Ecosystem Structure and Function Still Altered Two Decades After Short-Term Fertilization of a Seagrass Meadow

D. A. Herbert[1]* and J. W. Fourqurean[1,2]

[1]Department of Biological Sciences and Southeast Environmental Research Center, Florida International University, Miami, Florida 33199, USA; [2]Fairchild Tropical Botanic Garden, Goral Gables, Florida 33156, USA

ABSTRACT

An oligotrophic phosphorus (P) limited seagrass ecosystem in Florida Bay was experimentally fertilized in a unique way. Perches were installed to encourage seabirds to roost and deliver an external source of nutrients via defecation. Two treatments were examined: (1) a chronic 23-year fertilization and (2) an earlier 28-month fertilization that was discontinued when the chronic treatment was initiated. Because of the low mobility of P in carbonate sediments, we hypothesized long-term changes to ecosystem structure and function in both treatments. Structural changes in the chronic treatment included a shift in the dominant seagrass species from *Thalassia testudinum* to *Halodule wrightii*, large increases in epiphytic biomass and sediment chlorophyll-a, and a decline in species richness. Functional changes included increased benthic metabolism and quantum efficiency. Initial changes in the 28-month fertilization were similar, but after 23 years of nutrient depuration *T. testudinum* has reestablished itself as the dominant species. However, P remains elevated in the sediment and *H. wrightii* has maintained a presence. Functionally the discontinued treatment remains altered. Biomass exceeds that in the chronic treatment and indices of productivity, elevated relative to control, are not different from the chronic fertilization. Cessation of nutrient loading has resulted in a superficial return to the pre-disturbance character of the community, but due to the nature of P cycles functional changes persist.

Key words: phosphorus; nitrogen; nutrient retention; seagrass; diversity; respiration; productivity; benthic metabolism; eutrophication.

INTRODUCTION

Nutrient supply influences species composition and dominance in plant assemblages, and together these can shape the functional characteristics of ecosystems including habitat suitability, process rates, element storage, and element fluxes between trophic levels and among adjacent landscape components. Consequently, changes in the rate of nutrient supply can cause changes in ecosystem function (Chapin and others 1997). Historic nutrient enrichments associated either directly or indirectly with human manipulations of landscapes have caused changes, for example, eutrophication, that have altered both species composition and the stability of ecosystem functions (Sanderson and others 2004). In light of worldwide losses of species diversity (Vitousek and others 1997; Chapin and others 2000), an increasing reliance on the stability

*Corresponding author; e-mail: herbertd@fiu.edu

of ecosystem functions (Loreau and others 2001; Hector and Bagchi 2007), and efforts to restore affected ecosystems (Hobbs and Norton 1996), an understanding of how ecosystems respond to nutrient loadings and the cessation of nutrient loadings is essential. Here we report on a unique experiment in Florida Bay that documents ecosystem changes in response to nutrient loading of an oligotrophic ecosystem and two decades of nutrient depuration following the cessation of nutrient loading.

The composition of terrestrial plant communities generally changes with nutrient supply. Low nutrient supply typically favors slow-growing species that are effective in nutrient acquisition and use (Reader and others 1994; Guo and Berry 1998). Therefore, low nutrient supply limits species composition, richness, and diversity. Increased nutrient supply decreases nutrient competition and allows for greater species diversity (Schoener 1976; Abrams 1988; Herbert and others 2004). An increase in biomass resulting from increased nutrient supply can shift competition away from belowground resources to aboveground resources such as light, and this shift may result in species exclusions by fast-growing, superior light competitors (Olff and others 1993; Grace 1993; Wilson and Tilman 1995). Consequently, increased nutrient supply can shift the competitive balance away from slow-growing species and toward fast-growing species and it is possible that one or a few superior competitors will cause local extinctions at either end of a nutrient gradient (Margalef 1963; Huston and DeAngelis 1994; Abrams 1995). The emergent relationship between resource supply and species diversity is described as unimodal (Grime 1973, 1979; Al-Mufti and others1977) and the greatest diversity is theoretically attained where vegetation is simultaneously limited by multiple resources both aboveground and belowground (Herbert and others 2004).

The effects of nutrient supply on benthic marine vegetation can be similar to those demonstrated for terrestrial vegetation. Nutrient additions generally cause a shift from slow-growing to fast-growing species (Valiela and others 1992; Duarte 1995; Fourqurean and Rutten 2003); productivity, species richness, and diversity change with nutrient supply (Worm and others 2002; Nielsen 2003; Bracken and Nielsen 2004); and inter-species competition can produce unimodal diversity patterns across nutrient gradients (Hixon and Brostoff 1996; Korpinen and others 2007).

Functionally, increases in biomass, a shift from slow-growing to fast-growing species, or changes in litter quality (for example, nutrient content and decomposability) increases ecosystem net primary production (NPP) and respiration (R), and affects the quantity of organic matter (OM) that can be stored in biomass and sediments (Herbert and others 1999). In turn, NPP, R, and OM can drive changes in the rates of biogeochemical cycles. Such changes in ecosystem structure and function have been demonstrated in experimental nutrient additions (for example, Shaver and Chapin 1980; Vermeer 1986; Tilman 1987; Gough and others 1994), and are visible across landscapes as a consequence of animal behaviors via nutrient concentration and redistribution (for example, Coppock and others 1983a, b; Helfield and Naiman 2001; Bilby and others 2003; Ben-David and others 1998).

