Role of Benthic Communities in the Cycling and Balance of Nitrogen in Florida Bay

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EXECUTIVE SUMMARY

A study was conducted to measure major processes and rates of nitrogen cycling in representative basins of Florida Bay. Samples were collected in August 1999 and March 2000 at sites in six basins (Johnson Key, Rabbit Key, Rankin Bay, Terrapin Point, Little Madiera, and Sunset Cove), which span 30 km across an East-West transect of the Bay. These sites are representative of gradients of sediment depth, phosphorus and nitrogen limitation, and seagrass health. Using intact cores, measurements were made for sediment-water fluxes of O_2, N_2, NH_4^+, NO_3^- and PO_4^{3-} in light and dark incubations at vegetated (within dense beds) and unvegetated (in large bare patches) sites. Net fluxes of N_2 across the sediment-water interface were measured using a precise and novel technique that analyzes concentrations of nitrogen gas relative to those of the inert gas, argon. Data were also collected for sediment chlorophyll-*a* and C-N-P solid phase concentrations and for sediment pore water nutrient and sulfide concentrations. Sediment accretion rates were estimated by analyzing geochronology from vertical profiles of ^{210}Pb. In addition, we measured aboveground and belowground biomass of seagrasses at these stations, and analyzed plant tissues for concentrations of N and P.

Measured rates of denitrification (dark N_2 flux) were much higher than would be predicted from estimated N loading rates to Florida Bay. Overall, rates averaged 127 ± 87 $\mu mol\ m^{-2}\ h^{-1}$ in August and 65 ± 82 $\mu mol\ m^{-2}\ h^{-1}$ in March for all Bay sites. These rates are similar to values estimated for sediments in Chesapeake Bay and other eutrophic estuaries. We speculate that such high rates may be characteristic of shallow tropical ecosystems like Florida Bay with severely limited availability of phosphorus. Estimates of N fixation (gross N_2 fluxes in light) were large enough to balance denitrification in August but not so in March. Ammonium fluxes across the sediment-water interface were much smaller, and generally directed into the sediments in the light and from the sediments in dark. Nitrate and phosphate fluxes were negligible. We measured relative high biomass levels and photosynthetic rates for benthic microalgal communities at most Florida Bay sites.

Strong correlations between benthic chlorophyll-*a* and solute fluxes across the sediment water interface further suggest the importance of microphytobenthos. Estimated N budgets indicate that benthic algal uptake of N is one of the most important processes regulating N pools. Even in Rankin Bay, a major site of seagrass dieback, little ammonium and no nitrate escape from sediments to overlying water. Benthic algal assimilation and N_2 flux dominate the budget at this site. The absence of correlations between benthic community photosynthesis and respiration, however, suggests that other sources of organic matter, including seagrass exudates and detritus as well as epiphytes and phytoplankton, may also be important in fueling benthic respiration.

Nitrogen assimilation by the dominant seagrass, *Thalassia testudinum*, is an important term in the overall N budgets of the Bay. Seagrass uptake is, however, far more important in healthy beds like that at Rabbit Key than at dieback sites. Large pools of nitrogen are tied up in seagrass biomass, particularly at with healthy beds. Seagrass nitrogen pools in August and March are sufficient to support measured rates of denitrification for more than three years at healthy sites. Although our current research in Florida Bay is addressing indirect effects of seagrasses on N cycling, the study design of this previous study was not geared to measure N fluxes in sediments with seagrass roots.

While this study has provided important new information on nutrient biogeochemistry in Florida Bay sediments, many gaps remain in our overall understanding of these processes. Three key areas of research, which were not addressed in this study, have been identified as important. These are 1) the role of seagrasses in regulating rates and balance of N fixation and denitrification; 2) the rates and controls of P cycling in Bay sediments; 3) the relationships among biogeochemical cycles of N, P and organic carbon. Models that are used to guide management will eventually require a mechanistic understanding of major N and P cycling processes. We believe that our study represents a major first step towards this end.

INTRODUCTION

Seagrasses are conspicuous and productive components of temperate and tropical coastal ecosystems throughout the world (e.g., Kemp 2000). They provide both abundant food and shelter from predators for diverse fish and invertebrate populations (e.g., Lubbers et al. 1990). Plant communities also influence many physical, geological and biogeochemical processes in the sediments they inhabit (Kemp et al. 1984). In many cases, increased bottom friction from the seagrass canopy enhances trapping and binding of particulate organic detritus (e.g., Ward et al. 1984), which collects and decomposes in plant sediments to regenerate inorganic nutrients (e.g., Kenworthy et al. 1982). Thus, seagrasses may play an important role in the biogeochemistry of shallow coastal environments.

Although seagrasses derive much of the inorganic nutrients required to support their growth from sediment recycling processes (e.g., Lee and Dunton 1999), these processes are, in turn, influenced by the physiology and ecology of the plants themselves. For example, seagrasses tend to oxidize their rhizosphere by releasing photosynthetically produced dissolved oxygen from roots to sediments (e.g., Kemp and Murray 1986). In some instances, oxygen released from plant roots stimulates rhizosphere nitrification, which produces nitrate to support high rates of denitrification (e.g., Caffrey and Kemp 1992, Blackburn et al. 1994). Although coupled nitrification-denitrification is not always stimulated by seagrass oxygen release (e.g., Risgaard-Petersen et al. 1998), seagrass stimulation of denitrification appears to be a broadly reported phenomenon (Cornwell et al. 1999). Here, the resulting loss of fixed nitrogen could actually retard seagrass growth by limiting nitrogen availability (Caffrey and Kemp 1989).

Another important mechanism by which seagrasses can influence sediment biogeochemistry is root-release of dissolved organic matter (DOM) to the surrounding rhizosphere (e.g., Koepfler et al. 1993, Ziegler and Benner 1999). This input of DOM to sediment pore waters stimulates a range of bacterial metabolic pathways, including fixation of free nitrogen (Welch et al. 1997). In nitrogen limited environments, this

increased N-fixation would tend to enhance plant growth (e.g., O'Donohue et al. 1991). Root release of DOM also leads to increased rates of sulfate reduction in seagrass sediments (Holmer and Nielsen 1997). Sulfide, the primary metabolite of sulfate reduction is generally toxic to many seagrasses (e.g., Goodman et al. 1994, Erskine and Koch 2000). However, dissolved oxygen, which is released by seagrass roots on a diurnal cycle (e.g., Lee and Dunton 2000), tends to oxidize sulfide, precluding its accumulation and thereby improving growing conditions for these plants (e.g., Carlson et al. 1994). Clearly, seagrass-sediment interactions are numerous and complex, and the balance among these processes contributes to regulation of plant growth and survival.

One seagrass community that has received a great deal of attention over the past decade is that of Florida Bay. Although three seagrass species are abundant in this large shallow lagoonal ecosystem, one species, the turtlegrass (*Thalassia testudinum*) has dominated much of the Bay's bottom. In the late 1980's, however, a widespread pattern of *T. testudinum* dieback was observed (Zieman et al. 1999). Many theories have been proposed to explain this seagrass decline. These include unusual conditions of elevated salinity and temperature, accumulation of phytotoxic concentrations of sediment sulfide, outbreak of an infectious disease, and a broad pattern of eutrophication (Fourqurean and Robblee 1999). Many of these hypothesized mechanisms involve, either directly or indirectly, interactions between seagrass plants and sediment biogeochemical cycling of organic matter and nutrients.

A recent analysis of nitrogen and phosphorus inputs and outputs revealed that Florida Bay's nutrient budgets are generally dominated by advective exchanges at the eastern and western boundaries (Rudnick et al. 1999). There is some evidence that recent anthropogenic increases in nutrient loading may be degrading seagrass health in areas of the Bay (Tomasko and Lapointe 1991, Lapointe et al. 1994), but such effects appear to be restricted to a narrow region in the upper Florida Keys (Rudnick et al. 1999). In fact, seagrass growth in Florida Bay is generally limited by low concentrations of nutrients, particularly phosphorus, in sediment pore waters (Fourqurean et al. 1992, Koch et al. 2001). Although phosphorus availability tends to be more important than nitrogen in

limiting seagrass growth in shallow calcareous subtropical systems such as Florida Bay, modest elevation in P-loading from external sources may increase the relative importance of nitrogen (McGlathery et al. 1994). Very little is known, however, about factors regulating N and P concentrations in Florida Bay (e.g., Boyer et al. 1999). Preliminary analyses suggest that two processes, denitrification and nitrogen fixation, may be especially important in the N budget of Florida Bay (Rudnick et al. 1999). There is, however, surprisingly little known about the magnitudes or controls of processes, as well as other key pathways of N and P cycling. Here, we report on an integrated study of denitrification, nitrogen fixation, and related processes, at representative stations across the Bay in spring and summer seasons.

METHODS

Samples were collected from six basins (Table 1) in August 1999 and March 2000. At each station, duplicate flux cores and a single pore water core were collected from "vegetated" and "unvegetated" sites (4 total flux cores, 2 pore water cores). The cores from vegetated sites were collected from small (10 cm diameter) openings among *T. testidinum* vertical shoots; cores from unvegetated sites were collected from bare patches (1-10 m diameter) within the seagrass bed. At Rabbit Key, all 4 cores were collected in seagrass meadows because there were virtually no bare patches in that bed.

Table 1. Sampling Locations

ID	Reason For Inclusion
Rabbit Key	Healthy Grass Beds in West/Central Bay
Johnson Key	Site of Seagrass Dieback in West/Central Bay
Rankin Bay	Site of Major Seagrass Dieback in Central Bay
Terrapin Bay	Healthy grass beds in Northern Bay
Little Madiera	Strongly affected by freshwater pulsing
Sunset Cove	Anthropogenic N and P inputs from development

Seagrass biomass was sampled at four stations (Rabbit, Johnson, Rankin, Sunset Cove) in August 1999 and March 2000, and at the Little Madiera site in March only. At each station, triplicate plant samples were collected within 10 m of sediment sampling sites using an acrylic corer (15.5 cm diameter, 35 cm long) from randomly selected sites. In all cases, the corer was inserted into the sediments carefully (to avoid cutting seagrass leaves) to a sediment depth of approximately 25 cm. Although some roots of *T. testudinum* extend deeper than this sampling depth, most of the belowground biomass was captured in these samples (J. Fourqurean, personal communication). Sediments were vigorously washed from each plant sample in 1 mm mesh bags in the field and again in the laboratory under a stream of fresh water. Dead plant material was separated from each biomass sample and retained for subsequent analyses. Leaves were gently scraped free of calcium carbonate under a water stream. Plant samples were oven dried at 60° C until constant weight was achieved (usually after 48 hours).

Dried plant material was ground in a Wiley Mill and powdered with a mortar and pestle. Powdered samples were separated into two parts and stored in screw-capped vials for subsequent chemical analyses. The first part was used to measure plant C and N content with a Perkin-Elmer Model 240B CHN Analyzer. The second part of the dried, powdered material (approximately 3 mg) was analyzed for P content (Technicon Autoanalyzer) after digestion and extraction with potassium persulfate for 4 h (Strickland and Parsons 1972, Short et al. 1985).

Sediment pore water cores were sectioned into 2 cm horizons, centrifuged in 50 mL polycarbonate tubes, and syringe filtered (0.4 μm). The presence of hydrogen sulfide in most sediment horizons provided a solubility limit to dissolved iron (Morse et al. 1987), minimizing oxidation artifacts for soluble reactive phosphorus (Bray et al. 1994).

Sediment incubations were carried out in a circular incubator kept at ambient water temperature by the continuous pumping of Sunset Cove surface seawater. The incubation cores were immediately placed in the chamber upon arrival to a pier at Sunset Cove. The cores were gently bubbled overnight in a large pool of water collected from

each coring site. We have found that such overnight submersion of the cores minimized artifacts of gas exchange between water and the acrylic incubation core. Stirring was carried out by a suspended magnet in each core, with a central magnetic turntable used to turn the magnets. Early in the morning on the day after core collection, cores were sealed without any gas space and a dark incubation was initiated. Sampling intervals were 1.5-2 hours and water samples were collected at 4 time points. After the fourth time point, the sediments were illuminated with sunlight by removal of an opaque blanket and 3 more time points were collected at 1 hour intervals. The water that was removed was replaced by inflow from a carboy containing ambient water. Samples for gas analysis were collected in 7 mL ground glass stoppered tubes, forced by gravity flow from the ambient water. Mercuric chloride was added as a preservative and the sample tubes were stored underwater at ambient or sub-ambient temperatures. Such preservation and storage results in no storage artifact for periods greater than 5-6 weeks. Nutrient samples were collected in 20 mL syringes and filtered (0.2 μm). They were then frozen for subsequent analysis. At the end of the incubation, samples for chlorophyll *a* were collected using a cutoff syringe. Duplicates samples were collected to a depth of 0.6 cm and frozen in a 15 ml centrifuge tube until analysis.

Nitrate plus NO_2^- was analyzed colorimetrically after cadmium catalyzed reduction of NO_3^- (Parsons et al. 1984). Soluble reactive phosphorus (SRP) and NH_4^+ were analyzed colorimetrically following Parsons et al. (1984). Pore water H_2S was analyzed colorimetrically (Cline 1969). High precision (<0.05% COV) gas analyses was analyzed using a membrane inlet mass spectrometer (Kana et al. 1994; 1998) that provides high precision analyses of O_2/Ar and N_2/Ar ratios. This instrument system (Dissolved Gas Analyzer or DGA) allowed us to measure the net N_2 flux across the sediment-water interface. This system also allows us to measure both net denitrification (flux out of the sediment) and net nitrogen fixation (flux into the sediment) in our experiments. Corrections for the production of N_2O and NO in the mass spectrometer were applied (T. Kana, personal communication). The generation of O_2 in some illuminated incubations can lead to an apparent artifact in the N_2/Ar ratios. Oxygen bubbles strip N_2 relative to Ar, thus leading to an apparent decrease in the N_2/Ar ratio.

Although this can lead to a false nitrogen fixation rate, we avoided this problem by eliminating data where either O_2 reached super-saturation or bubbles were observed.

Measurements of total N in sediment solids were obtained with a Control Equipment CHN analyzer; to avoid solubilization of organic N, we did not eliminate the carbonates in the sediment (Schubert and Nielsen 2000). The analysis of total and inorganic P was carried out colorimetrically after HCl extractions of ashed and unashed sediment (Aspila et al. 1976). Sediment chlorophyll *a* was analyzed via HPLC after acetone extraction (Van Heukelem et al. 1994).

Sediment dating was carried out using the ^{210}Pb technique (Robbins 1978) that has been successfully applied to Florida Bay mud banks (Robbins et al. 2000). Sediment ^{210}Pb was measured as the daughter ^{210}Po after acid extraction. The sedimentation rate was estimated by a regression of the natural logarithm of excess ^{210}Po versus cumulative sediment mass.

RESULTS

Geochronology

The ^{210}Pb profiles generally showed indications of mixing near the sediment-water interface, as indicated by relatively constant activity for the top 12-20 cm (Figure 2). Such mixing phenomena are generally attributed to bioturbation by macrofauna, or perhaps disturbance by storms. Mudbanks in central Florida Bay generally did not exhibit such signs of disturbance (Robbins et al. 2000). We used a model which assumes constant ^{210}Pb input concentration and fitted the data to cumulative mass (Robbins et al. 2000) for the regions of these cores where exponential decay was evident. In all cases, we used 3-7 data points for regression and calculated a mass sedimentation rate (Table 2). The deep mixing at Sunset Cove precluded calculation of sedimentation rates; the profile at that site suggests deposition with a relatively recent, mobile mud layer on top of older

sediments. Sediment accretion rates ranged from about 500 to 2,200 g m^{-2} y^{-1} and were generally lower than found previously by Robbins et al. (2000) in mud banks (1,700-9,800 g m^{-2} y^{-1}). Given the possibility of deep mixing in our cores collected within each basin, all of our rates reported here should be regarded as maximum estimates.

