

Impacts of physical disturbance on ecosystem structure in subtropical seagrass meadows

Amanda S. Bourque^{1,2,*}, W. Judson Kenworthy³, James W. Fourqurean²

¹Habitat Restoration Program, Biscayne National Park, National Park Service, Homestead, FL 33033, USA

²Marine Science Program, Department of Biological Sciences, and Southeast Environmental Research Center, Florida International University, Miami, FL 33199, USA

³109 Holly Lane, Beaufort, NC 28516, USA

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 (C_{org}), 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 C_{org}, 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

—Resale or republication not permitted without written consent of the publisher—

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, Virnstein 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

*Corresponding author: amanda_bourque@nps.gov

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, Duntun & 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 CO₂ when soils are disturbed, which may contribute to climate change fueled by greenhouse gas emissions (Fourqurean et al. 2012b, Pendleton et al. 2012).

Tropical seagrass communities in the western Atlantic and Caribbean are generally thought to follow a facilitation model of succession following dis-

turbance (sensu den Hartog 1971, Connell & Slayter 1977, Zieman 1982, Williams 1990). Gap closure occurs primarily through clonal extension from adjacent populations (Bell et al. 1999, Rasheed 1999, Kenworthy et al. 2002, Fonseca et al. 2004, Uhrin et al. 2011) and more rarely from recruitment of vegetative fragments (Di Carlo et al. 2005). In larger disturbances, seedling recruitment may play a role initiating growth in central areas more distant from the colonizing edges (Olesen et al. 2004, Whitfield et al. 2004). Recovery following soil disturbance may take from several years to over a decade (Zieman 1976, Durako & Moffler 1985, Dawes et al. 1997, Kenworthy et al. 2002, Hammerstrom et al. 2007, Uhrin et al. 2011, Hall et al. 2012) due to the slow growth of late-successional species, the physical geometry of disturbances that slows seagrass colonization, and/or the susceptibility of disturbances to destabilization by erosion.

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 1996, 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.int-res.com/articles/suppl/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-

mated within randomly placed 0.25 m² PVC quadrats using a modified Braun-Blanquet (BB) cover-abundance scale (Fourqurean et al. 2001). Random points were generated using ESRI ArcMap 10 from shapefiles of each site and reference area. Our initial surveys indicated that our studied vessel groundings were between 2 and 41 m² in area; we sampled approximately 10% of each site area (or a minimum of 3 quadrats per site), with an equivalent number of quadrats sampled in the undisturbed reference area for each site (see Table S1).

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 (Fourqurean 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 grounding sites that ranged from 20 to 70 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 $C_{\text{org}} = \text{ca. } 0.38 \times \text{OM}$. 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

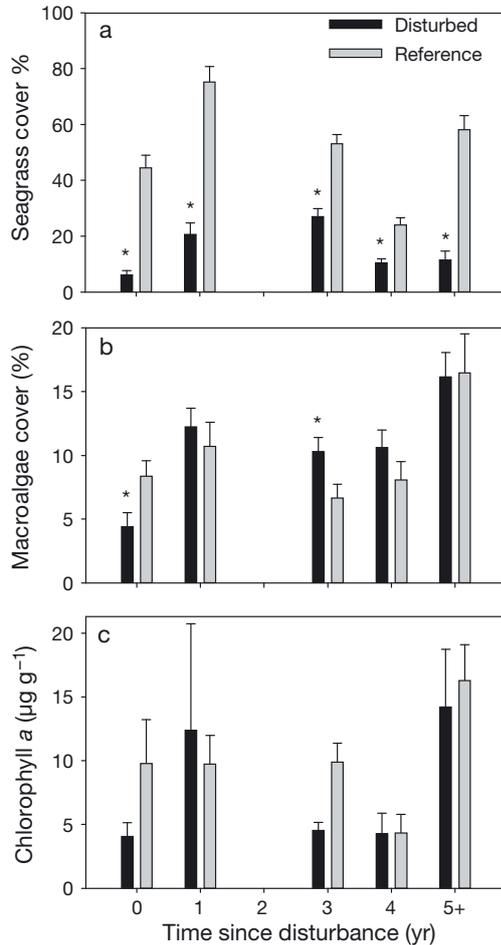


Fig. 1. Mean (\pm SE) (a) seagrass percent cover, (b) macroalgae percent cover, and (c) benthic chlorophyll a content at disturbed sites of known time since disturbance (black bars) and adjacent reference sites (gray bars). Asterisk indicates a statistical difference between disturbed and reference values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

Initial disturbance effects: loss of elemental stocks

Seagrass soils at the four 0 yr sites contained an average of $15.0 \pm 2.0 \text{ kg m}^{-3}$ of C_{org} in the top meter of soils. Soil nitrogen content was $0.9 \pm 0.0 \text{ kg m}^{-3}$, and phosphorus content was $0.072 \pm 0.003 \text{ kg m}^{-3}$ 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 (NH_4^+ and SRP) in the top 10 cm of disturbed soils of 0 yr sites were reduced by half relative to reference soils (NH_4^+ median 192.1 vs. $289.8 \mu\text{M}$, SRP median 1.3 vs. $3.1 \mu\text{M}$). 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 for the 1 and 4 yr old sites (Fig. 3).

