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Anna R. Armitage
Department of Biological Sciences and Southeast Environmental Research Center, Florida International University, armitage@fiu.edu

Thomas A. Frankovich
Marine Sciences Program, Department of Biological Sciences and Southeast Environmental Research Center, Florida International University,, tfrankov@fiu.edu

James W. Fourqurean
Marine Sciences Program, Department of Biological Sciences and Southeast Environmental Research Center, Florida International University,, fourqure@fiu.edu

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Long term effects of adding nutrients to an oligotrophic coastal environment

Running title:
Long term nutrient enrichment in seagrass

Anna R. Armitage
Department of Biological Sciences and Southeast Environmental Research Center
Florida International University
Miami, FL 33199

Current address:
Department of Marine Biology
Texas A&M University at Galveston
PO Box 1675
Galveston, TX 77553
Phone: 409-740-4842
Fax: 409-740-5001
Email: armitaga@tamug.edu

Thomas A. Frankovich
Department of Biological Sciences and Southeast Environmental Research Center
Florida International University
Miami, FL 33199

James W. Fourqurean
Department of Biological Sciences and Southeast Environmental Research Center
Florida International University
Miami, FL 33199

Author contributions:
ARA performed the research, developed methods, analyzed the data, and wrote the paper.
TAF performed the research, developed methods, and contributed to writing the paper.
JWF conceived of the study, developed methods, and contributed to writing the paper.

Abstract

Management of ecological disturbances requires an understanding of the time scale and dynamics of community responses to disturbance events. To characterize long-term seagrass bed responses to nutrient enrichment, we established six study sites in Florida Bay, USA. In 24 plots (0.25 m^2) at each site, we regularly added nitrogen (N) and phosphorus (P) in a factorial design for seven years. Five of the six sites exhibited strong P limitation. Over the first two years, P enrichment increased *Thalassia testudinum* cover in the three most P-limited sites. After three years, *Halodule wrightii* began to colonize many of the P-addition plots, but the degree of colonization was variable among sites, possibly due to differences in the supply of viable propagules. *Thalassia* increased its allocation to aboveground tissue in response to P enrichment; *Halodule* increased in total biomass but did not appear to change its aboveground: belowground tissue allocation. Nutrient enrichment did not cause macroalgal or epiphytic overgrowth of the seagrass. Nitrogen retention in the study plots was variable but relatively low, whereas phosphorus retention was very high, often exceeding 100% of the P added as fertilizer over the course of our experiments. Phosphorus retentions exceeding 100% may have been facilitated by increases in *Thalassia* aboveground biomass, which promoted the settlement of suspended particulate matter containing phosphorus. Our study demonstrated that low-intensity pulse (short-term) disturbance events such as phosphorus enrichment can initiate a slow, ramped successional process that may alter community structure over many years.

Key words: Aboveground and belowground biomass, epiphyte, eutrophication, macroalgae, nutrient, press, pulse, and ramp disturbances, seagrass

Introduction

Differences among plant species in their ability to compete with other species and utilize resources can dictate community composition and successional patterns after disturbance events (Grime 1977). Disturbance can be broadly defined to include alterations in resources (Pickett and others 1989), such as changes in the availability of limiting nutrients that subsequently alter plant community structure and composition (Fourqurean and others 1995; Siemann and Rogers 2003). These alterations are often caused by anthropogenic nutrient enrichment (Vitousek and others 1997), which can be characterized as pulse (short-term, discrete events), press (sudden events that maintain a constant level), or ramp (events that increase in intensity over time) disturbances depending on the intensity and persistence of the nutrient input (Lake 2000). The response of a system to any of these types of nutrient loading events is strongly dependent on landscape configuration and the availability of propagules (Lotze and others 2000), but in general, nutrient additions increase the biomass and growth rate of plants (Tilman 1987; Micheli 1999). Nutrient enrichment also frequently shifts the competitive balance from slower-growing species that dominate in low nutrient environments to faster-growing species (Duarte 1995; Bargali 1997).

Urbanized and developed shorelines make coastal ecosystems such as seagrass beds vulnerable to anthropogenic impacts. Proximity to urbanized and cultivated terrestrial landscapes exposes seagrass beds to runoff replete with anthropogenic nutrients, which can subsequently alter vital ecological processes and economic functions of seagrass beds (Martinetto and others 2006). Within seagrass beds, nutrient input often increases productivity and plant biomass (Lee and Dunton 2000) and facilitates the overgrowth or replacement of seagrass by fast-growing, opportunistic primary producers (Fourqurean and others 1995; McGlathery 2001).

Nutrient enrichment in seagrass beds may cause changes that extend over many years, especially in oligotrophic systems. For example, in a small-scale pulsed nutrient addition

experiment in seagrass beds in Florida Bay, the slow-growing species *Thalassia testudinum* originally responded to fertilization with increases in density and plant size; these increases remained until the fertilized sites were colonized by the faster growing species *Halodule wrightii* (Powell and others 1989; Fourqurean and others 1995). After that colonization event, *Thalassia* biomass and density began to decline, and within three years, *Halodule* biomass exceeded that of *Thalassia* (Fourqurean and others 1995). However, primary production in the fertilized plots remained higher than the surrounding area because of the greater mass-specific productivity of *Halodule*, even 20 years after cessation of fertilization (Herbert and Fourqurean 2008).

The fate of nutrients entering the system will have substantial impacts on ecosystem structure and function. If inputs of nitrogen and phosphorus, for example, are retained in the system, then even short-term pulsed or episodic deposition can have long-term impacts on community characteristics. If those nutrient inputs are quickly lost, then there will be a more rapid return to the base state. Herbert and Fourqurean (2008) found that the consequences of three years of fertilization, including increases in biomass, increases in biodiversity and enhanced primary productivity, persisted for over two decades following the cessation of fertilizer application in Florida Bay. Therefore, it is important to understand the storage of nutrients in the system in order to predict the long-term impacts of short-term changes in nutrient input.

Previous enrichment experiments performed at these sites have unequivocally demonstrated strong short-term responses (1.5 years) to phosphorus (P) enrichment at sites in eastern Florida Bay, where P addition increased *Thalassia* percent cover and productivity by approximately twofold (Armitage and others 2005). In contrast, *Thalassia* beds in western Florida Bay showed few responses to P addition on that time scale (Armitage and others 2005). However, the expected replacement of *Thalassia* with more opportunistic species like *Halodule* did not occur in that time frame (Powell and others 1989; Fourqurean and others 1995). Furthermore, the

storage of the experimental nutrient additions has not yet been quantified. Therefore, the objectives of the present study are to (1) characterize longer-term (seven years) response to experimental nutrient addition within the benthic producer community, and (2) quantify the fate of nutrients added to the system in order to better predict the long-term responses of seagrass bed structure to the low-intensity press disturbance events of phosphorus enrichment.