The ^{210}Pb inventories that were calculated by summation of excess ^{210}Pb within each core, were generally lower than expected from the atmospheric deposition of ^{210}Pb (~ 30 dpm cm^{-2}) and lower than the 24-98 dpm cm^{-2} found by Robbins et al. (2000) in bank sediments. The differences between basin and deep sediments suggest that ^{210}Pb and possibly fine-grained sediments are focused on to bank areas. Such focusing of ^{210}Pb into shallow water sediments has not been observed in other systems; indeed, most other aquatic systems tend to accumulate ^{210}Pb in deeper waters.

Table 2. Inventories, concentrations and rates of sediment and N burial for Florida Bay cores. N is the number of point used in the regression; COV is the coefficient of variation of the linear regression slope.

ID	^{210}Pb Inventory	Mixing Depth	Sedimentation Rate	N	COV	Burial N	N Burial Rate	N Burial Rate
	dpm cm^{-2}	cm	g m^{-2} y^{-1}		%	mg g^{-1}	g m^{-2} y^{-1}	□mol m^{-2} h^{-1}
Rabbit Key	11.7	12	1,008	3	8	6.6	6.6	59
Little Madeira	11.3	0	2,208	3	33	1.8	4.0	32
Sunset Cove	7.5	20				11.2		
Rankin Bay	7.0	0	699	7	17	3.2	2.2	18
Johnson Key	16.5	16	526	3	2	6.1	3.2	26
Crocodile Point	10.3	0	1,674	7	34	3.1	5.2	42

Seagrass Biomass and Nutrient Content.

Plant biomass (Table 3) collected at these sites was comprised almost exclusively by *T. testudinum*. Although small quantities of *Halodule wrightii* were also collected in cores from Johnson Key and Little Madiera Bay, these represent less than 1% of total seagrass biomass. Rabbit Key had the highest overall biomass values, with total biomass averaging around 2300 g dw m^{-2} for the two dates, and the ratio of below/aboveground (R/S) tissue ranging from 7-14. The next highest plant biomass was at Sunset Cove,

where totals ranged from 1100-1200 g dw m^{-2}, and R/S ratios ranging from only 3-5. Biomass and R/S ratios at the two main die-back sites, Rankin Key and Johnson Key, were substantially lower, with biomass values ranging from 200-400 g dw m^{-2} and from 400-500 g dw m^{-2}, respectively, and R/S ranging from 2-3. Biomass was intermediate (1043 g dw m^{-2}, R/S = 5) at Little Madiera Bay, where no significant dieback has been reported and P-limitation appears to be most severe (some dieback was reported at this station in summer 2000). Thus, plant biomass and R/S ratio appear to reflect effects of both dieback and P-limitation.

Seagrass tissues were analyzed for C, N and P content, with plant material separated into aboveground and belowground living tissues. Overall, leaf N and P content ranged from highs of 2.58 %N and 0.130 %P both at Sunset Cove to lows of 2.08 %N at Johnson Key and 0.07%P at Rabbit Key. In general, tissue nutrient contents were highest at Sunset Cove, with %N decreasing among sites in a westward direction and %P low at most sites. For all stations, N and P contents decreased consistently from aboveground to belowground tissues and from living to dead plant material (data not shown). Belowground (root and rhizome) tissues were lowest in Rabbit Key and Rankin Bay. There is some suggestion that tissue N and P contents were slightly higher in dieback areas (Johnson and Rankin) compared to Rabbit Key. C:P and N:P ratios for leaf tissues ranged from 800-1200 and 40-70 and were similar to mean values reported previously (C:P = 1070, N:P = 59, Fourqurean et al. 1992). These data do not follow the previously reported pattern (Fourqurean et al. 1992) of decreasing C:P ratios from eastern to western regions of the Bay.

Table 3. Seagrass biomass and tissue nutrient content measured at Florida Bay sites in August 1999 and March 2000. Given are mean values and standard errors (in parentheses) among three replicates.

Station	Date	Aboveground Tissues				Belowground Tissues			
		Biomass ($g\ dw\ m^{-2}$)	C (%)	N (%)	P (%)	Biomass ($g\ dw\ m^{-2}$)	C (%)	N (%)	P (%)
Johnson Key	Aug	165 (66)	--*	--	0.084 (0.033)	344 (156)	--	--	0.073 (0.033)
	Mar	114 (22)	32.5 (6.3)	2.08 (0.40)	0.106 (0.020)	286 (183)	32.7 (20.9)	1.29 (0.82)	0.065 (0.042)
Rabbit Key	Aug	272 (74)	--	--	0.076 (0.021)	1919 (178)	--	--	0.043 (0.004)
	Mar	163 (50)	33.6 (10.4)	2.16 (0.67)	0.070 (0.022)	2201 (513)	32.5 (7.6)	1.31 (0.31)	0.036 (0.008)
Rankin Bay	Aug	61 (51)	--	--	0.070 (059)	164 (83)	--	--	0.051 (0.025)
	Mar	108 (120)	33.7 (37.4)	2.27 (2.52)	0.072 (0.080)	339 (54)	30.2 (4.8)	1.44 (0.23)	0.033 (0.005)
Little Madiera[#]	Mar	178 (16)	34.2 (3.07)	2.09 (0.19)	0.097 (0.009)	865 (90)	33.6 (3.50)	1.56 (0.16)	0.048 (0.005)
Sunset Cove	Aug	206 (80)	--	--	0.130 (0.050)	1031 (160)	--	--	0.133 (0.021)
	Mar	263 (55)	34.6 (7.2)	2.58 (0.54)	0.810 (0.017)	801 (121)	32.3 (4.9)	2.12 (0.32)	0.65 (0.010)

*Data for C and N content unavailable for August sampling.
[#]No biomass samples collected in August at Little Madiera site.

Chlorophyll *a* and Nutrient Concentrations/Burial

Sediment chlorophyll *a* concentrations in August ranged from 8 to 86 mg m^{-2} (Table 4), similar to the range of 24 to 120 mg m^{-2} observed by Brand and Suzuki (1999). In 3 of the 5 sites at which both vegetated and unvegetated sediments were sampled, the unvegetated chlorophyll *a* was higher than at the corresponding vegetated site. There was no difference between vegetated and unvegetated cores at Sunset Cove, whereas at Little Madeira the vegetated site had much more chlorophyll *a*. In March 2000, the concentration of chlorophyll *a* decreased at all but one site, indicating a strong seasonality of benthic algal biomass. In March, only in the unvegetated Sunset Cove cores did the chlorophyll *a* concentrations exceed 25 mg m^{-2}; in August, 7 of 12 sites had chlorophyll *a* concentrations higher than 25 mg m^{-2}. This shift in biomass in surficial sediments suggests lower production (or possibly higher grazing) of microphytobenthos during cooler months.

Table 4. Chlorophyll-*a*, organic C and total N concentrations. Chlorophyll *a* is expressed on a square meter basis and is based on the mean of two analyses per core, with two cores for each site (n = 4). For Rabbit Key, n = 8. The mass of "algal" N associated with the chlorophyll *a* was estimated assuming a ratio of chlorophyll *a* mass (mg) to N (mmol) of 0.69 (50:1 C:Chl-*a*; 106:16 for C:N ratio). The organic C and N were from August cores collected from vegetated sites.

Station	Vegetated?	August 1999 Chlorophyll *a*	March 2000 Chlorophyll *a*	August Algal N	March Algal N	Organic C	Total N
		mg m^{-2}		mmol N m^{-2}		mg g^{-1}	
Rabbit Key	Vegetated	8±1	5 ± 2	6	3	39.7	4.9
Johnson Key	Vegetated	60±26	14 ± 4	41	10	36.4	4.6
	Unvegetated	86±2	18 ± 11	59	12		
Rankin Bay	Vegetated	21	8 ± 3	14	10	42.7	5.1
	Unvegetated	75±40	10 ± 1	52	7		
Terrapin	Vegetated	11±1	nd	8	nd	21.9	2.8
	Unvegetated	28±15	nd	19	nd		
Little Madeira	Vegetated	67±8	14 ± 6	46	10	22.9	2.2
	Unvegetated	17	21 ± 3	12	14		
Sunset Cove	Vegetated	42	8 ± 1	29	6	68.6	8.6
	Unvegetated	44±9	69 ± 19	30	48		

The concentrations of organic carbon (21.9-68.6 mg g^{-1}) and total N (1.8-11.2 mg g^{-1}) in surficial sediment (Table 4; Appendix I) tended to co-vary, with a molar C:N ratio of 9.8±1.1. Such molar ratios are consistent with an algal organic matter source (Cornwell et al. 1996). Total N concentrations decrease down-core (Appendix I) and the N data used to estimate the concentration of buried N is the mean of 8-10 and 18-20 cm core sections (for Johnson Key, we use only the 8-10 cm sections). These concentrations are presented in Table 1. The product of mass sedimentation rate and N concentration is a N burial rate (Table 1) expressed in g m^{-2} y^{-1} or in μmol m^{-2} h^{-1} (for comparison to our short-term flux calculations). Nitrogen burial rates ranged from 2.2 g m^{-2} y^{-1} at Rankin Bay to 6.6 g m^{-2} y^{-1} at Rabbit Key. Phosphorus data (not shown; Appendix I) are similar to those of Koch et al. (2001).

Sediment-Water Exchange

High rates of oxygen uptake were observed in dark incubations in August 1999 (Figure 3), with rates ranging from –1,268 to -2,626 μmol m^{-2} h^{-1}, and averaging –1,909 ± 396 μmol m^{-2} h^{-1}. In general, the duplicate cores from each incubation tracked each other quite well. The highest O_2 uptake was found in the high *Thalassia* biomass environment of Rabbit Key; the lowest was the unvegetated cores in Johnson Key. We observed modest differences between vegetated and unvegetated sediments, except at Johnson Key, where O_2 uptake by vegetated sediments were almost two-fold higher than in unvegetated sediments. Dark oxygen uptake in March averaged -1,900±1,137 μmol m^{-2} h^{-1}, similar to the August data. Higher site-to-site variability was observed, and differences between August and March rates for each site were considerable. A large decrease in oxygen uptake at Rabbit Key contrasted strongly with the large increase in O_2 uptake at Sunset Cove from August to March.

The illumination of sediments resulted in large changes in sediment-water O_2 exchange (Figure 4), with only 3 of 11 core sites showing net uptake of oxygen during August. In March, only 3 of 9 cores showed net O_2 uptake. In August, light O_2 uptake averaged 1743 ± 2,894 μmol m^{-2} h^{-1}; in March the average was 869 ± 1,631 μmol m^{-2} h^{-1}.

During both sampling times, the highest rates of O_2 production occurred in unvegetated cores at Sunset Cove; high rates were observed for both vegetated and unvegetated cores at Johnson Key and Terrapin Bay in August.

Relatively high rates of dark N_2 production were observed at most sites (Figure 5), averaging 127 ± 87 μmol N_2-N m^{-2} h^{-1} for August and 65±62 μmol N_2-N m^{-2} h^{-1} for March. Net N_2 exchange was zero in the dark at Terrapin in August and Little Madiera in March, and a small dark N_2 uptake was observed in the unvegetated cores at Johnson Key during March. The highest efflux rates observed in this program were found at the Rankin unvegetated and Little Madeira vegetated and unvegetated sites.

Illuminated N_2 flux incubations yielded N_2 fluxes both into and out of sediments (Figure 6), with August incubations averaging -203 ± 507 μmol m^{-2} h^{-1} and March incubations averaging –3 ± 88 μmol N_2-N m^{-2} h^{-1}. The unvegetated N_2 uptake at Sunset Cove averaged –1455 ± 245 μmol N_2-N m^{-2} h^{-1}, indicating extremely high rates of N_2 fixation at that site in August. During March, only Sunset Cove cores had N_2 uptake.

Dark fluxes of NH_4^+ showed high rates out of sediment at Rabbit and Johnson Key sites in August as well as Sunset unvegetated cores in March. The means of all NH_4^+ fluxes were, however, relatively low, being 16 ± 90 μmol m^{-2} h^{-1} in August and 12 ± 38 μmol m^{-2} h^{-1} in March. Light NH_4^+ fluxes were consistently lower than dark fluxes, averaging –25 ± 117 μmol m^{-2} h^{-1} in August and 6 ± 19 μmol m^{-2} h^{-1} in March. In August light NH_4^+ flux data exhibited greater site to site variability than did the March data.

Sediment Pore Waters

Vertical profiles of soluble reactive phosphorus (SRP), ammonium (NH_4^+) and hydrogen sulfide (H_2S) concentrations in sediment pore waters were generally higher in August than in March (Appendix III). Concentrations of H_2S were often very high, exceeding 1mM at 5 of 11 sites in August and at one site in March. Subsurface

concentrations of NH_4^+ exceeded 100 μM for all but one site in August and for 5 of 9 sites in March. Highest NH_4^+ concentrations were observed at Rankin Bight, a major dieback area, and Sunset Cove, which is influenced by anthropogenic sources. For both NH_4^+ and H_2S, concentrations tended to increase with depth, but often exhibited lower concentrations in the primary root zone (8-12 cm) at vegetated sites. We view the extremely high surface concentration of NH_4^+ (1601 μM) measured in the surface layer for Rabbit Key in August to be an anomaly. Concentrations of SRP were generally below 1-2 μM except in the surface layer (0-2 cm) in August, where concentrations approached 4-5 μM at 4 of 11 sites.

DISCUSSION

Denitrification in Florida Bay

Despite relatively low exogenous nutrient loading (Rudnick et al. 1999), rates of sediment denitrification were very high; rates at many sites were in excess of 100 μmol N_2-N m^{-2} h^{-1}. Dark rates of N_2 flux are at the high end for coastal marine ecosystems (Seitzinger 1988) and on a par with estimates for the eutrophic Chesapeake Bay (Kemp et al. 1990; Boynton et al. 1995). Similar high rates have been observed previously for some tropical seagrass sediments (Blackburn et al. 1994).

The direct N_2 flux method used here is the first application of this approach (using precise measurements of N_2/Ar ratios) to seagrass environments. This method avoids many of the limitations of other measurement approaches, such as the acetylene block technique, long-term direct N_2 measurement techniques via gas chromatography after purging, and sediment-water flux stoichiometry (Cornwell et al. 1999). The direct measurement of N_2 fluxes simplifies the estimation of denitrification. In shallow systems such as Florida Bay, the method also provides estimates of net nitrogen fixation as N_2 uptake by sediments in the light. Overall, fluxes of gaseous N_2 represents the largest exchange of inorganic N across the sediment-water interface in Florida Bay. Thus to a

large extent, factors which regulate the balance between denitrification and nitrogen fixation control the overall biogeochemistry and cycling or nitrogen in this system.

In sediments with microphytobenthos, coupled nitrification-denitrification is often enhanced (Risgaard-Petersen et al. 1994, Rysgard et al. 1995, An and Joye 2001) under sediment illumination because of increased nitrification. However, the inhibition of denitrification by benthic photosynthesis can also occur, particularly when denitrification is largely supported by water column nitrate (Christensen et al. 1990, Risgaard-Peteresen et al. 1994). High rates of benthic photosynthesis enhance the size of the habitat suited to nitrification via the deepening of oxygen penetration in the sediment. With low water column nitrate concentrations, the only potential nitrate source for denitrification is via nitrification.

