Impacts of physical disturbance on ecosystem structure in subtropical seagrass meadows

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ABSTRACT: Soil disturbance, a key contributor to physical degradation in seagrass ecosystems, can lead to long-term changes in ecosystem function. We used a chronosequence of vessel grounding disturbances of different ages (0 yr, 1 yr, 3 yr, 4 yr, 5+ yr) as a model for soil disturbance to test hypotheses that disturbance alters primary producer communities, soil properties, biogeochemical processes, and infauna communities in seagrass ecosystems and that altered structure and processes will change following disturbance through seagrass bed development and ecosystem recovery. Disturbance involving excavated surface soils resulted in long-term loss of seagrass and macroalgae and stored organic carbon, nitrogen, and phosphorus. Disturbed sites were characterized by reductions in variables related to organic matter and inorganic nutrient content. Disturbance altered habitat quality for some taxa including amphipods, as evident from differences in invertebrate community structure. These impacts persisted in study sites for 5+ yr after the disturbance, likely because of physical and chemical soil modification accompanied by slow development of the seagrass community. We estimate that disturbance from 0.4 m deep excavations led to losses of 6.0 kg m⁻² organic C (Corg), 0.4 kg m⁻² N, and 0.03 kg m⁻² P from the disturbed areas. First-order conservative estimates of scarring excavation rate in Miami–Dade County, Florida, USA, suggest potential annual fluxes of 1.1 × 10⁶ kg Corg, 74 000 kg N, and 5500 kg P from seagrass soils in the region. Our findings suggest that vessel grounding disturbances create complex and long-term resource losses that are undervalued by resource trustees.

KEY WORDS: Ecosystem function · Blue carbon · Nitrogen · Phosphorus · Infauna · Macroalgae · Biscayne National Park · Soil · Sediment

INTRODUCTION

Seagrasses are ecosystem engineers (sensu Jones et al. 1994, Orth et al. 2006, van der Heide et al. 2012), and seagrass soils have larger nutrient pools (Fourqurean et al. 1992a, Duarte et al. 2005), higher organic matter content (Kenworthy 1981, Pedersen et al. 1997), more sulfate reduction activity (Isaksen & Finster 1996, Holmer & Duarte 2003), greater nitrogen fixation (Patriquin & Knowles 1972, Capone & Taylor 1980), higher benthic microalgal biomass (Bucolo et al. 2008), and more abundant and diverse microbial (Moriarty et al. 1985) and macrofaunal (Stoner 1980, Virmstein et al. 1983) communities than unvegetated sediments. Infauna play a major role in the transfer of carbon fixed by seagrasses and benthic microalgae to higher trophic levels (Summerson & Peterson 1984). Further, bioturbation by infauna irrigates and oxygenates shallow sediments, enhances benthic-pelagic fluxes, and stimulates primary production (Norkko et al. 2001, Lohrer et al. 2004, Montserrat et al. 2008). Soil structure is an important determinant of nutrient processing rates and storage capacity, affecting plant productivity, community
structure, and habitat quality (sensu Hall et al. 1997) for seagrass bed development and the associated organisms.

Seagrass ecosystems provide numerous goods and services to human populations, including shoreline protection, soil stabilization, water purification, and commercial and artisanal fisheries (Fonseca et al. 2000, Spalding et al. 2001) and are valued at an estimated US$ 19 000 ha$^{-1}$ yr$^{-1}$ (Costanza et al. 1997). Recent studies have emphasized that seagrass ecosystems also sequester large quantities of organic carbon, nitrogen, and phosphorus in their soils (Duarte et al. 2010, Fourqurean et al. 2012a). Stored carbon, particularly organic or ‘blue’ carbon stocks in seagrass soils, is considered an ecosystem service that was recently assigned a potential carbon credit value of US$ 7000 ha$^{-1}$ (Murray et al. 2011).

Loss of seagrass resources in coastal ecosystems is accelerating (Waycott et al. 2009), and physical disturbance from storm events, dredging, development, fishing gear impacts, and vessel groundings contribute to the declines (Short & Wyllie-Echeverria 1996, Orth et al. 2006, Grech et al. 2012). Seagrass meadows near population centers are subject to frequent and severe physical disturbance when vessels run aground (Zieman 1976, Sargent et al. 1995, Dunton & Schonberg 2002, Uhrin et al. 2011, Hallac et al. 2012). Vessel groundings can excavate plants and soils (Kenworthy et al. 2002, Hammerstrom et al. 2007, Di Carlo & Kenworthy 2008). The resulting disturbances represent harmful impacts on valuable resources, but they can provide an opportunity for studying severe physical disturbance and recovery in seagrass ecosystems (Uhrin et al. 2011).

Physical disturbances to seagrass meadows that disrupt the rhizosphere, such as from shellfish dredging (Neckles et al. 2005) or vessel groundings (Kenworthy et al. 2002, Di Carlo & Kenworthy 2008), are some of the most severe types of impacts that can occur in seagrass meadows. Soil disturbances can lead to long-term changes in ecosystem function, including primary production, nutrient cycling, and habitat provision for seagrass-associated organisms. Stored organic carbon may be redeposited to the sea floor near the disturbance, exported to adjacent water bodies, and/or be oxidized and released into the atmosphere as CO$_2$ when soils are disturbed, which may contribute to climate change fueled by greenhouse gas emissions (Fourqurean et al. 2012b, Pendleton et al. 2012).


