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PHOSPHORUS CYCLING IN TROPICAL CARBONATE SEDIMENT-SEAGRASS SYSTEMS

by

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ABSTRACT

PHOSPHORUS CYCLING IN TROPICAL CARBONATE SEDIMENT-SEAGRASS SYSTEMS

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Old Dominion University, 2013
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This thesis presents two studies focusing on phosphorus cycling in calcium carbonate sediments inhabited by seagrasses. Phosphorus is a major limiting nutrient for primary productivity in these sediments as well as in the overlying waters. In large part this is due to removal of phosphate from solution by adsorption and precipitation reactions.

In chapter II, the relationship between the size of the sedimentary phosphorus pool and the abundance of seagrass on the Great Bahama Bank, as well as the relationship between phosphorus content and grain size in the sediments, were examined to better understand the biogeochemistry of carbonate sediments and the associated sediment-seagrass interactions. Additionally, the depth distribution of fluoride in the pore waters was used to infer precipitation/dissolution of phosphate mineral phases that may occur during diagenesis. A strong positive relationship between the magnitude of the sedimentary phosphorus pool and seagrass density was observed. This association, along with phosphorus inventory calculations, suggests that seagrasses maintain high productivity through utilization of nutrient resources in the sediment. A likely mechanism to access these resources is seagrass-mediated metabolic carbonate dissolution. Additionally, a surface area control of phosphate is evident but not the

primary factor controlling phosphate adsorption. While results provide no evidence for carbonate fluorapatite precipitation, its presence may be masked by low rates of this transformation relative to the time scales of pore water advection.

In chapter III, sediment trap and tidal current flow data were examined to explore the physical/chemical factors that may influence the distribution and density of seagrass across the Great Bahama Bank. Sediment trap data were used to quantify the flux of phosphorus from the water column to the sediments. Sedimentation rates were correlated to tidal current flow amplitudes to elucidate the source of the phosphorus associated with particle deposition and to predict spatial patterns of the phosphorus deposition that may affect seagrass distribution across the Great Bahama Bank. The observation that the highest tidal flow velocities, sediment fluxes, and seagrass densities occur at sites geographically positioned on the bank margin suggests that tidal current flow in the LSI region strongly controls nutrient delivery and deposition.

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CHAPTER I

INTRODUCTION

The global phosphorus cycle can be separated into several components. Tectonic uplift and volcanic eruptions expose phosphorus-bearing rocks to the forces of weathering of phosphate from the continental crust. Following exposure of the rock, physical and chemical weathering produce soils and provide dissolved and particulate phosphorus to rivers that transport phosphorus to the ocean (Filippelli 2008). Once in the ocean, productivity at the sea surface assimilates inorganic phosphorus into organic matter. Most of this organic phosphate is remineralized within the euphotic zone (Bishop et al. 1977), but a small fraction of the organic productivity is exported from the euphotic zone in the form of fecal pellets and other large aggregates (Dugdale and Goening 1969; Eppley 1989). Remineralization causes the downward flux of this material to attenuate exponentially with depth until the residue is deposited on the sea floor (Martin 1987). Sedimentation leads to benthic regeneration of phosphorus. Finally, the remainder is buried either as particulate organic phosphorus or carbonate fluoroapatite until tectonic uplift brings the sediments back into contact with the weathering regime (Filippelli 2008).

Phosphorus weathered from continental rock is mainly delivered to the ocean by riverine transport of the dissolved and particulate phases (Benitez-Nelson 2000). Riverine particulate phosphorus exists as both inorganic phosphorus and organic

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phosphorus. Globally, rivers deliver 27 to 49 x 10^{10} mol/year of particulate inorganic phosphorus and 2.9 x 10^{10} mol/year of particulate organic phosphorus to the oceans each year (Compton et al. 2000). Rivers deliver 0.8-1.5 x 10^{10} mol/year of dissolved inorganic phosphorus and 0.6 x 10^{10} mol/year of dissolved organic phosphorus to the oceans (Compton et al. 2000). Anthropogenic effects have accelerated continental weathering in recent years as phosphorus from fertilizer, sewage, soil erosion, and paper pulp manufacturing is transported to the ocean by rivers (Carpenter et al. 1998; Bennett et al. 2001). The present day total river phosphorus flux ranges from 57 x 10^{10} to 100 x 10^{10} mol/year, approximately twice the pre-anthropogenic flux. Aerosols, volcanic ash, and mineral dust contribute phosphorus to the oceans through atmospheric deposition (Benitez-Nelson 2000). A significant amount of the riverine particulate phosphorus is sequestered in continental shelves and therefore is less important in open ocean processes (Seitzinger et al. 2005; Beusen et al. 2005). Hydrothermal activity on the ocean floor represents only a minor sink for phosphorus in the oceans (Edmond et al. 1979b); the dominant sink is sedimentation followed by subsequent burial in marine sediments (Filippelli 2008).