The co-occurrence of high rates of benthic algal production and denitrification may indicate minimal competition for N between primary producers (macrophytes and benthic algae) and nitrifying bacteria. In a P-limited system such as eastern Florida Bay, the high rates of exchange of N_2 may indicate that major N losses and gains from the sediments may not be a major control on the productivity of this ecosystem. In fact, P limitation may tend to regulate the balance of N cycling in the Bay.

The Role of Microphytobenthos in Florida Bay Nutrient Cycling

The rates of dark uptake of oxygen (sediment oxygen demand or SOD) are similar to many coastal environments and exhibit no simple temporal or spatial pattern. Rudnick et al. (1999) reported sediment oxygen demand rates of 1,700 to 3,300 $\mu mol\ m^{-2}\ h^{-1}$ at a site near Terrapin Bay. Sediment oxygen demand in the mangrove and pond environments of Taylor Slough in northern Florida Bay ranged from 800 to 2,500 $\mu mol\ m^{-2}\ h^{-1}$ and late October rates were considerably lower than July rates (Cornwell and Owens 2000). The production of oxygen, or a decrease of SOD during light incubations, points toward the important role of microphytobenthos to production in Florida Bay. As with

SOD, light O_2 fluxes varied considerably between sites and dates, though the high O_2 production measurements found at several sites in August were present only in Sunset Cove in March.

The differences between light and dark oxygen fluxes can be used as a measure of the production of benthic algae (gross O_2 production). A key assumption of this is that the rates of light and dark sediment respiration are the same; the production of oxygen in surficial sediment/algal layers may enhance sediment oxygen consumption by steepening the oxygen gradient. In addition, enhanced oxidation of reduced sulfides or other species may occur (Epping et al. 1999). Another assumption is that the production of oxygen for 2 to 3 hours after introducing sunlight can provide photosynthesis rates valid for the entire 12 hour time period. These assumptions are untested, but the high rates of benthic photosynthesis should provide approximations of ambient rates.

In the unvegetated sites in August, a positive correlation ($p < 0.01$) was observed between gross O_2 production and the concentration of chlorophyll *a* (Figure 9). This strong correlation indicates that the benthic chlorophyll is active and may well be a good predictor of benthic photosynthesis. A similarly good correlation is observed assuming a C:Chl*a* ratio of 50 and a photosynthetic quotient of 1.0, the slope of these relationships suggest a growth rate of 0.3 d^{-1} for benthic algae. Gross O_2 production at the vegetated sites was not significantly correlated to chlorophyll a, perhaps indicating different physiological responses to light, deposition of phytoplanktonic chlorophyll, and/or effects of seagrass shading. Given the lack of strong spatial relationships in the O_2 flux data, the general response of O_2 production to different levels of chlorophyll a is reassuring. The general levels of gross O_2 production (in some cases exceeding 5,000 $\mu mol\ m^{-2}\ h^{-1}$), suggest that benthic algal production may be an important part of the Florida Bay ecosystem.

In comparison to the expected reasonable match between primary production and respiration in water column oxygen cycling studies (e.g., Smith and Kemp 1995), it is clear that the large range in light oxygen fluxes does not match well with the much smaller range

in dark oxygen fluxes (Figure 10). Only for the unvegetated March sediments is there a significant correlation ($p < 0.05$). For the other sites, there appears to be no consistent pattern, with many points suggesting a predominance of primary production over respiration, and a number of sites showing the opposite trend. The uncoupling of production and respiration suggests that mass balances at these sites are strongly influenced by inputs of organic matter not produced at the surface of the sediments (seagrass, phytoplankton, or mangrove detritus) or by the loss of organic matter through either grazing or advective export after resuspension.

A significant correlation between light N_2 flux and chlorophyll *a* concentration was found for unvegetated sediments (Figure 11) during both August and March. The general decrease in N_2 fluxes with increasing chlorophyll *a* indicates the increasing importance of N fixation when benthic algal abundance increases. Whether this represents stimulation of N-fixing communities by enhanced organic matter supply (Welsh 2000) or some other control is not evident from these data.

Light and dark ammonium fluxes and chlorophyll *a* are correlated except for the March unvegetated data (Figure 12). High algal biomass and production lead to the increased uptake of NH_4^+ from the water column. Uptake during the dark may occur through algal uptake, although usually at a lower rate (Thornton et al. 1999). The ability of microphytobenthos to assimilate NH_4^+ from both the water and (probably) from the sediments indicate that these algal communities provide important regulation of fixed N fluxes at the sediment-water interface. The lack of nitrate fluxes into or out of sediments occurs because of low water column fluxes and the microbial efficiency of denitrification after nitrification.

Because of the high N nutritional need of benthic algae, an examination of the sum of the potential N sources can be a useful exercise. If we assume that benthic algae has a C:N and O_2:N ratio of 6.25, we can use the gross oxygen photosynthesis rates to estimate N demand. If we sum up potential contributions from ammonium uptake from the water column, decomposition, and N fixation, we can estimate an N supply. In August 1999, a

very significant positive correlation ($p < 0.01$) was observed between N supply and demand (Figure 13). A strong correlation ($p < 0.01$) was also observed in March 2000. In August, the slope of 1.3 was indistinguishable from 1; in March, apparent sources of N supply could meet 61% of our calculated N demand by microphytobenthos.

The Role of Seagrasses in Florida Bay Nitrogen Cycling

Large pools of N and P were residing in plant tissue material at these sites. At Rabbit Key in March, for example, *T. testudinim* leaves contained 250 mmol N m^{-2} and 3.6 mmol P m^{-2}, while belowground tissues held 2060 mmol N m^{-2} and 25.5 mmol P m^{-2}. An additional 646 mmol N m^{-2} and 2.3 mmol P m^{-2} was stored in recently dead detrital plant tissues. For comparative purposes, sediment porewater pools can be estimated assuming mean porewater concentrations of NH_4 and PO_4 of 150 μM and 1 μM, respectively, (e.g., Koch et al. 1999) over a 30 cm rooting zone. These concentrations would yield porewater inventories of approximately 23 mmol N m^{-2} and 0.15 mmol P m^{-2}, which are only 1% and 0.5% of the respective N and P pools in living plant tissues.

In general, it appears that, for *T. testudinum* in Florida Bay, productivity (P, g dw m^{-2} d^{-1}) can be described in terms of standing crop (B, g dw m^{-2}) by the following relationship (Zieman et al. 1989), $P = 0.058 + 0.018\ B$ ($r^2 = 0.92$). Because the intercept of this equation is essentially zero, we can use this relationship to compute the nitrogen demand associated with *T. testudinum* leaf production by simply multiplying estimates of N standing stock in seagrass leaves by 0.018. Nitrogen demand is estimated in Table 4.

Table 5. Estimated nitrogen pools and rates associated with seagrass biomass and productivity in Florida Bay study sites in August 1999 and March 2000.

Station	Date*	Aboveground Tissues		Belowground Tissues	
		N-Biomass* ($mmol\ m^{-2}$)	N-Production† ($mmol\ m^{-2}d^{-1}$)	N-Biomass ($mmol\ m^{-2}$)	N-Production† ($mmol\ m^{-2}d^{-1}$)
Johnson Key	Aug	245	4.41	317	0.63
	Mar	169	3.05	263	0.53
Rabbit Key	Aug	420	7.55	1796	3.59
	Mar	249	4.50	2060	4.12
Rankin Bay	Aug	99	1.78	169	0.34
	Mar	175	3.15	349	0.70
Little Madiera#	Mar	266	4.78	964	1.93
Sunset Cove	Aug	380	6.83	1561	3.12
	Mar	485	8.72	1213	2.43

* Assumes that N-content of seagrass biomass assumed was the same in August and March (Fourqurean et al. 1992).

No biomass samples were collected in August at Little Madiera site.

† Assumes production/biomass ratios of 0.018 d^{-1} (Zieman et al. 1989) for leaves and 0.002 d^{-1} (Patriquin 1973) for root/rhizome tissues.

Florida Bay Sediment Nitrogen Budgets

Mass budgets can provide useful perspective on nitrogen cycling processes in Florida Bay sediments. We recognize that measurements at two time points do not necessarily represent an average annual N budget. In lieu of a more complete data-set, these rates represent the best estimates of sediment N cycling processes currently available for Florida Bay. We do not present these budgets as well-constrained balances of all nitrogen fluxes and rates, but rather they are meant to provide a basis for quantitative comparisons among rates on either side of the input/output ledgers. We regard this as a provisional budget exercise, which will be greatly strengthened by the addition of further data being collected in 2000-2002.

Using the average of measured sediment flux rates from all sites, we calculated major inputs and losses of N to the Bay's DIN pool at our stations in August and March (Table 6). In this N budget, inputs are (1) ammonium generated from sediment mineralization and (2) nitrogen fixation. Losses include (3) uptake by benthic algae (estimated both from light O_2 fluxes, and from the difference between light and dark O_2 fluxes). Seagrass net uptake (4) is calculated from biomass/production relationships, and denitrification (5) is estimated from direct measurement (assuming that dark N_2 fluxes are representative of both light and dark denitrification). Interestingly, inputs and losses in August are not very different from those in March. However, a net imbalance equivalent to >50% of the inputs is noted, if we use benthic algal uptake associated with gross photosynthesis. Although other losses, such as grazing or export were not considered, a potentially important input which is not included but which might help to balance the N budget is N-fixation associated with seagrasses. On a whole system basis, the effect of benthic algae in N cycling rates in August is similar to that of seagrasses; algae are less important in March. Denitrification represents approximately 15-20% of all loss terms in the budget, and this is consistent with reports from other sediments dominated by microphytobenthic and seagrass communities (Sundback et al. 2000, Risgaard-Petersen and Ottosen 2000).

A second type of N-budget for Florida Bay was computed with respective to the sediment surface to contrast N fluxes for a basin experiencing major seagrass dieback, Rankin Bay, and a basin with healthy seagrasses, Rabbit Key. Here, inputs are N fluxes from water to sediments (and to plants rooted in the sediments), and outputs are N fluxes from the sediments to the overlying water (Table 7). For Rankin Bay, large seasonal shifts in inputs arise because of relatively high summer rates of N fixation and ammonium uptake. Much less seasonality in N input is calculated for Rabbit Key. For both areas, denitrification is a major pathway for N loss, representing 73-84% of N losses from sediments in Rankin and 34-62% of losses in Rabbit Bay. The high rate of ammonium efflux from sediments in August at Rabbit Key suggests large sources of NH_4^+ from N fixation and/or decomposition. It is somewhat surprising that most of ammonium produced in organic decomposition at Rankin Bay is shunted to N_2 loss via nitrification-denitrification. As suggested earlier, this may be a function of the relative excess of N relative to P for support of seagrass and algal growth. Overall, sediment burial is, as expected, a small component in these budgets.

Although our analyses suggest that both seagrasses and microphytobenthos have similar impacts on N cycling by direct uptake, there are huge differences in the N capital stored in their respective biomasses. The highest algal N pools (Table 4) are on the order of 50 mmol N m^{-2}, and values are much lower (< 20 mmol N m^{-2}) for most stations and dates. In contrast, seagrass biomass usually contained >> 500 mmol N m^{-2}, and values range from 2000 to 2,500 mmol m^{-2} at Rabbit Key and Sunset Cove (Table 5, sum of above and belowground). In principle, there is sufficient N contained in seagrass biomass to support observed rates of denitrification for three years. It might be anticipated, therefore, that nitrogen recycling in areas such as Rankin Bay, which have experienced major mortality of seagrasses through dieback, would support greatly elevated rates of denitrification and/or ammonium flux to overlying waters. This pattern was not seen in our data, but it appears that N demand by the active microphytobenthos community may be sufficient to mitigate partially against abrupt N losses.

While this study has provided important new information on nutrient biogeochemistry in Florida Bay sediments, many gaps remain in our overall understanding of these processes. Three key areas of research, which were not addressed in this study, have been identified as important. These are: 1) the role of seagrasses in regulating rates and balance of N fixation and denitrification; 2) the rates and controls of P cycling in Bay sediments; 3) the relationships among biogeochemical cycles of N, P and organic carbon. These key processes represent an important gap in our knowledge in this system. Models that are used to guide management will eventually require a mechanistic understanding of major N and P cycling processes. We believe that our study represents a major first step towards this end.

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Table 6. Estimated seasonal balances of nitrogen fluxes to and from pools of dissolved inorganic nitrogen in Florida Bay. Rates are calculated as means of all measurements at all sites (mmol N m^{-2} d^{-1}).

Rates	August	March
INPUTS		
1) NH_4^+ Regeneration	7.32	7.30
2) N_2 Fixation	3.96	0.74
Total Inputs	11.28	8.04
LOSSES		
3) Benthic Algal Uptake (Community Net Uptake)	7.01 (3.35)	5.32 (1.67)
4) Seagrass Net Uptake	7.06	6.78
5) Denitrification	3.05	1.56
Total Losses	17.12 (13.46)	13.66 (10.01)
Inputs - Losses	-5.84 (-2.18)	-5.62 (-1.97)

[1] Calculated from dark O_2 flux and assuming O_2:N = 6.25.
[2] Calculated as light plus N_2 fluxes divided by 2, assuming dark rates = 0, with 12 h darkness per day.
[3] Calculated from either light O_2 fluxes or as light plus dark O_2 fluxes (in parentheses), assuming O_2:N = 6.25, and that dark rates = 0.
[4] Calculated from leaf and root/rhizome growth times respective tissue %N (see Table X).
[5] Calculated as dark N_2 flux, assuming rates are same in light and dark.

Table 7. Estimated seasonal mean balances of nitrogen fluxes (mmol N m^{-2} d^{-1}) to and from sediment surface for two stations in Florida Bay.

Rates	Rankin		Rabbit	
	March	**August**	**August**	**March**
INPUTS				
1) N_2 Fixation	5.12	0.70	0.58	0.95
2) Sediment Uptake of NH_4^+ from Water	1.09	0	0	0
3) Seagrass Uptake of NH_4^+ from Water	0.89	1.57	3.77	2.25
Total Inputs	7.10	2.27	4.35	3.20
OUTPUTS				
4) Denitrification	3.72	2.18	2.78	2.57
5) NH_4^+ Efflux from Sediments	0.26	0.38	4.04	0.16
6) Sediment Burial	0.43	0.43	1.42	1.42
Total Outputs	4.41	2.99	8.24	4.15
Inputs - Losses	2.69	-0.72	-3.89	-0.95

[1] Calculated as light plus N_2 fluxes divided by 2, assuming dark rates = 0, with 12 h darkness per day.
[2] Calculated as light NH_4^+ fluxes across sediment-water interface.
[3] Calculated as leaf growth times tissue %N divided by 2, assuming half of the N assimilation comes from overlying water (see Lee and Dunton 1999).
[4] Calculated as dark N_2 flux, assuming rates are same in light and dark.
[5] Calculated as dark NH_4^+ fluxes across sediment-water interface.
[6] Calculated from ^{210}Pb methods (see Table 2).

REFERENCES

An, S. and S.B. Joye. 2001. Enhancement of coupled nitrification-denitrification by benthic photosynthesis in shallow estuarine sediments. Limnol. Oceanogr. 46: 62-74.

Aspila, K.I., H. Agemian. and A.S.Y. Chau. 1976. A semi-automated method for the determination of inorganic, organic and total phosphate in sediments. Analyst 101: 187-197.

Boyer, J. N., J. W. Fourqurean, R. D. Jones. 1999. Seasonal and long-term trends in the water quality of Florida Bay (1989-1997). Estuaries 22 (2B): 417-430.