Accumulations of nutrients and their effects on ecosystems persist long after additions have ceased. Losses by occlusion, grazing, hydrological export, and for N, denitrification, eventually return the system to an approximate balance of inputs and outputs. Accumulations of N in abandoned agricultural land generally return to pre-disturbance levels within years or decades, whereas geochemical adsorption and precipitation with carbonates and oxides of Fe and Al can function to retain P for centuries or even millennia (Sandor and Eash 1995; Compton and Boone 2000; McLauchlan 2006). Indeed, archeologists use soil phosphate levels to identify sites of past human occupation (Eidt 1977). The different behaviors of N and P similarly affect their retention times in benthic marine ecosystems. For example, N-driven changes in seagrass meadows are less likely to persist because of N losses via denitrification in the typically anoxic sediments (Stapel and others 2001). However, P-driven changes are likely to persist much longer because of a strong affinity between dissolved inorganic phosphorus and the carbonate sediments typical of many tropical seagrass ecosystems (Ruttenberg and Berner 1993; Jia-Zhang and others 2004). Ferdie and Fourqurean (2004) found that 49–82% of P added to a P-limited seagrass meadow in south Florida was retained in the system after 1 year, but less than 10% of added N was retained after 1 year in N-limited seagrass meadows.

Florida Bay provides an ideal setting for investigating the response of benthic macrophyte communities to nutrient supply. The distribution of seagrass species in Florida Bay is largely defined by spatial patterns of nutrient supply and limitation (Fourqurean and Zieman 2002). Phosphorus generally limits primary productivity within the bay, and increases in availability from east to west across

the bay (Fourqurean and others 1992a; Jia-Zhang and others 2004; Armitage and others 2005). In areas of clear water and low nutrient availability Florida Bay is characterized by the relatively slow-growing seagrass *Thalassia testudinum*, but slightly higher nutrient supply favors faster growing seagrass species including *Halodule wrightii* and *Syringodium filiforme*, which can displace *T. testudinum* in experimental fertilizations (Powell and others 1989; Fourqurean and others 1995; Ferdie and Fourqurean 2004; Armitage and others 2005). At Cross Bank in eastern Florida Bay there is a 23-year fertilization experiment that makes use of bird perches and a 23-year nutrient depuration involving the removal of earlier installed bird perches. The dominant seagrass species at Cross Bank is *T. testudinum* and the long-term fertilization has caused a shift in species dominance to *H. wrightii*.

Because of the low mobility of P in sediments we hypothesized that total P would be elevated in the P-limited carbonate sediments 23 years after fertilization was discontinued and there would be little residual N. It is likely that elevated sediment P provides an elevated P supply to plants, which will be evident in tissue nutrient contents and stoichiometry. In theory, altered nutrient supply affects ecosystem structure and function, so benthic community characteristics should differ among the continuously fertilized, previously fertilized, and unfertilized treatments in predictable ways. Functional changes were interpreted relative to productivity, respiration, sediment OM, and quantity of fast growing epiphytes and microalgae. Structural changes were assessed on the basis of benthic macrophyte biomass and species dominance, richness, and diversity.

METHODS

Study Area

The study area is located on Cross Bank, a shallow (<35 cm deep), narrow (100–200 m wide), seagrass-covered carbonate mud bank in east-central Florida Bay, extending west from 25°00.25′ N 80°33.5′ W to 25°00.6′ N 80°36.6′ W. Diurnal tides are less than 3 cm and there is a seasonal ±15 cm variation in depth that is driven by the prevailing northeast winds (Holmquist and others 1989). Seagrass cover is dominated by *T. testudinum* with sparse presence of *H. wrightii* (Powell and others 1989). Benthic macroalgae cover is dominated by *Penicillus capitatus*, *Halimeda monile*, and *Laurencia* sp., with sparse presence of *Batophora*, *Dictyota*, and *Jania* spp.

In 1981 Cross Bank was the site of a study on the feeding behavior of wading birds, which was facilitated by the installation of location marker stakes at 100 m intervals along the center of the Bank (Powell 1987). The markers consisted of 1.5 m long, 1.2 cm diameter PVC pipe with a 10 cm long wood block of construction grade 2″ × 4″ mounted on top. The stakes were used as roosting sites by two piscivorous seabirds, Royal Terns (*Sterna maxima*) and Double-crested Cormorants (*Phalacrocorax auritus*), which occupied these artificial roosts during 81% of daylight hours and 87% of dark hours. Defecation by the roosting seabirds delivered N (∼19.0 g m^{-2} y^{-1}) and P (∼3.29 g m^{-2} y^{-1}) to the benthic community, which caused an increase in seagrass density and a shift in species composition from *T. testudinum* to *H. wrightii* (Powell and others 1989; Fourqurean and others 1995).

Experimental Design and Statistical Analyses

In November 1983, 28 months after the stakes were installed; five of the stake locations (600 m, 1200 m, 1800 m, 2400 m and 3100 m from the eastern end of Cross Bank) were selected to determine the effect of the roosting birds on observed changes. Stakes at those locations were pressed into the sediment so that they no longer functioned as roosts. Two new stakes were installed 5 m from the original stake in a line perpendicular to the predominant direction of water flow (∼10°N to ∼190°S) with the original stake in the center. One of the new stakes was identical to the original stake and the other was cut to a point to prevent birds from roosting. The design provided five sites treated as blocks, each with three treatments including control, fertilized, and fertilized but discontinued. In November 2006 the sites were relocated for use in the present study. The original experimental design has been retained and treatments are henceforth referred to as (C) control, (F) chronic fertilization (∼76 g P m^{-2} and ∼440 g N m^{-2} over 23 years), and (D) discontinued fertilization (∼8 g P m^{-2} and ∼44 g N m^{-2} over 28 months) with 23 years of recovery. In keeping with the original experimental design (unless otherwise noted) samples were collected in replicates of four from all treatments within all blocks at standard locations along a transect in-line with the predominant water flow direction (50 cm N, 30 cm N, 30 cm S, and 50 cm S relative to stakes).

Analyses were performed using a mixed linear model procedure to account for the fixed effects of treatment and the random effects of block. The SAS MIXED procedure (Little and others 1996) is a

generalization of the standard linear model that permits data to exhibit correlation and non-constant variability. Means, variance, and covariance were modeled in a pair-wise manner to determine treatment differences. An alpha of 0.05 was used to determine significance in all cases. All results are presented in tabular form as arithmetic means and standard errors.