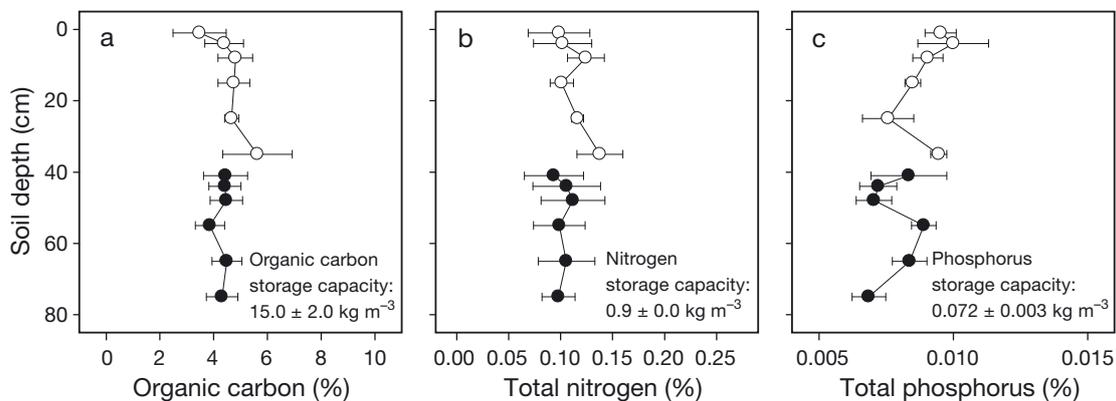


Fig. 2. Mean (\pm SE) (a) organic matter, (b) nitrogen, and (c) phosphorus content in soils from 0 yr old disturbed sites and adjacent reference sites. Data are from $7.6 \times 40 \text{ cm}$ cores collected from the bottom of disturbed sites that averaged approximately 40 cm deep (\bullet) or from the top 40 cm of the reference seagrass bed (\circ). 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