Burial in marine sediments occurs after transformation from dissolved to particulate forms in the upper water column. Phosphorus is exported from the surface waters as sinking particulate organic phosphorus (40%), authigenic particulate inorganic phosphorus formed when organic phosphorus is remineralized and reprecipitated as calcium fluorapatite (25%), labile particulate inorganic phosphorus (21%), and smaller amounts of detrital material (13%) (Faul et al. 2005). The majority of the phosphorus is remineralized in the water column, however 1% of the phosphorus carried to the deep sea by sinking particles is deposited into the sediments (Broeker and Peng 1982). Total phosphorus burial in marine sediments ranges from 9.3 x 10^{10} mol/year to 34 x 10^{10} mol/year (Berner and Berner 1996; Filippelli and Delaney 1996; Benitez-Nelson 2000). Specific forms of phosphorus found in this burial flux are phosphorus in organic matter, that associated with iron oxides, loosely sorbed phosphorus, and that present in authigenic minerals such as carbonate fluoroapatite (Ruttenberg and Berner 1993). Of the entire 9.3-34 x 10^{10} mol/year that is buried in marine sediments, 3.2 x 10^{10} mol/year is carbonate fluoroapatite and about the same amount is organic phosphorus (Berner and Berner 1996). Other estimates are almost 3-fold higher at 8 x 10^{10} mol/year for carbonate fluoroapatite burial and 5 x 10^{10} mol/year for burial of iron-bound/adsorbed phosphorus (Delaney 1998). It is difficult to ascertain the reasons for the differences in the estimates, but this level of uncertainty is not uncommon in geochemical budget calculations and suggests the need for additional work in this area.

Dissolved forms of phosphorus dominate the total oceanic phosphorus inventory of 3 x 10^{15} mol, and the total deep water inventory (2.9 x 10^{15} mol) is much larger than the surface inventory (0.1 x 10^{15} mol) (Broecker and Peng 1982). The phosphorus residence time in the oceans is between 16,000 and 38,000 years (Ruttenberg 1993). Studies have attempted to constrain global phosphorus budgets (Follmi 1996; Baturin 2001; Filippelli and Delaney 1994); however, this has proven to be a difficult task mainly because phosphorus is rapidly exchanged between its various reservoirs and anthropogenic sources such as fertilizers, animal wastes, and municipal sewage have proven significant but fluctuate in magnitude over time.

In contrast to a more comprehensive understanding in other oceanic environments, carbonate-dominated systems are not well-constrained, especially in terms of fluxes and fate of phosphorus to the oceans. Carbonate sediments are found in shallow water environments in tropical and subtropical regions of the world because calcium carbonate solubility increases with increasing pressure, decreasing temperature and higher CO_2 content (Morse and Mackenzie 1990).

Primary productivity in tropical carbonate systems is limited by phosphorus rather than nitrogen which typically limits productivity in temperate and open ocean systems (Smith 1984; Smith and Atkinson 1984). One factor that contributes to phosphorus limitation in tropical systems is the widespread occurrence of nitrogen fixation (Carpenter and Capone 1981). This is seen in subtropical carbonate sediments of the Bahamas and Bermuda where pore water ratios of dissolved inorganic nitrogen to phosphorus are on the order of 40 to 50 (Gaudette and Lyons 1980; Short et al. 1985; Morse et al. 1987), and in Florida Bay sediments where this ratio is on the order of 90 to 900 (Fourqurean 1992a).

Another important difference that contributes to phosphorus limitation in tropical carbonate systems is that phosphate adsorbs strongly to the surface of calcite and aragonite particles. Kinetic studies suggest a multi-step model for the interaction of phosphate with solid phase carbonates in which the initial rapid uptake of phosphate from solution is followed by much slower removal from solution (deKanel and Morse 1978). This behavior is attributed to either an exponential decrease in surface reaction sites over time or a linear decrease in activation energy for surface adsorption. More recent studies (Froelich 1988; McGlathery et al. 1994) confirm a two-step process in adsorption precedes mineral crystallization. This process sets adsorption in calcareous sediments apart from adsorption in temperate siliclastic sediments because, phosphate is no longer available to oxidative processes once crystallized. Studies show adsorption is the reason carbonate sediments typically have low concentrations of phosphate in pore waters (Morse and Cook 1978), as indicated by intertidal macroalgae on the Atlantic coast switching from being nitrogen limited to being phosphorus limited as the environment shifts from temperate siliclastic systems to tropical carbonate systems (Lapointe et al. 1992).