Sediment Chemistry and Chlorophyll Content

Surface sediments were collected for determination of bulk density, organic matter content (OM), and elemental content (C, N, P). Four cores (1.15 cm diameter, 5.0 cm depth) from all treatments within each block were collected. Cores were transferred to pre-weighed 20 ml glass scintillation vials and dried at 70°C for 48 h to obtain a dry weight. Dry samples were ground using a ceramic mortar and pestle. P content was determined by dry-oxidation, acid hydrolysis extraction followed by colorimetric analysis of phosphate concentration (Fourqurean and others 1992b). Total C and N content were determined using a CHN analyzer (Fisons NA1500). Sediment organic C (SOC) was determined as the difference between total C and the C remaining after 4 h of thermal decomposition of organic matter at 500°C, both measured by the CHN analyzer (Hirota and Spyzer 1975; Froelich 1980; King and others 1998). Element contents were calculated as % dry weight and element ratios were calculated on a molar basis.

Another four sediment cores (1.15 cm diameter, 1.0 cm depth) were used to determine chlorophyll-a (chl-a) content (mg m^{-2}) as a proxy for sediment microalgal abundance. Samples were transferred into 20 ml glass scintillation vials and placed on ice in the dark. In the lab, 10 ml of 100% acetone was added to wet samples for chl-a extraction, and content was measured fluorometrically (Strickland and Parsons 1972) with a Gilford Fluoro IV Spectrofluorometer (excitation = 435 nm, emission = 667 nm).

Benthic Macrophyte Biomass, Species Composition, and Chemistry

All aboveground biomass was sampled from four 10 cm × 10 cm quadrats in all treatments within each block. Biomass was separated by species. Epiphytic material adhering to seagrass leaves was removed by scraping with a razor blade and placed into pre-weighed 20 ml glass scintillation vials and stored at −20°C. Seagrass leaf material and aboveground macroalgae thalli from each

quadrat was pooled by species, dried at 70°C, and ground to a fine powder. Macroalgae biomass was corrected for calcium carbonate content by combustion of sub-samples at 500°C for 5 h, and organic C (OC) was estimated assuming 40% of organic matter (OM) loss on ignition. Macrophyte nutrient content was determined following the procedures described for sediment nutrient content.

Epiphyte Chlorophyll and Biomass Estimate

Epiphytic chl-a content was analyzed following the method used for sediment chl-a content. Twenty ml of 90% acetone were added to each vial. Vials were shaken and stored at −20°C for a minimum of 72 h. Epiphyte mass was estimated from chl-a mass and an autotrophic index of 0.2 μg Chl-a mg^{-1} epiphyte consistent with earlier measurements throughout Florida Bay (Frankovich and Fourqurean 1997).

Photosynthesis and Respiration

Benthic metabolism was measured by in situ dissolved O_2 (DO) production and consumption in 20 l chambers centered 30 cm approximately 190° south (down current) from each stake. A single incubation was completed per treatment in all blocks. All measurements were taken between November 30 and December 1, 2006. Chambers were constructed from Nalgene clear polycarbonate 20 l carboys with tops cut off, inverted, and pressed into the sediment by at least 10 cm. Aerial coverage was 0.062 m^2 (inside dia. = 28 cm) but volume varied as a function of height of the chamber top above the sediment, ranging from 14 to 20 l depending on water depth (20–31 cm). A well-mixed DO environment in the chamber was maintained by water circulated via submersible water pump (180 l/h flow capacity) powered by a 6 V battery pack and a 1.7 W solar panel (Silicon Solar Inc., San Diego, CA, USA). DO (mg m^{-3}) was measured with a YSI Environmental DO200 DO/temperature probe inserted through a port in the top of the chamber directly into the stream from the water pump. Benthic respiration was measured as the rate of DO change (mg m^{-2} min^{-1}) in chambers when darkened by an opaque cover. After completion of respiration measurements the covers were removed and DO measurements continued in daylight-illuminated chambers for a measurement of net benthic DO production. DO consumed in the dark chambers was added to the DO produced in light chambers for an estimate gross benthic DO production. Incubation periods in

the light and dark were between 120 and 190 min depending on the rate of DO change. All light incubations were initiated at mid-day, but light conditions varied. Average incident photosynthetically active radiation (PAR) was measured at 1-min intervals near the water surface with a LI-COR LI190SB-L Quantum Sensor (LI-COR, Lincoln, Nebraska) to determine DO production per mole quanta. Chamber tops were always within 2–5 cm of the water surface so no light attenuation correction for water depth was applied. Rates of gross primary production (GPP) and NPP were converted to units of carbon (mg C m^{-2} h^{-1}) using photosynthetic and respiratory quotients of 1.2 and 1.0, respectively (Oviatt and others 1986). Net benthic C production (mg C m^{-2} d^{-1}) was calculated for 24 h assuming a 10.3 h photoperiod.

RESULTS

Sediment Chemistry

After 23 years of continuous fertilization (treatment F) total sediment P concentrations were elevated by more than 30 times over control (Table 1). Of greater interest, P concentrations in discontinued fertilizations (treatment D) were elevated 44% over control. However, there were no differences in sediment N concentrations. SOC concentrations in D and F were similar ($P = 0.46$) but greater than control by 13.5 and 17.8%, respectively. Molar C:P and N:P ratios were driven by P, and although molar C:N was slightly elevated in F, differences in C:N between treatments were small.

The Benthic Community

The seagrass species dominance shift from T. testudinum to H. wrightii reported by Fourqurean

and others (1995) has continued through 23 years of F treatments and has apparently not deviated from its current representation (95.5 ± 2.3%) in the last 17 years (Figure 1). H. wrightii in treatment D, which received 28 months continuous fertilization, apparently reached its highest relative abundance at some time after fertilization ceased in1983. The highest recorded relative abundance of H. wrightii was 66% of the total aboveground seagrass biomass 4 years after cessation. Data are not available for 1984–1986. Within 6 years T. testudinum biomass began to increase in D treatments, and by 12 years represented 90% of the aboveground seagrass biomass.