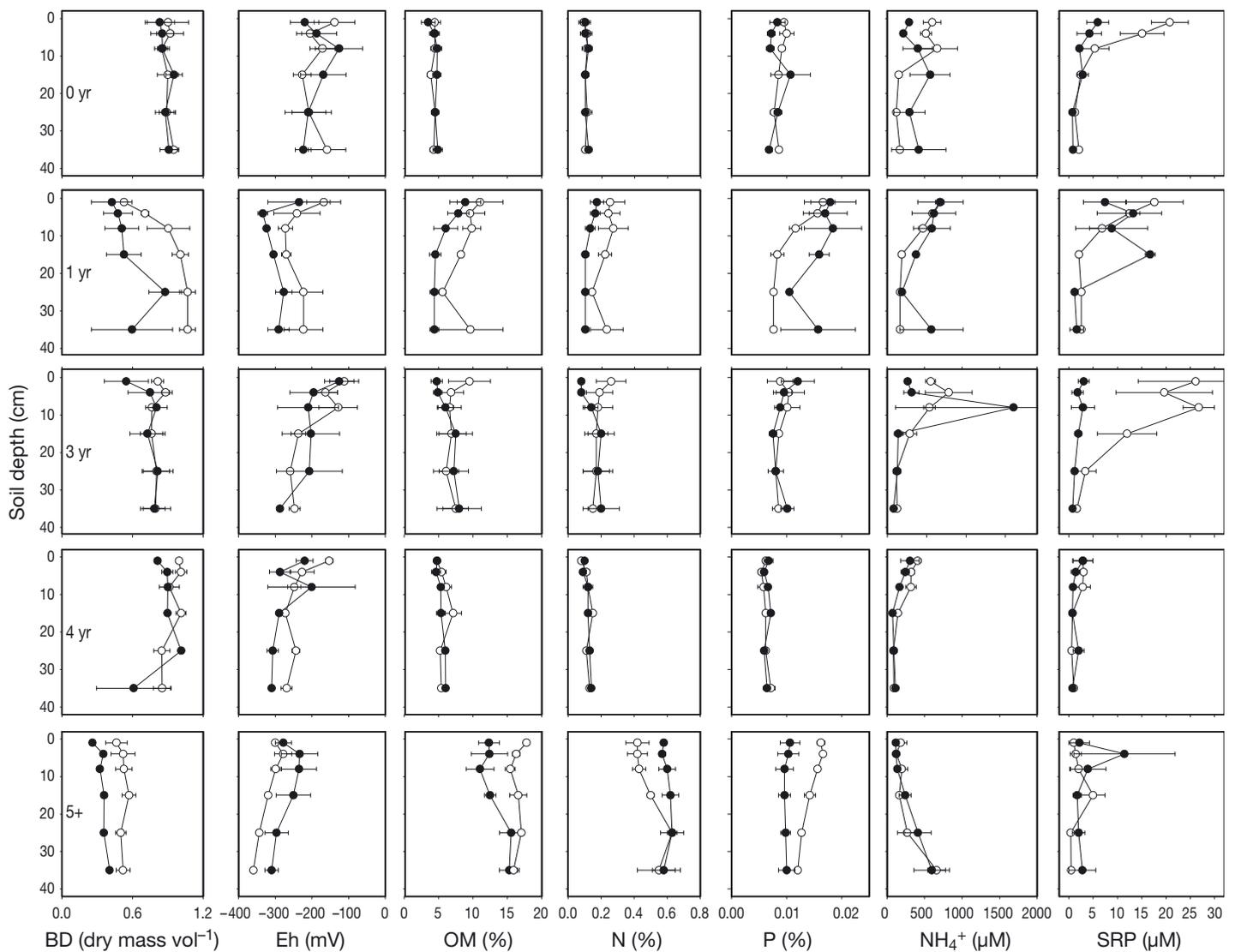


Fig. 3. Mean (\pm SE) depth profiles for soil bulk density (BD), redox potential (Eh), organic matter (OM), nitrogen, and phosphorus content and for porewater ammonium and soluble reactive phosphorus (SRP) concentrations. Values are from 7.6×40 cm soil cores collected from disturbed sites of known time since disturbance (\bullet) and adjacent reference sites (\circ)

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 NH_4^+ , 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 \times 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).

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

Variable	Organic matter status (PC1, 52.2%)	Porewater nutrient pools (PC2, 21.3%)
Bulk density	0.48	0.14
Redox potential	0.34	-0.18
Organic matter	-0.50	-0.01
Total nitrogen	-0.49	0.03
Phosphorus	-0.36	-0.42
Ammonium	0.05	-0.65
Soluble reactive phosphorus	0.20	-0.59