Methods

Study design

To evaluate the long-term effects of N and P enrichment across a P-availability gradient within Everglades National Park in Florida Bay, we used a three-way repeated measures ANOVA design, where the factors were P addition, N addition, and site. The original study concept had two sites nested in each of three major regions of the Bay: Northeast, Interior-Central, and Gulf, as defined by Zieman et al. (1989) based on macrophyte and sediment characteristics. However, subsequent analyses revealed that the region designation did not follow expected nutrient-limitation patterns (Armitage and others 2005). Therefore, we considered site to be a factor with six independent levels. In September 2002 we established six study sites (all depths < 2 m) in Florida Bay. The three eastern sites (Duck, South Nest, Bob Allen; see map in Digital Appendix 1) were characterized by a sparse, short *T. testudinum* canopy with some calcareous green macroalgae, primarily *Penicillus* spp. These three sites occurred in an area of severe P limitation (Fourqurean and Zieman 2002; Armitage and others 2005). Two middle sites (Rabbit Key, Nine Mile Bank) occurred in a region of intermediate P limitation (Fourqurean and Zieman 2002) and featured a dense, tall *T. testudinum* canopy and little macroalgae. The westernmost site (Sprigger Bank) was located in a region that may experience both N and P limitation and was characterized by a dense macroalgal-*Syringodium filiforme* (manatee grass)-*T.*

testudinum assemblage. At each site we established 24 0.25-m^2 study plots demarcated with a PVC frame secured to the benthos at one meter intervals.

We randomly assigned treatments (control [C], nitrogen only [N], phosphorus only [P], both nitrogen and phosphorus [NP]) to six plots per site (at Sprigger Bank, replication decreased to three due to the loss of 12 plots from erosion and boat disturbance over the course of the study). N was added in the form of slow release nitrogen fertilizer (Polyon, Pursell Technologies Inc., 38-0-0) and P as granular phosphate rock (Multifos, IMC Global, $Ca_3(PO_4)_2$). Loading rates of 1.43 g N m^{-2} d^{-1} and 0.18 g P m^{-2} d^{-1} (molar N:P ratio 17.6:1) were selected based on potential sewage loading rates (MCSM 2001) and previous studies in the region (Ferdie and Fourqurean 2004). We began bimonthly applications of fertilizer in September 2002 by sprinkling granular fertilizer evenly on the sediment surface and gently working it into the sediment by hand. Sediment in the control plots was similarly disturbed but no fertilizer was added. Benthic fertilizer applications ensured accessibility of nutrients to both aboveground and benthic primary producers (Ferdie and Fourqurean 2004; Mutchler and others 2004). Earlier studies confirmed that this protocol was effective in enriching sediment, seagrass tissue, and seagrass epiphytes (Armitage and others 2005). Bimonthly fertilization continued through April 2006, at which point a portion of each plot was destructively sampled for belowground biomass (see detailed methods below). After a 16-month recovery period, quarterly fertilization was resumed in August 2007 and continued through the end of the study in June 2009.

Temporal patterns

Every three months from October 2002 to August 2005, we recorded macrophyte percent cover, epiphyte biomass, benthic microalgal biomass, and seagrass and epiphyte tissue nutrient content. Macrophyte percent cover monitoring continued as frequently as logistics permitted;

measurements were taken in September 2007, April 2008, September 2008, December 2008, and June 2009.

We determined macrophyte (seagrass and macroalgae) percent cover using a modified Braun-Blanquet (BB) abundance scale used for extensive monitoring in this region (Fourqurean and others 2001). On this scale, 0 = absent; 0.1 = one individual, <5% cover; 0.5 = few individuals, <5% cover; 1 = many individuals, <5% cover; 2 = 5–25% cover; 3 = 25–50% cover; 4 = 50–75% cover; and 5 = 75–100% cover. Seagrass cover measurements began in October 2002; macroalgal measurements were initiated in February 2004.

We measured seagrass photosynthetic epiphyte biomass by collecting two *T. testudinum* short-shoots from each plot and removing the epiphytes by gently scraping the leaves with a razor blade. Epiphytes were freeze dried and pigments extracted with 90% acetone. The chlorophyll *a* (chl *a*) concentration was determined using a Shimadzu RF-Mini 150 fluorometer with low bandwidth filters (Welschmeyer 1994) following calibration with a chl *a* standard using a Shimadzu UV Mini 1240 spectrophotometer and the spectrophotometric equations of Jeffrey and Humphrey (1975). Epiphyte biomass is reported as μg chl *a* cm^{-2} of seagrass leaf. Due to logistical constraints, epiphytes were collected quarterly from October 2002 through August 2005 and in April 2006 and April 2008.

We measured the N and P content and calculated the molar N:P ratio of dried seagrass leaves for each of the sampling events through April 2006. N contents were determined using a CHN analyzer (Fisons NA1500). P contents were determined by a dry-oxidation, acid hydrolysis extraction followed by a colorimetric analysis of phosphate concentration of the extract (Fourqurean and others 1992a).

All data collected over time were analyzed with three-way repeated measures ANOVA, where the fixed factors were ± P, ± N, and site. Variances were tested for homoscedasticity with

the F_{max} test and data were log transformed to conform to the assumptions of ANOVA. To compensate for potential violations of sphericity in the data, Greenhouse-Geisser corrections are reported.

Biomass and nutrient budget

To assess macrophyte (seagrass and macroalgae) and epiphyte biomass responses to the enrichment treatments, we destructively sampled a portion of each plot in April 2006. Using a circular core (15 cm diameter) to subsample biomass in each plot, we removed all aboveground and belowground tissue to a depth of 15 cm. Cores were frozen pending processing in the lab. Plants were separated by species, and for seagrass, tissue was divided into aboveground (photosynthetic) and belowground tissue (rhizomes + roots + other non-photosynthetic tissue). Epiphytes were removed from seagrass leaves by gently scraping with a razor blade. Macroalgal tissue was rinsed to remove adhered sediments but epiphytes were not removed from the complex thalli. Seagrass and macroalgae tissues were dried at 60˚C and weighed to determine biomass.

To determine the fate of added nutrients, we recorded the N and P content of each component of the system. Following the collection of biomass cores in April 2006, we measured the N and P content (as described above) of dried seagrass (aboveground and belowground), macroalgal and epiphyte tissues. Sediment cores were not collected in April 2006, so we estimated sediment N and P content using sediment nutrient data from cores (1 cm diameter, 5 cm deep) that were collected from each plot in February 2004. Since these cores were taken earlier in the study, it is likely that we underestimated the sediment nutrient content at the time the plant biomass was recorded.

To determine the long-term importance of nutrient enrichment, we calculated the retention efficiency of nitrogen and phosphorus within 0.25 m^3 compartments (50 x 50 x 100 cm)

containing 200 L of water column and 50 L of sediment (sensu Ferdie and Fourqurean 2004). The components included in the calculation were seagrass leaves (separated by species), seagrass belowground tissue (separated by species), macroalgae, *T. testudinum* epiphytes, sediment, and water column. Quantities of nutrients in each component were calculated as nutrient content as a percent of dry weight and biomass (g dry weight). Average values for each treatment at each site were used in the budget calculation. Water column nutrient concentrations from April 2006 were obtained from the Southeast Environmental Research Center Water Quality Monitoring Network at Florida International University. Calculations included net system retention ([total system nutrient (g), enriched] - [total system nutrient (g), control] and retention efficiency ([net system retention (g)/mass applied (g) x 100%).