Total aboveground biomass varied between treatments with D having nearly twice that of control, but not significantly greater than F (Table 2). Benthic macroalgae were a substantial component in C and D treatments (32 and 12%, respectively) consisting primarily of Laurencia sp., and two calcareous green species, P. capitatus, and H. monile (Figure 2). In F treatments Laurencia represented 7% of biomass, whereas P. capitatus, and H. monile were not present. Epiphyte loads, estimated by chlorophyll-a content, were six times greater in F than in control (Table 2) and are a substantial component of aboveground totals in F. Epiphyte loads in D were elevated 43% over control. Sediment microalgae concentrations in F were about 3–4 times greater than in D or control.

Although the macrophyte community on Cross Bank is not particularly species-rich, there were differences between treatments (Table 2). Richness in D treatments was elevated relative to F but not C, whereas C appeared somewhat elevated relative to F ($P = 0.089$). Species richness also tended to increase asymptotically with sediment TP ($R^2 = 0.67$, $P < 0.01$) but declined with the high TP concentrations present in F treatments (Figure 3).

Table 1. Sediment Carbon, Nitrogen, and Phosphorus Content

Variable	Treatment mean (SE)			Pair-wise comparison P statistic		
	C	D	F	C × D	C × F	D × F
P (%)	0.0062 (0.0004)	0.0089 (0.0007)	0.2200 (0.0402)	0.008	<0.001	<0.001
N (%)	0.250 (0.011)	0.262 (0.014)	0.294 (0.026)	0.369	0.104	0.160
C (%) (organic)	2.08 (0.04)	2.36 (0.06)	2.45 (0.13)	0.012	0.036	0.459
C:P	892 (41)	767 (53)	44 (7.1)	0.054	<0.001	<0.001
C:N	10.0 (0.26)	10.5 (0.21)	9.6 (0.22)	0.334	0.049	0.014
N:P	92 (6)	73 (6)	4.6 (0.9)	0.033	<0.001	<0.001

Treatment means with standard errors in brackets. P statistic generated from a mixed linear model pair-wise comparison. Treatments: C = control, D = discontinued fertilizations, F = continuous fertilizations. Percentages are on a mass basis. Ratios are on a molar basis.
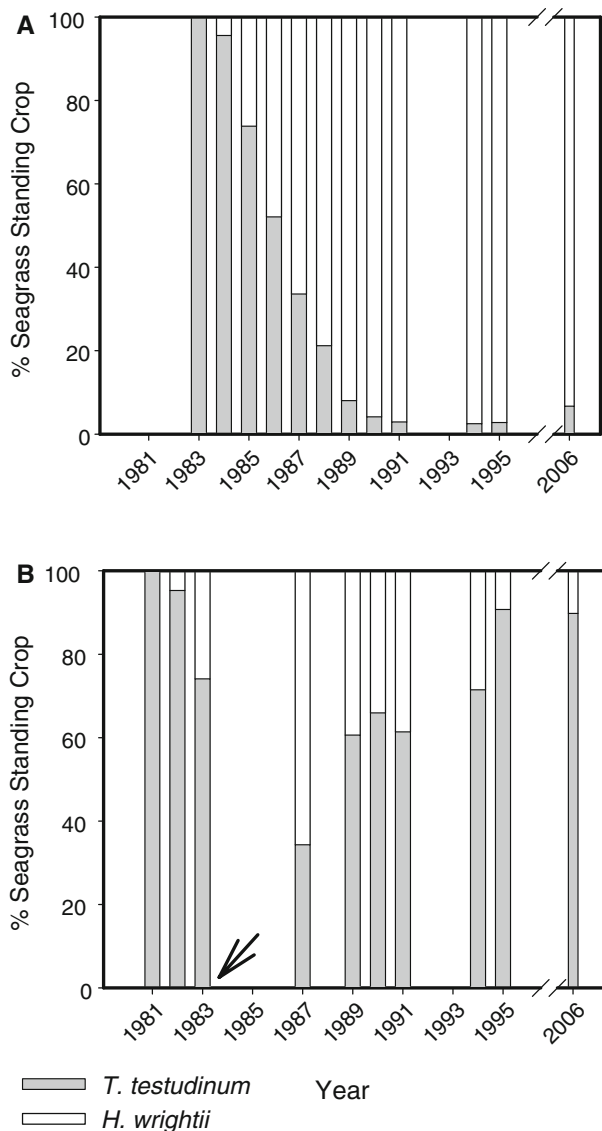
Figure 1. Changes in seagrass species composition illustrating the shifts in dominance between *T. testudinum* and *H. wrightii* under conditions of (**A**) long-term continuous fertilization and (**B**) short-term fertilization that was discontinued after 28 months. Stacked bars represent percent composition by each of the two species present. The first bar on the left indicates species composition when fertilization was initiated. The arrow in panel B indicates the time at which fertilization was discontinued.

Shannon–Wiener diversity, which incorporates evenness of community composition, was greater in C than in F, but did not distinguish control from D (Table 2).

Seagrass Foliar Tissue Chemistry

H. wrightii was rarely present in control treatments and so its foliar chemistry was completed for F and D

treatments only. However, *H. wrightii* N and P concentrations measured in D treatments were comparable to earlier control measurements (Powell and others 1989). *H. wrightii* N and P concentrations were elevated in F over D treatments by approximately 17 and 100%, respectively (Table 3). *T. testudinum* also responded to treatments with elevated P concentrations in D and F relative to C and in F relative to D. There was a higher N concentration in F compared to D, but no difference between F and C. Nutrient ratios analogous to Redfield Ratio but adjusted for the structural tissues of macrophytes have been proposed (Atkinson and Smith 1983; Duarte 1990) and applied to *T. testudinum* throughout Florida Bay to describe relative limitation to seagrasses by N or P (Fourqurean and Zieman 2002). A molar C:N:P ratio of 550:30:1 has been accepted as optimal. In all treatments foliar C:N in both *T. testudinum* and *H. wrightii* was near an adjusted Redfield Ratio of 18.3 indicating no N limitation. C:P and N:P in leaves of both *H. wrightii* and *T. testudinum* in F treatments were also very near adjusted Redfield Ratios (550 and 30, respectively). Increased C:P and N:P of *H. wrightii* and *T. testudinum* leaves in D treatments indicates limitation by P, whereas extreme limitation was indicated for *T. testudinum* in C.