Previous studies of post-disturbance recovery in seagrass ecosystems have typically focused on rapid assessments of plant cover and abundance metrics (e.g. Williams 1990, Fonseca et al. 1996a, 2000, Dawes et al. 1997, Kenworthy et al. 2002, Whitfield et al. 2004, Hammerstrom et al. 2007, Di Carlo & Kenworthy 2008, Uhrin et al. 2011) or on associated nekton (e.g. Fonseca et al. 1996b, Bell et al. 2001, Uhrin & Holmquist 2003) as proxies for recovery of ecological services. Studies on recovery of the entirety of ecosystem structure are lacking. The heavy focus on vegetation in analysis of recovery relies on an assumption that the recovery of seagrasses is tightly coupled with the structure and function of the benthic soils during the recovery process. However, this assumption has never been tested. In addition, minimal work has been done on the effects of acute physical disturbance on seagrass infauna (but see Sheridan 2004). Disturbance effects have been described for infauna in other marine ecosystems (e.g. storm impacts: Dobbs & Vozarik 1983, Hall 1994, Posey & Lindberg 1995, Zajac et al. 1998; or trawling impacts: Collie & Hall 2000, Kaiser et al. 2006), where post-disturbance recovery may be affected by altered sediment structure, as well as by the timing, duration, and spatial scales of the disturbance.

Our study aimed to fill information gaps that exist regarding the impacts of severe physical disturbance on seagrass ecosystem structure by using vessel grounding sites as model disturbances and contrasting the disturbed sites with undisturbed reference seagrass beds. Undisturbed, unconsolidated soils provide substrate for seagrass colonization and contain reservoirs of nutrients and organic matter that di-
rectly benefit maintenance and development of a seagrass meadow, which in turn enriches and structures the soils. This positive feedback loop is destroyed by excavation, and regaining this linkage is an important but poorly understood part of the recovery process. We examined primary producers, soil properties, and macroinvertebrate infauna for variables essential to habitat quality, nutrient storage, carbon sequestration, and ecosystem metabolism. In the absence of a priori knowledge of our study variables, we used a chronosequence of vessel grounding sites to evaluate impacts of recent disturbances on these variables. In addition, by making the assumption that disturbances of different ages may reveal different stages of ecological recovery, we used the chronosequence to evaluate how altered ecosystem structure changed with time. We hypothesized that: (1) vessel groundings that excavate soils impact seagrass ecosystem structure and function, specifically by altering abundance in the primary producer and macroinvertebrate communities, modifying soil properties and biogeochemical processes, and removing sequestered carbon and other soil nutrients, and (2) these impacts change structure and process with time following disturbance through succession and ecosystem recovery.

**MATERIALS AND METHODS**

**Study system**

Southern Biscayne Bay is 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 & Fourqurean 2013). The limited available information on infauna in seagrass soils of this area (Roessler 1971, McLaughlin et al. 1983) suggests that these communities are typical of those found in subtropical seagrass meadows.

Many shallow seagrass shoals (<1 m deep) in this area are heavily impacted by vessel groundings where seagrass has been removed and soil excavated in discrete areas, similar to the widespread damage observed throughout the shallow water south Florida marine ecosystem (Sargent et al. 1995, Kenworthy et al. 2002, Kirsch et al. 2005, McNeese et al. 2006, Uhrin et al. 2011, Bourque & Fourqurean 2013). Our study evaluated vessel excavation disturbances to seagrass ecosystem structure on multiple seagrass shoals: Cutter Bank (latitude 25.36719° N, longitude 80.27095° W), Arsenicker Bank (25.37399° N, 80.28430° W), East Featherbed Bank (25.50696° N, 80.21666° W), and Biscayne Channel (25.65363° N, 80.16725° W).

**Experimental design**

We evaluated the effects of vessel groundings on ecosystem structure and the changes to ecosystem structure that occur through time following disturbance. We used a chronosequence approach to assess primary producers, soil properties, and macroinvertebrate infauna communities at multiple vessel grounding sites and adjacent undisturbed seagrass meadows on these shoals. Fourteen vessel grounding sites of known age (i.e. time since disturbance) were identified (see Table S1 in the Supplement; www.intres.com/articles/supp/m540p027_supp.pdf) where soils were excavated to a mean depth of 0.5 m (depth range 0.1 to 1.6 m). These sites ranged in area from 2 to 41 m², with a mean area of 22 m². Two to 4 sites were assigned to each age group rounded to the nearest 6 mo increment (0 yr, 4 sites; 1 yr, 2 sites; 3 yr, 3 sites; 4 yr, 2 sites; and 5+ yr, 3 sites). No sites could be attributed to a 2 yr old age group. Most sites were documented following the initial disturbance and were easily relocated for this study from GPS coordinates obtained during original grounding site assessments. The 3 sites in the 5+ yr age group were not documented upon occurrence but were known from aerial photography to be at least 5 yr old. Each site was sampled once during the period February–March 2011. As is implicit in chronosequence studies (Johnson & Miyanishi 2008), we made the assumption of steady state in the seagrass communities over time in the absence of disturbance; hence, we assumed undisturbed seagrass meadows within 2 m of each grounding site best represented the undisturbed condition of our vessel grounding sites.

