Soil condition and fertilization treatments were randomly assigned to sites. Note the disturbed sites and the sites that were filled were not recent disturbances, but rather were known to be a minimum of five years old based on knowledge of disturbance features at Cutter Bank (Bourque, unpublished).

Reference and reference + plots for soil and invertebrate parameters were established by delineating 32 m^2 circular plots around randomly selected points in a seagrass-vegetated area of the shoal that showed no signs of recent vessel grounding disturbance. For seagrass community parameters, undisturbed seagrass meadows within a 2 m buffer encircling each disturbed or filled site were sampled for reference conditions. Sites were sampled following implementation of a restoration project that was completed in January–February 2010. For soils and invertebrate parameters, sampling began within a month of restoration completion, and was repeated at 3, 6, 9, and 12 months following restoration (i.e., February, May, August, November 2010 and February 2011). The seagrass community was sampled only at months 0, 6, and 12 months following restoration.

2.3. Seagrass community characterization

To evaluate the status of the macrophyte community at each site, seagrass and macroalgae abundance was estimated within randomly placed 0.25 m^2 PVC quadrats, using a modified Braun-Blanquet (BB) cover-abundance scale (Fourqurean et al., 2001). While many taxa of macroalgae were encountered in our surveys, only the calcareous green macroalgae from the genera *Halimeda*, *Penicillus*, and *Udotea* were common, so we have restricted our analysis of macroalgae data to this group. Ten percent of each site area was sampled.

2.4. Soil core collection and processing

We sampled a suite of twelve soil properties that are indicators of structure and function in seagrass ecosystems, including benthic microalgae (primary production, habitat quality); pH, redox potential, organic matter content, and porewater sulfide (benthic

metabolism and remineralization); bulk density, water content, and particle size (nutrient exchange); and nitrogen and phosphorus in soil and porewater (nutrient storage). Soils were sampled by collecting 7.3 cm × 40 cm cores from each site using a piston corer. Three cores were haphazardly collected per site per sampling event, and replicate data were averaged for analysis. Following collection, core tubes were immediately plugged at both ends, and temporarily stored in the dark in a vertical position in ambient seawater until processed.

Cores were extruded and sectioned into six depth horizons (0–2 cm, 2–6 cm, 6–10 cm, 10–20 cm, 20–30 cm, and 30–40 cm in a nitrogen-filled glovebox. The pH and redox potential (E_h) of soils from each homogenized depth horizon were measured in the glovebox. Depth horizons were then subsampled for analysis of benthic microalgal biomass (as chlorophyll *a,* chl *a*), soil physical properties (bulk density, water content, particle size, organic matter content, total nitrogen, total phosphorus), and porewater constituents (ammonium (NH_4^+), soluble reactive phosphorus (SRP), and dissolved sulfide (DS)). Soils for porewater extraction were placed into 50 ml centrifuge tubes and capped inside the glove box, centrifuged for five minutes at 3000 rpm, and returned to the glovebox. Extracted porewater was filtered through GF-C in-line syringe filters and subsampled into two aliquots for analysis of NH_4^+/SRP and DS. Samples for DS were fixed with 1 M ZnAc in a 1:10 dilution (Holmer et al., 2001) and stored at room temperature; all other soil and porewater samples were frozen at −20 °C until further analysis.

Benthic microalgal biomass was measured for the 0–2 cm horizon only. Soils were freeze-dried and pigments extracted with 90% acetone for 72 h at −20 °C, and chl *a* content (μg g^{-1}) was measured flourometrically (Strickland and Parsons, 1972) on a Shimadzu RF 5301PC spectrofluorophotometer (excitation = 435 nm, emission = 667 nm). Soil bulk density (BD) was measured as dry mass per unit volume. Water content (WC) was determined as proportional mass loss after drying soils at 75 °C for 48 h. Grain size contributions were determined through sieve analysis (Folk, 1974; Ingram, 1971) for the 0 and 12 month samples. Particle size class contributions were determined for gravel ($\Phi < -1$), sand ($-1 \leq \Phi < 4$), silt ($4 \leq \Phi < 8$), and clay ($\Phi \geq 8$). Organic matter content (OM) was measured as loss on ignition (LOI) at 500 °C for four hours (Gross, 1971). Soil total nitrogen (N) was determined using a CHN elemental analyzer (Fisons NA1500). Total P (P) was determined through a dry-oxidation, acid hydrolysis extraction followed by colorimetric analysis of phosphate concentration in the extract (Fourqurean et al., 1992). Elemental content was calculated on a dry weight basis as [mass of element/dry weight of sample] × 100%. Elemental ratios were calculated as molar ratios.

Porewater samples for NH_4^+ and SRP were acidified to a pH of 2 with 6 *N* HCl, and sparged with nitrogen gas to drive off hydrogen sulfide prior to analysis. Porewater NH_4^+ concentrations were measured colorimetrically with the indo-phenol blue method (Koroleff, 1969, Parsons et al., 1984). Soluble reactive phosphorus (SRP) concentrations were measured colorimetrically using the ascorbate method (Parsons et al., 1984). Porewater sulfide concentrations were determined spectrophotometrically following the methods of Cline (1969).

2.5. Infauna core collection and processing

The macroinvertebrate infauna community was sampled with 7.3 cm × 10 cm soil cores collected by hand. Three cores were haphazardly collected from each site at the 0, 3, 6, and 12 month sampling events. Core contents were sieved through 500 μm mesh. Material retained on the sieve was fixed in 4% seawater-buffered formalin for several weeks, rinsed, and stored in 90% ethanol. Samples were stained with Rose Bengal and organisms were separated from soil and detritus. Infauna were then counted and sorted by coarse taxonomic level, usually to class or order. We did not measure biomass of the organisms we sampled.

2.6. Data analysis

Seagrass and macroalgae BB scores from the seagrass community surveys were converted to percent cover data using the midpoint of the percent cover range corresponding to each BB score, and percent cover values were averaged for each site.

We explored soil structure among treatments using principal components analysis (PCA) with the software Primer-e (Clarke and Gorley, 2006). The PCA allowed us to reduce data complexity and extract composite variables that explained maximum variability in the soil properties. Nine soil variables were included in the PCA: BD, pH, Eh, OM, N, P, NH_4^+, SRP, and DS. Prior to analysis, soil variable data were log-transformed to reduce skewness and normalized to place variables on comparable and dimensionless scales. Multivariate differences in soil properties among treatments were visualized with a PCA ordination. We attributed ecological relevance to PC axes with eigenvalues >1, with interpretation based on soil variables that were strongly correlated with each PC axis.

Principal coordinates analysis (PCO) was used to evaluate multivariate infauna community structure. Infauna community characteristics including taxonomic richness (*S*), evenness (Pielou's *J′*, Simpson's λ'), diversity (Shannon-Weaver, *H′*), and dominance (Simpson, $1-\lambda'$) were calculated from multivariate infauna community data. The similarity percentages procedure (SIMPER, Clarke and Gorley, 2006) was used to determine infauna taxonomic similarity within the disturbed and reference sites. SIMPER analysis also identified the contribution of the most abundant taxa in each analysis to within group similarity.