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

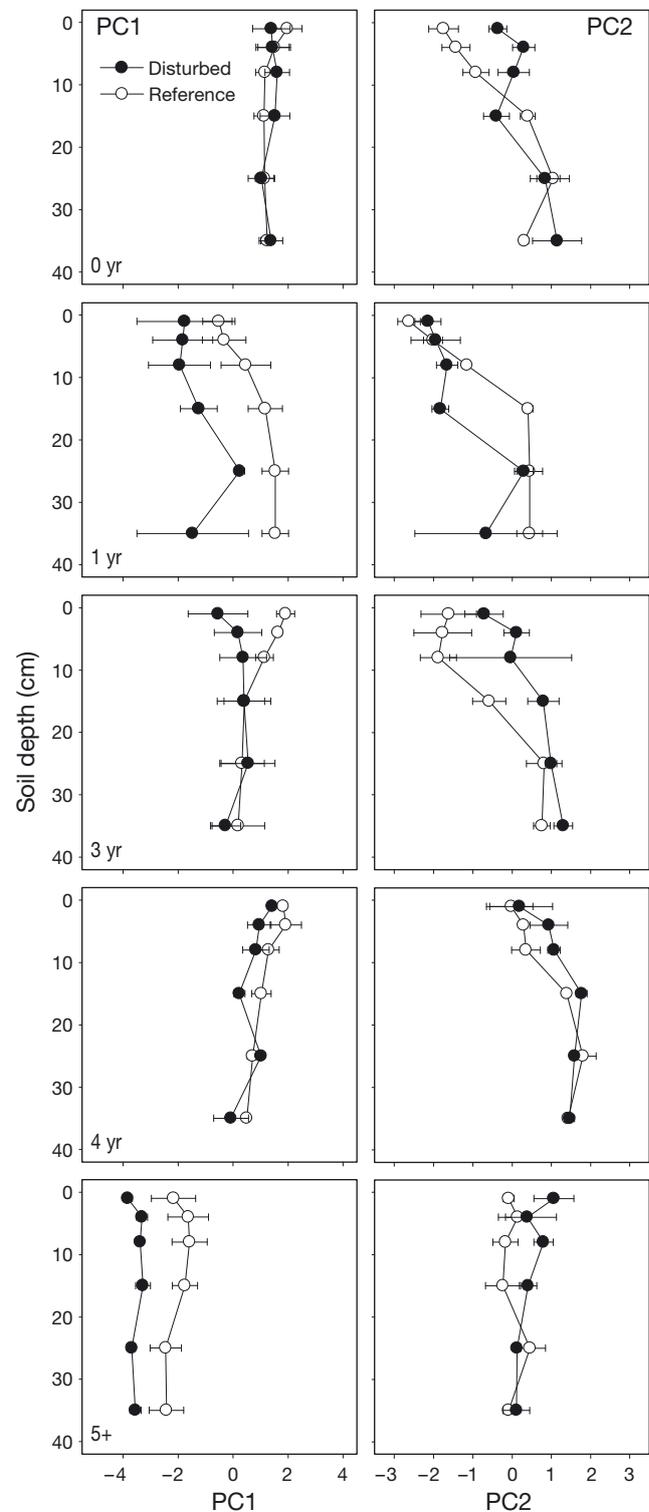


Fig. 4. Mean (\pm SE) depth profiles for principal component (PC) scores extracted from a multivariate data set of soil and porewater variables sampled from 7.6×40 cm cores collected from disturbed sites of known time since disturbance (\bullet) and adjacent reference sites (\circ). PC1 is interpreted as the soil organic matter content, and PC2 is interpreted to represent porewater inorganic nutrient pools

Table 3. Results of PERMANOVA tests of Disturbance Status (DS; disturbed, reference), time since disturbance (Age; 0, 1, 3, 4, 5+ yr), and pairwise tests of DS within Age levels, on principal component scores representing organic matter content (PC1) and inorganic porewater nutrient pools (PC2). Depth was a covariate in the model. p-values in **bold** indicate statistical significance at $\alpha = 0.05$. Refer to 'Materials and methods' for soil variables included in analysis

Source	PC1: organic matter content				PC2: porewater inorganic nutrients			
	df	MS	Pseudo- <i>F</i>	p	df	MS	Pseudo- <i>F</i>	p
Depth	1	1.8	1.8	0.181	1	51.5	66.4	0.001
DS	1	1.6	1.6	0.228	1	10.1	13.0	0.001
Age	4	99.8	99.1	0.001	4	13.5	17.4	0.001
DS × Age	4	12.5	12.4	0.001	4	2.7	3.5	0.010