Following this destructive sampling of biomass, the plots were undisturbed (no sampling or fertilization) for a period of 16 months, after which the holes created by the core extractions had filled in and were no longer visible, and the seagrass canopies had apparently recovered. The enrichment effects were still visually evident, so we resumed the study in August 2007 and continued with quarterly fertilization and semiannual monitoring of plant percent cover.

Biomass data were analyzed with a three-way fixed factor ANOVA (P addition, N addition, and site) following verification of homoscedasticity with the F_{max} test. Biomass data were log transformed if necessary to conform to the assumptions of ANOVA.

Results

Temporal responses

Seagrass leaf nutrient content reflected nutrient treatments, though the magnitude of the responses varied among sites and over time. A highly significant date x site x P interaction (df = 39, F = 2.3, $p < 0.001$) was driven by the large decrease in *Thalassia* leaf N:P ratio in P addition treatments at all sites except for the westernmost site, Sprigger Bank (Fig. 1, Digital Appendix

2a). The magnitude of the response to P addition was largest at the three eastern sites and intermediate at Rabbit Key and Nine Mile Bank. A significant 4-way interaction between date, site, P addition, and N addition (df = 31, F = 1.5, p = 0.031) was driven by higher leaf N:P ratios in NP relative to P only treatments at Duck and Bob Allen Keys on most dates.

The response of *Thalassia* percent cover (as represented by the Braun-Blanquet cover score) varied with site and over time (Digital Appendix 2b). *Thalassia* cover increased in P addition treatments (P alone and with nitrogen), but only at the three eastern sites (date x site x P df = 52, F = 7.6, p < 0.001; Fig. 2). At those sites, *Thalassia* response to P addition peaked approximately two years into the study (September 2004-February 2005), after which *Thalassia* cover declined to control levels in all treatments at most sites. The exception was Bob Allen Key, where *Thalassia* cover decreased but remained measurably higher in P addition plots.

There were no interactions between N and P addition for *Thalassia* cover, but there was a significant date x site x N addition interaction (df = 52, F = 1.7, p = 0.001; Digital Appendix 2b). This interaction may have been driven by higher *Thalassia* cover in NP relative to P-only treatments at some sites (Duck, Bob Allen) on some dates (May 2004 – May 2005) (Fig. 2).

There was a significant interaction between date, site, and P addition for *Halodule* percent cover (df = 23, F = 4.2, p < 0.001; Digital Appendix 2b). This interaction was driven by a proliferation of *Halodule* in P addition plots starting in the fourth year of the study at all sites except Sprigger Bank (Fig. 2). *Halodule* rarely occurred in our control or N only plots. In two of the three eastern sites (Duck and Bob Allen), *Halodule* cover was equivalent to or higher than *Thalassia* cover. There were no significant N effects on *Halodule* cover, and no N x P interactions.

A third species of seagrass, *Syringodium filiforme*, was common at the westernmost site, Sprigger Bank. No statistical analyses were performed on its cover because it occurred only at

that site, but qualitative observations suggest that it was consistently more abundant than *Thalassia* (Fig. 2f). *Halodule* was not found at Sprigger Bank on any of the sampling dates.

Cover of the two dominant macroalgal groups, calcified green algae and uncalcified red algae, varied over time, though the nature of the temporal changes differed between sites (red macroalgae date x site df = 7, F = 37.6, $p < 0.001$; green macroalgae date x site df = 7, F = 11.7, $p < 0.001$; Digital Appendix 2c, Fig. 3). Overall, macroalgal cover was higher at Sprigger Bank than at all other sites. There were marginally significant site x P (df = 1, F = 4.4, p = 0.045) and site x N (df = 1, F = 4.6, p = 0.042) interactions for red macroalgae (Digital Appendix 2c), but the magnitude of the site and date effects were much larger than any nutrient addition effects. There were no N x P interactions for either type of macroalgae.

Thalassia epiphyte biomass (μg chl *a* cm^{-2} seagrass leaf) was lower in P and NP treatments on some dates at Bob Allen (date x site x P df = 18, F = 3.0, $p < 0.001$; Digital Appendix 2d, Fig. 4). Epiphyte biomass was higher at Sprigger Bank than at all other sites, and the magnitude of the site effect was much larger than the temporally variable P-addition effect. Epiphyte biomass did not change in response to nitrogen addition, and there were no N x P interactions.

Biomass

Aboveground *Thalassia* biomass was impacted by P addition, but that effect varied among sites, as revealed by a significant site x P interaction (df = 5, F = 8.8, $p < 0.001$; Digital Appendix 2e, Fig. 5a). Relative to controls, aboveground *Thalassia* biomass was 2.8-6.7 times higher in P-addition plots at the three eastern bay sites, Duck, South Nest, and Bob Allen. There was no substantial change in aboveground biomass among treatments at the three western sites.

The effect of P addition on belowground *Thalassia* biomass varied significantly among sites (site x P df = 5, F = 5.2, $p < 0.001$; Digital Appendix 2e, Fig. 5b). Belowground biomass was 1.7 times higher in P addition plots at Bob Allen Keys and about 25% lower in P addition plots at

Rabbit and Nine Mile Bank. There was no substantial change in absolute belowground biomass among treatments at the other three sites.

The effect of P addition on the ratio of aboveground to belowground *Thalassia* biomass also varied significantly among sites (site x P df = 5, F = 4.8, p = 0.001; Digital Appendix 2e, Fig. 5c). Relative to controls, the ratio was 3.3-4.5 times higher (i.e., more relative aboveground biomass) in P-addition plots at the three eastern bay sites. There was no substantial change in the ratio among treatments at the three western sites.

Halodule biomass was patchy and was entirely absent from a large number of plots; precluding statistical analyses. However, *Halodule* biomass was substantially higher in P-addition plots (alone or with nitrogen) at Duck and Bob Allen Keys than in control or nitrogen-only plots (Fig. 6). At Rabbit Keys and Nine Mile Bank, *Halodule* biomass was highest in NP addition plots. *Halodule* was absent from Sprigger bank and occurred in only one P-addition plot at South Nest Key.

Macroalgal biomass was highly variable among sites, precluding statistical analyses. Overall, there was no macroalgal proliferation or overgrowth of the seagrasses in enriched plots. Calcareous green algae (*Penicillus* spp. and *Halimeda* spp.) were the most common genera, with substantially higher biomass at Sprigger Bank than at all other sites (Fig. 7). Uncalcified red algae (e.g., *Polysiphonia* spp., *Laurencia intricata, Palisada poiteaui*) were more common in the eastern bay (Fig. 7).