We used Permutational Analysis of Variance (PERMANOVA, Anderson et al., 2008) to test for the effects of soil condition, fertilization, and time since restoration on chl *a* content, macroalgae and seagrass percent cover, soil particle size-class composition, ecological relevance represented by PC scores derived from the PCA, multivariate infaunal abundance, and univariate infauna diversity metrics. A three-factor analysis was not possible for macroalgae and seagrass cover because of a lack of data for reference + sites at the 0 mo time interval. As a result, the PERMANOVA analysis of macroalgae and seagrass cover was conducted with two factors: time since restoration, and a combined factor of soil condition × fertilization with five levels (i.e., disturbed, disturbed+, filled, filled+, and reference). PERMANOVA analyses of chl *a,* macroalgae and seagrass cover, soil parameters, and univariate invertebrate diversity metrics were conducted on Euclidean distance resemblance matrices. PERMANOVA analysis of multivariate infauna abundance data was based on the binomial deviance dissimilarity measure (Anderson and Millar, 2004). Resemblance matrices were calculated from square root transformed macroalgae and seagrass cover data and from log transformed data for other parameters. Soil depth was used as a covariate for PERMANOVA analysis of soil properties, requiring the use of Type I sums of squares; otherwise, Type III sums of squares were used in the PERMANOVA routines. Significance values for PERMANOVA tests were based on 999 permutations of residuals under reduced models. Bonferroni corrections were applied to multiple comparisons tests following PERMANOVA analyses.

Distance-based linear modeling (DistLM) and distance-based redundancy analyses (dbRDA) (Anderson et al., 2008; Legendre and Anderson, 1999; McArdle and Anderson, 2001) were used to determine relationships between infauna community abundance data and multivariate data on sediment properties. Parameters for the DistLM routine, which is analogous to linear multiple

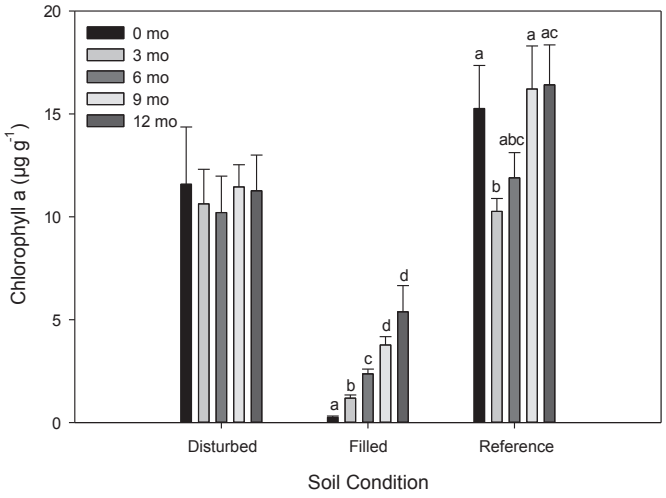

Fig. 1. Mean ± se benthic chlorophyll *a* concentrations in 7.6 × 2 cm cores collected from study sites sampled repeatedly over one year following restoration (0, 3, 6, 9 and 12 months). Soil condition treatments included disturbed, filled, and reference sites ($n = 6$ sites per treatment). Letters indicate statistical significance ($\alpha = 0.05$) of comparisons among sampling events within each treatment, determined through PERMANOVA pairwise tests of time steps (i.e. means with the same letter are not significantly different from each other).

regression, included the Best selection procedure and the Akaike Information Criteria corrected for small sample sizes (AICc; Akaike, 1973; Burnham and Anderson, 2002); the procedure was run with 9999 permutations. Sediment data from the top three depth horizons (0–2 cm, 2–6 cm, 6–10 cm) were weighted proportionally and combined for comparison with the infauna data, which was also collected from the top 10 cm of sediment. Sediment data were log-transformed prior to analysis to reduce skewness. PCA, PCO, infauna diversity, SIMPER, PERMANOVA, DistLM, and dbRDA analyses were conducted with PERMANOVA + for PRIMER (Clarke and Gorley, 2006; Anderson et al., 2008).

3. Results

3.1. Chlorophyll a content

Soil condition status during the first year post-restoration at the Cutter Bank sites affected soil microphytobenthos abundance. Chl *a* content across all samples ranged from 10.6 ± 1.7 to 16.4 ± 1.9 μg g^{-1} (Fig. 1). Chl *a* content varied among soil condition treatments and time (PERMANOVA, $p < 0.001$; Table 1), but not with fertilization ($p = 0.263$), so results are presented for the main soil condition treatments (i.e. disturbed, filled, reference). Chl *a* content was highest at the reference sites (PERMANOVA pairwise tests, $p < 0.002$), and there was some variation among sampling events. Chl *a* content was lower in disturbed sites, ranging from 10.6 ± 1.7 to 11.6 ± 2.8 μg g^{-1}, and values did not vary with time (PERMANOVA pairwise tests, $p < 0.05$; Fig. 1). The filled sites had the lowest overall chl *a* content (PERMANOVA pairwise tests, $p < 0.002$), ranging from 0.2 ± 0.1 to 5.4 ± 1.3 μg g^{-1}. Chl *a* content at filled sites increased steadily with each time step (PERMANOVA pairwise tests, $p < 0.05$), but remained lower than disturbed or reference sites at the one year mark.

Table 1
Results of PERMANOVA tests of soil condition (SC: disturbed, filled, reference) × fertilization (Fe: −, +), and time since restoration (Ti) on soil chlorophyll *a* content and particle size classes. Ti for chlorophyll *a* includes five sampling events (0, 3, 6, 9 and 12 mo post restoration), and two events (0 and 12 mo post restoration) for particle size classes. Pairwise tests were conducted on the soil condition term in the chlorophyll *a* analysis. *p* values in bold text indicate statistical significance at $\alpha < 0.05$.

Source	Tests of chl *a* content				Tests of particle size			
	df	MS	Pseudo-F	*p*	df	MS	Pseudo-F	*p*
Soil condition	2	21.4	415.8	**0.001**	2	398.8	365.2	**0.001**
Fertilization	1	0.1	1.4	0.263	1	0.8	0.8	0.539
Time	4	1.1	21.5	**0.001**	1	1.5	1.4	0.236
SC × Fe	2	0.1	1.0	0.378	2	5.6	5.1	**0.001**
SC × Ti	8	0.7	14.4	**0.001**	2	1.5	1.3	0.233
Fe × Ti	4	0.0	0.9	0.500	1	2.9	2.6	**0.040**
SC × Fe × Ti	8	0.1	1.9	0.091	2	1.7	1.5	0.147
Residual	60	0.1			92	100.5	1.1	
Pairwise tests on soil condition					t			*p*
Disturbed, filled					21.6			0.001
Disturbed, reference					3.7			0.002
Filled, reference					30.9			0.001

3.2. Seagrass community structure

The reference seagrass community at Cutter Bank was characterized by dense *T. testudinum* (median percent cover 60.3%) mixed with sparse calcareous green macroalgae (median percent cover 9.3%). Mean macroalgae cover in filled sites (4.2 ± 1.4%) was lower than reference cover (9.5 ± 1.1%), but did not vary from reference values for the other soil condition treatments (PERMANOVA, $p = 0.014$; Table 2; Fig. 2). Across treatments, macroalgae cover approximately doubled (4.9 ± 1.2% to 11.2 ± 2.1%) over the yearlong study (PERMANOVA, $p = 0.010$). By the end of the first year post-restoration, calcareous green macroalgae cover in restoration sites ranged from 33% (filled+) to 216% (disturbed) of reference values. Seagrass cover in reference areas (60.3 ± 1.2%) was 4–12 time higher than in restoration sites (PERMANOVA, $p < 0.001$; Table 2; Fig. 2). Across all treatments, seagrass cover declined over the course of the study (PERMANOVA, $p = 0.033$), and ranged from 6% (filled+) to 19% (disturbed) of reference cover one year post-restoration.