Residual	157	1.0			157	0.8		
Pairwise tests on DS within Age levels	Age (yr)	<i>t</i>	p	Age (yr)	<i>t</i>	p		
	0	0.1	0.883	0	2.8	0.008		
	1	4.0	0.001	1	1.6	0.112		
	3	2.0	0.060	3	3.6	0.005		
	4	2.5	0.022	4	1.4	0.197		
	5+	6.0	0.001	5+	2.4	0.028		

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

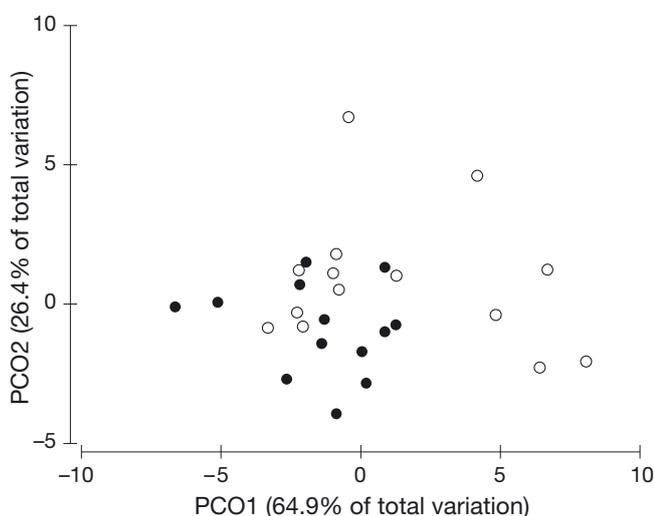


Fig. 5. Principle coordinates analysis (PCO) ordination of multivariate infaunal community samples from disturbed sites of known time since disturbance (●) and adjacent reference sites (○)

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*; Zieman 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 (Zieman 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 C_{org} , 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-

balance 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 $185\,000 \text{ m}^2 \text{ yr}^{-1}$ 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_{org} , N, and P loss from excavated soils as $6 \text{ kg } C_{\text{org}} \text{ m}^{-2}$, 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_{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 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_{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_{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.