Boynton, W.R., J.H. Garber, R. Summers and W. M. Kemp. 1995. Inputs, transformations and transport of nitrogen and phosphorus in Chesapeake Bay and selected tributaries. Estuaries 18: 285-314.

Blackburn, T. H., D. B. Nedwell and W. J. Wiebe. 1994. Active mineral cycling in a Jamaica seagrass sediment. Mar. Ecol. Prog. Ser. 110: 233-239.

Brand, L.E. and M. Suzuki. 1999. Distribution of benthic chlorophyll Florida Bay sediments. Abstract, 1999 Florida Bay and Adjacent Marine Systems Science Conference, p. 129.

Caffrey, J. M. and W. M. Kemp. 1989. Nitrogen cycling in sediments with estuarine populations of *Potamogeton perfoliatus* and *Zostera marina*. Mar. Ecol. Progr. Ser. 66: 147-160.

Caffrey, J. M. and W. M. Kemp. 1991. Seasonal and spatial patterns of oxygen production, respiration and root-rhizome release in *Potamogeton perfoliatus* L. and *Zostera marina*. L. Aquat. Bot. 40: 109-128.

Caffrey, J. M. and W. M. Kemp. 1992. Influence of the submersed plant, *Potamogeton perfoliatus* L., on nitrogen cycling in estuarine sediments: Use of ^{15}N techniques. Limnol. Oceanogr. 37: 1483-1495.

Carlson, P. R., and L. Yarbro and T. Barber. 1994. Relationship of sediment sulfide to mortality of *Thalassia testudinum* in Florida Bay. Bull. Mar. Sci. 54: 733-746.

Christensen, P.B., L. P. Nielsen., J. Sorenson and N. P. Revsbech. 1990. Denitrification in nitrate-rich streams: diurnal and seasonal variation related to benthic oxygen metabolism. Limnol. Oceanogr. 35: 640-651.

Cline, J.D., 1969. Spectrophotometric determination of hydrogen sulfide in natural waters. Limnol. Oceanogr. 14: 454-458.

Cornwell, J.C., J. C. Stevenson, D. J. Conley, and M. Owens. 1996. A sediment chronology of Chesapeake Bay eutrophication. Estuaries, 19: 488-499.

Cornwell, J.C. and M. S. Owens. 2000. Nitrogen cycling in Florida Bay mangrove environments: sediment-water exchange and denitrification. Final Report to South Florida Water Management District.

Cornwell, J. C., W. M. Kemp and T. M. Kana. 1999. Denitrification in coastal ecosystems: Environmental controls and aspects of spatial and temporal scaling. J. Aquat. Ecol. 33: 41-54.

Epping, E.H.G., A. Khalili and R. Thar. 1999. Photosynthesis and dynamics of oxygen consumption in a microbial mat as calculated from transient oxygen microprofiles. Limnol. Oceanogr. 44:1936-1948.

Erskine, J. M. and M. S. Koch. 2000. Sulfide effects on *Thalassia testudinum* carbon balance and adenylate energy charge. Aquatic Bot. 67: 275-285.

Fong, P, M. E. Jacobson, M. C. Mescher, D. Lirman and M. C. Harwell. 1997. Investigating the management potential of a seagrass model through sensitivity analysis and experiments. Ecol. Appl. 7: 300-315.

Fourqurean, J. W., J. C. Zieman, and G. Powell. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. Limnol and Oceanogr. 37: 162-171.

Fourqurean, J. W. and M. B. Robblee. 1999. Florida Bay: a history of recent ecological changes. Estuaries 22 (2B): 345-357.

Goodman. J., K. Moore, and W. Dennison. 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. Aquat. Bot. 50: 37-47.

Jensen, H. S., K. J. McGlathery, R. Marino and R. W. Howarth. 1998. Forms and availability of sediment phosphorus in carbonate sand of Bermuda seagrass beds. Limnol. Oceanogr. 43: 799-810.

Holmer, M. and S. L. Nielsen. 1997. Sediment sulfur dynamics related to biomass-density patterns in *Zostera marina* (eelgrass) beds. Mar. Ecol. Prog. Ser. 146: 163-171.

Kana, T.M. et al., 1994. Membrane inlet mass spectrometer for rapid high-precision determination of N_2, O_2, and Ar in environmental water samples. Anal. Chem. 66: 4166-4170.

Kana, T.M., M. B. Sullivan., J.C. Cornwell and , K. Groszkowski. 1998. Denitrification in estuarine sediments determined by membrane inlet mass spectrometry. Limnology and Oceanography, 42: 334-339.

Kemp, W.M., W.R. Boynton, R.R. Twilley, J.C. Stevenson, and L.G. Ward. 1984. Influences of submersed vascular plants on ecological processes in upper Chesapeake Bay, In V.S. Kennedy (ed.), Estuaries as filters. Academic Press, New York, pp. 367-394.

Kemp, W.M. and L. Murray. 1986. Oxygen release from roots of the submersed macrophyte, *Potamogeton perfoliatus* L.: Regulating factors and ecological implications. Aquatic Bot. 26:271-283.

Kemp, W. M., P. A. Sampou, J. M. Caffrey, M. Mayer, K. Henriksen and W. R. Boynton. 1990. Ammonium recycling versus denitrification in Chesapeake Bay sediments. Limnol. Oceanogr. 35: 1545-1563.

Kemp, W. M. 2000. Seagrass ecology and management: An introduction, pp. 1-8, In: S. Bortone (ed.) Seagrasses: Monitoring, ecology, physiology and management. CRC Press, Boca Raton, FL .

Kenworthy, W. J., J. Zieman, G. W. Thayer. 1982. Evidence for the influence of seagrasses on the benthic nitrogen cycle in a coastal plain estuary near Beaufort, North Carolina (USA). Oecologia. 54: 152-158.

Kenworthy, W. J. and G. W. Thayer. 1982. Production and decomposition of the roots and rhizomes of seagrasses, *Zostera marina* and *Thalassia testudinum* in temperate and subtropical marine ecosystems. Bull. Mar. Sci. 35: 364-379.

Koepfler, E. T., R. Benner, P. A Montagna. 1993. Variability of dissolved organic carbon in sediments of a seagrass bed and an unvegetated area within an estuary in southern Texas. Estuaries. 16: 391-404.

Koch, M. S., R. E. Benz and D. T. Rudnick. 2001. Solid-phase phosphorus pools in highly organic carbonate sediments of northeastern Florida Bay. Estuar. Coastal Shelf Sci. 52: 279-291.

Lapointe, B. E., D. Tomasko, and W. R. Matzie. 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. Bull. Mar. Sci. 54: 696-717.

Lee, K.-S. and K. H. Dunton. 1999. Inorganic nitrogen acquisition in the seagrass *Thalassia testudinum*: Development of a whole-plant nitrogen budget. Limnol. Oceanogr. 44: 1204-1215.

Lee, K.-S. and K. H. Dunton. 2000. Diurnal changes in pore water sulfide concentrations in the seagrass *Thalassia testudinum* beds: The effects of seagrasses on sulfide dynamics. J. Exp. Mar. Biol. Ecol. 255: 201-214.

Lubbers, L., W. R, Boynton and W. M. Kemp. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. Mar. Ecol. Progr. Ser. 65: 1-14.

McGlathery, K. J. R. Marino and R. W. Howarth. 1994. Variable rates of phosphate uptake by shallow marine carbonate sediments: Mechanisms and ecological significance. Biogeochemistry. 25: 127-146.

Parsons, T.R., Y. Maita, and C. M. Lalli. 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press, New York, 173 pp.

Patriquin, D. 1973. Estimation of growth rate, production and age of the marine angiosperm *Thalassia testudinum* Konig. Contr. Mar. Sci. 13: 111-123.

Risgaard-Petersen, N., N. Rysgaard,, L. P. Nielsen, and N. P. Revsbech. 1994. Diurnal variation of denitrification and nitrification in sediments colonized by benthic microphytes. Limnol. Oceanogr. 39: 573-579.

Risgaard-Petersen, N., T. Dalsgaard, S. Risgaard, P. B. Christensen, J. Borum, K. McGlathery, L. P. Nielsen. 1998. Nitrogen balance of a temperate eelgrass *Zostera marina* bed. Mar. Ecol. Prog. Ser. 174: 281-291.

Risgaard-Petersen, N. L. Ottosen. 2000. Nitrogen cycling in two temperate *Zostera marina* beds: seasonal variation. Mar. Ecol. Prog. Ser. 198: 93-107.

Robbins, J.A., 1978. Geochemical and geophysical applications of radioactive lead. In: J. O. Naraigu (ed.). The Biogeochemistry of Lead in the Environment. Elsevier, New York, pp. 285-405.

Robbins, J.A. et al., 2000. Time-averaged fluxes of lead and fallout radionuclides to sediments in Florida Bay. J. Geophy. Res. (Oceans), 105(C12): 28805-28821.

Rudnick, D. T., Z. Chen, D. L. Childers, J. N. Boyer, T. D. Fontaine. 1999. Phosphorus an nitrogen inputs to Florida Bay: the importance of the Everglades watershed. Estuaries. 22 (2B): 398-416.

Rudnick, D.T., S. Kelly, K. Picard, J.C. Cornwell and M.S. Owens. 1999. Benthic nutrient fluxes near Florida Bay's mangrove ecotone. Abstract, 1999 Florida Bay and Adjacent Marine Systems Science Conference. p. 102.

Rudnick, D.T., S. Kelly, C. Donovan, J.C. Cornwell, and M.S. Owens. 2001. Patterns of inorganic nutrient flux from Northern Florida Bay sediments. Abstract, 2001 Florida Bay Science Conference. p. 96.

Rysgaard, S. P. B. Christensen, and L. P. Nielsen. 1995. Seasonal variation in nitrification and denitrfication in estuarine sediment colonized by benthic microalgae and bioturbating infauna. Mar. Ecol. Prog. Ser. 126: 111-121.

Sundack, K., A. Miles, and E. Goransson. 2000. Nitrogen fluxes, denitrification and the role of microphytobenthos in microtidal shallow water sediments: An annual study. Mar. Ecol. Prog. Ser. 200:59-76.

Schubert, C.J. and Nielsen, B., 2000. Effects of decarbonation on $\delta^{13}C$ values in marine sediments. Mar. Chem. 72: 55-59.

Seitzinger, S.P., 1988. Denitrification in freshwater and coastal marine ecosystems: ecological and geochemical significance. Limnol. Oceanogr. 33: 702-724.

Short, F. T., M. Davis, R. Gibson, C. Zimmerman. 1985. Evidence for phosphorus limitation in carbonate sediments of the seagrass, *Syringodium filiforme*. Est. Coast. Shelf Sci. 20: 419-430.

Smith, E. M. and W. M. Kemp. 1995. Seasonal and regional variations in plankton community production and respiration for Chesapeake Bay. Mar. Ecol. Progr. Ser. 116: 217-231.

Thornton, D.C.O., G.J.C. Underwood and D.B. Nedwell. Effect of illumination and emersion period on the exchange of ammonium across the sediment-water interface. Mar. Ecol. Prog. Ser.. 184:11-20.

Tomasko, D. A. and B. E. Lapointe. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: Field observations and experimental studies. Mar. Ecol. Prog. Ser. 73: 9-17.

Van Heukelem, L., A. J. Lewitus, T. M. Kana, and N. E. Craft. 1994. Improved separations of phytoplankton pigments using temperature-controlled high performance liquid chromatography. Mar. Ecol. Prog. Ser. 114: 303-313.

Ward, L.G., W.M. Kemp and W.R. Boynton. 1984. The influence of water depth and submerged vascular plants on suspended particulates in a shallow estuarine embayment. Mar. Geol. 59:85-103.

Welsh, D. T., S. Bourques, R. de Wit, I. Auby. 1997. Effect of plant photosynthesis, carbon sources and ammonium availability on nitrogen fixation rates in the rhizosphere of *Zostera noltii*. Aquat. Microbial Ecol. 12: 285-290.

Welsh, D.T., 2000. Nitrogen fixation in seagrass meadows: Regulation, plant-bacteria interactions and significance to primary productivity. Ecol. Letters 3: 58-71.

Ziegler, S., and R. Benner. 1999. Dissolved organic carbon cycling in a subtropical seagrass-dominated lagoon. Mar. Ecol. Prog. Ser. 180: 149-160.

Zieman, J. C., J. W. Fourqurean and R. Iverson. 1989. Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. Bull. Mar. Sci. 44: 292-311.

Zieman, J. C., J. W. Fourqurean and T. A. Frankovich. 1999. Seagrass die-off in Florida Bay: Long-term trends in abundance and growth of Turtle Grass, *Thalassia testudinum*. Estuaries. 22 (2B): 460-470.

Appendix I. Solid Phase Analyses

Table I-1. Vertical profiles of water content and ^{210}Pb.

This table shows data from six long cores collected in August 1999 for solid phase analysis and ^{210}Pb dating. Percent water was determined by drying at 65 C. The dry content was determined by measuring the volume of collected sediment, then determining the dry mass for a given volume. Cumulative mass is the sum of mass at the bottom of each succeeding sediment section, while mid-point mass is the cumulative mass at the middle of each section. The ^{210}Pb activity is determined by alpha counting of ^{210}Po; secular equilibrium is assumed.

Table I-2. Solid phase nutrient profiles.

This table presents nutrient data from the long cores collected in August 1999 (see Table I-1). Total P and inorganic P are determined by 1 N HCl extractions of ashed and unashed samples. Organic C and total N in the 0-2 cm sections are determined by CHN analyzer after acidification to remove carbonate minerals. The total N in the 8-10 and 18-20 cm sections is determined by CHN analyzer; samples were not acidified.

Table I-1.

Location	Depth	Water Content	Dry Content	Cumulative Mass	Mid-Point Mass	^{210}Pb Activity
	cm	%	g cm^{-3}	g cm^{-2}	g cm^{-2}	dpm g^{-1}
Rabbit Key	0-2	64.6	0.452	0.90	0.45	2.80
	2-4	63.5	0.476	1.86	1.38	3.17
	4-6	64.1	0.462	2.78	2.32	3.50
	6-8	65.5	0.438	3.66	3.22	3.13
	8-10	62.6	0.470	4.60	4.13	3.47
	10-12	61.1	0.511	5.62	5.11	3.29
	12-14	63.0	0.481	6.58	6.10	
	14-16	64.4	0.445	7.47	7.02	2.67
	16-18	68.2	0.398	8.26	7.87	
	18-20	68.4	0.393	9.05	8.66	2.27
	20-25	66.7	0.400	11.05	10.05	2.00
	25-27	70.6	0.337	11.72	11.39	1.76
Little Madeira	0-2	57.6	0.568	1.14	0.57	4.90
	2-4	55.1	0.684	2.50	1.82	3.39
	4-6	52.8	0.729	3.96	3.23	4.21
	6-8	53.1	0.668	5.30	4.63	3.69
	8-10	44.5	1.235	7.77	6.53	3.52
	10-12	45.1	0.872	9.51	8.64	2.31
	12-14	43.7	0.847	11.21	10.36	
	14-16	43.1	0.932	13.07	12.14	2.75
	16-18	43.3	2.758	18.59	15.83	
	18-20	42.6	0.921	20.43	19.51	2.19
	20-25	42.7	0.800	24.43	22.43	2.60
	25-30	38.5	0.933	29.09	26.76	2.41
Sunset Cove	0-2	92.4	0.078	0.16	0.08	3.76
	2-4	90.2	0.100	0.36	0.26	
	4-6	89.6	0.109	0.57	0.46	5.21
	6-8	88.6	0.118	0.81	0.69	
	8-10	87.5	0.135	1.08	0.95	5.05
	10-12	84.5	0.167	1.41	1.25	
	12-14	86.8	0.140	1.69	1.55	
	14-16	83.9	0.170	2.03	1.86	4.69
	16-18	85.6	0.154	2.34	2.19	
	18-20	83.8	0.176	2.70	2.52	5.36
	20-25	68.0	0.367	4.53	3.61	
	25-30	51.9	0.601	7.54	6.03	2.12
	30-35	68.1	0.396	9.52	8.53	2.14

Table I-1 continued.