Table 2
Results of PERMANOVA tests of the factors soil condition × fertilization (SCFE: disturbed, disturbed + fertilized, filled, filled + fertilized, reference), and time since restoration (Ti: 0, 6, and 12 months) on total seagrass cover and total calcareous green macroalgae cover. Pairwise tests were conducted on the soil condition and time terms for both variables. *p* values in bold text indicate statistical significance at $\alpha = 0.05$ for main effects and pairwise tests on time, and at Bonferroni-corrected $\alpha = 0.005$ for pairwise tests on SCFE.

Source	Tests of macroalgae cover				Tests of seagrass cover			
	df	MS	Pseudo-F	*p*	df	MS	Pseudo-F	*p*
SCFE	4	5.4	3.7	**0.014**	4	121.3	102.1	**0.001**
Time	2	16.7	11.5	**0.010**	2	4.4	3.8	**0.033**
SCFE × Ti	8	2.3	1.6	0.200	8	1.0	0.8	0.592
Residual	57	1.5			57	1.2		
		t	*p*			*t*	*p*	
Pairwise tests on SCFE								
Disturbed, disturbed+		1.5	0.153			1.9	0.084	
Disturbed, filled		3.3	0.010			3.4	**0.004**	
Disturbed, filled+		2.6	0.026			4.3	**0.005**	
Disturbed, reference		1.2	0.239			10.3	**0.001**	
Disturbed+, filled		0.7	0.530			1.9	0.079	
Disturbed+, filled+		0.5	0.628			2.0	0.067	
Disturbed+, reference		1.4	0.144			12.2	**0.001**	
Filled, filled+		0.2	0.851			0.4	0.657	
Filled, reference		2.9	**0.004**			13.9	**0.001**	
Filled+, reference		2.5	0.014			15.0	**0.001**	
Pairwise tests on time since restoration								
0 mo, 6 mo		4.4	**0.003**			1.8	0.088	
0 mo, 12 mo		4.0	**0.001**			2.5	**0.022**	
6 mo, 12 mo		0.3	0.762			0.9	0.387	

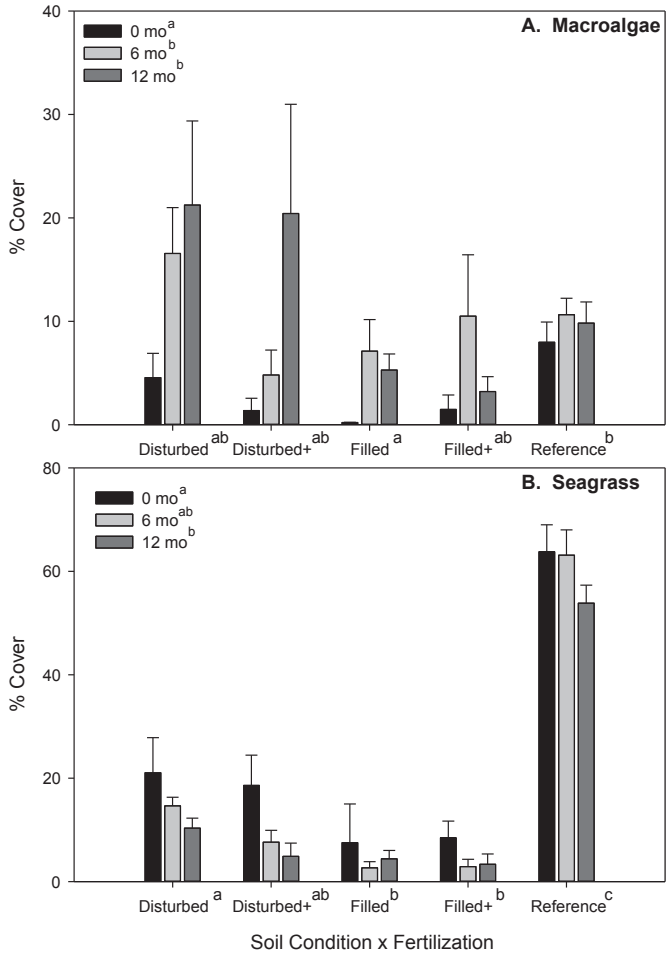

Fig. 2. Mean ± se macroalgae (top) and seagrass (bottom) percent cover at 0, 6, and 12 months post restoration for sites with disturbed, disturbed + fertilized, filled, filled + fertilized, and reference soil condition. Letters indicate statistical significance of PERMANOVA pairwise tests of time since restoration ($\alpha = 0.05$) and of the combined factor soil conditions × fertilization (Bonferroni-corrected $\alpha = 0.005$) on percent cover (i.e. within a factor, means with the same letter are not significantly different from each other).

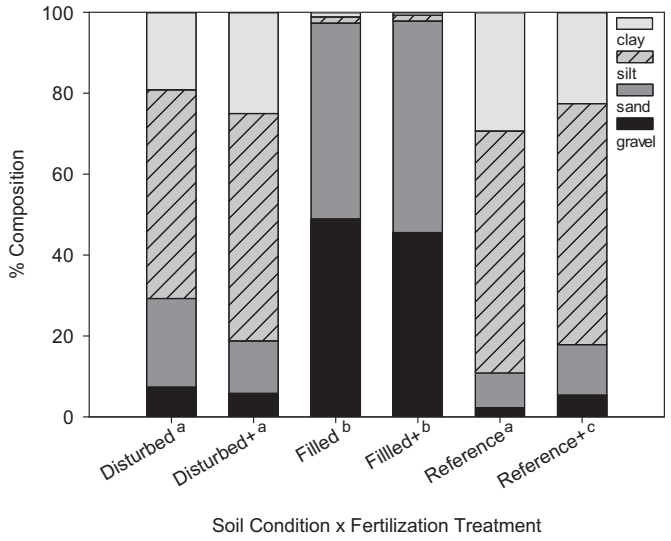

Fig. 3. Soil particle size class (clay, silt, sand, gravel) composition at study sites of soil condition (disturbed, filled, and reference) × fertilization treatments. Data are from 7.6 × 40 cm cores collected from study sites at 0 and 12 months post restoration. Data in bars are pooled over soil depth and time within each treatment. Letters indicate statistical significance ($\alpha = 0.05$) among treatments determined through PERMANOVA pairwise tests between treatments (i.e. means with the same letter are not significantly different from each other).

3.3. Particle size composition

At Cutter Bank, reference soils were dominated by silt (59.8 ± 3.4%) and clay (29.3 ± 3.0%), with small sand (8.6 ± 1.5%) and gravel (2.3 ± 0.9%) fractions (Fig. 3). Multivariate soil profiles (% clay, silt, sand, gravel) differed among soil condition treatments (PERMANOVA, $p < 0.001$; Table 1), but not with fertilization or time ($p > 0.236$). Disturbed sites had similar composition as reference soils, but filled sites were much coarser, consisting predominately of sand (50.3 ± 1.8%) and gravel (47.3 ± 1.9%). Fertilization affected the grain size distribution in restoration treatments in different ways (PERMANOVA, soil condition × fertilization, $p < 0.001$), suggesting that either the physical presence of the stake or the bird feces dropped around the stakes influenced grain size distribution. However, the only significant pairwise comparison was that coarser grain sizes were observed around bird stakes in reference seagrass meadows (PERMANOVA pairwise tests, $p < 0.008$).