Benthic Metabolism

Respiration in darkened chambers was nearly identical in F and D treatments, elevated by about 60% over control (Table 4). Net DO production in illuminated chambers was also elevated in F and D treatments over control, by 5 and 3.5 times, respectively (Figure 4). Although production was generally higher in F than in D, variance was large and in two of the blocks there were reversals in which productivity in D was greater than in F. Similar patterns were measured for gross DO production and quantum efficiency of DO production. Net benthic production for 24 h including a 10.3 h photoperiod indicated that controls were net heterotrophic, whereas F treatments were net autotrophic during this early winter incubation (Table 4). Discontinued fertilization treatments were on average slightly net autotrophic but variability was high.

DISCUSSION

Increased P availability, measured as pore water PO_4^{3-} (Powell and others 1989) and total sediment P (this study), has produced changes in ecosystem structure and function at Cross Bank, which is located in an otherwise P deficient, oligotrophic region of Florida Bay. Earlier measured changes in the continuously fertilized treatments included an

Table 2. Characteristics of the Benthic Plant Community

Variable	Treatment mean (SE)			Pair-wise comparison P statistic		
	C	D	F	C × D	C × F	D × F
Epiphyte chl-a (mg m^{-2})	0.53 (0.07)	0.93 (0.10)	3.29 (0.28)	0.049	0.001	0.002
Sediment chl-a (mg m^{-2})	10.8 (1.12)	13.6 (1.34)	39.7 (6.83)	0.136	0.006	0.014
Benthic macroalgae (g m^{-2})	18.3 (5.7)	13.2 (4.7)	5.7 (5.3)	0.811	0.022	0.046
Seagrass (g m^{-2})	36.3 (7.3)	92.8 (16.2)	57.9 (3.6)	0.019	0.028	0.059
Total biomass (g m^{-2})	57.3 (12.0)	110.6 (12.6)	79.8 (4.4)	0.033	0.106	0.074
Shannon–Wiener H′	0.718 (0.137)	0.684 (0.104)	0.358 (0.106)	0.859	0.007	0.128
Species richness	2.2 (0.22)	2.9 (0.23)	1.7 (0.18)	0.108	0.089	0.006

Treatment means with standard errors in brackets. P statistic generated from a mixed linear model pair-wise comparison. Treatments: C = control, D = discontinued fertilizations, F = continuous fertilizations. All values are for aboveground biomass only. Total biomass includes an estimate of epiphyte mass estimated from chl-a mass and an autotrophic index of 0.2 μg Chl-a mg^{-1} epiphyte (Frankovich and Fourqurean 1997).
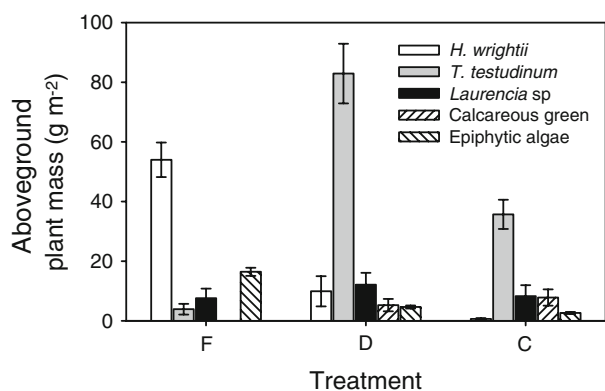

Figure 2. Aboveground plant mass by treatment and species groups. Values do not include sediment microalgae. Calcareous green algae have been decalcified. Epiphyte mass was estimated from chl-a mass and an autotrophic index of 0.2 μg Chl-a mg^{-1} epiphyte (Frankovich and Fourqurean 1997). Bars represent means ± 1SE. Treatments: C = control, D = discontinued fertilizations, F = continuous fertilizations.

increase in seagrass biomass within 2 years, and a shift in species dominance from *T. testudinum* to *H. wrighti* within 7 years (Powell and others 1989; Fourqurean and others 1995). Discontinued nutrient enrichment caused the community to slowly revert to *T. testudinum* dominance, but other nutrient-related changes in structure and function have remained after 23 years, and those changes are the result of the persistence of P in the ecosystem. Functional changes have included increased rates of benthic respiration and net production, increased quantum efficiency, and increased nutrient storage in the sediment. The functional change in habitat quality for dependent species was not directly assessed, although impacts on bivalve and gastropod
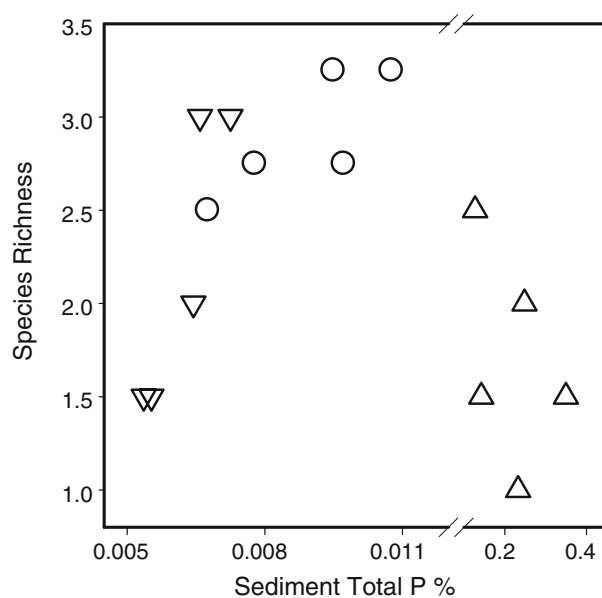

Figure 3. Benthic macrophyte species richness versus sediment total P concentration. All experimental blocks and treatments are represented. Control = downward triangle, discontinued fertilization = circle, continuous fertilization = upward triangle.

assemblages have been examined and a decline in species richness and abundance recorded in F treatments (Ferguson 2008). These long-term effects of short-term and chronic nutrient enrichments are the focus of this discussion.