Nutrient retention budget

Nitrogen and phosphorus concentrations in seagrass above- and belowground tissue, macroalgal tissue, *Thalassia* epiphytes, soil, and the water column are reported in Digital Appendix 3. There was little (< 31%) nitrogen retention in nitrogen-only plots at most sites, except for one of the western sites, Nine Mile Bank (Table 1). At the three eastern sites, nitrogen

retention was higher (24-85%) in plots where both nitrogen and phosphorus were added. Nearly all of the phosphorus added to the experimental plots was retained in the study plots, particularly within the sediment and belowground *Thalassia* tissue (Table 1). In most cases, phosphorus retention appeared to be greater than 100%, suggesting that the plants or soils were scavenging phosphorus from other sources.

Discussion

The release from phosphorus limitation caused both acute and longer-term effects on community composition and biomass. Immediate effects of enrichment included an increase in *Thalassia* cover, but these short-term effects did not reflect the long-term, ecosystem level responses. Rather, the most striking outcome of nutrient enrichment in our study was a gradual shift in seagrass species from *Thalassia* to *Halodule*, with a concurrent increase in *Halodule* biomass. As an ecological opportunist with a high potential intrinsic rate of growth, *Halodule* has been shown to overgrow *Thalassia* in nutrient-replete conditions in Florida Bay (Fourqurean and others 1995).

Despite the strong *Halodule* response to P addition, the degree of *Halodule* colonization was independent of the severity of phosphorus limitation at each site. Heterogeneity in the supply of viable propagules may have driven the differences in *Halodule* colonization among sites (Lotze and others 2000). One of the most P-limited sites, South Nest Key, had little *Halodule* colonization until the seventh year of the study, whereas the other severely P-limited sites experienced substantial *Halodule* colonization after three years of fertilization. In two of the less P-limited sites, Rabbit Key and Nine Mile Bank, *Halodule* colonized a few plots after one year of fertilization, but did not spread into other plots during the rest of the study period. This spatial heterogeneity in *Halodule* recruitment, both within and among sites, strongly suggests that the community response to nutrient enrichment is largely influenced by the existing bank of viable

seagrass material and the stochastic landings of opportunistic *Halodule* propagules in our plots. Propagule dispersal has been shown to influence species composition in wetland (Campbell and others 2003), marine (Reed and others 2000), and terrestrial (Dosch and others 2007) habitats. The high level of small- (within sites) and large-scale (among sites) spatial heterogeneity in *Halodule* density suggests that the supply of propagules via dispersal is highly variable, even when potential parent plants are established close by (Fourqurean and others 1995).

Overgrowth of fast-growing macro- or epiphytic algae is a commonly reported manifestation of enrichment in seagrass beds (e.g., Duarte 1995; Valiela and others 1997; Hauxwell and others 2001; Hughes and others 2004), but we did not detect any algal proliferation in enriched plots despite the high nutrient loading rates and long duration of our experiments. Our results parallel other regional studies of the controls of epiphytic and macroalgal abundance and further suggests that algal loads do not universally increase in seagrass beds during eutrophication. In Florida Bay, nutrient availability explained only a small proportion of the variation in epiphyte loads (Frankovich and Fourqurean 1997), and in a recent analysis, epiphyte loads were independent of natural gradients in nutrient availability across the seagrass beds of southern Florida (Fourqurean and others 2010). Macroalgal species composition was highly variable among sites (Armitage and others 2005; Armitage and Fourqurean 2009), and this uneven species distribution may have obscured a bay-level macroalgal response to nutrients. Alternatively, nutrient enrichment may have increased the nutritional quality of algal tissue, subsequently stimulating herbivory and effectively preventing algal overgrowth (Heck and others 2006).

Thalassia increased its allocation to aboveground biomass in enriched treatments, consistent with fertilization responses observed in other seagrass species (e.g., Short 1983; Perez and others 1994; Lee and Dunton 1999). Similar allocation strategies in nutrient-replete conditions have been detected in terrestrial grassland systems (Haase and others 2008; Johnson and others 2008).

Our study also agrees with previous work showing that enrichment does not cause *Halodule* to increase its allocation to aboveground tissue (Dunton 1996), although total *Halodule* biomass in control and nitrogen-only plots was very low, limiting our ability to accurately calculate aboveground: belowground biomass ratios in those treatments.

A substantial portion of the nutrients that were experimentally added to this system were retained in the sediment and belowground seagrass tissue, similar to findings at sites on the ocean side of the Florida Keys (Ferdie and Fourqurean 2004). Although the sediment and root tissue contained higher absolute quantities of nitrogen than of phosphorus, percent retention of phosphorus was remarkably high, often over 100% of the P added as fertilizer over the course of our experiments. Furthermore, we likely underestimated sediment nutrient content because those measurements were collected earlier in the study. Therefore, our determinations of P content in the sediment are conservative and suggest that P retention may be even higher than we calculated. Organic acid exudates from *Thalassia* roots can extract phosphorus bound to carbonate sediments like those in Florida Bay (Long and others 2008). Therefore, the dense aggregations of *Thalassia* roots in P-enriched plots may have been able to scavenge phosphorus from pools deeper in the sediment (Holmer and others 2006). Accordingly, the highest P retention (> 200%) in our study occurred in the two sites with the highest seagrass biomass (Rabbit Key and Nine Mile Bank, Fig. 5).

An alternative or complimentary mechanism driving the greater than 100% phosphorus retention rates may be linked to the entrapment of dissolved inorganic phosphorus (DIP) in the dense seagrass beds in P-enriched treatments. In carbonate environments, DIP quickly binds to particulate matter and settles to the substrate (de Kanel and Morse 1978). Further, seagrass ecosystems trap sediments and organic matter from the water column, so that on average, 50% of the organic matter deposited in seagrass beds worldwide comes from allochthonous sources

(Kennedy and others in review). These sediments contain both organic and inorganic P. Since the rate of particle trapping increases in denser seagrass beds (Eckman 1983; Boström and Bonsdorff 2000), the increased aboveground seagrass biomass in P-addition plots may have accelerated P capture from the water column.

At most sites, phosphorus retention was greater than 100%, but the westernmost site, Sprigger Bank, had relatively low (< 67%) P retention. We may have underestimated sediment P content, suggesting that absolute P retention may actually be higher than 67%. Nevertheless, Sprigger Bank had markedly lower P retention relative to the other five study sites. This is likely a consequence of the higher energy environment of Sprigger Bank, which receives higher tidal exchange and wave energy than our other sites within the protected waters of Florida Bay. This higher energy environment probably led to increased sediment resuspension and the loss of shed seagrass leaves, compared to the more quiescent inner bay sites. Similarly, Ferdie and Fourqurean (2004) found P retention was much higher in protected inshore sites compared with more exposed sites further offshore in the backreef environment of the Florida Keys. In addition, even though nutrient uptake rates tend to be higher in high velocity environments (Morris and others 2008), most of the plant biomass at the Sprigger site was macroalgae (Fig. 7). Belowground seagrass biomass, where much of the phosphorus was retained in the other sites, was quite low (Fig. 5b), limiting the size of the potential P sink at that site.