3.4. Soil properties

In reference soils, water content ranged from 64 ± 5.4% to 81.0 ± 0.7% and did not vary with depth below the top 2 cm of soil (Supplemental Figure S1). Bulk density ranged from 0.18 ± 0.01 g ml^{-1} to 0.41 ± 0.10 g ml^{-1}, and was lower in the top 2 cm of soils than in the deeper horizons. Soil pH ranged from 6.56 ± 0.02 to 7.38 ± 0.02 and generally decreased with depth below 30 cm. Soils were strongly reduced, and redox potential decreased with depth over the all depth horizons, ranging from −278.3 ± 23.3 mv to −359.6 ± 0.9 mv. Organic matter content ranged from13.8 ± 1.2% to 18.3 ± 0.5% and tended to increase with depths below 6 cm. Nitrogen content was fairly constant, ranging from 0.52 ± 0.01% to 0.67 ± 0.01%, and did not vary with depth (Supplemental Figure S2). Total phosphorus content was very low (0.011 ± 0.001% to 0.019 ± 0.002%) and decreased with depth. Ammonium (83.0 ± 6.4 μm to 842.9 ± 108.9 μm), SRP (0.09 ± 0.02 μm to 18.8 ± 4.5 μm), and DS (76.4 ± 9.0 μm to 3157.5 ± 241.7 μm) concentrations all ranged widely. Ammonium and DS increased with depth, while SRP showed no trends with depth. Porewater profiles showed some anomalies that contribute to the wide-ranging values. Specifically, NH_4^+ and SRP profiles for the 6 month sampling event were elevated in the top 20 cm of soils relative to profiles from the other four sampling events. Dissolved sulfide profiles increased substantially with soil depth for the 12 month profile relative to the previous sampling events.

Soil properties in disturbed and filled sites differed from those in the reference sites. Qualitatively, the most obvious differences were found in the filled sites, and related to soil texture and oxidation-reduction status. Because we observed complex patterns in individual soil properties with depth, soil condition, fertilization, and time (Supplemental Figures S1 and S2), we chose to use a PCA to reduce the dimensionality of this data set for analysis, rather than statistically examining how each soil property varied with treatment, depth, and time. We observed multiple collinear relationships among the soil properties measured, allowing us to define composite variables that described the major ways that soil properties varied by treatment, time and depth. PCA extracted two principal components that together described 75.3% of the variation in the original data. PC1 was positively correlated with OM and N and negatively correlated with BD, pH, Eh, and P, and explained

Table 3
Principal components analysis (PCA) eigenvectors and percent variation explained for PC axes with eigenvalues > 1.0 extracted from multivariate data set of soil and porewater variables from study sites of soil condition (disturbed, filled, reference) × fertilization treatments. See Fig. 4 for corresponding ordination.

Variable	PC1 (57.0%)	PC2 (18.3%)
Bulk density	0.4	0.15
pH	0.39	−0.12
Redox Potential	0.37	−0.21
Organic matter	−0.42	−0.1
Nitrogen	−0.41	−0.09
Phosphorus	0.37	0.13
Ammonium	0.05	0.65
Soluble reactive phosphorus	−0.01	0.61
Dissolved sulfide	−0.28	0.31

57% of variation in the data set (Table 3). We interpreted PC1 to represent soil OM. Inorganic nutrients in the porewater (NH_4^+ and SRP) were both positively correlated with PC2 (18.3% of variance explained), and we described PC2 as representing dissolved inorganic nutrients. Dissolved sulfide was not strongly correlated with either axis. The effects of soil condition status on multivariate soil properties during the first year post-restoration at the Cutter Bank sites were evident in the PCA ordination visualized for the soil condition × fertilization factor (Fig. 4). Soils from filled and filled + samples were characterized by low PC1 scores (indicating high BD, P, pH, and Eh and low OM and N), and clearly separated from disturbed, disturbed+, reference, and reference + samples. There was considerable overlap among disturbed, disturbed+, reference, and reference + samples in this ordination, characterized by high PC1 scores, thus high OM and N content. Samples from reference sites had higher soil organic content (PC1 scores) than disturbed, disturbed+, and reference + samples. There was little difference among any treatments for porewater nutrient concentrations (as indicated by PC2 scores).

Our composite variables (PC1 and PC2) were affected by soil condition status (PERMANOVA, $p < 0.001$; Table 4, Fig. 5). Each soil condition treatment (disturbed, filled, reference) differed from the others for both composite variables (PERMANOVA pairwise tests, $p < 0.001$). Organic matter content (PC1) was highest in reference sites, lower content in disturbed sites, and nearly absent in filled sites. Noticeable trends of porewater nutrient patterns among soil condition × fertilization treatments were lacking, though concentrations in filled and filled + treatments were more variable than in

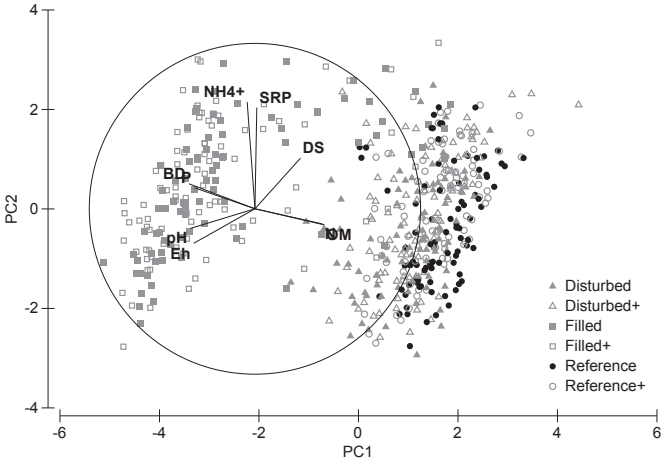

Fig. 4. Principal components analysis (PCA) ordination with PCA eigenvector overlay of multivariate soil data, visualized for soil condition (disturbed, filled, and reference) × fertilization treatment. Refer to Methods for soil variables included in the PCA.

Table 4
Results of PERMANOVA analyses of soil condition (SC: disturbed, filled, reference), fertilization (Fe: −, +), and time since restoration (Ti: 0, 3, 6, 9 and 12 months) on principal component scores extracted from a Principal Component Analysis of multivariate soil properties. PC1 is interpreted as soil organic matter content, and PC2 is interpreted as inorganic porewater nutrients. Pairwise tests were conducted on the soil condition × fertilization interactions. Refer to Methods for soil variables included in analyses. Soil depth was included as a covariate. p values in bold text indicate statistical significance at $\alpha < 0.05$.

Source	Tests of PC1 scores				Tests of PC2 scores			
	df	MS	Pseudo-F	p	df	MS	Pseudo-F	p
Depth	1	219.5	301.3	**0.001**	1	388.1	152.3	**0.001**
Soil condition	2	1034.4	1419.6	**0.001**	2	1086.9	426.7	**0.001**
Fertilization	1	1.0	1.4	0.232	1	13.5	5.3	**0.002**
Time	4	10.3	14.1	**0.001**	4	93.2	36.6	**0.001**
SC × Fe	2	3.0	4.2	**0.022**	2	11.6	4.6	**0.001**
SC × Ti	8	5.9	8.1	**0.001**	8	23.6	9.3	**0.001**
Fe × Ti	4	1.3	1.8	0.136	4	3.5	1.4	0.149
SC × Fe × Ti	8	0.6	0.8	0.603	8	2.8	1.1	0.309
Residual	509	0.7			509	2.5		
Pairwise tests on SC × Fe			t	p			t	p
Disturbed, Disturbed+			0.1	0.137			2.7	**0.001**
Filled, Filled+			2.2	**0.023**			1.5	0.094
Reference, Reference+			0.7	0.497			2.9	**0.001**

the other treatments. Concentrations were highest in the 6 month samples (from August 2010) across all soil condition × fertilization treatments.