**Seagrass community characterization**

To evaluate natural recovery of the seagrass community in vessel grounding disturbances, seagrass and macroalgae (mainly calcareous green algae) cover was documented at each site. Cover was esti-
Soil core collection and processing

Soils were sampled for a suite of properties that are important indicators of structure, function, and processes in seagrass ecosystems including: benthic microalgae (indicative of primary production, habitat quality); redox potential and organic matter content (benthic metabolism and remineralization); water content and bulk density (nutrient exchange); and nitrogen and phosphorus in soil and porewater (nutrient storage). Soils were sampled by collecting 7.3 × 40 cm cores from each grounding site and from undisturbed reference seagrass beds using a piston corer (see the Table 1). Three soil cores were haphazardly collected from each of the three 5+ yr old sites and from their reference areas, respectively, and replicate data were averaged for analysis. For sites in the remaining age groups, a single core was haphazardly collected from each grounding feature and from the adjacent undisturbed reference seagrass bed. The decision to collect only one core sample per feature was dictated by limited resources available for sample processing, collection, and analysis. We recognize that this lack of replication introduces the possibility that within-feature spatial variability was not captured by our sampling approach.

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 6 depth horizons (0–2, 2–6, 6–10, 10–20, 20–30, and 30–40 cm) in a nitrogen-filled glovebox. The pH and redox potential (Eh) 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, organic matter content, total nitrogen, total phosphorus), and porewater constituents (ammonium [NH4+], and soluble reactive phosphorus [SRP]). Soils for porewater extraction were placed into 50 ml centrifuge tubes and capped inside the glove box, centrifuged for 5 min at 3000 rpm, and returned to the glovebox. Extracted porewater was filtered through GF-C (1.2 µm) in-line syringe filters and subsampled into 2 aliquots for analysis of NH4+ and SRP (20 ml). 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 fluorometrically (Strickland & 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. Organic matter content (OM) was measured as loss on ignition (OM or proportional mass loss of dry soils following combustion at 500°C for 4 h; 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 (Fourquean et al. 1992b). 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 NH4+ 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 NH4+ 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).

Infauna core collection and processing

The macroinvertebrate infauna community was sampled with separate 7.3 × 10 cm soil cores collected by hand (see Table S1). Three cores were haphazardly collected from each of the 5+ yr old sites and from their reference areas, respectively. For sites in the remaining age groups, a single core was haphazardly collected from each grounding feature and from the adjacent undisturbed reference seagrass meadow. 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.

Data analysis

Nutrient storage estimates for seagrass soils were developed using disturbance and reference soil cores from recent vessel grounding impacts (i.e. 0 yr sites). Storage estimates were then used to quantify nutrient loss resulting from the disturbances. The disturbance cores (40 cm long, n = 4) were collected from the bottom of the seagrass soils with a depth of 2 to 70 cm, with an average depth of 40 cm (see Table S1). Reference cores (40 cm long, n = 4) were collected in seagrass soils within 2 m of the grounding incidents. For the 0 yr sites, we vertically superimposed reference core values over disturbance core values to provide estimates of pre-impact conditions. The disturbance cores were 80 cm deep, with an average depth of 40 cm (see Table S1). Reference cores (40 cm long, n = 4) were collected in seagrass soils within 2 m of the grounding incidents. For the 0 yr sites, we vertically superimposed reference core values over disturbance core values to provide estimates of pre-impact conditions in the top 80 cm of soils. Soil OM content has been shown to be a good predictor of soil organic carbon ($C_{org}$) in subtropical seagrass meadows (e.g. Florida Bay, USA, Shark Bay, Australia) with relatively high $C_{org}$ content (Fourqurean et al. 2012b). We used OM content as a proxy for $C_{org}$ content, using a ratio of $C_{org}$ = ca. 0.38 × OM. Loss of nutrients (i.e. $C_{org}$, N, P) stored in the top 80 cm of soils resulting from grounding disturbances was calculated using the volume, bulk density, and nutrient content of each core slice. To enable description of our results in the context of published reports of storage per cubic meter in other locations (Fourqurean et al. 2012b), we extrapolated mass loss to a depth of 1 m, making the assumption that bulk density and elemental content for the 80–100 cm range did not differ from the deepest 10 cm slice of the disturbance cores. We felt this was a reasonable assumption, given that for nearby Florida Bay seagrass soils, Fourqurean et al. (2012b) documented little change in $C_{org}$ content in the 80–100 cm horizon. We then calculated the nutrient storage in the top 1 m of reference soils and developed estimates of elemental loss for the recent (0 yr) disturbances studied. We also estimated loss of organic $C_{org}$ contained in seagrasses destroyed by the recent disturbances. We assumed that $C_{org}$ content in seagrass dry mass is approximately 35% and used relationships between $T. testudinum$ BB scores to aboveground biomass (Fourqurean et al. 2001), and ratios of aboveground to belowground biomass in $T. testudinum$ (Fourqurean & Zieman 1991), to estimate seagrass biomass loss at the 4 sites.

Prior to 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. Seagrass and macroalgae percent cover values and chl a values were square root-transformed to reduce skewness and stabilize variance. Soil variable data were log-transformed to reduce skewness and normalized to place variables on comparable and dimensionless scales. Principal components analysis (PCA) was used to reduce data complexity and extract composite variables that explained maximum variability in the soil properties. Seven soil variables were included in the PCA: BD, Eh, OM, N, P, $NH_4^+$, and SRP. For all age groups except the 5+ yr group, values at each depth horizon for each core collected per age group were considered a sample. For those sites in the 5+ yr age group where we collected 3 replicate cores per site, values at each depth horizon were averaged across replicate cores prior to analysis. Differences in multivariate soil properties between disturbed and reference sites were visualized with a PCA ordination. We attributed ecological relevance to the PC axes with eigenvalues >1, with interpretation based on soil property variables that were strongly correlated with each PC axis.