Elevated nutrient inputs caused by defecation of roosting seabirds was sufficient to change the sediment P environment in the long-term, persisting more than two decades after removal of bird perches despite the expected sediment erosion losses and accumulations of P-deficient carbonates

Table 3. Seagrass Species Nutrient Content and Stoichiometry

Variable	Treatment mean (SE)			Pair-wise comparison P statistic		
	C	**D**	**F**	**C × D**	**C × F**	**D × F**
H. wrightii						
P (%)	–	0.105 (0.005)	0.210 (0.013)	–	–	0.008
N (%)	–	2.70 (0.092)	3.15 (0.079)	–	–	0.051
C:P	–	1086 (35)	543 (37)	–	–	0.003
C:N	–	19.0 (0.442)	15.9 (0.27)	–	–	0.019
N:P	–	57.2 (2.17)	34.3 (2.93)	–	–	0.022
T. testudinum						
P (%)	0.095 (0.005)	0.125 (0.014)	0.190 (0.013)	0.030	0.001	0.006
N (%)	2.46 (0.052)	2.39 (0.039)	2.57 (0.035)	0.245	0.131	0.029
C:P	1098 (63)	885 (86)	598 (77)	0.027	0.001	0.015
C:N	18.4 (0.33)	19.5 (0.41)	18.1 (0.32)	0.030	0.366	0.016
N:P	59.4 (3.32)	45.0 (3.80)	32.4 (3.27)	0.007	0.001	0.023

Treatment means with standard errors in brackets. P statistic generated from a mixed linear model pair-wise comparison. Treatments: C = control, D = discontinued fertilizations, F = continuous fertilizations. Percentages are on a mass basis. Ratios are on a molar basis. H. wrightii was absent from control treatments.

Table 4. Components of Benthic Production

Variable	Treatment mean (SE)			Pair-wise comparison P statistic		
	C	**D**	**F**	**C × D**	**C × F**	**D × F**
DO consumption (mg m^{-2} min^{-1})	3.35 (0.30)	5.05 (0.64)	5.51 (0.59)	0.0494	0.0160	0.631
Gross DO production (mg m^{-2} min^{-1})	5.33 (0.33)	11.97 (1.39)	16.09 (1.84)	0.004	<0.001	0.136
Quantum efficiency (mg DO μmole PAR^{-1})	86 (8.3)	197 (22)	254 (24)	0.005	<0.001	0.136
NPP (mg m^{-2} h^{-1})	100 (20)	347 (2)	530 (69)	0.013	<0.001	0.117
GPP (mg m^{-2} h^{-1})	301 (19)	650 (77)	860 (99)	0.045	<0.001	0.158
Net benthic production (mg C m^{-2} d^{-1})	−1312 (364)	54 (912)	1616 (461)	0.177	<0.001	0.187

Treatment means with standard errors in brackets. P statistic generated from a mixed linear model pair-wise comparison. Treatments: C = control, D = discontinued fertilizations, F = continuous fertilizations. Gross dissolved O₂ (DO) production is the sum of DO consumption and net DO production. Estimates of net primary productivity (NPP) and gross primary production (GPP) were converted to units of carbon using photosynthetic and respiratory quotients of 1.2 and 1.0, respectively (Oviatt and others 1986). Benthic production estimates are for 24 h with a 10.3 h photoperiod.

formed biogenically or as precipitates. The elevated pore water PO_4^{3-} measured by Powell and others (1989) is evidence that P was accumulating in quantities that could saturate carbonate binding sites in surface sediments, allowing P to penetrate downward. Accumulated deep pools of P are now a likely source to surface pools, which are elevated by 44%. This long-term change is the consequence of 28 months of elevated P inputs totaling approximately 8 g P m^{-2}. Sediments accumulating P for 23 years in the continuously fertilized treatments may be even more resistant to a return to pre-disturbance conditions.

Phosphorus limitation, measured as foliar C:P and N:P of *H. wrightii* and *T. testudinum*, was evident in both control and D treatments, but not in F treatments. *T. testudinum* foliar N:P in control was typical for central to NE Florida Bay, but in D

treatments were more typical of W Florida Bay, where P is less limiting (Fourqurean and others 1992a). This line of evidence suggests there has been a long-term increase in plant-available P in discontinued fertilizations.

Low SOC:N in F treatments indicates the possibility of N accumulation. Acetylene reduction activity associated with *H. wrightii* from F treatments (Powell and others 1989) suggest that N fixation could contribute to N pools when P supply is sufficient, which would prevent a shift to N limitation (Vitousek and Howarth 1991). However, comparatively high SOC:N in D treatments where sediment P is also elevated indicates that low SOC:N in F treatments is likely a direct contribution from bird feces. Much of the N in feces is relatively insoluble uric acid and may accumulate in sediments, but the minor decrease in SOC:N in F
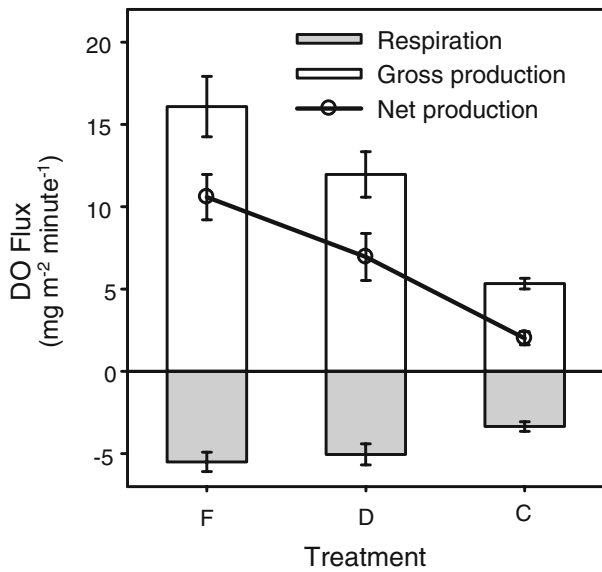
Figure 4. In situ chamber measured dissolved O_2 (DO) flux. *Open bars* (above the zero reference line) represent gross O_2 production in full daylight; *shaded bars* (below the zero reference line) represent O_2 consumption in darkened chambers, and *open bullets* represent net O_2 production. Treatments: C = control, D = discontinued fertilizations, F = continuous fertilizations.