In the oligotrophic Florida Bay environment, *Thalassia* is the dominant seagrass species in Florida Bay. *Thalassia* dominance in nutrient-poor conditions is likely due to its low demand for phosphorus, relative to *Halodule* demands (Fourqurean and others 1992b). In enriched conditions, *Halodule* proliferation and subsequent decreases in *Thalassia* abundance may be attributable to light competition, where *Halodule* production of aboveground runners limited the light available to the *Thalassia* canopy underneath it (Fourqurean and others 1995).

The colonization-competition theory of community organization predicts that the initial colonizing species after a disturbance will be the inferior competitor (Tilman and Wedin 1991). Although *Halodule* is generally considered an opportunistic species that quickly colonizes following physical disturbances (Gallegos and others 1994; Robbins and Bell 2000; Sheridan 2004; Di Carlo and Kenworthy 2008), in this study, *Halodule* was slow to colonize, probably due to the small size and patchiness of a viable propagule supply. Furthermore, *Halodule* persisted in the enriched plots for an extended period, possibly because P concentrations in the sediment can remain high for decades following enrichment (Herbert and Fourqurean 2008). Changes in resource levels have been shown to facilitate species invasions in grasslands as well, where opportunistic species can capitalize on increased nutrient availability and, once established, accelerate the displacement of the species that were previously present (Siemann and Rogers 2003).

The time scale of species shifts in response to ecosystem disturbances is linked to several factors, including the supply of viable propagules (Lotze and others 2000), competitive dynamics (Fourqurean and others 1995; Rose and Dawes 1999), and resource limitation (Armitage and others 2005). In some cases, communities can recover more quickly from occasional pulsed disturbance events than from long-term, low-intensity press disturbances (Detenbeck and others 1992). In Florida Bay, however, even short-term disturbance events such as phosphorus enrichment can initiate a slow, ramped successional process that will continue over many years, possibly decades, because of the efficient retention of the limiting resource, phosphorus, in the ecosystem (Herbert and Fourqurean 2008). This extended time scale must be considered in the management and monitoring of disturbances.

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Figure and table captions

Table 1: Nutrient retention budget for plots with nitrogen (N) and/or phosphorus (P) added at six sites in Florida Bay. Budget was calculated in April 2006 after 3.5 years of experimental fertilization. Retention efficiencies are reported in percentages; all other units are in grams within 0.25 m^3 compartments (50 x 50 x 100 cm) containing 200 L of water column and 50 L of sediment. Average plant and sediment values for each treatment are used in the budget.

Figure 1: Changes in the molar N:P ratio of *Thalassia testudinum* aboveground tissue over time and in response to nutrient (nitrogen, N and phosphorus, P) enrichment. Sites are listed in order from east to west. Bars represent standard error.

Figure 2: Changes in *Thalassia testudinum* and *Halodule wrightii* Braun-Blanquet percent cover score over time and in response to nutrient enrichment. There were no significant nitrogen effects and no nitrogen x phosphorus interactions; therefore, only control and nitrogen + phosphorus treatments are shown for clarity. Sites are listed in order from east to west. Bars represent standard error. $^{\phi}$Note that grey symbols at Sprigger represent *Syringodium filiforme*; *Halodule* was absent at that site.

Figure 3: Changes in uncalcified red and calcareous green macroalgae Braun-Blanquet percent cover score over time and in response to nutrient enrichment. There were no significant nitrogen x phosphorus interactions; therefore, only control and nitrogen + phosphorus treatments are shown for clarity. Sites are listed in order from east to west. Bars represent standard error.

Figure 4: Changes in *Thalassia testudinum* epiphyte chlorophyll *a* concentration (μg cm^{-2} of seagrass leaf) over time and in response to nutrient (nitrogen, N and phosphorus, P) enrichment. Sites are listed in order from east to west. Bars represent standard error.

Figure 5: *Thalassia testudinum* aboveground and belowground biomass (g/m^2) at six sites after four years of nutrient (nitrogen, N and phosphorus, P) enrichment. Bars represent standard error. Note different y-axes.

Figure 6: *Halodule wrightii* aboveground and belowground biomass (g/m^2) at six sites after four years of nutrient (nitrogen, N and phosphorus, P) enrichment. Bars represent standard error. Note different y-axes.

Figure 7: Macroalgal aboveground biomass (g/m^2) at six sites after four years of nutrient enrichment. Note different y-axis scale for Sprigger (f).

Digital Appendix 1: Map of Florida Bay and study sites.

Table 1

Duck						
	Nitrogen			Phosphorus		
Treatment	C	N	NP	C	P	NP
Sediment	61.4	140.2	145.6	2.1	56.3	50.6
Thalassia aboveground tissue	5.2	10.4	25.5	0.2	1.3	1.7
Thalassia belowground tissue	61.0	52.5	72.6	1.4	8.9	7.6
Other seagrass aboveground tissue	0.0	0.0	8.0	0.0	0.2	0.5
Other seagrass belowground tissue	0.0	0.4	19.1	0.0	0.5	2.2
Macroalgae	9.2	1.9	1.2	0.1	0.0	0.0
Thalassia epiphytes	0.5	0.7	1.0	0.0	0.1	0.1
Water	0.1	0.1	0.1	0.0	0.0	0.0
Total system	137.3	206.1	273.0	3.8	67.2	62.7
Net retention		68.8	135.7		63.4	58.9
Mass applied		376.3	376.3		47.3	47.3
Retention efficiency (%)		**18.3**	**36.1**		**134.2**	**124.6**
S Nest						
	Nitrogen			Phosphorus		
Treatment	C	N	NP	C	P	NP
Sediment	43.0	49.0	127.0	1.5	38.5	49.8
Thalassia aboveground tissue	16.9	15.2	44.8	0.4	2.2	2.0
Thalassia belowground tissue	43.8	61.2	61.0	0.8	7.6	7.5
Other seagrass aboveground tissue	0.0	0.0	0.0	0.0	0.0	0.0
Other seagrass belowground tissue	0.0	0.0	0.0	0.0	0.0	0.0
Macroalgae	6.2	3.5	4.8	0.1	0.1	0.1
Thalassia epiphytes	1.3	1.5	1.8	0.1	0.2	0.2
Water	0.1	0.1	0.1	0.0	0.0	0.0
Total system (g)	111.4	130.4	239.5	2.9	48.6	59.5
Net retention (g)		19.1	128.2		45.8	56.6
Mass applied (g)		376.3	376.3		47.3	47.3
Retention efficiency (%)		**5.1**	**34.1**		**96.8**	**119.8**

Table 1 (continued):