Differences in multivariate infauna community structure (i.e. abundance data simultaneously analyzed for multiple taxa) between disturbed and reference sites were visualized using principal coordinates analysis (PCO, Anderson et al. 2008). The SIMPER procedure (Clarke & Gorley 2006) was used to determine infauna taxonomic similarity within the disturbed and reference sites. SIMPER also identified the relative taxonomic contributions of the most abundant taxa in each analysis.

We used permutational analysis of variance (PERMANOVA, Anderson et al. 2008) to test for the effects of disturbance status (i.e. disturbed vs. reference) and time since disturbance (i.e. age) on univariate ecological relevance as represented by PC scores derived from soil properties and on seagrass percent cover, macroalgae percent cover, benthic chl a content, and multivariate infauna abundance.

For soil parameters, seagrass percent cover, macroalgae percent cover, and benthic chl a content, the PERMANOVA analyses were conducted on Euclidean distance resemblance matrices as suggested by Clarke & Gorley (2006). PERMANOVA analysis of multivariate infauna structure was conducted on...
log(x + 1)-transformed data using the binomial deviance dissimilarity measure (Anderson & Millar 2004) as an improvement on the Bray-Curtis dissimilarity measure. Soil depth was used as a covariate for PERMANOVA of soil properties, requiring the use of Type I sums of squares; otherwise, Type III sums of squares were used in the PERMANOVA routines.

Significant Disturbance Status (DS) × Age interactions were followed with pairwise permutational tests of DS within each age level. Significance values for PERMANOVA tests were based on 999 permutations of residuals under reduced models.

PCA, PCO, infauna diversity, PERMANOVA, and SIMPER analyses were conducted with PERMANOVA+ for PRIMER (Clarke & Gorley 2006, Anderson et al. 2008). Analyses of recovery status for seagrass, macroalgae, and chl a data were conducted with SPSS 20.0 (IBM).

### RESULTS

**Primary producer abundance**

Disturbance effects were evident in seagrass cover relative to the reference seagrass meadows (PERMANOVA, p < 0.001; Table 1, Fig. 1a). Mean seagrass percent cover within the very recent disturbances (6.2 ± 1.5%) was approximately 15% of that in the reference seagrass meadows (44.4 ± 4.5%). Seagrass cover in disturbed sites was lower than in reference meadows for sites of every age group (PERMANOVA pairwise tests, p < 0.001; Table 1, Fig. 1a).

A clear disturbance effect was not observed in macroalgae cover in our chronosequence sites (PERMANOVA, p = 0.686; Table 1, Fig. 1b). Macroalgae cover in 0 yr groundings (4.4 ± 1.1%) was reduced to approximately half of the cover in the reference seagrass community (PERMANOVA pairwise test, p < 0.013; Table 1, Fig. 1b). However, this reduction did not persist in the older disturbed sites, and macroalgae cover in the disturbed 3 yr old sites exceeded reference cover (PERMANOVA pairwise test, p = 0.036; Table 1, Fig. 1b).

Microphytobenthos abundance (as assessed by chl a content of surficial soils) ranged from 4.1 ± 1.1 to 14.2 ± 1.1 µg g⁻¹. No disturbance effect was detected (PERMANOVA, p = 0.175; Table 1, Fig. 1c).

<table>
<thead>
<tr>
<th>Source</th>
<th>Seagrass cover (%)</th>
<th>Macroalgae cover (%)</th>
<th>Benthic chl a content</th>
<th>Multivariate infaunal abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>DS</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
</tr>
<tr>
<td>Disturbance Status (DS; disturbed, reference) × Age (0, 1, 3, 4, 5+ yr)</td>
<td>1 182.7 18.7 0.001</td>
<td>1 643.3 14.4 0.001</td>
<td>1 35.9 8.0 0.001</td>
<td>386 4.5 3.1 0.001</td>
</tr>
<tr>
<td>Age</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
</tr>
<tr>
<td>Age (yr)</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
</tr>
<tr>
<td>Pairwise tests on DS within Age levels</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
<td>df ME Pseudo-F p</td>
</tr>
<tr>
<td>0</td>
<td>1 77.4 0.001</td>
<td>1 5.6 0.001</td>
<td>4 4.7 0.001</td>
<td>4 17.4 0.001</td>
</tr>
<tr>
<td>0.013</td>
<td>0 2.6 0.013</td>
<td>0 1.0 0.033</td>
<td>0 1.3 0.251</td>
<td>0 1.0 0.351</td>
</tr>
</tbody>
</table>

Table 1. Results of PERMANOVA tests of Disturbance Status (DS; disturbed, reference) and time since disturbance (Age; 0, 1, 3, 4, 5+ yr), on square root-transformed seagrass percent cover, macroalgae percent cover, benthic chlorophyll a content, and on log(x + 1)-transformed multivariate infaunal abundance data. p-values in bold indicate statistical significance at α = 0.05. Significant DS × Age interactions were followed with pairwise permutational tests of DS within each age level.
Initial disturbance effects: loss of elemental stocks