Porewater nutrients, but not OM content, were affected by fertilization (PERMANOVA, $p < 0.001$; Table 4; Fig. 5). In soil condition × fertilization pairs, porewater nutrient concentrations were elevated for the fertilized sites within the disturbed/disturbed+ and reference/reference + pairs (PERMANOVA pairwise tests, $p < 0.001$), but not in the filled/filled + pair. Both composite variables covaried with depth (PERMANOVA, $p < 0.001$). Across all soil condition × fertilization treatments, OM and porewater nutrient pools tended to increase with depth, largely driven by increases in disturbed and filled treatments.

3.5. Infaunal community structure

Infaunal community analysis was conducted on samples from the 3, 6, and 12 month time steps. A total of 7225 individual organisms of 27 infauna taxa were identified from 159 cores (Supplemental Table S1). Across the three sampling events, mean abundance per core ranged from 35.1 ± 3.9 organisms for all disturbed cores to 61.8 organisms for all reference + cores. Taxonomic richness ranged from 5.5 ± 0.5 taxa per core for all disturbed + cores to 7.1 ± 0.1 taxa per core for all reference + sites.

We did not observe infaunal community structure converging with reference communities in the course of the study. Infauna community abundance differed among the soil condition treatments (PERMANOVA, $p = 0.001$; Table 5), and each treatment supported different communities (PERMANOVA pairwise tests, $p < 0.001$). Infauna communities also differed with each time step (PERMANOVA, $p = 0.001$). There was an interaction between soil condition × time (PERMANOVA, $p = 0.002$). Fertilization was not a source of variation in the infauna community data set. Structure in infauna communities was evident in the PCO ordination (Supplemental Table S2, Supplemental Figure S3). Disturbed and reference samples separated along PCO1, though there was some overlap between these two groups. Communities from filled samples clustered separately from disturbed and reference samples along PCO2. Within each treatment, samples also clustered by time step. Communities from filled samples clustered separately from

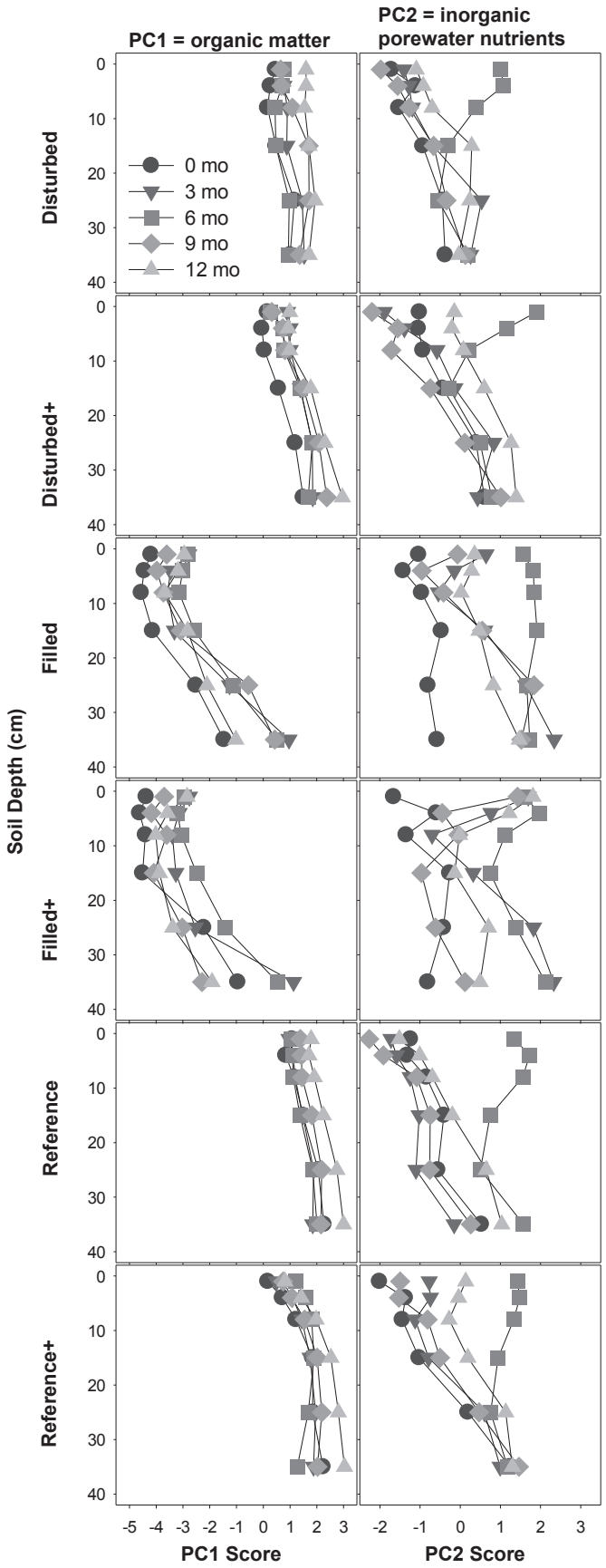

Fig. 5. Soil depth profiles for mean ± se Principal Component (PC) scores extracted from the multivariate data set of soil variables sampled from study sites from soil condition (disturbed, filled, and reference) × fertilization treatments. PC1 is interpreted as a soil organic matter content and PC2 represents dissolved inorganic nutrients in the porewaters.

disturbed and reference samples along PCO2. Cumaceans, amphipods, and tanaidaceans contributed to the separation of communities in reference and reference + sites, as determined by strong correlations of those taxa ($r > 0.7$) with PCO1. Oligochaete and nematode abundances, respectively, were strongly negatively with PCO2 indicating that these taxa were important in distinguishing disturbed and reference samples from filled samples.

SIMPER analysis revealed that polychaetes and nematodes contributed strongly to similarity within samples from each soil condition treatment (Supplemental Table S3). Oligochaetes were abundant in disturbed and reference samples, but not in filled samples. Amphipods were important contributors to filled and reference samples, but not to disturbed samples.

Soil condition explained significant variance in univariate metrics of infaunal abundance (PERMANOVA, $p = 0.001$; Table 5; Fig. 6), evenness ($p = 0.003$), diversity ($p = 0.001$), and dominance ($p = 0.001$). Abundance in disturbed samples was lower than in reference samples (PERMANOVA pairwise tests, $p = 0.001$), but disturbed and reference samples did not differ on the basis of evenness, diversity, or dominance. Abundance, evenness, diversity, and dominance were all lower in filled samples than in reference samples (PERMANOVA pairwise tests, $p < 0.004$).

Time since restoration explained variation in infauna abundance, richness, and diversity (PERMANOVA, $p = 0.001$; Table 5; Fig. 6). Values for each of these metrics were higher at the 3 month sampling event than at the 6 month and 12 month events (PERMANOVA pairwise tests, $p < 0.004$). Time affected infauna abundance differently among the soil condition treatments (soil condition × time, PERMANOVA, $p = 0.001$; Table 5). Abundance in the reference treatment was lower at the 6 and 12 month sampling events that at the 3 month (PEMANOVA pairwise tests, $p < 0.002$; data not shown).

Infauna abundance was the only metric for which the fertilization factor explained variation (PERMANOVA, $p = 0.039$; Table 5). Across treatments, abundance was about 18% higher (41.8 ± 3.9 organisms per core) in the fertilized treatments than in unfertilized treatments (49.4 ± 4.0 per core; PERMANOVA pairwise tests, $p = 0.034$).