Bob Allen						
	Nitrogen			Phosphorus		
Treatment	C	N	NP	C	P	NP
Sediment	108.2	161.1	281.8	4.1	45.3	40.6
Thalassia aboveground tissue	9.9	4.4	58.0	0.2	3.1	2.5
Thalassia belowground tissue	45.8	21.5	124.5	1.0	17.0	11.1
Other seagrass aboveground tissue	0.0	0.0	6.2	0.0	0.3	0.2
Other seagrass belowground tissue	0.7	0.0	11.3	0.0	0.9	0.8
Macroalgae	1.6	0.0	4.8	0.0	0.1	0.2
Thalassia epiphytes	0.1	0.0	0.8	0.0	0.1	0.0
Water	0.1	0.1	0.1	0.0	0.0	0.0
Total system (g)	166.3	187.1	487.6	5.3	66.8	55.5
Net retention (g)		20.8	321.2		61.5	50.2
Mass applied (g)		376.3	376.3		47.3	47.3
Retention efficiency (%)		**5.5**	**85.4**		**130.2**	**106.3**

Rabbit						
	Nitrogen			Phosphorus		
Treatment	C	N	NP	C	P	NP
Sediment	340.7	432.6	331.6	13.1	201.5	191.6
Thalassia aboveground tissue	57.1	69.4	69.9	2.2	3.7	4.6
Thalassia belowground tissue	226.8	236.9	217.3	12.0	41.2	37.1
Other seagrass aboveground tissue	0.0	0.0	3.5	0.0	0.0	0.2
Other seagrass belowground tissue	0.0	0.0	9.7	0.0	0.0	1.2
Macroalgae	0.0	0.0	0.0	0.0	0.1	0.0
Thalassia epiphytes	2.0	3.4	3.2	0.2	0.5	0.8
Water	0.0	0.0	0.0	0.0	0.0	0.0
Total system (g)	626.6	742.4	635.2	27.5	247.0	235.6
Net retention (g)		115.7	8.6		219.5	208.1
Mass applied (g)		376.3	376.3		47.3	47.3
Retention efficiency (%)		**30.8**	**2.3**		**464.6**	**440.4**

Table 1 (continued):

Nine Mile						
	Nitrogen			Phosphorus		
Treatment	C	N	NP	C	P	NP
Sediment	258.4	652.1	361.7	15.0	175.7	95.9
Thalassia aboveground tissue	43.5	84.4	53.7	1.4	3.0	3.0
Thalassia belowground tissue	240.1	262.4	200.7	11.6	23.8	27.4
Other seagrass aboveground tissue	0.0	0.3	5.7	0.0	0.0	0.2
Other seagrass belowground tissue	0.0	1.1	26.5	0.0	0.0	1.1
Macroalgae	0.6	0.0	0.0	0.0	0.0	0.0
Thalassia epiphytes	2.2	3.4	2.4	0.3	0.3	0.3
Water	0.0	0.0	0.0	0.0	0.0	0.0
Total system (g)	544.9	1003.7	650.6	28.3	202.8	127.8
Net retention (g)		458.8	105.8		174.4	99.4
Mass applied (g)		376.3	376.3		47.3	47.3
Retention efficiency (%)		**121.9**	**28.1**		**369.2**	**210.4**
Sprigger						
	Nitrogen			Phosphorus		
Treatment	C	N	NP	C	P	NP
Sediment	107.8	134.3	99.2	19.0	41.1	37.5
Thalassia aboveground tissue	2.3	0.0	5.8	0.2	0.8	0.4
Thalassia belowground tissue	9.6	11.7	15.8	2.9	5.0	3.1
Other seagrass aboveground tissue	15.9	51.1	39.0	1.5	2.6	4.3
Other seagrass belowground tissue	58.1	83.9	62.5	9.3	13.3	9.2
Macroalgae	25.2	28.4	38.3	0.9	2.1	1.7
Thalassia epiphytes	0.7	0.2	0.2	0.1	0.1	0.0
Water	0.0	0.0	0.0	0.0	0.0	0.0
Total system (g)	219.6	309.6	260.9	33.8	65.1	56.3
Net retention (g)		89.9	41.2		31.3	22.5
Mass applied (g)		376.3	376.3		47.3	47.3
Retention efficiency (%)		**23.9**	**11.0**		**66.3**	**47.5**

Digital Appendix 2: Summaries of statistical results.

Digital Appendix 2a: Summary of three-way repeated measures ANOVA for the effects of site, nitrogen (N) addition, and phosphorus (P) addition on *Thalassia testudinum* leaf N:P ratio. Mean square and df values for within-subjects effects are adjusted with the Greenhouse-Geisser correction. **Bold** indicates statistically significant effects at $p \leq 0.05$.

	df	MS	F	p
Within-subjects effects				
Date	8	6590.2	44.2	<0.001
Date*Site	39	1736.7	11.7	<0.001
Date*P	8	2978.4	20.0	<0.001
Date*N	8	117.4	0.8	0.611
Date*P*N	8	202.6	1.4	0.213
Date*Site*P	39	341.6	2.3	<0.001
Date*Site*N	39	121.4	0.8	0.783
Date*Site*P*N	31	230.7	1.5	0.031
Error	548	149.0		
Between-subjects effects				
Site	5	39693.3	307.5	<0.001
P	1	139991.0	1084.5	<0.001
N	1	6164.3	47.7	<0.001
P*N	1	56634	4.4	0.04
Site*P	5	7418.9	57.5	<0.001
Site*N	5	293.1	2.3	0.057
Site*P*N	4	223.9	1.7	0.152
Error	70	129.1		

Digital Appendix 2b: Summary of three-way repeated measures ANOVA for the effects of site, nitrogen (N) addition, and phosphorus (P) addition on (a) *Thalassia testudinum* and (b) *Halodule wrightii* Braun-Blanquet cover scores. Mean square and df values for within-subjects effects are adjusted with the Greenhouse-Geisser correction. **Bold** indicates statistically significant effects at $p \leq 0.05$.

(a) *Thalassia testudinum*

	df	MS	F	p
Within-subjects effects				
Date	10	0.32	51.3	<0.001
Date*Site	52	0.10	15.9	<0.001
Date*P	10	0.08	13.5	<0.001
Date*N	10	0.01	1.8	0.051
Date*P*N	10	0.01	0.9	0.548
Date*Site*P	52	0.05	7.6	<0.001
Date*Site*N	52	0.01	1.7	0.001
Date*Site*P*N	52	0.01	1.3	0.070
Error	1127	0.01		
Between-subjects effects				
Site	5	7.90	238.4	<0.001
P	1	2.31	69.6	<0.001
N	1	0.02	0.6	0.457
P*N	1	0.02	0.6	0.427
Site*P	5	0.55	16.7	<0.001
Site*N	5	0.05	1.3	0.246
Site*P*N	5	0.01	0.4	0.871
Error	108	0.03		

(b) *Halodule wrightii*

	df	MS	F	p
Within-subjects effects				
Date	5	1.09	74.1	<0.001
Date*Site	23	0.15	10.3	<0.001
Date*P	5	0.44	29.5	<0.001
Date*N	5	0.01	0.9	0.493
Date*P*N	5	0.01	0.44	0.802
Date*Site*P	23	0.06	4.2	<0.001
Date*Site*N	23	0.01	0.5	0.976
Date*Site*P*N	23	0.01	0.7	0.869
Error	544	0.01		
Between-subjects effects				
Site	5	0.39	11.3	<0.001
P	1	1.52	44.2	<0.001
N	1	0.07	2.2	0.142
P*N	1	0.02	0.5	0.476
Site*P	5	0.15	4.3	0.001
Site*N	5	0.02	0.7	0.654
Site*P*N	5	0.02	0.7	0.625
Error	120	0.03		

Digital Appendix 2c: Summary of three-way repeated measures ANOVA for the effects of site, nitrogen (N) addition, and phosphorus (P) addition on (a) uncalcified red macroalgae and (b) calcified green macroalgae Braun-Blanquet cover scores. Mean square and df values for within-subjects effects are adjusted with the Greenhouse-Geisser correction. **Bold** indicates statistically significant effects at $p \leq 0.05$.