Seagrass soils at the four 0 yr sites contained an average of $15.0 \pm 2.0$ kg m$^{-3}$ of C$_{org}$ in the top meter of soils. Soil nitrogen content was $0.9 \pm 0.0$ kg m$^{-3}$, and phosphorus content was $0.072 \pm 0.003$ kg m$^{-3}$ at these sites. The total volume of soil excavated from the 40 yr grounding sites was approximately 32.6 m$^3$. We thus estimate that the grounding events responsible for these 4 disturbances resulted in the removal, redistribution and potential loss of approximately 489 kg of buried soil C$_{org}$ and 2.6 kg of C$_{org}$ contained in lost seagrass biomass from the vessel grounding disturbances. In addition, 29.3 kg of N, and 2.3 kg of P, respectively, were removed from these sites (Fig. 2).

Soil properties

Recently disturbed (0 yr) sites differed little from reference sites in terms of BD (median 0.8 vs. 0.9 g ml$^{-1}$), Eh (median $-273$ vs. $-220$ mV), OM (median 6.1 vs. 4.9%), N (median 0.14 vs. 0.11%), or P (median 0.0084 vs. 0.0082%; Fig. 3). Porewater nutrient concentrations ($\text{NH}_4^+$ and SRP) in the top 10 cm of disturbed soils of 0 yr sites were reduced by half relative to reference soils ($\text{NH}_4^+$ median 192.1 vs. 289.8 µM, SRP median 1.3 vs. 3.1 µM). Disturbance effects on soil properties showed variable patterns for different site age groups. For example, BD, OM, and N were reduced in the 1 yr old disturbances but greater than reference soils in the 5+ yr old sites (Fig. 3). SRP concentrations were up to 5 times lower in the 3 yr old groundings than in reference soils but similar to reference values in the 1 and 4 yr old disturbances (Fig. 3).

Fig. 1. Mean (±SE) (a) seagrass percent cover, (b) macroalgae percent cover, and (c) benthic chlorophyll a content at disturbed sites of known time since disturbance (black bars) and adjacent reference sites (gray bars). Asterisk indicates a statistical difference between disturbed and reference values on square root-transformed values within an age group (PERMANOVA pairwise tests, $\alpha = 0.05$)

Fig. 2. Mean (±SE) (a) organic matter, (b) nitrogen, and (c) phosphorus content in soils from 0 yr old disturbed sites and adjacent reference sites. Data are from 7.6 × 40 cm cores collected from the bottom of disturbed sites that averaged approximately 40 cm deep (●) or from the top 40 cm of the reference seagrass bed (○). Reference cores superimposed over disturbance cores enable 80 cm deep soil profiles. Capacity values quantify organic carbon, nitrogen, and phosphorus stocks in the top meter of soil and potential loss of buried resources per unit area in disturbances that excavate the top meter of soil.
The main variation in soil properties, as elucidated in the PCA, related to the OM content (PC1; higher OM, N; lower BD, Eh) and dissolved inorganic nutrients (PC2; higher NH4+, SRP) (Table 2, Fig. 4). We interpreted PC1 as a proxy for the OM content of seagrass soils, and PC2 to represent the availability of dissolved inorganic nutrients.

OM content as represented by PC1 scores did not vary with soil depth (p = 0.181) or by DS (p = 0.228) but did vary with site age (Age) and the Disturbance × Age interaction (PERMANOVA, p < 0.001; Table 3, Fig. 4). OM content (PC1 score) was lower in disturbance samples than in reference samples at 1, 4, and 5+ yr old sites (PERMANOVA, p < 0.002; Table 3, Fig. 4).

Porewater nutrient pools, as represented by PC2 scores, increased with soil depth (p < 0.001) and varied by DS, age, and the 2-factor interaction (PERMANOVA, p < 0.010; Table 3, Fig. 4). Concentrations were higher in disturbance samples than in reference samples from 0, 3, and 4 yr old sites (PERMANOVA, p < 0.028; Table 3, Fig. 4).

**Infauna community structure and diversity**

A total of 3635 individual organisms of 29 infauna taxa were identified from 13 disturbance sites and 14 reference sites (see Table S2 in the Supplement).
Thirty-three percent of the organisms collected were from disturbance sites, and 67% were from reference sites. Infaunal community structure differed between the disturbance and reference samples (PERMANOVA, p = 0.016; Table 1). This difference between communities was visible in the PCO ordination, where disturbance site cores separated from reference site cores along PCO1, though with some overlap between the 2 groups (Table S3 in the Supplement, Fig. 5). Tanaidacea, Nemertinea, Isopoda, Polychaeta, and Ophiuroidea abundance contributed to the differences between disturbance and reference cores, as indicated by strong positive correlations (>0.7) with PCO1 (Table S3). SIMPER analysis revealed that polychaetes and nematodes made substantial contributions (23.4–38.6%, Table S4 in the Supplement) to similarity within both disturbance and reference samples, as did oligochaetes to a lesser extent (12.8–17.9%). Amphipods contributed 13.0% to reference site similarity (Table S4) but less (4.2%) to similarity within disturbance samples.