Acknowledgements. This work was supported by Biscayne National Park and Florida International University. We thank M. Tongue, E. McGrath, D. Crossett, C. Johnson, K. Slattery, J. Martens, P. Parker, J. Drake, A. Perez, G. Puig-Santana, and R. Decker for assistance. Mote Marine Laboratory (Sarasota, FL) assisted with invertebrate analyses. This is contribution #757 of the Southeast Environmental Research Center, Florida International University.

LITERATURE CITED

- Admirall W (1984) The ecology of sediment-inhabiting diatoms. *Prog Phycol Res* 3:269–322
- Anderson M, Millar R (2004) Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. *J Exp Mar Biol Ecol* 305:191–221
- Anderson M, Gorley R, Clarke K (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Bell SS, Robbins BD, Jensen SL (1999) Gap dynamics in a seagrass landscape. *Ecosystems* 2:493–504
- Bell S, Brooks RA, Robbins BD, Fonseca MS, Hall MO (2001) Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biol Conserv* 100:115–123
- Bell S, Hall M, Soffian S, Madley K (2002) Assessing the impact of boat propeller scars on fish and shrimp utilizing seagrass beds. *Ecol Appl* 12:206–217
- Bourque A, Fourqurean J (2013) Variability in herbivory in subtropical seagrass ecosystems and implications for seagrass transplanting. *J Exp Mar Biol Ecol* 445:29–37
- Bucolo P, Sullivan MJ, Zimba PV (2008) Effects of nutrient enrichment on primary production and biomass of sediment microalgae in a subtropical seagrass bed 1. *J Phycol* 44:874–881
- Burfeind D, Stunz G (2006) The effects of boat propeller scarring intensity on nekton abundance in subtropical seagrass meadows. *Mar Biol* 148:953–962
- Capone D, Taylor B (1980) Microbial nitrogen cycling in a seagrass community. In: Kennedy V (ed) *Estuarine perspectives*. Academic Press, New York, NY, p 153–162
- Clarke K, Gorley R (2006) PRIMER v6. Prim v6 user manual/tutorial. PRIMER-E, Plymouth
- Collie J, Hall S (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. *J Anim Ecol* 69:785–798
- Connell JH, Slayter RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *Am Nat* 111:1119–1144
- Costanza R, D'Arge R, de Groot R, Farber S and others (1997) The value of the world's ecosystem services and natural capital. *Nature* 387:253–260
- Dawes C, Andorfer J, Rose C, Uranowski C, Ehringer N (1997) Regrowth of the seagrass *Thalassia testudinum* into propeller scars. *Aquat Bot* 59:139–155
- den Hartog C (1971) The dynamic aspect in the ecology of seagrass communities. In: Zavodnik D (ed) *Proceedings of the Sixth European Symposium on Marine Biology*. *Thalass Jugoslavica* 7:101–112
- Dernie K (2003) Recovery rates of benthic communities following physical disturbance. *J Anim Ecol* 72:1043–1056
- Di Carlo G, Kenworthy WJ (2008) Evaluation of above-ground and below-ground biomass recovery in physically disturbed seagrass beds. *Oecologia* 158:285–298
- Di Carlo G, Badalamenti F, Jensen A (2005) Colonisation process of vegetative fragments of *Posidonia oceanica* (L.) Delile on rubble mounds. *Mar Biol* 147:1261–1270
- Dobbs FC, Vozarik JM (1983) Immediate effects of a storm on coastal infauna. *Mar Ecol Prog Ser* 11:273–279
- Duarte C, Chiscano C (1999) Seagrass biomass and production: a reassessment. *Aquat Bot* 65:159–174
- Duarte CM, Holmer M, Marba N (2005) Plant–microbe interaction in seagrass meadows. In: Kristensen E, Haese RR, Kostka E (eds) *Interactions between macro- and microorganisms in marine sediments*. American Geophysical Union, Washington, DC, doi:10.1029/CE060p0031
- Duarte C, Marbà N, Gacia E, Fourqurean JW, Beggins J, Barrón C, Apostolaki E (2010) Seagrass community metabolism: assessing the carbon sink capacity of seagrass meadows. *Global Biogeochem Cycles* 24:GB4032, doi:10.1029/2010GB003793
- Dunton K, Schonberg S (2002) Assessment of propeller scarring in seagrass beds of the south Texas coast. *J Coast Res* SI37:100–110
- Durako MJ, Moffler MD (1985) Observations on the reproductive ecology of *Thalassia testudinum* (Hydrocharitaceae). III. Spatial and temporal variations in reproductive patterns within a seagrass bed. *Aquat Bot* 22:265–276
- Fonseca MS, Kenworthy WJ, Colby DR, Rittmaster KA, Thayer GW (1990) Comparisons of fauna among natural and transplanted eelgrass *Zostera marina* meadows: criteria for mitigation. *Mar Ecol Prog Ser* 65:251–264
- Fonseca MS, Kenworthy WJ, Courtney FX (1996a) Development of planted seagrass beds in Tampa Bay, Florida, USA. I. Plant components. *Mar Ecol Prog Ser* 132:127–139
- Fonseca MS, Meyer DL, Hall MO (1996b) Development of planted seagrass beds in Tampa Bay, Florida, USA. II. Faunal components. *Mar Ecol Prog Ser* 132:141–156
- Fonseca M, Julius B, Kenworthy W (2000) Integrating biology and economics in seagrass restoration: How much is enough and why? *Ecol Eng* 15:227–237
- Fonseca MS, Whitfield PE, Judson Kenworthy W, Colby DR, Julius BE (2004) Use of two spatially explicit models to determine the effect of injury geometry on natural resource recovery. *Aquat Conserv Mar Freshw Ecosyst* 14:281–298
- Fourqurean JW, Zieman JC (1991) Photosynthesis, respiration and whole plant carbon budget of the seagrass *Thalassia testudinum*. *Mar Ecol Prog Ser* 69:161–170