The adsorption of phosphate onto carbonate grains reduces the biological availability of reactive phosphorus. The most significant biota for the current project is seagrasses - rooted marine flowering plants which are abundant in carbonate sediments throughout the world's shallow, tropical oceans (Hartog 1970). The Great Bahama Bank is an ideal site for seagrasses because the oligotrophic waters are shallow and highly transparent, with little suspended sediment or phytoplankton to block light penetration needed for productivity (Dierrsen et al. 2010). High resolution ocean color data collected across the Great Bahama Bank revealed that seagrass productivity was 292 g C m^{-2} y^{-1} (Dierrsen et al. 2010). In comparison, phytoplankton primary productivity measured across the same region of the Bahamas Bank is only 9 g C m^{-2} y^{-1} (Behrenfield and Falkowski 1997). Across the entire Bahama Bank, seagrass ecosystems represent 0.04% of the total ocean productivity of 48×10^{15} g C yr^{-1} (Longhurst et al. 1995). Globally, if seagrass productivity is consistent across the 800,000 km^2 area of all shallow water carbonate sediment banks throughout the world (Milliman 1993), productivity in carbonate sediment-seagrass systems accounts for approximately 0.3% of the global annual ocean productivity (Dierrsen et al. 2010).

The Great Bahama Bank supports beds of several seagrass species; *Thalassia testudinium* (turtle grass), *Syringodium filiforme* (manatee grass), *Halodule wrightii* (shoal grass), and *Halophila engelmannii* (star grass), all of which play a role in the processing and cycling of nutrients in these oligotrophic waters. This is done by maintaining high productivity through utilization of nutrient resources in the sediment (Short 1987; Powell et al. 1989; Fourqurean et al. 1992a). While the dominant processes for nitrogen regeneration are similar in tropical carbonate sediments and temperate siliclastic sediments, the dynamics of phosphorus are very different due to the adsorption of phosphate ions onto carbonate minerals that dominate many tropical sediments (deKanel and Morse 1978; Froelich 1988; McGlathery et al. 1994). Dissolved phosphate regenerated from organic matter decomposition is removed by seagrass root uptake or adsorption onto carbonate grains (Short 1987), effectively depleting the pore waters of dissolved inorganic phosphorus (Short et al. 1990). As a result, phosphorus often limits primary production in tropical carbonate marine environments (Powell et al. 1991; Lapointe et al. 1992).

Since the phosphate bound in the carbonate matrix is biologically unavailable, seagrass-mediated carbonate dissolution may facilitate remobilization of the phosphorus bound to carbonate minerals or incorporated in mineral phases such as carbonate fluoroapatite (CFA) (Burdige and Zimmerman 2002). Seagrasses facilitate carbonate dissolution by the input of photosynthetically produced oxygen from the roots and rhizomes, driving the microbial production of respiratory acid (CO_2) that dissolves carbonate minerals (Burdige and Zimmerman 2002). Dissolution of the carbonate matrix in the rhizosphere releases phosphate to the pore waters that can then be taken up by seagrass roots, supporting plant growth (Jensen et al. 1998). The possibility of CFA acting as a source of phosphate is consistent with the results of Ruttenberg (1992). Her sequential extraction method SEDEX uses a weak acid to promote the dissolution of carbonate sediments and extraction of CFA. While evidence for liberation of phosphate by the mechanism of seagrass-mediated carbonate dissolution may seem contradictory to previous findings of phosphorus limitation in carbonate-dominated systems, such phosphate release may be too slow to support maximum growth rates at more oligotrophic sites such as the Bahamas, and it is this competition between biotic and abiotic uptake that may explain the phosphorus limitation observed for seagrasses growing in calcareous sediments (Jensen et al. 1998).