3.6. Environmental predictors of infauna community structure

Total nitrogen, mean grain size, and water content were excluded from the DistLM analysis due to high correlation ($|r|>0.95$) with organic matter content and bulk density. The dbRDA ordination visualizes infauna community samples coded by soil condition treatment as constrained by environmental variables (Fig. 7). Infauna samples from filled sites separated from disturbed and reference samples in the ordination. Disturbed and reference samples overlapped completely, contrary to what was observed in the unconstrained PCO ordination (Supplemental Figure S3), where there was some separation between the two treatments. The first three dbRDA axes explained 94.1% of the fitted variation, and 43.1% of the variation in the resemblance matrix (Fig. 7), and are likely capturing substantial information about the infauna community structure at these sites as influenced by environmental predictors.

There was a strong negative correlation between SRP concentration and dbRDA1 (DistLM, $r = -0.82$). OM content had a strong negative loading on dbRDA2 (DistLM, $r = -0.77$). BD was positively correlated with dbRDA3 (DistLM, $r = 0.77$) and a negative correlation with NH_4^+ ($r = -0.56$). Phosphorus and pH did not load

Table 5
Results of PERMANOVA analyses of soil condition (SC: Disturbed (D), Filled (F), Reference (R)), fertilization (Fe: −, +), and time since restoration (Ti: 3, 6, and 12 months) on infauna community structure and diversity metrics. *p* values in bold text indicate statistical significance at $\alpha < 0.05$. Superscript letters indicate significance among factor levels at $\alpha = 0.05$ (means for levels with the same letter are not significantly different from each other).

Source	df	MS	Pseudo-F	*p*	Source	df	MS	Pseudo-F	*p*
Multivariate Abundance					*Pielou's J'*				
Soil condition (D^a, F^b, R^c)	2	38.6	11.7	**0.001**	Soil condition (D^a, F^b, R^a)	2	0.056	8.66	**0.003**
Fertilization	1	8.8	2.7	0.078	Fertilization	1	0.008	1.17	0.307
Time (3^a, 6^b, 12^c mo)	2	53.3	16.1	**0.001**	Time	2	0.001	0.12	0.874
SC × Fe	2	2.2	0.7	0.644	SC × Fe	2	0.002	0.29	0.738
SC × Ti	4	12.3	3.7	**0.002**	SC × Ti	4	0.010	1.60	0.197
Fe × Ti	2	1.8	0.5	0.719	Fe × Ti	2	0.009	1.44	0.277
SC × Fe × Ti	4	1.6	0.5	0.833	SC × Fe × Ti	4	0.003	0.44	0.805
Residual	36	3.3			Residual	36	0.006		
Abundance					*Shannon-Weaver H'*				
Soil condition (D^a, F^a, R^b)	2	1521.9	9.2	**0.001**	Soil condition (D^{ab}, F^a, R^b)	2	0.335	9.58	**0.001**
Fertilization (+ > −)	1	779.5	4.7	0.039	Fertilization	1	0.000	0.00	0.964
Time (3^a, 6^b, 12^b mo)	2	1548.6	9.4	**0.001**	Time (3^a, 6^b, 12^b mo)	2	0.307	8.77	**0.001**
SC × Fe	2	60.3	0.4	0.679	SC × Fe	2	0.004	0.12	0.890
SC × Ti	4	2116.9	12. 8	**0.001**	SC × Ti	4	0.078	2.24	0.086
Fe × Ti	2	341.4	2.1	0.142	Fe × Ti	2	0.017	0.48	0.600
SC × Fe × Ti	4	112.7	0.7	0.624	SC × Fe × Ti	4	0.061	1.73	0.169
Residual	36	165.6			Residual	36	0.035		
Richness					*Simpson's λ'*				
Soil condition	2	13.9	3.4	0.053	Soil condition (D^a, F^b, R^a)	2	0.078	14.33	**0.001**
Fertilization	1	1.9	0.5	0.505	Fertilization	1	0.000	0.01	0.945
Time (3^a, 6^b, 12^b mo)	2	43.9	10.7	**0.001**	Time	2	0.002	0.40	0.648
SC × Fe	2	2.0	0.5	0.633	SC × Fe	2	0.001	0.14	0.866
SC × Ti	4	6.7	1.6	0.184	SC × Ti	4	0.014	2.56	0.053
Fe × Ti	2	0.9	0.2	0.800	Fe × Ti	2	0.003	0.63	0.566
SC × Fe × Ti	4	9.9	2.4	0.071	SC × Fe × Ti	4	0.004	0.78	0.553
Residual	36	4.093			Residual	36	0.005		

clearly onto the first three axes. These correlations indicate that high OM content in the disturbed and reference soils, and high BD, NH_4^+, and SRP in the filled soils are important drivers of the observed infauna community structure across soil condition treatments.

DistLM marginal tests that fit each environmental variable individually to the infauna community data showed that every variable except NH_4^+ concentration was individually related to infauna community abundance (DistLM marginal tests, $p < 0.020$). DistLM returned a best multivariate predictor model explaining infauna community structure across Soil condition treatments that included OM, BD, pH, NH_4^+, SRP, and P (DistLM, $r^2 = 0.43$). However, the solutions for the seven best models all had AICc values within two units of each other, so all may be considered viable (Burnham and Anderson, 2002). The ten best models included all included NH_4^+, SRP, bulk density, organic matter content, and NH_4^+ concentration. All but one model included OM, and none included Eh, DS, or chl *a* as predictor variables.

4. Discussion

Soil properties and benthic infaunal community structure were clearly different between disturbed sites and reference seagrass meadows in our study sites. Given that the initial disturbance caused by these groundings resulted in loss of the seagrass community and erosion, this was not surprising. We found soil properties and macrophyte community structure to be markedly influenced by the restoration techniques employed, and that two common restoration techniques – filling vessel grounding scars and fertilizing the damaged areas by encouraging birds to roost above them – act independently to influence ecosystem structure. Filling disturbances initially altered seagrass ecosystem structure by creating a soil matrix with different physical properties, low organic matter content and nutrient pools, and lower macrophyte cover and microalgal abundance relative to the undisturbed ecosystem. The filled sites were also characterized by different infauna community structure than the undisturbed seagrass meadow. Adding a fertilizer source via bird roosting stakes increased porewater nutrient pools at disturbed and reference sites, but not at filled sites.

Calcareous green macroalgae cover was variable in disturbed and restored sites during the first year post-restoration, but did approach convergence with reference cover for all treatments except the filled sites. Seagrass cover did not increase in any of the restoration treatments during the first year post-restoration. These findings are consistent with observed patterns of tropical seagrass bed development, in which turf and calcareous green macroalgae initially colonize disturbances, followed by rapidly growing seagrass species. Bed development culminates with a monospecific climax community dominated by slower-growing species, or a mixed community of climax and successional species (Kenworthy et al., 2002; Rollon et al., 1999; Whitfield et al., 2002; Williams, 1990; Zieman, 1982). It has been proposed (Williams, 1990) that these patterns indicate a facilitation (sensu Connell and Slayter, 1977) model of succession: early colonizers stabilize soils and help build nutrient pools that eventually provide for colonization by climax species. At an experimental scale, Hammerstrom et al. (2007) found a greater degree of recovery of the seagrass community after one year in unfilled and filled excavations of south Florida seagrass meadows. However, because gap closure in seagrass meadows occurs primarily through clonal extension (Bell et al., 1999; Fonseca et al., 2004; Kenworthy et al., 2002; Rasheed, 1999; Uhrin et al., 2011; Zieman, 1976), colonization of larger gaps, such as with our disturbed and filled sites, is expected to require more time than in small experimental plots.