- Fourqurean JW, Zieman JC, Powell G (1992a) Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. *Mar Biol* 114:57–65
- Fourqurean JW, Zieman JC, Powell G (1992b) Phosphorus limitation of primary production in Florida Bay: evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnol Oceanogr* 37:162–171
- Fourqurean JW, Willisie A, Rose CD, Rutten L (2001) Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Mar Biol* 138: 341–354
- Fourqurean J, Duarte C, Kennedy H, Marba N and others (2012a) Seagrass ecosystems as a globally significant carbon stock. *Nat Geosci* 5:505–509
- Fourqurean J, Kendrick G, Collins L, Chambers R, Vanderkluft M (2012b) Carbon, nitrogen and phosphorus storage in subtropical seagrass meadows: examples from Florida Bay and Shark Bay. *Mar Freshw Res* 63:967–983
- Grech A, Chartrand-Miller K, Erfemeijer P, Fonseca M and others (2012) A comparison of threats, vulnerabilities and management approaches in global seagrass bioregions. *Environ Res Lett* 7:024006
- Gross M (1971) Carbon determination. In: Carver R (ed) *Procedures in sedimentary petrology*. Wiley, New York, NY, p 653
- Hall L, Krausman P, Morrison M (1997) The habitat concept and a plea for standard terminology. *Wildl Soc Bull* 25: 173–182
- Hall M, Kenworthy W, Merrello M (2012) Experimental evaluation of techniques to restore severe boat damage in south Florida seagrass habitats. Final Report to Florida's State Wildlife Grant Program, Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Conservation Commission, Tallahassee, FL
- Hall S (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanogr Mar Biol Annu Rev* 32:179–239
- Hallac D, Sadle J, Pearlstine L, Herling F, Shinde D (2012) Boating impacts to seagrass in Florida Bay, Everglades National Park, Florida, USA: links with physical and visitor-use factors and implications for management. *Mar Freshw Res* 63:1117–1128
- Hammerstrom KK, Kenworthy WJ, Whitfield PE, Merello MF (2007) Response and recovery dynamics of seagrasses *Thalassia testudinum* and *Syringodium filiforme* and macroalgae in experimental motor vessel disturbances. *Mar Ecol Prog Ser* 345:83–92
- Hemminga MA, Duarte CM (2000) *Seagrass ecology*. Cambridge University Press, Cambridge
- Holmer M, Duarte CM (2003) Sulfur cycling and seagrass (*Posidonia oceanica*) status in carbonate sediments. *Biogeochemistry* 66:223–239
- Irlandi EA, Orlando BA, Biber P (2004) Drift algae–epiphyte–seagrass interactions in a subtropical *Thalassia testudinum* meadow. *Mar Ecol Prog Ser* 279:81–91
- Isaksen MF, Finster K (1996) Sulphate reduction in the root zone of the seagrass *Zostera noltii* on the intertidal flats of a coastal lagoon (Arcachon, France). *Mar Ecol Prog Ser* 137:187–194
- Johnson EA, Miyaniishi K (2008) Testing the assumptions of chronosequences in succession. *Ecol Lett* 11:419–431
- Jones C, Lawton J, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- Kaiser M, Clarke K, Hinz, Austen MCV, Sommerfield PJ, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. *Mar Ecol Prog Ser* 311:1–14
- 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
- Kenworthy W, Fonseca M, Whitfield P, Hammerstrom K (2002) Analysis of seagrass recovery in experimental excavations and propeller-scar disturbances in the Florida Keys National Marine Sanctuary. *J Coast Res* 37: 75–85
- Kirsch K, Barry K, Fonseca M, Whitfield P, Meehan S, Kenworthy W, Julius B (2005) The Mini-312 Program—an expedited damage assessment and restoration process for seagrasses in the Florida Keys National Marine Sanctuary. *J Coast Res* SI40:109–119
- Koroleff F (1969) Direct determination of ammonia in natural waters as indophenol blue. *Int Cons Explor Sea* CM 9: 19–22
- Lamote M, Dunton K (2006) Effects of drift macroalgae and light attenuation on chlorophyll fluorescence and sediment sulfides in the seagrass *Thalassia testudinum*. *J Exp Mar Biol Ecol* 334:174–186
- Larson F, Sundback K (2008) Role of microphytobenthos in recovery of functions in a shallow-water sediment system after hypoxic events. *Mar Ecol Prog Ser* 357:1–16
- Lohrer AM, Thrush SF, Gibbs MM (2004) Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431:1092–1095
- Marba N, Holmer M, Gacia E, Barron C (2006) Seagrass beds and coastal biogeochemistry. In: Larkum AWD, Orth RJ, Duarte CM (eds) *Seagrasses: biology, ecology, and conservation*. Springer, Dordrecht, p 135–157
- McLaughlin PA, Treat SAF, Thorhaug A, Lemaitre R (1983) A restored seagrass (*Thalassia*) bed and its animal community. *Environ Conserv* 10:247–254
- McNeese PL, Kruer CR, Kenworthy WJ, Schwartzschild AC, Wells P, Hobbs J (2006) Topographic restoration of boat grounding damage at the Lignumvitae Submerged Land Management Area. In: Treat SF, Lewis RR (eds) *Seagrass restoration: success, failure, and the cost of both*. Lewis Environmental Services, Velrico, FL, p 131–146
- Micheli F, Bishop M, Peterson C, Rivera J (2008) Alteration of seagrass species composition and function over two decades. *Ecol Monogr* 78:225–244
- Montserrat F, Van Colen C, Degraer S, Ysebaert T, Herman P (2008) Benthic community-mediated sediment dynamics. *Mar Ecol Prog Ser* 372:43–59
- Moriarty DJ, Boon PI, Hansen JA, Hunt WG and others (1985) Microbial biomass and productivity in seagrass beds. *Geomicrobiol J* 4:21–51
- Murray B, Pendleton L, Jenkins W, Sifleet S (2011) Green payments for blue carbon: economic incentives for protecting threatened coastal habitats. Nichols Institute Report 11-04. Nichols Institute for Environmental Policy Solutions, Durham, NC
- Neckles HA, Short FT, Barker S, Kopp BS (2005) Disturbance of eelgrass *Zostera marina* by commercial mussel *Mytilus edulis* harvesting in Maine: dragging impacts and habitat recovery. *Mar Ecol Prog Ser* 285:57–73
- Norkko A, Hewitt J, Thrush S, Funnell G (2001) Benthic-pelagic coupling and suspension-feeding bivalves: linking site-specific sediment flux and biodeposition to benthic community structure. *Limnol Oceanogr* 46:2067–2072