**DISCUSSION**

We documented that vessel grounding disturbances (mean depth of 0.5 m) in seagrass ecosystems that excavated surface soils affected seagrass and macroalgae abundance, some soil properties, and infaunal invertebrate communities. Initial effects on primary producers included loss of aboveground cover of seagrass and macroalgae. Although we did not directly measure biomass, the disturbance excavations were deep enough to remove belowground seagrass rhizome and root biomass (sensu Di Carlo & Kenworthy 2008). Recovery to reference levels

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**Table 2. Principal components analysis (PCA) eigenvectors for PC axes with eigenvalues >1.0, extracted from multivariate data sets of soil and porewater variables sampled from 7.6 × 40 cm cores collected from disturbed and reference sites**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Organic matter status (PC1, 52.2%)</th>
<th>Porewater nutrient pools (PC2, 21.3%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulk density</td>
<td>0.48</td>
<td>0.14</td>
</tr>
<tr>
<td>Redox potential</td>
<td>0.34</td>
<td>−0.18</td>
</tr>
<tr>
<td>Organic matter</td>
<td>−0.50</td>
<td>−0.01</td>
</tr>
<tr>
<td>Total nitrogen</td>
<td>−0.49</td>
<td>0.03</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>−0.36</td>
<td>−0.42</td>
</tr>
<tr>
<td>Ammonium</td>
<td>0.05</td>
<td>−0.65</td>
</tr>
<tr>
<td>Soluble reactive</td>
<td>0.20</td>
<td>−0.59</td>
</tr>
<tr>
<td>phosphorus</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---

**Fig. 4. Mean (±SE) depth profiles for principal component (PC) scores extracted from a multivariate data set of soil and porewater variables sampled from 7.6 × 40 cm cores collected from disturbed sites of known time since disturbance (●) and adjacent reference sites (○). PC1 is interpreted as the soil organic matter content, and PC2 is interpreted to represent porewater inorganic nutrient pools.**
occurred in the first year for benthic microalgae. By Year 1, calcareous green macroalgae cover returned to or exceeded reference values in grounding disturbance sites of all ages, with the exception of recent disturbances. In contrast, seagrass cover remained lower than in reference sites for all disturbance age groups we studied. These results are consistent with prior disturbance studies and knowledge of successional patterns in tropical seagrass ecosystems, in which the first colonizers are usually turf and calcareous green macroalgae (Zieman 1976, 1982, Williams 1990, Rollon et al. 1999, Kenworthy et al. 2002, Whitfield et al. 2002, Uhrin et al. 2011).

Likewise, disturbed sites were characterized by detectable and long-term changes in soil properties, organic content, and porewater nutrients that did not return to reference levels in the 5 yr time frame captured in our study. Loss of plant cover, belowground seagrass biomass, and organic matter from surficial soils disrupted a major source of nutrients that typically occur in an undisturbed seagrass meadow. Our data indicate that important ecological services (e.g. nutrient storage and nutrient cycling) normally provided by undisturbed seagrass meadows (Hemminga & Duarte 2000, Marba et al. 2006) are severely impaired by physical disturbances and continue to be impaired during the earliest stages of recovery.

Following excavation of seagrass soils, seagrasses and rhizophytic algae may not be able to grow down abrupt steep slopes, such as typically exist in these disturbances, to recolonize the area (Kenworthy et al. 2002, Whitfield et al. 2002). Plant material or seeds falling into the excavation may encounter soils that are qualitatively different from the surrounding seagrass beds, with lower OM content and depleted porewater SRP, which may further impair a rapid recovery of the disturbance. Drift algae, sponges, and seagrass detritus often accumulate in the bottom of excavations and may cause light limitation, increase soil sulfides, and cause hypoxic conditions (Kenworthy et al. 2002, Lamote & Dunton 2006, but see Irlandi et al. 2004). The potential for re-accumulation of sequestered resources can only be realized with the slow reestablishment of the seagrass community, as our results suggest.

At disturbed sites, infauna community structure differed from reference sites for all disturbance age levels.

![Fig. 5. Principle coordinates analysis (PCO) ordination of multivariate infaunal community samples from disturbed sites of known time since disturbance (●) and adjacent reference sites (○)](image-url)}

<table>
<thead>
<tr>
<th>Source</th>
<th>PC1: organic matter content</th>
<th>PC2: porewater inorganic nutrients</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>MS</td>
</tr>
<tr>
<td>Depth</td>
<td>1</td>
<td>1.8</td>
</tr>
<tr>
<td>DS</td>
<td>1</td>
<td>1.6</td>
</tr>
<tr>
<td>Age</td>
<td>4</td>
<td>99.8</td>
</tr>
<tr>
<td>DS × Age</td>
<td>4</td>
<td>12.5</td>
</tr>
<tr>
<td>Residual</td>
<td>157</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Pairwise tests on DS within Age levels:

<table>
<thead>
<tr>
<th>Age (yr)</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.1</td>
<td>0.883</td>
</tr>
<tr>
<td>1</td>
<td>4.0</td>
<td>0.001</td>
</tr>
<tr>
<td>3</td>
<td>2.0</td>
<td>0.060</td>
</tr>
<tr>
<td>4</td>
<td>2.5</td>
<td>0.022</td>
</tr>
<tr>
<td>5+</td>
<td>6.0</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Likewise, disturbed sites were characterized by detectable and long-term changes in soil properties, organic content, and porewater nutrients that did not return to reference levels in the 5 yr time frame captured in our study. Loss of plant cover, belowground seagrass biomass, and organic matter from surficial soils disrupted a major source of nutrients that typically occur in an undisturbed seagrass meadow. Our data indicate that important ecological services (e.g. nutrient storage and nutrient cycling) normally provided by undisturbed seagrass meadows (Hemminga & Duarte 2000, Marba et al. 2006) are severely impaired by physical disturbances and continue to be impaired during the earliest stages of recovery.