Benthic microalgae perform important functions in shallow coastal soils by fixing carbon, oxygenating surficial soils, and providing food sources to meio- and macrofauna (Moncreiff et al., 1992; Pollard and Kogure, 1993). In our study, benthic microalgae did not respond to nutrient input, suggesting that the microalgae

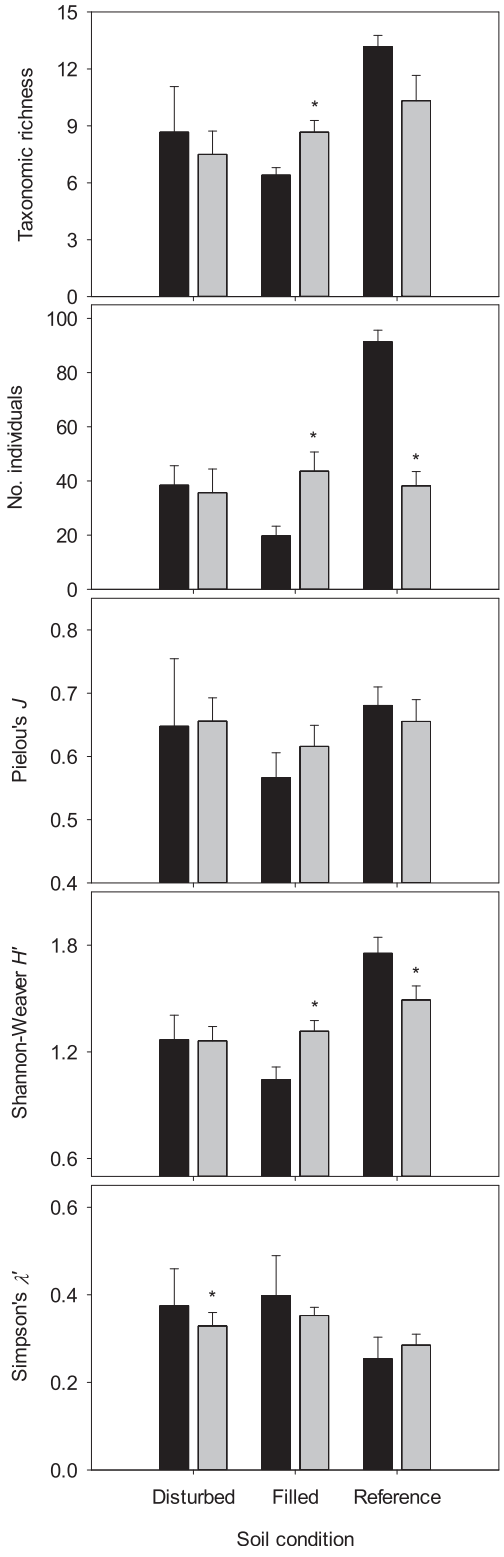

Fig. 6. Mean ± se infaunal community diversity metrics from study sampled at 0 (dark bars) and 12 (light bars) months post-restoration. Soil condition treatments included disturbed, filled, and reference sites. Data for reference sites are from 3 and 12 month sampling events. Asterisks indicate significance at $\alpha = 0.05$ between time steps within treatments.

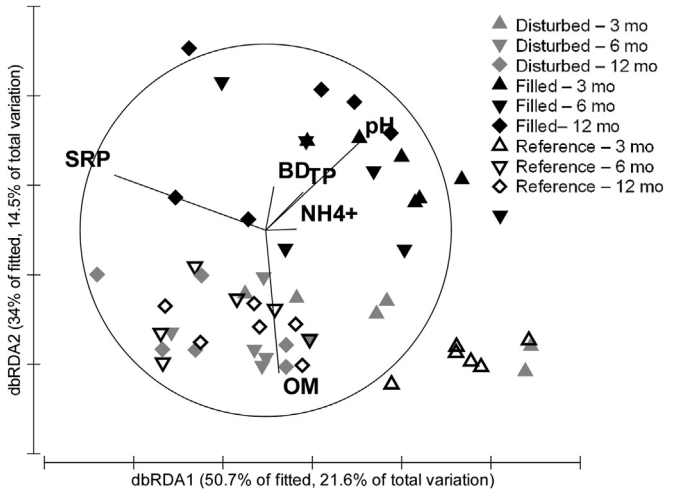

Fig. 7. dbRDA ordination of the best fit DistLM model of multivariate infaunal community data versus log transformed environmental variables from Cutter Bank sites. Data are from 3, 6, and 12 month sampling events, visualized by sampling event within soil condition treatments (disturbed, filled, reference). Data from fertilization treatments are pooled with corresponding soil condition treatments.

are not nutrient limited at this location, but microalgal response to nutrient addition in seagrass soils can be variable and may reflect complex interactions between biotic and abiotic factors (Armitage et al., 2006, 2005). We saw a clear pattern of increasing benthic microalgal abundance in the filled sites over the course of the study. Recovery of benthic microalgae following disturbance occurs relatively quickly due to rapid rates of growth and reproduction (Larson and Sundback, 2008; Montserrat et al., 2008) and the motility of some benthic diatom taxa (Admirall, 1984) may enable rapid colonization of new substrate. Though chl *a* content did not yet reach levels of the surrounding seagrass meadow, the observed increase is nonetheless an early indicator of developing structure and function.

Excavation of soils by vessel groundings removes the vital substrate needed by seagrasses and rhizophytic macroalgae to thrive. Filling excavations stabilizes the site and helps to prevent further site damage through erosion caused by currents or severe storms (e.g., Whitfield et al., 2002; Uhrin et al., 2011). Gap closure in seagrass meadows occurs primarily through clonal extension (Kenworthy et al., 2002; Rasheed, 1999; Zieman, 1976), and seagrass and rhizophytic algae may be not be able to extend down abrupt steep slopes such as typically exist in grounding disturbances (Kenworthy et al., 2002; Whitfield et al., 2002). For these reasons, filling excavations to grade is considered a critical step in the recovery process, especially for larger and deeper disturbances (Uhrin et al., 2011). Our sampling design used undisturbed seagrass meadows on Cutter Bank to assess reference conditions, assuming that these reference areas represented the undisturbed condition of our disturbed sites. This approach requires an assumption of steady state in the seagrass communities over time in the absence of disturbance. It is possible that these undisturbed beds sites were either initially different from the sites that were to be disturbed, or that the state of the undisturbed meadow has changed since the time of the disturbances. However, we have noticed no marked changes in the nature of the undisturbed seagrass meadows in this area over the last decade, and the disturbed sites occur in a relatively homogenous expanse of seagrass meadow. Inclusion of disturbed but unrestored sites (i.e. those with no intervention) provides some information as to site status without intervention.

We found very low soil organic content at sites filled with quarried sand, and organic content did not increase in the short term. In seagrass meadows redeveloping from an unvegetated state, OM can accumulate in the soils during the recolonization process (Barrón et al., 2004; Cebrián and Pedersen, 2000; McGlathery et al., 2012; Pedersen et al., 1997). Sources of OM

include dead roots and rhizomes; root exudates; organic particles and litter buried by sedimentation and bioturbation; and benthic microalgal exudates (Holmer et al., 2001; Pedersen et al., 1997). Organic matter content in filled sites is expected to remain low until these sites support dense seagrass communities.