Location	Depth	Water Content	Dry Content	Cumulative Mass	Mid-Point Mass	^{210}Pb Activity
	cm	%	g cm^{-3}	g cm^{-2}	g cm^{-2}	dpm g^{-1}
Rankin Bay	0-2	84.8	0.164	0.33	0.16	4.76
	2-4	78.9	0.239	0.81	0.57	3.65
	4-6	76.6	0.272	1.35	1.08	4.79
	6-8	68.8	0.368	2.09	1.72	3.46
	8-10	59.5	0.505	3.10	2.59	3.31
	10-12	62.0	0.502	4.10	3.60	2.67
	12-14	61.7	0.494	5.09	4.59	2.22
	14-16	56.5	0.544	6.17	5.63	2.09
	16-18	58.2	0.555	7.28	6.73	
	18-20	50.3	0.677	8.64	7.96	2.05
	20-25	49.7	0.694	12.11	10.37	
	25-30	52.4	0.640	15.31	13.71	1.84
	30-35	46.5	0.729	18.95	17.13	
	35-40	45.8	0.718	22.55	20.75	1.68
	40-45	48.9	0.713	26.11	24.33	2.05
Johnson Key	0-2	83.2	0.187	0.37	0.19	4.19
	2-4	79.3	0.234	0.84	0.61	3.61
	4-6	63.0	0.455	1.75	1.30	3.87
	6-8	75.5	0.286	2.32	2.04	4.06
	8-10	70.4	0.361	3.05	2.68	4.04
	10-12	68.6	0.376	3.80	3.42	3.15
	12-14	73.2	0.314	4.43	4.11	
	14-16	75.4	0.280	4.99	4.71	3.57
	16-18	74.6	0.291	5.57	5.28	
	18-20	66.6	0.402	6.37	5.97	2.32
	20-25	49.9	0.678	9.76	8.07	1.57
	25-30	46.3	0.743	13.48	11.62	1.61
	30-35	37.8	0.954	18.25	15.86	1.25
Crocodile Point	0-2	56.9	0.570	1.14	0.57	3.81
	2-4	51.8	0.646	2.43	1.79	2.83
	4-6	49.6	0.674	3.73	3.08	3.90
	4-6 r	53.4	0.618			
	6-8	45.6	0.757	5.24	4.48	2.50
	8-10	50.2	0.683	6.61	5.92	3.14
	10-12	52.4	0.628	7.86	7.23	2.38
	12-14	42.1	0.789	9.44	8.65	2.15
	14-16	40.9	0.807	11.05	10.25	2.01
	16-18	44.0	0.828	12.71	11.88	
	18-20	48.5	0.692	14.09	13.40	1.84
	20-25	45.5	0.777	17.98	16.04	
	25-30	47.0	0.731	21.64	19.81	1.85
	30-35	41.3	0.880	26.04	23.84	1.78

Table I-2.

Location	Depth	Total P	Inorganic P	Organic C	Total N	Location	Depth	Total P	Inorganic P	Organic C	Total N
	cm	μg g^{-1}	μg g^{-1}	mg g^{-1}	mg g^{-1}		cm	μg g^{-1}	μg g^{-1}	mg g^{-1}	mg g^{-1}
Rabbit Key	0-2	247.4	156.3	39.7	4.9	Rankin Bay	0-2	275.7	160.4	42.7	5.1
	2-4	262.2	164.5				2-4	266.7	143.6		
	4-6	251.8	152.0				4-6	271.1	160.4		
	6-8	258.0	149.7				6-8	236.8	142.2		
	8-10	260.4	125.6		6.0		8-10	178.9	106.3		3.6
	10-12	205.0	104.0				10-12	221.6	128.4		
	12-14	166.8	93.9				12-14	243.2	134.5		
	14-16	194.5	90.2				14-16	213.0	116.6		
	16-18	186.7	76.4				16-18	206.7	120.7		
	18-20	185.7	86.0		7.1		18-20	174.6	95.9		2.8
	20-25	177.6	74.9				20-25	224.7	125.0		
	25-27	165.3	69.7				25-30	230.8	125.3		
							30-35	217.8	125.4		
Little Madeira	0-2	95.5	47.4	22.9	2.2		35-40	213.5	121.6		
	2-4	84.7	49.5				40-45	256.5	153.3		
	4-6	73.9	39.6								
	6-8	66.8	38.3			Johnson Key	0-2	419.6	220.2	36.4	4.6
	8-10	50.9	25.0		2.0		2-4	404.1	219.7		
	10-12	42.5	23.2				4-6				
	12-14	35.5	17.1				6-8	412.3	202.9		
	14-16	36.3	17.7				8-10	406.1	200.7		6.1
	16-18	41.8	16.6				10-12	374.4	214.5		
	18-20	27.3	18.8		1.6		12-14	454.6	252.1		
	20-25	28.4	17.6				14-16	438.5	243.5		
	25-30	32.5	15.2				16-18	409.4	243.7		
							18-20	449.0	370.1		
Sunset Cove	0-2	248.9	109.8	68.6	8.6		20-25	199.9	160.9		
	2-4	341.3	151.1				25-30	199.8	163.1		
	4-6	331.9	158.2				30-35	131.4	100.6		
	6-8	372.5	171.7								
	8-10	333.8	173.3		11.7	Crocodile Point	0-2	114.6	76.5	21.9	2.8
	10-12	309.8	151.8				2-4	86.6	69.0		
	12-14	347.3	138.4				4-6	100.4	70.0		
	14-16	285.6	117.7				6-8	96.6	63.9		
	16-18	306.8	120.2				8-10	63.0	42.6		3.4
	18-20	286.5	106.1		10.7		10-12	69.7	65.8		
	20-25	196.0	63.9				12-14	76.9	45.6		
	25-30	95.4	21.7				14-16	65.0	29.3		
	30-35	102.6	38.5				16-18	49.2	42.5		
							18-20	87.1	61.5		2.8
							20-25	100.7	49.5		
							25-30	103.0	49.6		
							30-35	84.4	45.5		

Appendix II. Summary of Flux Data

See Methods Section for details of analyses.

Table II-1. Net sediment-water fluxes of O_2, N_2 and NH_4^+ in cores.

Station	Vegetated?	Illumination	August O_2 Flux	March O_2 Flux	August N_2-N Flux	March N_2-N Flux	August NH_4^+ Flux	March NH_4^+ Flux
			$\mu mol\ m^{-2}\ h^{-1}$					
Rabbit Key	Vegetated	Dark	-2,626 ± 483	-847 ± 386	116 ± 38	107 ± 33	118 ± 34	2 ± 22
		Light	-1,260 ± 157	-298 ± 199	68 ± 93	28 ± 71	219 ± 12	11 ± 36
Johnson Key	Vegetated	Dark	-2,176 ± 979	-973	169 ± 3	62 ± 48	207 ± 87	-35
		Light	2,442 ± 3,394	-685 ± 685	21	121 ± 160	-50 ± 113	0 ± 0
	Unvegetated	Dark	-1,268 ± 206	-1,338	94 ± 23	-21 ± 21	-29	0 ± 20
		Light	4,799 ± 590	1,282 ± 1,423	0 ± 0	45 ± 85	-118 ± 15	8 ± 8
Rankin Bay	Vegetated	Dark	-1,521	-1,835	65	88	29	0
		Light	3,490	630 ± 1,030	-258 ± 118	11 ± 78	-95 ± 23	8
	Unvegetated	Dark	-1,947 ± 228	-1,418 ± 152	245	94 ± 20	-18 ± 16	19 ± 19
		Light	3,259 ± 1,339	107 ± 434	-286 ± 223	54	-87 ± 17	36 ± 21
Terrapin	Vegetated	Dark	-1,645 ± 101	nd	0 ± 0	Nd	71 ± 56	Nd
		Light	-753 ± 44	nd	107 ± 78	Nd	121	Nd
	Unvegetated	Dark	-1,621 ± 29	nd	0 ± 0	Nd	57 ± 70	Nd
		Light	159 ± 759	nd	33	Nd	33 ± 121	Nd
Little Madeira	Vegetated	Dark	-1,872 ± 62	-2,456 ± 658	260 ± 7	0 ± 0	-72 ± 36	-14 ± 68
		Light	-2,000 ± 669	0 ± 0	236	0 ± 0	-67 ± 85	-18 ± 18
	Unvegetated	Dark	-2,062 ± 292	-925 ± 68	183 ± 42	0 ± 0	-83 ± 65	34 ± 70
		Light	1,518 ± 592	0 ± 0	-291 ± 233	0 ± 0	-105 ± 63	29 ± 29
Sunset Cove	Vegetated	Dark	-1,859	-3,201 ± 891	100	81 ± 101	-54 ± 2	0 ± 0
		Light	-25	-135 ± 135	0 ± 0	-121 ± 69	45 ± 54	2 ± 35
	Unvegetated	Dark	-2,397 ± 25	-4,106 ± 768	162 ± 3	170 ± 48	-51	100 ± 100
		Light	7,541 ± 362	4,784 ± 751	-1,455 ± 244	-166 ± 10	-170 ± 17	-24 ± 48

Appendix III. Sediment Pore Water Data

Table III-1. August 1999 Pore Water Data.

Table III-2. March 2000 Pore Water Data.

Pore water was obtained via centrifugation. Where data are missing, there was an insufficient volume of water was available for analysis. Low water recoveries were generally observed in deeper sediment sections that consisted of very coarse-grained shell hash.

Table III-1. August 1999 Pore Water Data.

	Depth	SRP	NH_4^+	H_2S
Little Madiera Vegetated	0-2	4.9	90.1	387
	2-4	1.8	331.3	1191
	6-8	2.7		1300
	14-16			
Little Madiera Unvegetated	0-2	0.5	35.2	29
	2-4	1.1	35.2	10
	6-8	1.1	264.0	10
	14-16	1.1	204.3	98
Rankin Vegetated	0-2	0.5	75.8	140
	2-4	1.1	288.3	436
	6-8	1.1	189.4	507
	14-16	1.1	177.5	393
Rankin B. unveg	0-2	0.6	26.8	70
	2-4	1.1	25.6	137
	6-8	1.1	261.0	1216
	14-16	1.3	864.0	723
Sunset C. veg	0-2	4.9	32.8	65
	2-4	1.1	51.9	132
	6-8	1.1	287.9	1037
	14-16	1.3	284.9	728
Sunset C. unveg	0-2	0.4	59.0	190
	2-4	0.8	69.8	141
	6-8	1.1	183.4	254
	14-16	1.5	249.1	128

	Depth	SRP	NH_4^+	H_2S
Johnson Vegetated	0-2	4.9	28.0	23
	2-4	1.1	92.5	226
	6-8	1.1	117.7	221
	14-16	1.5	144.6	158
Johnson Unvegetated	0-2	0.6	14.9	138
	2-4	1.3	74.6	333
	6-8	1.3	168.5	405
	14-16	1.1	189.4	158
Rabbit Vegetated	0-2	0.8	1601.8	83
	2-4	1.1	265.6	267
	6-8		562.5	
	14-16			
Crocodile Point Vegetated	0-2	3.5	110.4	10
	2-4	1.3	125.9	94
	6-8	1.3	210.3	76
	14-16	1.3	108.8	143
Crocodile Point Unvegetated	0-2	0.9	269.2	863
	2-4	1.8	721.7	1393
	6-8			
	14-16			

Table III-2. March 2000 Pore Water Data.

	Depth	SRP	NH_4^+	H_2S
Little Madiera Vegetated	0-2	0.1	36.2	8
	2-4	0.2	48.5	7
	6-8			
	14-16			
Little M. unveg	0-2	0.3	27.2	8
	2-4	0.3	53.0	10
	6-8	0.2	65.2	5
Rankin B. veg	0-2	0.4	152.6	127
	2-4	1.6	738.4	484
	6-8		502.0	
	14-16		216.4	
Rankin B. unveg	0-2	0.5	241.1	291
	2-4		539.0	735
	6-8			
	14-16			
Sunset C. veg	0-2	0.2		5
	2-4	0.2	17.1	24
	6-8	1.2	104.4	918
	10-12	1.5	311.6	863
Sunset C. unveg	0-2	0.6	161.6	577
	2-4	1.3	273.6	878
	6-8	1.7	672.8	1126
	14-16	1.8	913.6	748

	Depth	SRP	NH_4^+	H_2S
Johnson veg	0-2	1.4	29.5	83
	2-4	0.2	49.6	104
	6-8	0.3	70.8	265
	14-16	0.1	68.0	24
Johnson unveg	0-2	0.2	36.2	26
	2-4	0.1	87.7	83
	6-8	0.1	115.6	80
	14-16	0.3	73.6	8
Rabbit	0-2	0.3	44.0	7
	2-4	1.0	42.9	31
	6-8		56.8	34
	14-16			

Figure Legends

Figure 1. Map of study sites

Figure 2. Pb-210 profiles.

Figure 3. Dark sediment oxygen fluxes for vegetated and unvegetated sediments during August 1999 and March 2000. The error bars represent ranges of duplicate cores.

Figure 4. Light sediment oxygen fluxes for vegetated and unvegetated sediments during August 1999 and March 2000. The error bars represent ranges of duplicate cores.

Figure 5. Dark N_2-N fluxes for vegetated and unvegetated sediments during August 1999 and March 2000. The error bars represent ranges of duplicate cores.

Figure 6. Light N_2-N fluxes for vegetated and unvegetated sediments during August 1999 and March 2000. The error bars represent duplicate cores. Data for August Sunset Cove unvegetated cores did not scale with other data; rates are $-1{,}455 \pm 245$ μmol N_2-N m^{-2} h^{-1}.

Figure 7. Dark NH_4^+ fluxes for vegetated and unvegetated sediments during August 1999 and March 2000. The error bars represent duplicate cores.

Figure 8. Light NH_4^+ fluxes for vegetated and unvegetated sediments during August 1999 and March 2000. The error bars represent duplicate cores.