treatments relative to the rate of loading ($\sim$19.0 g $N\,m^{-2}\,y^{-1}$) suggests that N was either remineralized and lost to the system by diffusion and volatilization or was washed down-current before it could be buried. Despite the N delivery rate it is unlikely that seagrasses have responded to N. Leaf stoichiometry from control suggests that N is available in surplus relative to P, and in F treatments, where P has been retained, foliar N:P does not indicate a shift from P limitation to N limitation. It is more likely that seagrass biomass at Cross Bank is limited by some factor other than nutrient supply in F treatments, for example, light availability or sediment sulfide concentrations.

The increase in seagrass biomass and changes in species composition in continuously fertilized treatments have persisted in the long-term and have apparently not deviated from the current relative dominance of *H. wrightii* during the past 17 years (95.5 ± 2.3% of total seagrass biomass). In the shorter-term nutrient enrichments *H. wrightii* also invaded and began to displace *T. testudinum*. Upon cessation of nutrient enrichments *H. wrightii* represented 26% of aboveground seagrass biomass (Fourqurean and others 1995) and continued to increase in dominance. Four years after cessation *H. wrightii* represented 66% of aboveground sea-grass biomass, but the species was in a phase of

decline. Peak dominance of *H. wrightii* was proba-bly reached in the intervening years for which data are unavailable. By 12 years (1995) *T. testudinum*, which had returned to dominance, represented 90% of the aboveground seagrass biomass. Clearly, continuous enrichment was necessary to maintain dominance by *H. wrightii* and without continuous external supplies the available P pools were soon depleted (within 5 years) to a point where *H. wrightii* could no longer maintain its dominance. However, despite 23 years of depuration, P has remained sufficiently elevated to support an established *H. wrightii* component in the commu-nity where previously it was not present.

Total aboveground dry mass, including decalci-fied algae and epiphytic microalgae, was greatest where sediment P was elevated above control. D treatments had marginally greater mass than F ($P = 0.074$) because of dominant species charac-teristics. Specifically, *T. testudinum* shoots, which were less densely distributed than *H. wrightii*, were much larger than *H. wrightii* shoots, especially with elevated sediment P (Powell and others 1989). When *H. wrightii* was dominant, all macroalgae with the exception of epiphytic *Laurencia* were excluded. Simplification of the benthic macroalgal community and reduction in macroalgal biomass was not compensated by elevated epiphytic mass in F treatments. Fourqurean and others (1995) sug-gested that competition for light was the likely cause for the shift in seagrass species composition between treatments. Light limitation where *H. wrightii* is dominant may also affect habitat suitability for calcareous green and other benthic algae.

Shannon–Wiener diversity was greatest in the control treatment, suggesting that low seagrass biomass and density allowed greater evenness of species distribution. Species richness, however was unimodally distributed relative to increasing P supply. The establishment of *H. wrightii* with ele-vated sediment P increased richness, but at the highest P concentrations other species were dis-placed. The overall pattern was to increase species richness with nutrient supply, but at some thresh-old P concentration the dominance of one species, *H. wrightii*, caused a reduction of species richness. The transitions from species effective in nutrient acquisition or efficient in nutrient use to species effective in light interception or efficient in light use, as is the likely case here, illustrates the importance of hypothesized trade-offs in functional characteristics to competitive success (Tilman 1982, 1990; Aerts 1990; Wilson and Tilman 1991; Aerts and Chapin 2000). Such trade-offs have been used

to explain unimodal relationships between species richness and diversity when resources are spatially or temporally homogeneous (Tilman 1982, 1990; Huston and DeAngelis 1994; Abrams 1995; Herbert and others 2004).

Changes in benthic nutrient pools, nutrient inputs, species composition and biomass were accompanied by functional changes in productivity and respiration. Control GPP (301 mg C m^{-2} h^{-1}) was comparable to in situ rates elsewhere. In lower Laguna Madre, TX, *T. testudinum* GPP averaged 81–233 mg C m^{-2} h^{-1} in chambers and 56–366 mg C m^{-2} h^{-1} using the open-water method (Ziegler and Bennar 1998). *H. wrightii* GPP in upper Laguna Madre, TX, was 161 mg C m^{-2} h^{-1} by the open water method (Odum and Hoskin 1958). In the Cross Bank experiment elevated GPP (650 mg C m^{-2} h^{-1}) in D treatments provides evidence of a functional change that has persisted more than two decades. Net benthic production estimates indicate that Cross Bank is net heterotrophic in the winter months, yet remained net autotrophic with elevated sediment TP.