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At disturbed sites, infauna community structure differed from reference sites for all disturbance age levels.
groups that we studied, including for crustaceans that form the basis of local fisheries (e.g. decapod shrimp) and that are important prey species (e.g. amphipods). However, numerical abundance did not differ between disturbed and reference sites. Our results suggest that disturbance sites may be supporting different infaunal communities, though numerical recovery may have occurred. Infaunal communities can change rapidly in disturbed soils, and colonization patterns may exhibit variable spatial and temporal responses to disturbance (Santos & Simon 1980, Zajac & Whitlatch 1982, Zajac et al. 1998, Schaffner 2010, Whomersley & Huxham 2010). Our findings are consistent with studies of less mobile epibenthic species (Uhrin & Holmquist 2003). More mobile epibenthic and nektonic communities have not been found to differ between disturbed seagrass habitat and reference meadows (Bell et al. 2002, Uhrin & Holmquist 2003, Burfeind & Stunz 2006), perhaps because of the ability of such species to readily seek habitat in adjacent undisturbed areas.

We propose that the apparent shift in infauna community composition we observed in disturbance sites can be explained by reduced habitat quality in these sites. Recovery of infaunal communities in unvegetated fine-grained unconsolidated soils following disturbance has been reported to occur in about a year (e.g. Collie & Hall 2000, Dernie 2003, Skilleter et al. 2006). However, in seagrass ecosystems, plant community structure provides additional habitat complexity and quality (e.g. belowground structure, soil organic matter, and food resources) when compared to unvegetated soils (Orth et al. 1984, Summerson & Peterson 1984). The slow recovery of seagrasses at the disturbed sites, where seagrass cover is, at most, only about 20% of that in the undisturbed meadow, may explain the community differences that we observed. Recovery of epibenthic faunal communities has been shown to track development of the seagrass community in transplanted seagrass sites (Fonseca et al. 1990), and it follows that a similar trajectory would apply to infauna.

Disturbances in subtropical seagrass meadows are first colonized by rapidly growing algae, and seagrasses follow, with the faster-growing seagrass species (e.g. Halodule wrightii and Syringodium filiforme in the Caribbean) colonizing before the slower-growing species (e.g. Thalassia testudinum; Ziemann 1982, Williams 1990, Rollon et al. 1999, Kenworthy et al. 2002, Whitfield et al. 2002). Seagrass species have different physical characteristics that include varying ratios of aboveground to belowground biomass (Ziemann 1982, Duarte & Chiscano 1999, Di Carlo & Kenworthy 2008). Early colonizers, like rhizophytic macroalgae, possess shallower and less belowground biomass than do climax seagrass species such as T. testudinum. Infaunal abundance and diversity were shown to be reduced in seagrass meadows dominated by early successional seagrass species, with reductions driven by structural characteristics of the seagrasses (Micheli et al. 2008). Likewise, the less complex belowground physical structure provided by the macroalgae community at our study sites may be supporting an altered infaunal community relative to the undisturbed seagrass meadow.

Our study sites were tens of square meters in size. At this scale, infaunal organisms are likely to actively migrate or be transported from the surrounding seagrass meadows into the disturbance sites during recolonization, though larval recruitment may also occur (Savidge & Taghon 1988). Habitat quality, including food availability, will be an important factor in the ability of disturbed 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 of benthic microalgae following disturbance occurred relatively quickly, likely because of rapid rates of growth and reproduction (Larson & Sundback 2008, Montserrat et al. 2008) and recolonization by mobile diatom taxa (Admirall 1984). Our results are consistent with this pattern. Development of microalgal resources is likely to be an important factor in the recovery of infauna communities following disturbance.