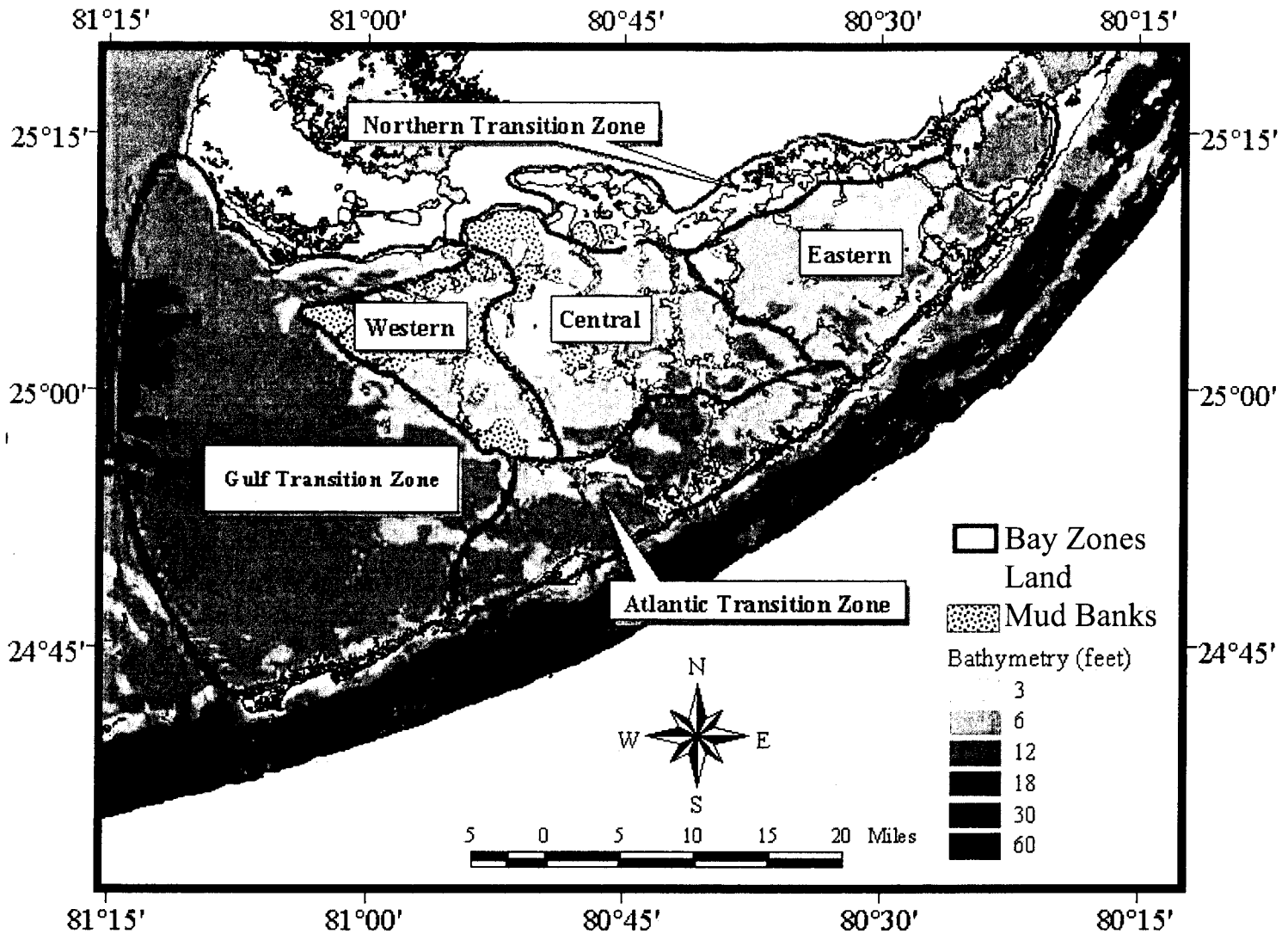
Figure 9. Gross oxygen production as a function of chlorophyll-*a*, separated into months and treatments. The production is calculated at the difference between light O_2 fluxes and dark O_2 fluxes. For the August and March unvegetated flux cores, a significant ($p < 0.01$) positive correlation was calculated.

Figure 10. Dark versus light O_2 fluxes. Given is 1:1 line for dark and light fluxes. The only significant correlation is for March unvegetated sediments ($r = 0.69$, $df = 8$, $p < 0.05$)

Figure 11. Sediment-water exchange of N_2 versus sediment chlorophyll-*a* under illuminated conditions. For August and March unvegetated sediments, N_2-N fluxes are significantly correlated ($p < 0.01$) with chlorophyll-*a* (Aug, $r = 0.98$; Mar, $r = 0.86$).

Figure 12. Sediment-water exchange of NH_4^+ as a function of chlorophyll a concentration. All NH_4^+ and chlorophyll-*a* data are significantly correlated ($p < 0.01$) except for the March vegetated dark data.

Figure 13. Nitrogen demand versus measured sources of N supply. Nitrogen demand was calculated from gross O_2 production rates, dividing them by 6.25. The nitrogen supply is the net N flux of the sediment plus N inputs from decomposition. Both months have a significant relationship ($p < 0.01$).



1. **Rabbit Key**
2. **Johnson Key**
3. **Rankin Bay**
4. **Terrapin Bay**
5. **Little Madeira Bay**
6. **Sunset Cove**

Figure 1

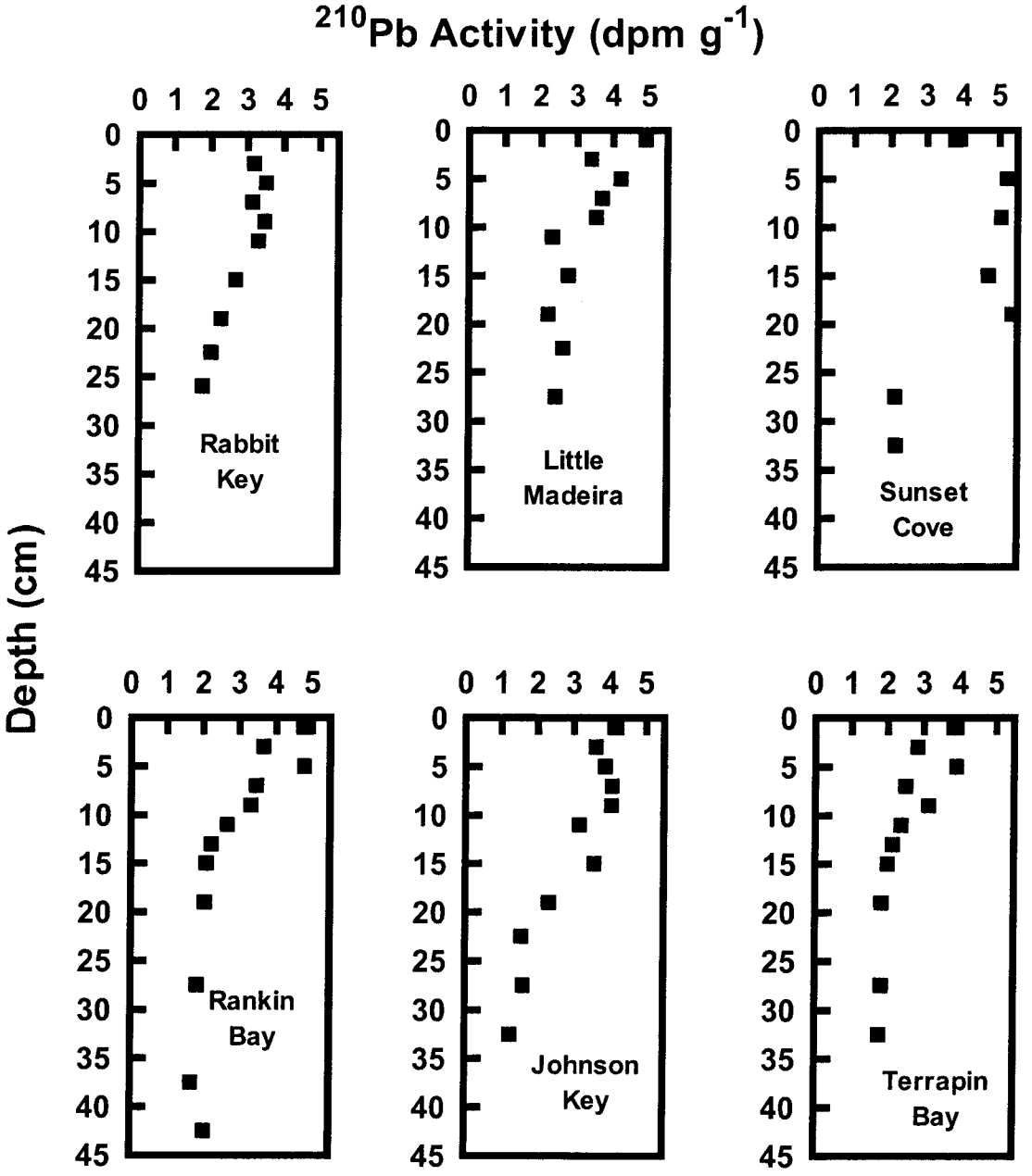

^{210}Pb Activity (dpm g^{-1})
Depth (cm)
0 1 2 3 4 5
0 5 10 15 20 25 30 35 40 45
Rabbit Key
Little Madeira
Sunset Cove
Rankin Bay
Johnson Key
Terrapin Bay

Figure 2.

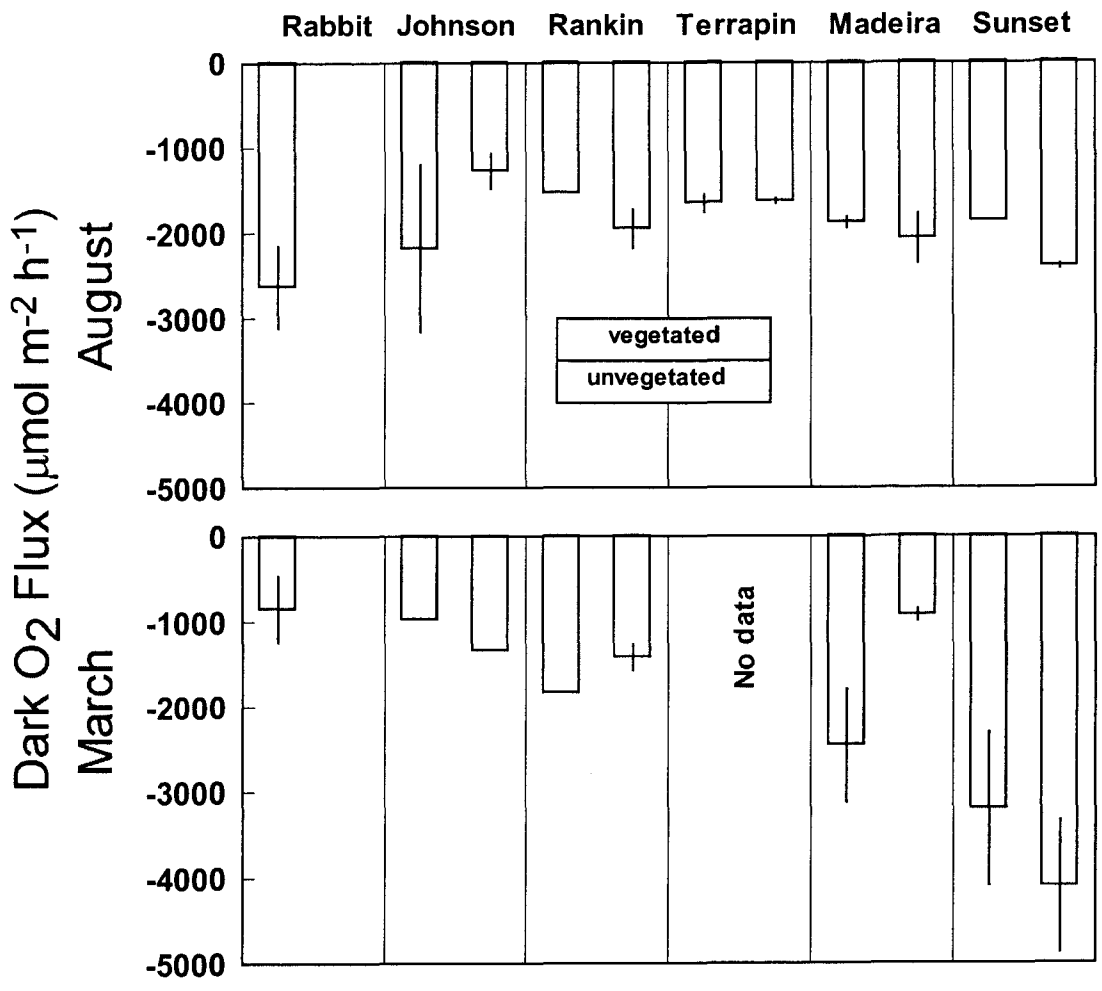

Rabbit
Johnson
Rankin
Terrapin
Madeira
Sunset
0
-1000
-2000
-3000
-4000
-5000
vegetated
unvegetated
August
March
Dark O2 Flux (μmol m-2 h-1)
No data

Figure 3.

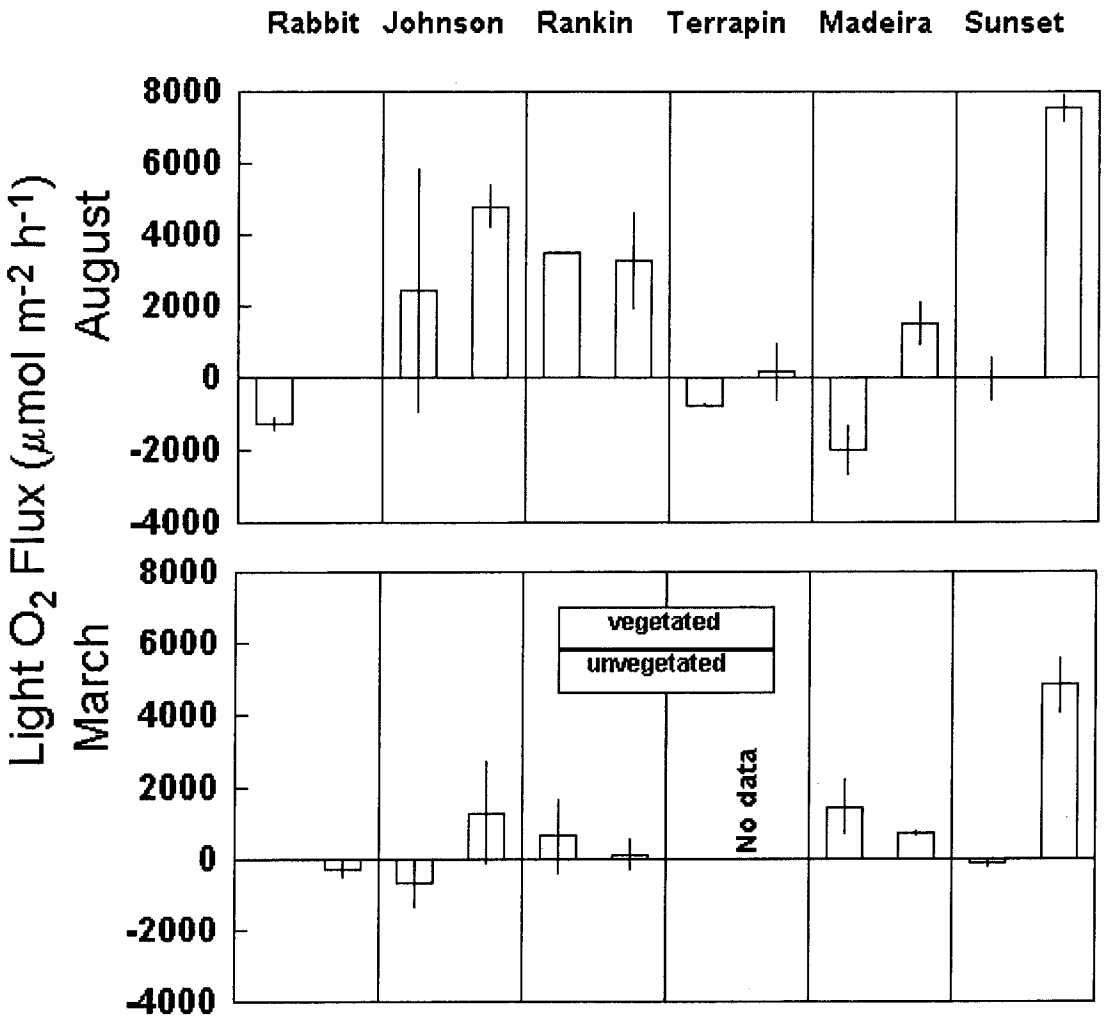

Rabbit
Johnson
Rankin
Terrapin
Madeira
Sunset
Light O_2 Flux (μmol m^{-2} h^{-1})
August
March
8000
6000
4000
2000
0
-2000
-4000
vegetated
unvegetated
No data

Figure 4.