(a) Uncalcified red macroalgae

	df	MS	F	p
Within-subjects effects				
Date	7	0.35	35.4	<0.001
Date*Site	7	0.37	37.6	<0.001
Date*P	7	0.01	0.7	0.636
Date*N	7	0.01	1.2	0.314
Date*P*N	7	0.01	1.4	0.219
Date*Site*P	7	0.01	1.4	0.214
Date*Site*N	7	0.02	1.6	0.129
Date*Site*P*N	7	0.01	0.8	0.608
Error	185	0.01		
Between-subjects effects				
Site	1	1.74	232.8	<0.001
P	1	0.01	0.7	0.398
N	1	0.09	12.5	0.002
P*N	1	<0.01	0.4	0.540
Site*P	1	0.03	4.4	0.045
Site*N	1	0.03	4.6	0.042
Site*P*N	1	<0.01	<0.1	0.992
Error	26	0.01		

(b) Calcified green macroalgae

	df	MS	F	p
Within-subjects effects				
Date	7	0.13	16.2	<0.001
Date*Site	7	0.10	11.7	<0.001
Date*P	7	0.01	1.6	0.150
Date*N	7	0.01	1.6	0.136
Date*P*N	7	0.01	1.0	0.452
Date*Site*P	7	0.01	0.6	0.767
Date*Site*N	7	0.01	1.4	0.215
Date*Site*P*N	7	0.01	1.2	0.313
Error	171	0.01		
Site	1	4.15	445.7	<0.001
P	1	0.03	3.8	0.063
N	1	0.01	0.8	0.379
P*N	1	0.03	2.9	0.100
Site*P	1	0.02	1.8	0.187
Site*N	1	<0.01	0.3	0.569
Site*P*N	1	0.01	0.8	0.367
Error	26	0.01		

Digital Appendix 2d: Summary of three-way repeated measures ANOVA for the effects of site, nitrogen (N) addition, and phosphorus (P) addition on *Thalassia* epiphyte chlorophyll *a* concentration. Mean square and df values for within-subjects effects are adjusted with the Greenhouse-Geisser correction. **Bold** indicates statistically significant effects at $p \leq 0.05$.

	df	MS	F	p
Within-subjects effects				
Date	6	0.17	20.7	<0.001
Date*Site	18	0.17	20.7	<0.001
Date*P	6	0.02	2.7	0.013
Date*N	6	0.01	0.6	0.739
Date*P*N	6	<0.01	0.5	0.831
Date*Site*P	18	0.02	3.0	<0.001
Date*Site*N	18	0.01	0.8	0.713
Date*Site*P*N	18	0.01	0.7	0.769
Error	500	0.01		
Between-subjects effects				
Site	3	1.10	119.2	<0.001
P	1	0.03	3.5	0.064
N	1	<0.01	<0.1	0.917
P*N	1	<0.01	0.1	0.822
Site*P	3	0.07	7.8	<0.001
Site*N	3	0.01	0.7	0.550
Site*P*N	3	<0.01	0.4	0.783
Error	85	0.01		

Digital Appendix 2e: Summary of three-way ANOVA for the effects of site, nitrogen (N) addition, and phosphorus (P) addition on (a) *Thalassia* aboveground biomass, (b) *Thalassia* belowground biomass, and (c) the ratio of aboveground to belowground *Thalassia* biomass. **Bold** indicates statistically significant effects at $p \leq 0.05$.

(a) *Thalassia* aboveground biomass

	df	MS	F	p
Site	5	1.87	21.1	<0.001
P	1	3.30	37.2	<0.001
N	1	0.02	0.2	0.626
P*N	1	0.03	0.3	0.557
Site*P	5	0.78	8.8	<0.001
Site*N	5	0.07	0.8	0.584
Site*P*N	4	0.03	0.3	0.868
Error	93	0.09		

(b) *Thalassia* belowground biomass

	df	MS	F	p
Site	5	2.08	63.2	<0.001
P	1	0.01	0.3	0.558
N	1	0.02	0.5	0.479
P*N	1	0.03	0.9	0.346
Site*P	5	0.17	5.2	<0.001
Site*N	5	0.04	1.2	0.304
Site*P*N	5	0.03	1.0	0.411
Error	93	0.03		

(c) Ratio of aboveground to belowground *Thalassia* biomass

	df	MS	F	p
Site	5	0.69	13.0	<0.001
P	1	1.47	27.5	<0.001
N	1	0.07	1.3	0.262
P*N	1	0.17	3.2	0.077
Site*P	5	0.26	4.8	0.001
Site*N	5	0.12	2.3	0.055
Site*P*N	4	0.04	0.7	0.577
Error	91	0.05		

Digital Appendix 3: Seagrass tissue nutrient content in control (C) and enriched plots (nitrogen, N; phosphorus, P; nitrogen + phosphorus, NP) at size sites in Florida Bay. -- indicates that the component was not present in that treatment. Water column data were obtained at each site but not within the treatment plots.