Another key difference between filled sites and the undisturbed ecosystem was particle size composition. In seagrass ecosystems, soil grain size and porosity affects exchange of soil pore water with overlying waters (Koch, 2001). Grain size is correlated with pore water exchange (Fourqurean et al., 1992), and thus nutrients and also toxic compounds such as sulfide may accumulate faster and at higher concentrations in fine-grained soils relative to coarse soils. To avoid erosion, soils used in seagrass restoration projects are typically far coarser than ambient soils (e.g., McNeese et al., 2006; Hall et al., 2012b), as was the case with our fill treatments. Turbidity created during fill placement can be difficult to control with fine soils, and there also is concern that fine soils may wash away from the site with tides and wave energy. The silt/clay fraction of fill material used in this restoration project ranged from 1% to 6%, within the range of soils that *T. testudinum* is known to grow in (Koch, 2001), but far lower than ambient soils at Cutter Bank. Fine soils are expected to increase in the fill sites as the seagrass community develops with time and seagrass blades entrain particles from the water column (Terrados and Duarte, 2000), but these sites will likely always remain coarser than the surrounding soils.

The sand used to fill grounding excavations had elevated P content compared to soils found in the nearby reference areas, and may have been quarried from bedrock containing phosphorus deposits (Marquez et al., 2008). Using fertilizer to aid restoration is desirable in P-limited seagrass ecosystems (Kenworthy et al., 2000), hence the use of bird roosting stakes to deliver phosphorus (Fourqurean et al., 1995). However, even small P inputs can have long lasting effects in this system. For example, following the experimental use of bird roosting stakes, with a P loading rate of 3.29 g m^{-2} y^{-1} (Powell et al., 1989), elevated P content in soils was detected over twenty years later (Herbert and Fourqurean, 2008), so it is likely that the P deposited at our filled sites will influence community structure at the filled sites for decades.

Release of P from the sand fill could have potentially serious ramifications, including localized eutrophic effects (e.g., changes in seagrass community structure, water column phytoplankton blooms), or export to and enrichment of adjacent ecosystems including coral reefs. Carbonate dissolution is one mechanism by which P tightly sorbed to carbonate particles is released into the rhizosphere and becomes available for uptake by seagrasses or release to the water column (Burdige and Zimmerman, 2002; Erftemeijer and Middelburg, 1993; Jensen et al., 1998). The range of pH values recorded in our study was surprisingly low (median pH 7.0) in disturbed and reference soils. This may reflect intense benthic metabolism associated with remineralization of OM or with sulfide oxidation (Jensen et al., 1998). These pH values are within the range at which carbonate dissolution should occur. The median pH for fill sites was 7.7. If pH drops through time in sites with P-enriched fill, the release of ecologically significant quantities of P could result. Of further concern is that bird stakes are often placed in restoration sites receiving fill material. If the fill is P-enriched, additional nutrient input via bird stakes could compound these effects. Further work is needed on the nature of the material used for fill in seagrass restoration sites, to include reviewing locations of quarries in relation to know bedrock P deposits. We recommend that fill be analyzed for P content prior to use in restoration projects, and that caution be exercised when deciding to use bird stakes in conjunction with fill of unknown origin and P content.

Infaunal communities at fill sites did not converge with reference communities during the first year post restoration, exhibiting reduced abundance, evenness, and diversity, and greater dominance than reference communities. However, both the number of individuals and taxonomic richness at the fill sites increased over the course of our study, suggesting that the infauna community may have entered a recovery trajectory. Infaunal communities can change rapidly in disturbed soils, and may exhibit variable spatial and temporal responses to disturbance in patterns of colonization (Santos and Simon, 1980; Schaffner, 2010; Whomersley and Huxham, 2010; Zajac and Whitlatch, 1982; Zajac et al., 1998). In our study, diversity was highest in reference and disturbed samples, indicating more developed infaunal communities than in filled sites. While polychaetes were the dominant taxa in all three restoration treatments, they had a third greater contribution to group similarity in the filled samples, than in the disturbed and reference samples. Dominance values for filled samples reflect this composition, and were higher than for disturbed and reference sites. These results suggest that infaunal communities at the disturbed and filled sites may be at early (albeit differing) points along the successional trajectory. In our restoration analysis, the disturbed sites were known to be at least five years old at the time of our study, and represented the status of the filled sites before they were filled. The disturbed sites were viewed as a “status quo” option from a management perspective, representing the ecosystem state if no restoration actions were taken. The status of the infaunal community at disturbed sites indicates that they are further along this trajectory. For example taxonomic richness, evenness, diversity, and dominance did not differ between disturbed and reference samples. However, community and total abundance was lower in disturbed than in reference samples, indicating that numerical recovery has not occurred.

We propose that the altered infauna communities we observed in restoration sites can be explained by reduced habitat quality in these sites. In seagrass ecosystems, plant community structure provides habitat complexity and more food resources, when compared to unvegetated soils (Orth et al., 1984; Summerson and Peterson, 1984). The slow recovery of the macrophytes may explain the differences in abundance that we observed. Infaunal abundance and diversity has shown to be reduced in seagrass meadows dominated by successional seagrass species, driven by structural characteristics of the seagrasses (Micheli et al., 2008). In transplanted seagrass sites, recovery of epibenthic infaunal communities has been shown to track development of the seagrass community (Fonseca et al., 1990), and it follows that a similar trajectory would apply to infauna.

Habitat quality, including food availability, will be an important factor in the ability of these sites to support recolonization by infauna. Benthic microalgae are a primary food source for many infauna species. Occupying the surficial soils, benthic microalgae are prone to impacts of physical disturbance of the soils. However, recovery following disturbance occurs relatively quickly due to rapid rates of growth and reproduction (Larson and Sundback, 2008; Montserrat et al., 2008) and recolonization by mobile diatom taxa (Admirall, 1984). Our results are consistent with this pattern. In our analysis, soil chl *a* in the fill sites increased steadily over the course of the first year following restoration. While fill site chl *a* only reached approximately half of the reference levels, this rapid development is likely to be an important factor in the recovery of infauna communities following restoration.

Infaunal communities had strong relationships to soil properties among treatments, and in particular between filled vs. disturbed and reference sites. The material used as fill in these restoration sites was much coarser in texture that the ambient soils. It remains to be seen whether physico-chemical differences in fill sites from the surrounding seagrass meadow will affect the recovery trajectory of seagrasses and infauna. This seems possible, given the

particle coarseness, lack of OM, and high P content that we documented in the fill sites. Documented recovery of infaunal communities typically occurs within a year following physical disturbance to soft soils (e.g. Collie and Hall, 2000; Dernie, 2003; Skilleter et al., 2006). However, most studies of these recovery dynamics focus on native soil that has been disturbed. The fill sites we studied involved terrestrially-sourced material with distinct properties relative to the surrounding area. We are unaware of studies that have examined infauna colonization dynamics in seagrass restoration sites involving fill placement, so we looked to studies of colonization in dredge spoil deposits as an analogue. Reports of infaunal community recovery time in dredge spoil deposited in seagrass habitat range from over a year (i.e. recovery not detected during the first year of monitoring) to ten years (reviewed in Sheridan, 2004a,b).

5. Conclusions

Our study provides new insight into the effects of seagrass restoration methods on ecosystem structure, when previous work has focused primarily on restoration effects on plant and epibenthic fish and invertebrates, or on small-scale experimental sites. Filling and fertilizing did not result in convergence of seagrass, microalgae, or soil response variables between restoration and reference sites in the first year post-restoration, suggesting that future studies of the recovery of seagrass community structure and function need to be conducted over much longer time scales. Filling excavations is an important step to prevent erosion, but at least in the initial months following restoration, resulting soil structure and nutrient pools may constrain rapid development of the seagrass community and associated infauna.

More rapid recovery trajectories suggested by experimental-scale studies likely underestimate recovery for restoration-scale projects. Evaluation of seagrass ecosystems including soils and invertebrate communities should be conducted over longer periods of time following restoration, in order to gain knowledge of the characteristics of restored seagrass ecosystems and to calibrate expectations of recovery trajectories.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2014.03.001.

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