Seagrass soils in southern Biscayne Bay and in many areas of south Florida are heavily impacted by vessel groundings (Sargent et al. 1995, Kirsch et al. 2005, Uhrin et al. 2011, Hallac et al. 2012). Our study demonstrates that substantial quantities of Corg, nitrogen, and phosphorus are buried in the seagrass soils of southern Biscayne Bay and that mechanical disturbance by motor vessel groundings may be responsible for the removal and redistribution of these nutrients from the disturbance sites, which could lead to losses from the seagrass systems in Biscayne Bay. For an upper estimate of the potential flux of C and nutrients from disturbed soils, we made the assumption that soil excavated by vessel groundings was either lost from Biscayne Bay or redistributed and deposited in an oxic environment where the organic matter would be more rapidly remineralized. Combining our calculations of elemental storage in seagrass soils with knowledge of cumulative distur-
bance levels enables first-order estimates of elemental fluxes from the disturbed soils at a regional scale. For example, Sargent et al. (1995) reported a total areal extent of $488 \times 10^6 \text{ m}^2$ of moderate to dense seagrasses in Miami-Dade County, FL (the county that contains our study sites, Biscayne Bay, Biscayne National Park, and the urban area of Miami). Of this area, 2.7% was reported as ‘moderately scarred’ (i.e. propeller excavations comprise 5 to 20% of the total area), and 3.1% of the area was reported as ‘severely scarred’ (i.e. >20% of the area excavated by propellers). If we use the lowest end of the scarring intensity ranges provided by Sargent et al. (1995), and assume that 5% of the moderately scarred area and 20% of the severely scarred area have been excavated by propellers, then we can conservatively estimate a total area of $3.7 \times 10^6 \text{ m}^2$ of propeller damage in Miami-Dade County seagrass beds. Further, if we assume that the lifespan for a propeller scar in *T. testudinum*-dominated seagrass meadows is 20 yr (Kenworthy et al. 2002), then 5% of the cumulative disturbance estimate, or $185 \times 10^6 \text{ m}^2 \text{ yr}^{-1}$ can be used as a yearly estimate of newly excavated seagrasses. If we then assume an average disturbance depth of 0.4 m, we can extrapolate our estimates of $C_{\text{org}}$, N, and P loss from excavated soils as 6 kg $C_{\text{org}} \text{ m}^{-2}$, 0.4 kg N m$^{-2}$, and 0.03 kg P m$^{-2}$. We calculate a preliminary estimate of the maximum potential flux of $C_{\text{org}}$ out of seagrass soils of $1.1 \times 10^6 \text{ kg yr}^{-1}$ across Miami-Dade County as a result of boat groundings, coupled with potential N and P flux estimates of $74,000 \text{ kg yr}^{-1}$ and $5550 \text{ kg yr}^{-1}$, respectively. These first-order estimates are in need of improvement through consideration of spatial variation in soil nutrient environments and more current estimates of regional motor vessel disturbance regimes.

The fate of these fluxes also needs further study, as some of the material will likely be redeposited within the system, and some fraction will fuel processes in the water column or be transported out of the system. The release of nutrients stored in seagrass soils may have complex ramifications. The loss of large stocks of P in an already P-limited ecosystem may severely affect recovery of the seagrass. In the P-limited coastal ecosystems of south Florida (Powell et al. 1989, Fourqurean et al. 1992b), release of even small quantities of P could locally stimulate benthic algae or phytoplankton blooms to the detriment of seagrass meadows, or be exported to adjacent ecosystems (Fourqurean et al. 2012b).

According to our results, organic carbon storage in Biscayne Bay is similar in magnitude to stocks in 2 other subtropical seagrass ecosystems (Florida Bay, USA, and Shark Bay, Australia) for which $C_{\text{org}}$ stocks have been quantified (Fourqurean et al. 2012b). Awareness of the magnitude and potential economic value of carbon stored in seagrass soils as a blue carbon resource is relatively recent (Duarte et al. 2010, Murray et al. 2011, Fourqurean et al. 2012a) and has not to date been factored into economic calculations of seagrass damage assessment and restoration (Fonseca et al. 2000). Disturbance of $C_{\text{org}}$ stocks may result in redistribution to a state subject to accelerated oxidation and/or CO$_2$ release to the atmosphere. Thus, vessel groundings and other physical human disturbances may lead to vulnerability or loss of blue carbon resources. Managers and regulators should consider incorporating this resource loss into considerations of impact severity and the economics of damage assessment and restoration.

**CONCLUSION**

Our study is among the first to quantify loss of stored nutrients in seagrass soils following disturbance and to evaluate the assumption that the recovery of seagrasses following disturbance is tightly coupled with the structure and function of the seagrass soils during the recovery process. Vessel grounding disturbances in seagrass meadows resulted not only in loss of seagrasses and calcareous green macroalgae, but also loss of soils containing C, N and P, and an altered invertebrate community with a lower diversity. These impacts persisted in study sites that were up to 5 yr or older in age since disturbance, though indicators of ecosystem development related to primary production and nutrient accumulation were observed. We acknowledge that our study focused on relatively recent disturbances, and ecosystem recovery trajectories following disturbance should be established over longer time frames. However, our study supports links among soil structure and function, seagrass recovery, and the reestablishment of trophic linkages and secondary production in disturbed seagrass ecosystems.

Given the extensive vessel grounding disturbances in south Florida seagrass meadows, potential cumulative impacts should be of substantial concern to resource managers. Our results underscore the severity of these types of resource disturbances and reinforce the potential need for active restoration efforts. Vessel grounding disturbances create more complex and long-term resource losses than previously understood and acknowledged. Further, these disturbances drive a substantial flux of CO$_2$, N, and P...
from the seagrass soils with potential pathways into the water column and atmosphere. Relying solely on specific ecosystem components, such as metrics of seagrass cover, to evaluate resource impacts will likely lead to underestimation of both the severity and natural recovery time of the disturbances, especially with those involving soil excavation. Continued work on quantifying and valuing ecosystem-level impacts of physical disturbance to seagrass ecosystems will help ensure that disturbance to these valuable resources is more accurately quantified and will provide increased impetus for the protection of seagrass ecosystems.

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LITERATURE CITED


Bourque et al.: Disturbance and seagrass ecosystem structure


Kenworthy W (1981) The interrelationship between seagrasses, Zostera marina and Halodule wrightii, and the physical and chemical properties of sediments in a mid-Atlantic coastal plain estuary near Beaufort, North Carolina (USA). University of Virginia, Charlottesville, VA


Ziemann J (1976) The ecological effects of physical damage from motor boats on turtle grass beds in southern Florida. Aquat Bot 2:127–139


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