- Olesen B, Marba N, Duarte CM, Savelle RS, Fortes MD (2004) Recolonization dynamics in a mixed seagrass meadow: the role of clonal versus sexual processes. *Estuaries* 27:770–780
- Orth R, Heck K, Van Montfrans J (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. *Estuaries Coasts* 7:339–350
- Orth R, Carruthers T, Dennison W (2006) A global crisis for seagrass ecosystems. *Bioscience* 56:987–996
- Parsons TR, Yoshiaki M, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, New York, NY
- Patriquin D, Knowles R (1972) Nitrogen fixation in the rhizosphere of marine angiosperms. *Mar Biol* 16:49–58
- Pedersen MF, Duarte CM, Cebrián J (1997) Rate of changes in organic matter and nutrient stocks during seagrass *Cymodocea nodosa* colonization and stand development. *Mar Ecol Prog Ser* 159:29–36
- Pendleton L, Donato D, Murray B, Crooks S and others (2012) Estimating global 'blue carbon' emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS ONE* 7:e43542
- Posey M, Lindberg W (1996) Influence of storm disturbance on an offshore benthic community. *Bull Mar Sci* 59: 523–529
- Powell GVN, Kenworthy WJ, Fourqurean JW (1989) Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bull Mar Sci* 44:324–340
- Rasheed M (1999) Recovery of experimentally created gaps within a tropical *Zostera capricorni* (Aschers.) seagrass meadow, Queensland Australia. *J Exp Mar Biol Ecol* 235: 183–200
- Roessler M (1971) Environmental changes associated with a Florida power plant. *Mar Pollut Bull* 2:87–90
- Rollon R, De Ruyter Van Steveninck E, Van Vierssen W, Fortes M (1999) Contrasting recolonization strategies in multi-species seagrass meadows. *Mar Pollut Bull* 37: 450–459
- Santos SL, Simon JL (1980) Response of soft-bottom benthos to annual catastrophic disturbance in a south Florida estuary. *Mar Ecol Prog Ser* 3:347–355
- Sargent F, Leary T, Crews D, Kruer C (1995) Scarring of Florida's seagrasses: assessment and management options. Florida Marine Research Institute Technical Report TR-1. Florida Marine Research Institute, St. Petersburg, FL
- Savidge WB, Taghon GL (1988) Passive and active components of colonization following two types of disturbance on intertidal sandflat. *J Exp Mar Biol Ecol* 115:137–155
- Schaffner LC (2010) Patterns and rates of recovery of macrobenthic communities in a polyhaline temperate estuary following sediment disturbance: effects of disturbance severity and potential. *Estuaries Coasts* 33:1300–1313
- Sheridan P (2004) Recovery of floral and faunal communities after placement of dredged material on seagrasses in Laguna Madre, Texas. *Estuar Coast Shelf Sci* 59:441–458
- Short FT, Wyllie-Echeverria S (1996) Natural and human-induced disturbance of seagrasses. *Environ Conserv* 23: 17–27
- Skilleter GA, Cameron B, Zharikov Y, Boland D, McPhee DP (2006) Effects of physical disturbance on infaunal and epifaunal assemblages in subtropical, intertidal seagrass beds. *Mar Ecol Prog Ser* 308:61–78
- Spalding M, Taylor M, Martins S, Green E, Edwards M (2001) The global distribution and status of seagrass ecosystems. Discussion paper prepared for the UNEP-WCMC Global Seagrass Workshop. UNEP–WCMC, Cambridge
- Stoner A (1980) The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bull Mar Sci* 30:537–551
- Strickland J, Parsons T (1972) Determination of particulate carbon. In: A practical handbook of seawater analysis, 2nd edn, Bull 167. Fish Res Board Canada, Ottawa
- Summerson HC, Peterson CH (1984) Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Mar Ecol Prog Ser* 15:63–77
- Uhrin AV, Holmquist JG (2003) Effects of propeller scarring on macrofaunal use of the seagrass *Thalassia testudinum*. *Mar Ecol Prog Ser* 250:61–70
- Uhrin AV, Kenworthy WJ, Fonseca MS (2011) Understanding uncertainty in seagrass injury recovery: an information-theoretic approach. *Ecol Appl* 21:1365–1379
- van der Heide T, Eklöf J, van Nes E, van der Zee E and others (2012) Ecosystem engineering by seagrasses interacts with grazing to shape an intertidal landscape. *PLoS ONE* 7:e42060
- Virnstein R, Mikkelsen P, Cairns K, Capone M (1983) Seagrass beds versus sand bottoms: the trophic importance of their associated benthic invertebrates. *Fla Sci* 46: 363–381
- Waycott M, Duarte CM, Carruthers T, Dennison W and others (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc Natl Acad Sci USA* 106:12377–12381
- Whitfield PE, Kenworthy WJ, Hammerstrom KK, Fonseca MS (2002) The role of a hurricane in the expansion of disturbances initiated by motor vessels on seagrass banks. *J Coast Res* 37SI:86–99
- Whitfield PE, Kenworthy WJ, Durako MJ, Hammerstrom KK, Merello MF (2004) Recruitment of *Thalassia testudinum* seedlings into physically disturbed seagrass beds. *Mar Ecol Prog Ser* 267:121–131
- Whomersley P, Huxham M (2010) Response of intertidal macrofauna to multiple disturbance types and intensities—an experimental approach. *Mar Environ Res* 69: 297–308
- Williams SL (1990) Experimental studies of Caribbean seagrass bed development. *Ecol Monogr* 60:449–469
- Zajac RN, Whitlatch RB (1982) Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonization. *Mar Ecol Prog Ser* 10:1–14
- Zajac R, Whitlatch R, Thrush S (1998) Recolonization and succession in soft-sediment infaunal communities: the spatial scale of controlling factors. *Hydrobiologia* 375-376:227–240
- Zieman J (1976) The ecological effects of physical damage from motor boats on turtle grass beds in southern Florida. *Aquat Bot* 2:127–139
- Zieman J (1982) The ecology of the seagrasses of south Florida: a community profile. US Fish Wildl Serv Off Biol Serv Washingt FWS/OBS-82. Department of Environmental Sciences, Virginia University, Charlottesville, VI