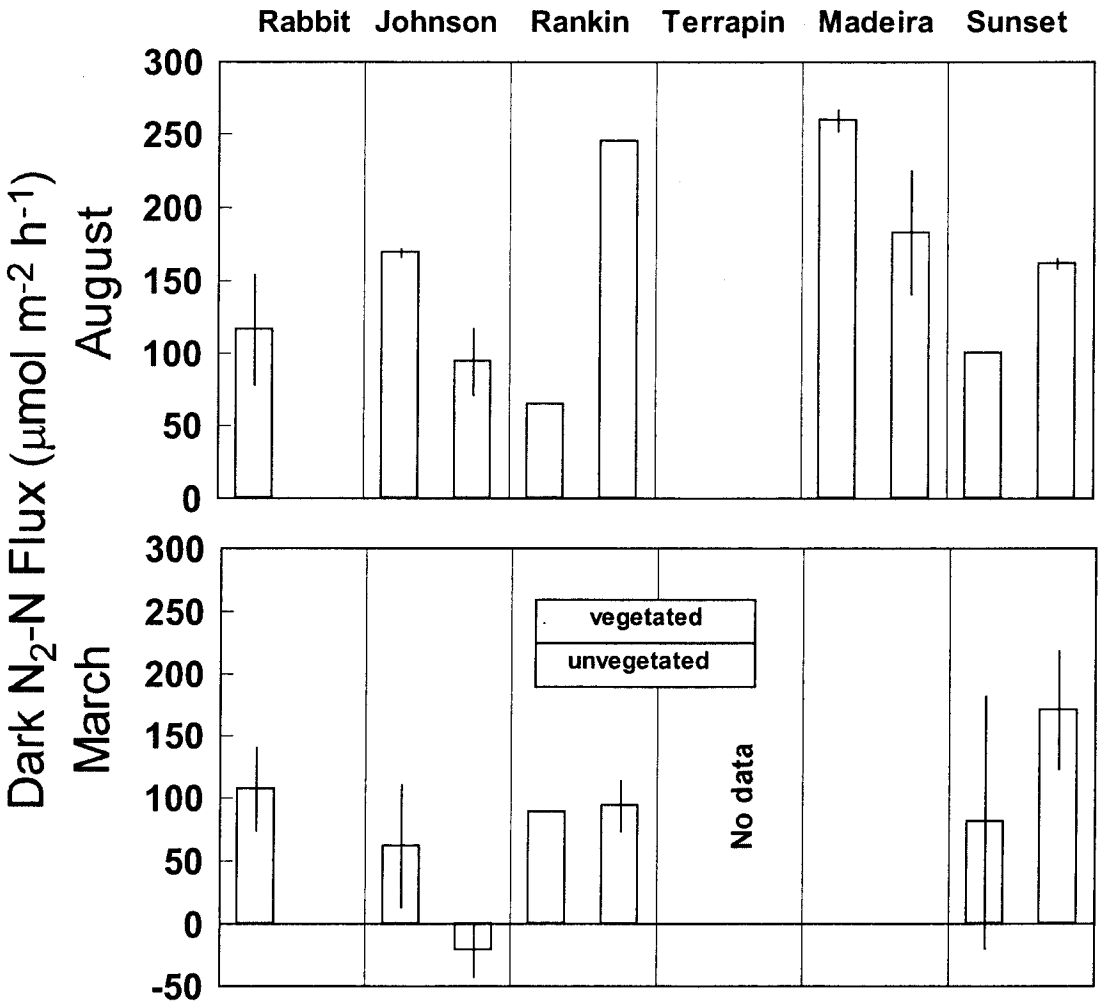

Rabbit
Johnson
Rankin
Terrapin
Madeira
Sunset
Dark N_2-N Flux (μmol m^{-2} h^{-1})
August
March
300
250
200
150
100
50
0
-50
vegetated
unvegetated
No data

Figure 5.

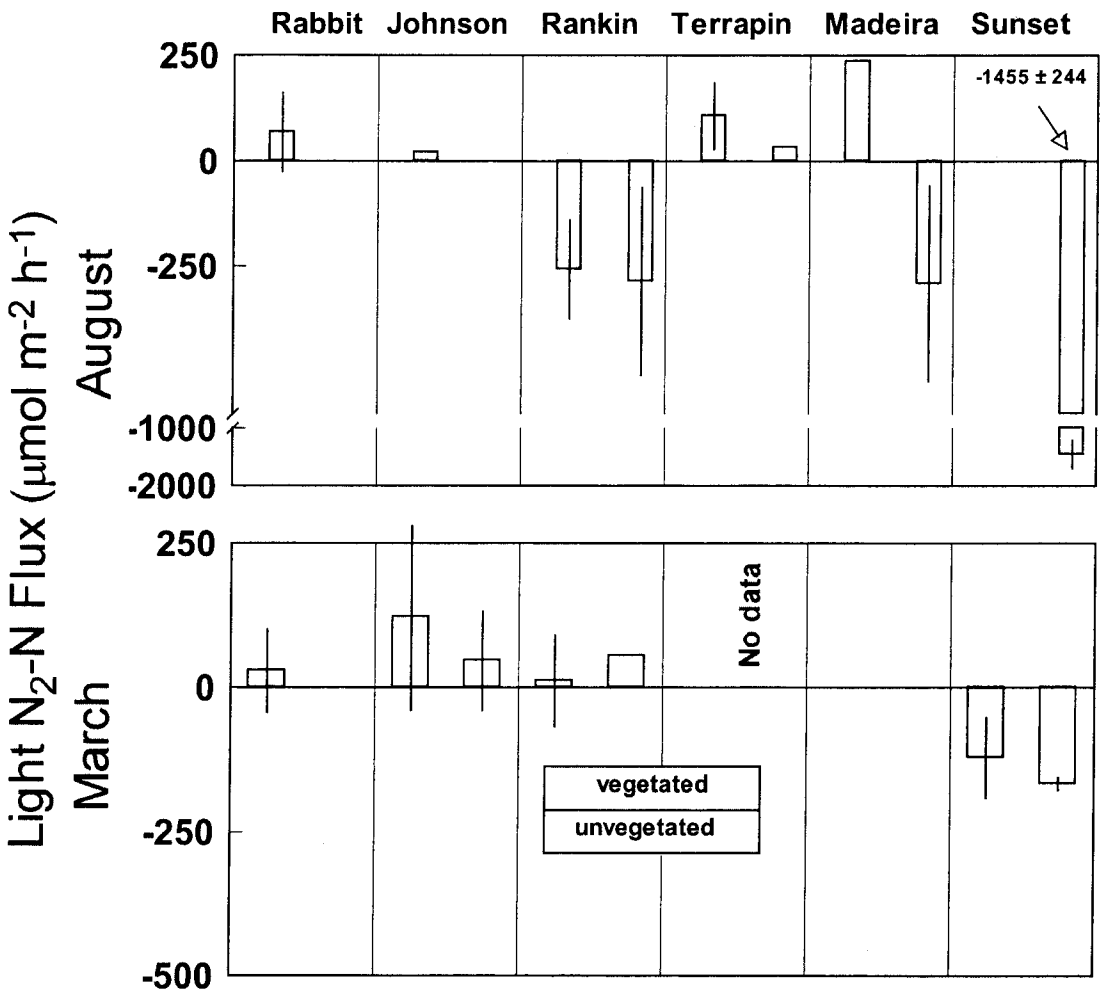

Rabbit
Johnson
Rankin
Terrapin
Madeira
Sunset
250
0
-250
-1000
-2000
-1455 ± 244
August
March
Light N_2-N Flux (µmol m^{-2} h^{-1})
250
0
-250
-500
No data
vegetated
unvegetated

Figure 6

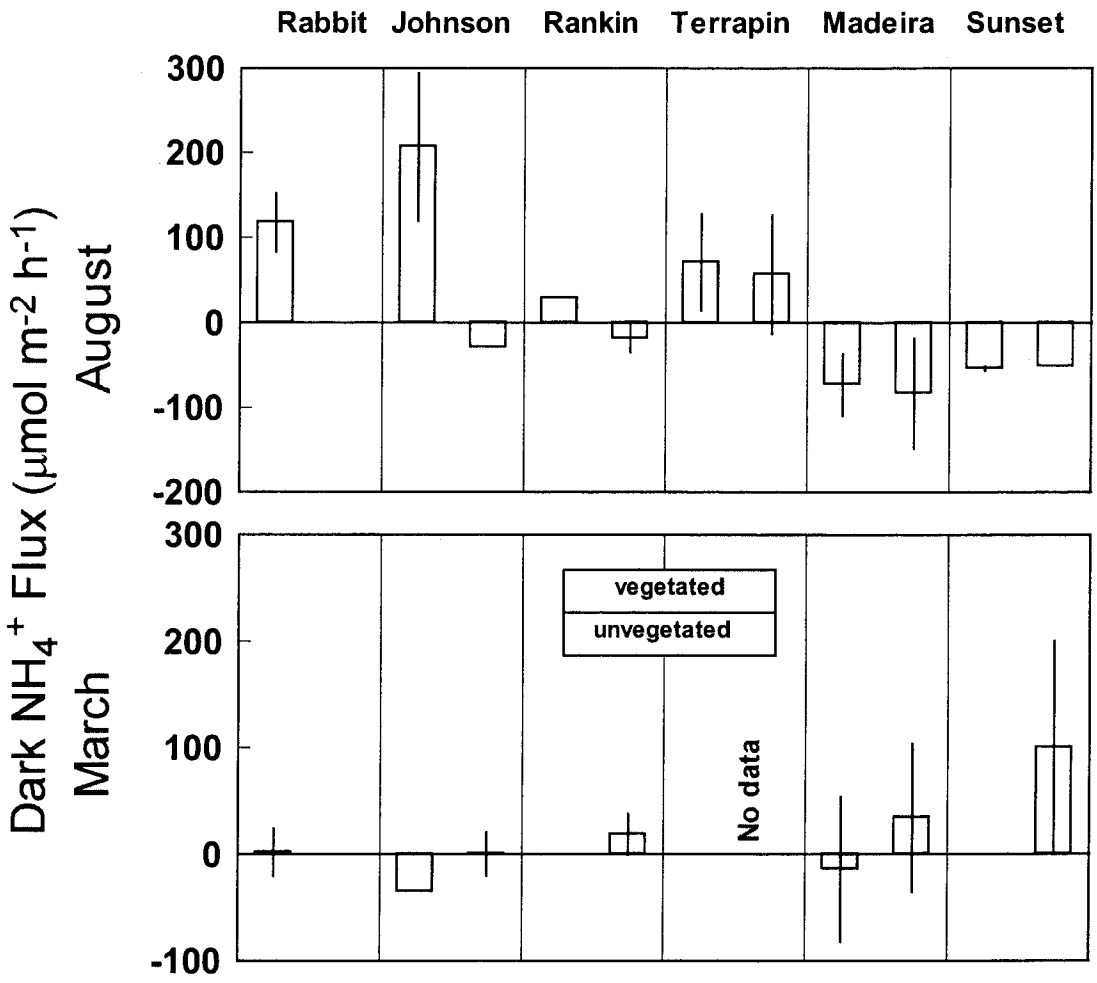

Rabbit
Johnson
Rankin
Terrapin
Madeira
Sunset
300
200
100
0
-100
-200
Dark NH_4^+ Flux (μmol m^{-2} h^{-1})
August
March
vegetated
unvegetated
No data

Figure 7

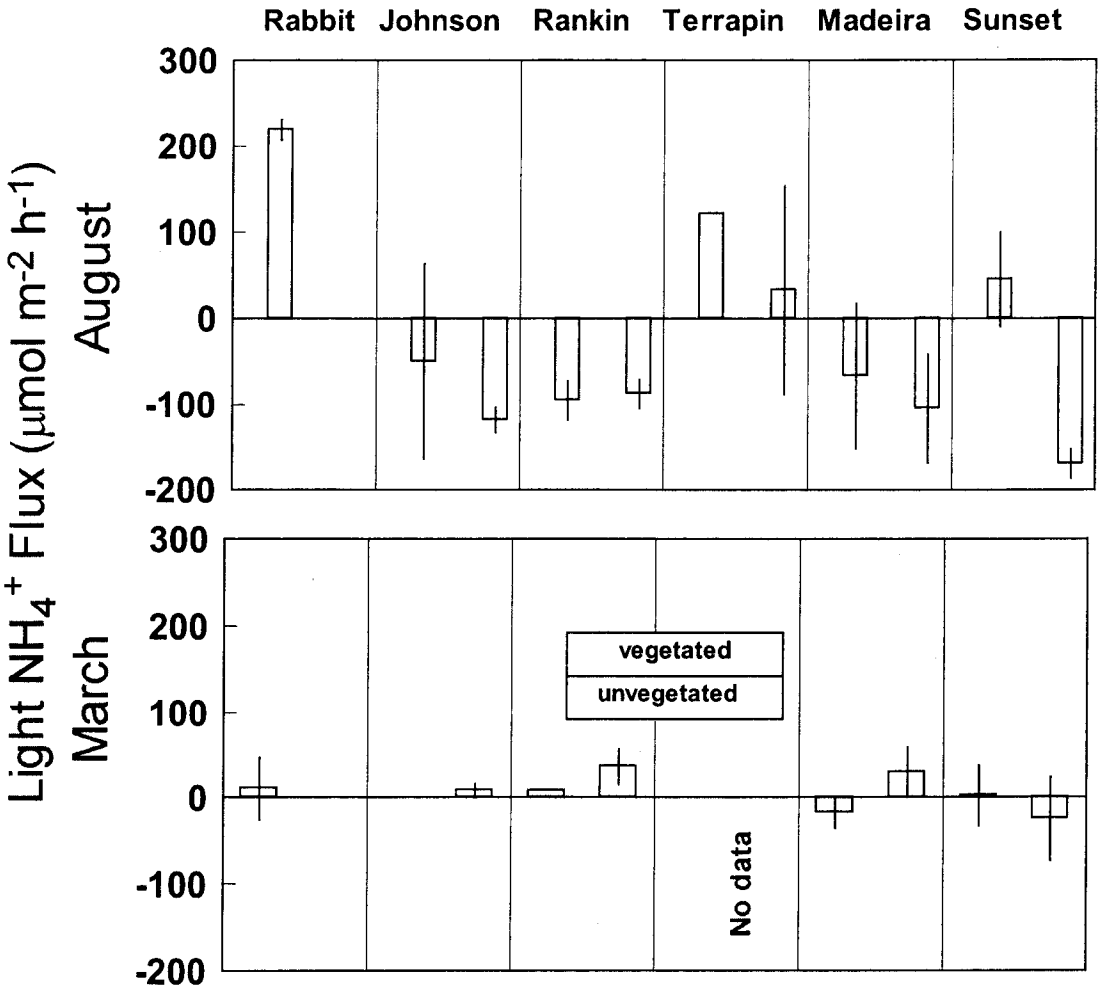

Rabbit
Johnson
Rankin
Terrapin
Madeira
Sunset
300
200
100
0
-100
-200
Light NH_4^+ Flux (μmol m^{-2} h^{-1})
August
March
vegetated
unvegetated
No data