Elevated respiration in D and F treatments correspond to elevated plant biomass including epiphytes and sediment microalgae. This elevated respiration also includes components of the community that we did not measure such as epifauna, burrowing macrofauna, and the community of microbial decomposers, all of which increase complexity of the system and have some level of dependence on the macrophyte community. Evidence for this increased community complexity can also be inferred from the size of the SOC pools. Although SOC changed little across treatments productivity was increased threefold in D and fivefold in F treatments. Because of the rhizomatous growth form of seagrasses, much of that productivity is allocated to rhizomes and roots. In F treatments rhizomes and roots account for 44–60% of *H. wrightii* mass and 74–88% of *T. testudinum* mass, and in control 80–98% of *T. testudinum* mass (Powell and others 1989). Roots and rhizomes senesce, die, and decompose in place contributing directly to SOC. Consequently, elevated rates of productivity must be matched by increased rates of decomposition in F and D treatments to account for the relatively constant SOC pool size across treatments, and this is reflected by the rate of DO consumption. This increase in decomposition rate may provide an alternative explanation for the observed shift in seagrass species composition. Anoxic conditions typical of the carbonate sediments in seagrass communities in Florida Bay and elsewhere can result in high levels of sulfate reduction to

sulfide during decomposition (Carlson and others 1994), and the greater the decomposable SOC pool the greater the accumulation of sulfide (Koch and others 2007; Ruiz-Halpern and others 2008). Because *H. wrightii* typically has a shallow root zone and has the ability to produce "aerial" rhizomes, a mechanism advantageous in light competition (Fourqurean and others 1995; Kenworthy and Schwarzschild 1998), it may be less susceptible to sulfide toxicity than the more deeply rooted *T. testudinum*, which varies little in its aboveground versus belowground biomass ratio.

In response to ecosystem-scale eutrophication sediment and epiphytic microalgae may become dominant in benthic ecosystems (Diaz and others 1990; Corredor and others 1999; Duarte 1995). Fertilization experiments elsewhere in Florida Bay have shown that epiphytes respond to fertilization even when N and P are added directly into the sediments (Ferdie and Fourqurean 2004; Armitage at al 2005). So it is interesting that although sediment and epiphytic microalgae were greatly increased in F treatments at Cross Bank, they never became dominant. This suggests that (1) the nutrient supply rate was insufficient for microalgal biomass to increase to the point where the extremes of eutrophication became manifest or (2) the nutrient supply rate in these small islands of P enrichment could support microalgal dominance, but top–down grazing pressure exerted control over the system. There is only weak correlation of epiphyte abundance with the large nutrient availability gradient in Florida Bay (Frankovich and Fourqurean 1997). It remains untested but this weak correlation has been interpreted to indicate that factors other than nutrient availability, like grazing pressure from herbivores, are as important as nutrient availability in controlling epiphyte abundance in this system.

Evidence for the larger-scale effects of seabird behavior on nearshore eutrophication and ecosystem structure was detailed in another Florida Bay study that compared benthic vegetation near islands having established bird colonies with that near islands without colonies (Powell and others 1991). The fast-growing seagrasses *Ruppia maritima* and *H. wrightii* were dominant near the bird-colonized islands, whereas *T. testudinum* was dominant near uncolonized islands and offshore from both colonized and uncolonized islands. Seagrasses nearest to the bird colony islands were more densely covered with epiphytes than in the surrounding seagrass beds by an order of magnitude (Frankovich and Fourqurean 1997), and observed thick benthic microalgal mats in areas within 10 m

of the colonized islands, devoid of seagrass, were thought to be the result of high nutrient supply rates from bird guano.

The response of seagrass ecosystems to marked increases and decreases in nutrient supply rates has an important application in restoration ecology. Seagrass meadows are under threat of loss worldwide (Orth and others 2006) and considerable effort is expended to repair damage to these ecosystems caused by human activity. In the tropical Western Atlantic, differences in growth rate and growth form lead to differential successes of seagrass transplants into damaged areas. *T. testudinum*, which is often the dominant species in damaged seagrass meadows, has a poor record of success in transplantation (Fonseca and others 1987). Recently, there has been an increase in the application of a novel fertilization technique that attempts repair or replacement of damaged *T. testudinum*-dominated seagrass meadows. By placing artificial bird perches in damaged areas, seabirds are encouraged to roost, and while roosting they defecate into the water below the perch (Kenworthy and others 2000). This seabird activity fertilizes the immediate area under the perches and encourages the growth of the fast-growing seagrass *H. wrightii* (Powell and others 1989; Fourqurean and others 1995; Kenworthy and others 2000). In most cases the dense fields of bird perches used in these projects are designed to be temporary. The *H. wrightii*-dominated community that develops functions to stabilize sediments and provide critical habitat, but it is much different than the *T. testudinum* community that existed prior to damage. With discontinued fertilization the community may return to its original composition, as in the present study.

By revisiting Cross Bank, the site of the original bird-stake fertilization experiments in Florida Bay, we have demonstrated that there can be a superficial return to the pre-disturbance character of an ecosystem in a relatively short period of time after cessation of the nutrient loading disturbance. However, because of the nature of element cycles, functional changes can persist for many decades. Even though this experiment delivered large inputs of nutrients in a rather specialized form to small areas within an otherwise oligotrophic landscape, we argue that our results are applicable to the understanding of eutrophication of coastal ecosystems in general. In oligotrophic systems, even large inputs of limiting nutrients do not lead to consistent measurable increases in concentrations of inorganic forms of the limiting nutrient because of rapid uptake by primary producers, hence nutrient loading to coastal ecosystems likely occurs in complexed organic and inorganic forms. Once these nutrients are captured in a benthic system, they have the potential to drive long-lasting changes in the ecosystem if recycled and retained in the system. In N-limited coastal ecosystems, recovery from N loading may be delayed for years or decades because of continued delivery and recycling from accumulated sediment N pools (for example, Carstensen and others 2006). Here we demonstrate that P is effectively captured and retained in a dynamic, shallow-water benthic ecosystem and continues to have effects for decades after an episodic deposition. It is likely that internal recycling will delay P limited ecosystems from responding to nutrient abatement longer than N-limited systems because there is no comparable process to denitrification for P removal. From this we should temper our expectations for coastal ecosystem responses to the abatement of nutrient pollution. Decades may be required to realize benefits from regulatory actions to control nutrient input to aquatic ecosystems.

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