	Thalassia testudinum				*Halodule wrightii*			
	C	N	P	NP	C	N	P	NP
Duck								
Aboveground %N	1.95 ± 0.11	1.81 ± 0.01	1.97 ± 0.15	1.88 ± 0.07	--	--	2.40	2.42 ± 0.36
Aboveground %P	0.05 ± 0.00	0.05 ± 0.00	0.15 ± 0.01	0.13 ± 0.01	--	--	0.14	0.15 ± 0.03
Belowground %N	0.91 ± 0.03	0.92 ± 0.07	0.97 ± 0.08	1.26 ± 0.09	--	0.77	1.03	1.53 ± 0.05
Belowground %P	0.02 ± 0.00	0.02 ± 0.00	0.12 ± 0.01	0.14 ± 0.02	--	0.02	0.11	0.17 ± 0.01
South Nest								
Aboveground %N	2.45 ± 0.17	2.19 ± 0.09	2.14 ± 0.13	2.14 ± 0.09	--	--	--	--
Aboveground %P	0.06 ± 0.00	0.05 ± 0.00	0.11 ± 0.01	0.10 ± 0.01	--	--	--	--
Belowground %N	1.14 ± 0.06	1.23 ± 0.07	1.30 ± 0.10	1.37 ± 0.09	--	--	1.23	--
Belowground %P	0.02 ± 0.00	0.02 ± 0.00	0.23 ± 0.04	0.18 ± 0.02	--	--	0.06	--
Bob Allen								
Aboveground %N	2.39 ± 0.06	2.48 ± 0.13	2.21 ± 0.03	2.46 ± 0.12	--	--	2.45 ± 0.45	2.87 ± 0.07
Aboveground %P	0.05 ± 0.00	0.05 ± 0.00	0.19 ± 0.02	0.11 ± 0.01	--	--	0.14 ± 0.01	0.15 ± 0.05
Belowground %N	1.06 ± 0.07	1.01 ± 0.07	1.16 ± 0.06	1.25 ± 0.05	0.88 ± 0.05	--	1.21 ± 0.19	1.29 ± 0.01
Belowground %P	0.02 ± 0.00	0.03 ± 0.01	0.21 ± 0.03	0.11 ± 0.01	0.02 ± 0.00	--	0.11 ± 0.02	0.09 ± 0.01
Rabbit								
Aboveground %N	2.08 ± 0.07	2.24 ± 0.05	1.95 ± 0.06	2.26 ± 0.04	--	--	--	3.40 ± 0.06
Aboveground %P	0.08 ± 0.00	0.08 ± 0.00	0.17 ± 0.01	0.14 ± 0.01	--	--	--	0.19 ± 0.02
Belowground %N	1.08 ± 0.04	1.19 ± 0.05	1.11 ± 0.05	1.27 ± 0.09	--	--	--	1.87 ± 0.06
Belowground %P	0.06 ± 0.00	0.05 ± 0.00	0.26 ± 0.03	0.22 ± 0.03	--	--	--	0.22 ± 0.02
Nine Mile								
Aboveground %N	2.12 ± 0.04	2.60 ± 0.29	2.04 ± 0.06	2.29 ± 0.05	--	2.43	--	2.84 ± 0.10
Aboveground %P	0.07 ± 0.00	0.08 ± 0.00	0.14 ± 0.01	0.13 ± 0.01	--	0.07	--	0.13 ± 0.01
Belowground %N	0.98 ± 0.04	0.99 ± 0.02	0.92 ± 0.02	1.10 ± 0.05	--	1.10 ± 0.2	1.12	1.45 ± 0.09
Belowground %P	0.05 ± 0.00	0.04 ± 0.00	0.14 ± 0.01	0.15 ± 0.01	--	0.06 ± 0.01	0.09	0.10 ± 0.02
Sprigger					*Syringodium filiforme*			
Aboveground %N	1.17	--	1.37	0.65	1.92 ± 0.08	2.93 ± 0.13	1.86 ± 0.15	2.62 ± 0.03
Aboveground %P	0.08	--	0.15	0.12	0.17 ± 0.05	0.19 ± 0.01	0.27 ± 0.01	0.27 ± 0.06
Belowground %N	0.52	1.11	0.94	1.10	0.67 ± 0.03	1.08 ± 0.09	0.72 ± 0.09	1.07 ± 0.08
Belowground %P	0.16	0.22	0.24	0.21	0.11 ± 0.05	0.13 ± 0.01	0.19 ± 0.00	0.16 ± 0.01

Digital Appendix 3 (continued):

	C	N	P	NP	C	N	P	NP
	Macroalgae				*Thalassia* epiphytes			
Duck								
%N	1.12 ± 0.13	1.32 ± 0.63	--	1.04	0.46 ± 0.10	0.58 ± 0.15	0.53 ± 0.07	0.52 ± 0.06
%P	0.01 ± 0.00	0.01 ± 0.00	--	0.02	0.02 ± 0.00	0.02 ± 0.00	0.05 ± 0.01	0.05 ± 0.01
South Nest								
%N	0.84 ± 0.09	1.07 ± 0.06	1.36 ± 0.08	1.55 ± 0.29	0.33 ± 0.04	0.35 ± 0.07	0.41 ± 0.05	0.39 ± 0.03
%P	0.02 ± 0.00	0.01 ± 0.00	0.02 ± 0.00	0.03 ± 0.01	0.02 ± 0.00	0.02 ± 0.00	0.03 ± 0.00	0.04 ± 0.00
Bob Allen								
%N	1.00 ± 0.44	--	1.23 ± 0.32	1.56 ± 0.42	0.57 ± 0.05	0.81	0.62 ± 0.09	0.75 ± 0.08
%P	0.02 ± 0.01	--	0.08	0.05 ± 0.01	0.02 ± 0.00	0.03	0.08 ± 0.03	0.05 ± 0.00
Rabbit								
%N	--	--	1.34 ± 0.10	--	0.70 ± 0.06	0.79 ± 0.07	0.58 ± 0.04	0.70 ± 0.06
%P	--	--	0.05 ± 0.01	--	0.06 ± 0.00	0.06 ± 0.01	0.16 ± 0.02	0.22 ± 0.10
Nine Mile								
%N	2.15	--	--	--	0.62 ± 0.06	0.55 ± 0.03	0.61 ± 0.03	0.63 ± 0.07
%P	0.06	--	--	--	0.08 ± 0.04	0.05 ± 0.00	0.07 ± 0.00	0.06 ± 0.00
Sprigger								
%N	1.02 ± 0.01	1.10 ± 0.38	1.03 ± 0.14	1.43 ± 0.36	0.41	--	0.46	0.49
%P	0.03 ± 0.00	0.05 ± 0.01	0.04 ± 0.00	0.07 ± 0.02	0.04	--	0.06	0.07
	Sediment				Water column (ppm)			
Duck								
%N	0.12 ± 0.01	0.28 ± 0.09	0.12 ± 0.00	0.29 ± 0.09	0.37			
%P	0.00 ± 0.00	0.00 ± 0.00	0.11 ± 0.02	0.10 ± 0.02	0.01			
South Nest								
%N	0.09 ± 0.01	0.10 ± 0.01	0.11 ± 0.02	0.25 ± 0.13	0.34			
%P	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.02	0.10 ± 0.02	0.01			
Bob Allen								
%N	0.22 ± 0.01	0.32 ± 0.05	0.21 ± 0.01	0.56 ± 0.19	0.40			
%P	0.01 ± 0.00	0.01 ± 0.00	0.09 ± 0.02	0.08 ± 0.02	0.01			
Rabbit								
%N	0.68 ± 0.05	0.87 ± 0.05	0.66 ± 0.04	0.66 ± 0.02	0.20			
%P	0.03 ± 0.00	0.03 ± 0.00	0.38 ± 0.08	0.40 ± 0.18	0.01			
Nine Mile								
%N	0.52 ± 0.02	1.30 ± 0.29	0.50 ± 0.02	0.72 ± 0.10	0.14			
%P	0.03 ± 0.00	0.03 ± 0.00	0.35 ± 0.07	0.19 ± 0.03	0.01			
Sprigger								
%N	0.22 ± 0.02	0.27 ± 0.10	0.16 ± 0.01	0.20 ± 0.02	0.08			
%P	0.04 ± 0.00	0.03 ± 0.00	0.08 ± 0.02	0.08 ± 0.03	0.01			