Figure 8

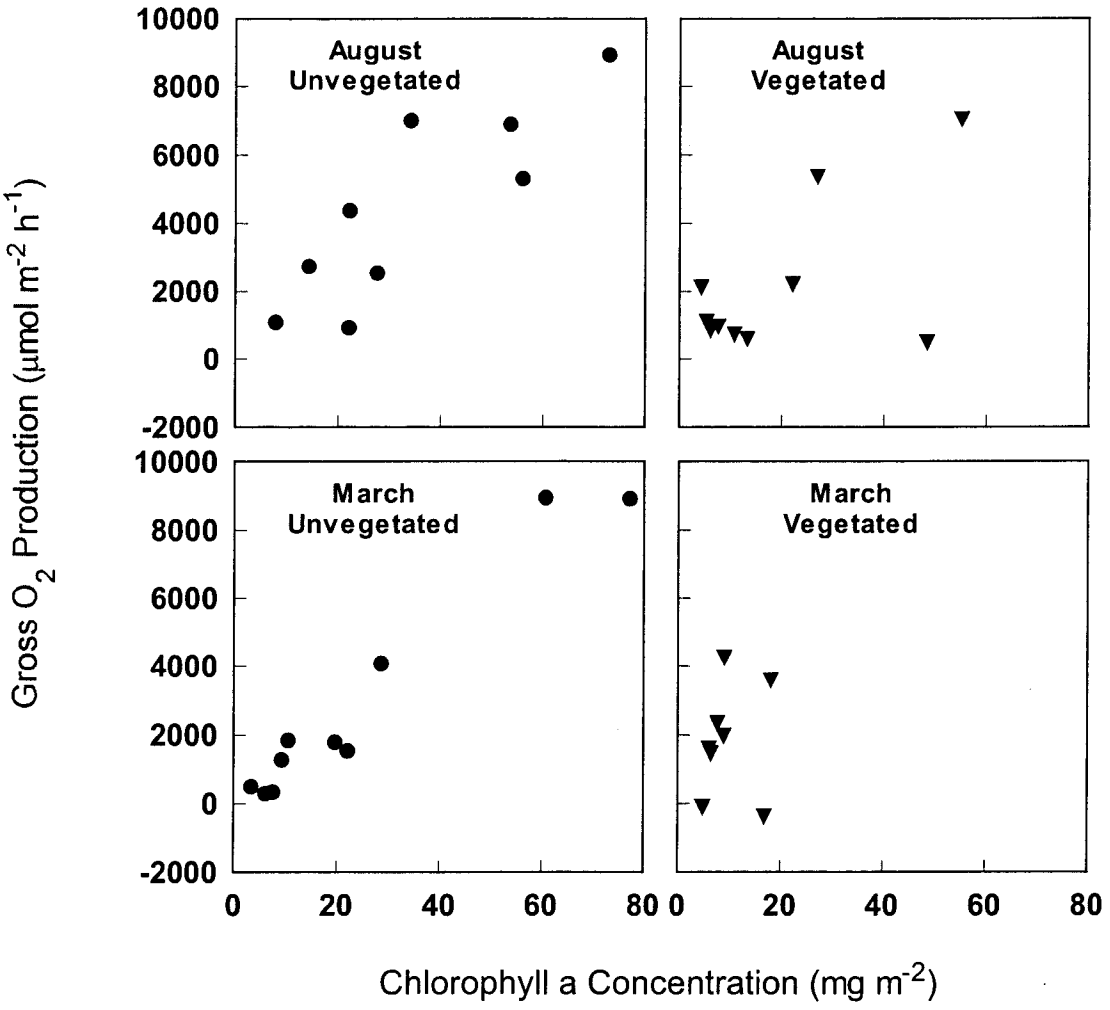

August
Unvegetated
August
Vegetated
March
Unvegetated
March
Vegetated
10000
8000
6000
4000
2000
0
-2000
0
20
40
60
80
Gross O_2 Production (µmol m^{-2} h^{-1})
Chlorophyll a Concentration (mg m^{-2})

Figure 9

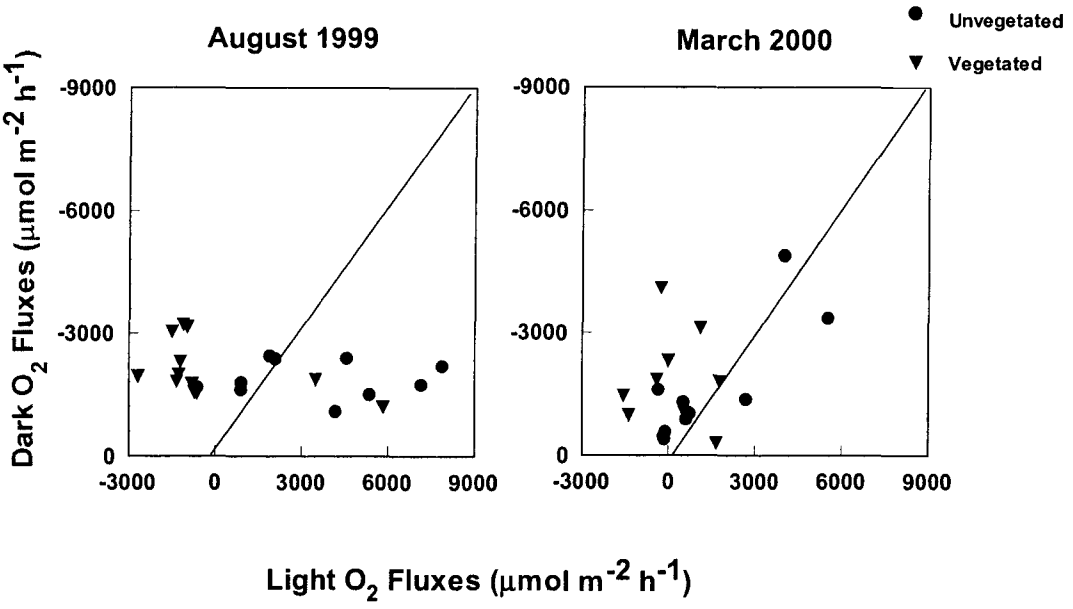

August 1999
March 2000
Unvegetated
Vegetated
Dark O_2 Fluxes (μmol m^{-2} h^{-1})
-9000
-6000
-3000
0
-3000
0
3000
6000
9000
Light O_2 Fluxes (μmol m^{-2} h^{-1})

Figure 10

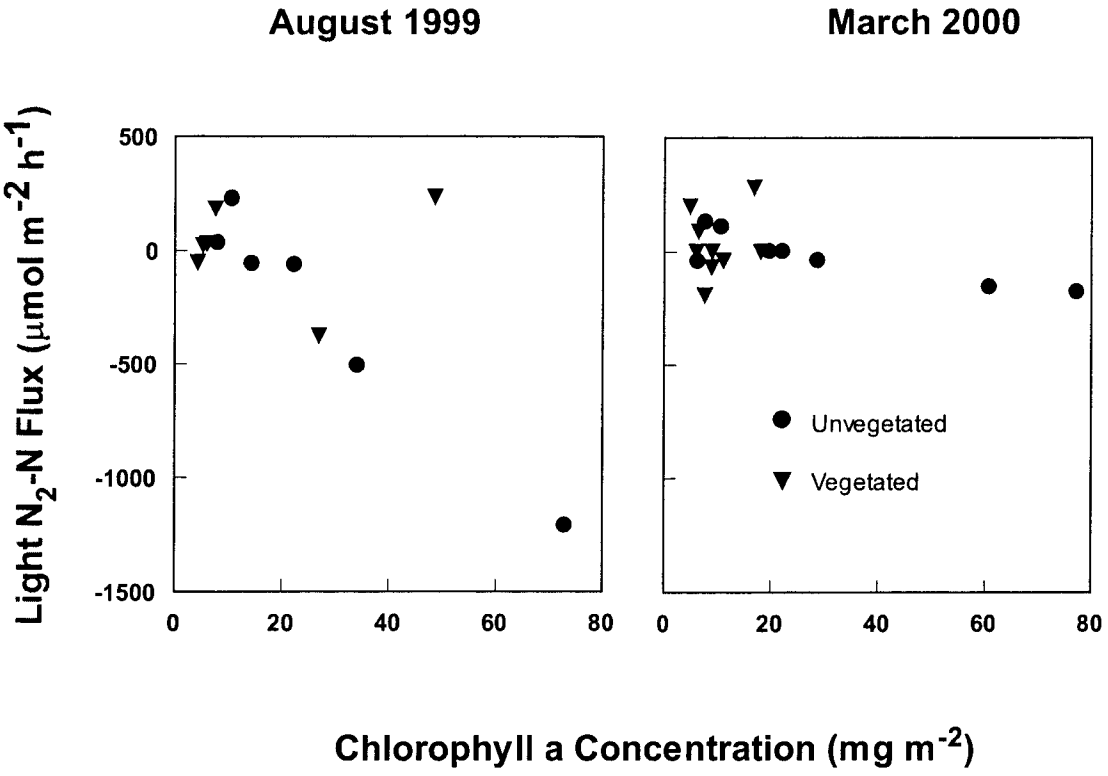

August 1999
March 2000
Light N_2-N Flux (μmol m^{-2} h^{-1})
500
0
-500
-1000
-1500
0
20
40
60
80
Unvegetated
Vegetated
Chlorophyll a Concentration (mg m^{-2})

Figure 11

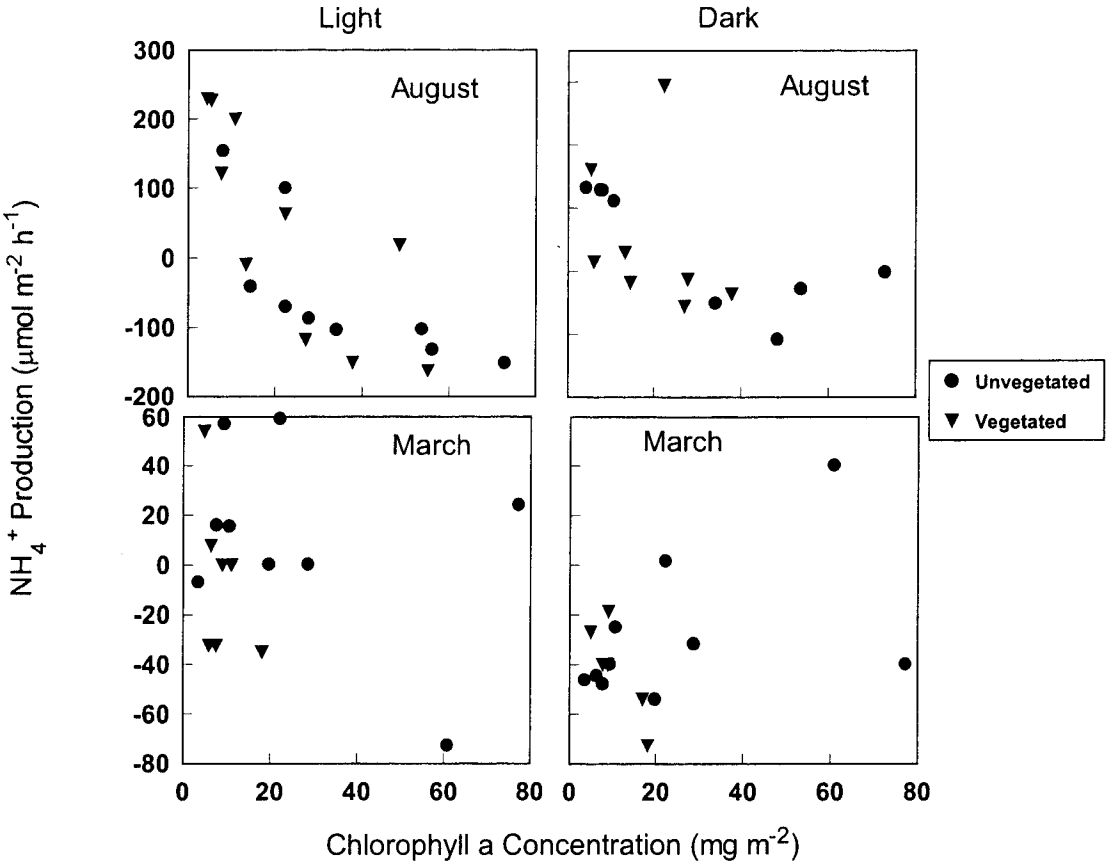

Light
Dark
August
August
March
March
300
200
100
0
-100
-200
60
40
20
0
-20
-40
-60
-80
0
20
40
60
80
NH_4^+ Production (µmol m^{-2} h^{-1})
Chlorophyll a Concentration (mg m^{-2})
Unvegetated
Vegetated

Figure 12

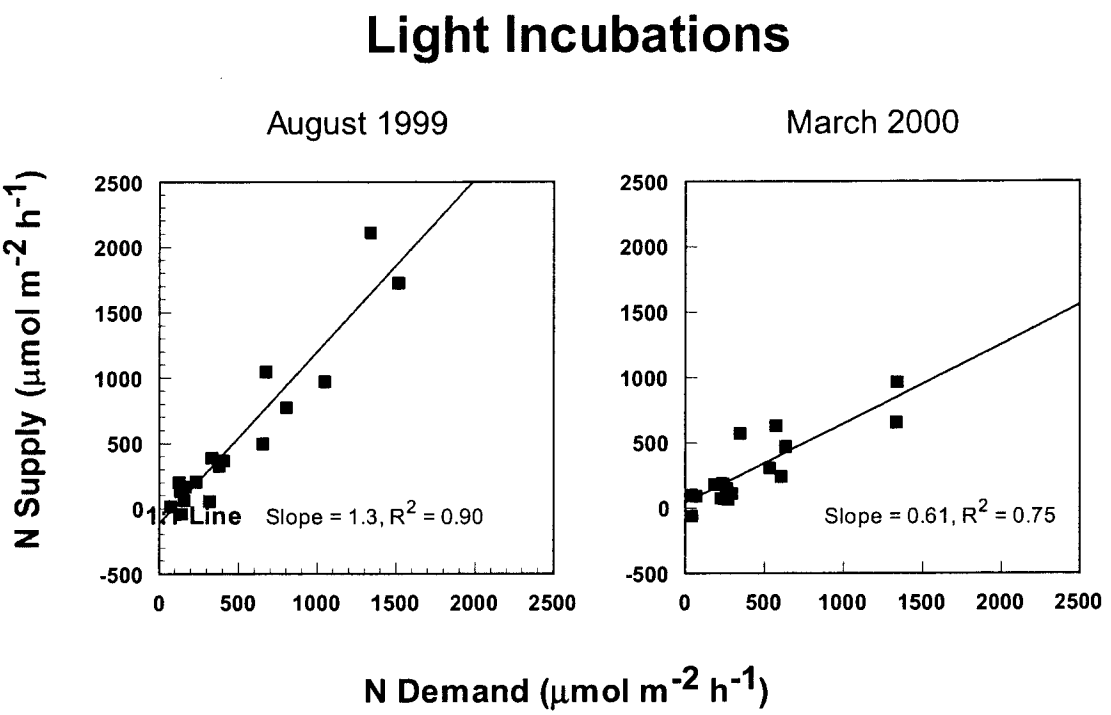

Light Incubations
August 1999
March 2000
N Supply (μmol m-2 h-1)
N Demand (μmol m-2 h-1)
1:1 Line
Slope = 1.3, R2 = 0.90
Slope = 0.61, R2 = 0.75
2500
2000
1500
1000
500
0
-500
0
500
1000
1500
2000
2500

Figure 13