Another important factor influencing the ability of sediments to retain phosphorus includes the formation of secondary authigenic phases during carbonate mineral diagenesis (Ruttenberg and Berner 1993). Mineral-bound phosphate can take a number of different forms including biogenic hydroxyapatite from the hard parts of marine fish (Suess 1981; Lowestam and Weiner 1989; Schenau and de Lange 2000), detrital fluoroapatite of igneous or metamorphic origin, and the most important form of mineral phosphate in marine sediments, authigenic carbonate fluoroapatite, also known as the mineral francolite (Ruttenberg and Berner 1993; Delaney 1998), which represents approximately half of the phosphorus buried in marine sediments (Ruttenberg 1993). Authigenic carbonate fluoroapatite forms not only in the traditional upwelling regimes, but also can form continental margin sediments in the absence of upwelling as well as in deep-sea sediments (Ruttenberg 1993; Ruttenberg and Berner 1993; Filippelli and Delaney 1996; Slomp et al., 1996; Delaney 1998), suggesting that its formation may be more important in the oceanic phosphorus cycle than previously thought.

Another important point to come out of these recent observations is the concept of sink-switching during diagenesis (Ruttenberg and Berner 1993). Sink-switching implies that reactive phosphorus is deposited in sediments in labile forms such as organic, iron-bound, or biogenic mineral phosphorus. That which is not returned to the overlying waters as a benthic flux of phosphate via remineralization or reductive dissolution is transformed in sediments to a more stable burial phase, authigenic carbonate fluoroapatite (Ruttenberg 1993). Calcium carbonate minerals undergo well-documented dissolution and precipitation reactions during diagenesis. Since the fluoride content of the major phosphatic mineral phases is high, dissolved fluoride concentrations during diagenesis could vary due to reactions such as precipitation and dissolution (Rude and Aller 1991). More specifically, fluoride mobilized during carbonate dissolution can be lost to the overlying water by exchange, incorporated into reprecipitating calcium carbonate, or incorporated into precipitating carbonate fluoroapatite (Rude and Aller 1991). Several studies (Ruttenberg and Berner 1993; Froelich et al. 1983) have observed a decrease in fluoride concentration with depth in the pore waters. The most common explanation for this decrease is authigenic precipitation of carbonate fluorapatite. Conversely, Rude and Aller (1991) observed elevated fluoride concentrations in pore waters, suggesting that dissolution of carbonate fluorapatite, not precipitation, dominates. Since burial in sediments controls the inventory of oceanic phosphorus and therefore biological production over geologic timescales, it is important to quantify phosphorus burial by constraining phosphorus adsorption as well as precipitation and dissolution of authigenic fluoride-bearing mineral phases that may also contain phosphorus.

This thesis presents two independent, yet closely related, studies focusing on phosphorus cycling in calcium carbonate sediment-seagrass systems. The work was performed to answer several questions:

1. Is there a relationship between the size of the sedimentary phosphorus pool and the abundance of seagrass on the Bahamas Bank?
2. Is there a relationship between phosphorus content and grain size in the sediments of Great Bahama Bank?
3. Can fluoride in pore waters be used as a tracer to establish the activity of authigenic fluoride-bearing phosphatic mineral phases that may occur during carbonate diagenesis?
4. How does biogeochemistry interact with geography and local physical oceanography to determine the large-scale pattern of seagrass distribution?

Answers to these questions will help us better understand the biogeochemistry of carbonate sediments and the associated sediment-seagrass interactions, as well as provide new information about the maintenance of important coastal ecosystems and the impacts of these sedimentary processes on the regional and global carbon cycle.

CHAPTER II

SEDIMENT PHOSPHORUS DISTRIBUTIONS

II -1. Introduction

Phosphorus is an essential element for all life and therefore impacts primary production rates in the ocean. Mostly in freshwater, but also in certain marine and estuarine environments, phosphate is considered the macronutrient that limits primary production. Over millions of years, phosphate has functioned as the ultimate limiting nutrient and thus regulates atmospheric carbon dioxide through its draw-down by photosynthetic activity (van Capellen and Berner 1989). For these reasons it is important to elucidate and quantify the factors controlling phosphate dynamics in the environment.

One particular environment of the ocean in which little is known about phosphorus cycling is calcium carbonate-rich shallow marine sediments. These environments, which include carbonate banks and bays, coral reefs, and tropical and subtropical continental shelves, represent only about 8% of the area of the modern ocean, however they account for approximately 40% of the global oceanic carbonate production and accumulation (Milliman 1993). Carbonate production and accumulation impacts the cycling of phosphorus, which strongly adsorbs to the surface of calcite and aragonite particles (deKanel and Morse 1978). In addition to sorption reactions, precipitation of phosphate minerals such as hydroxyapatite and carbonate fluoroapatite is thermodynamically favored in calcareous sediments (Gaudette and Lyons 1980). The precipitation of apatite as well as adsorption of phosphorus onto carbonate grains leads to retention of reactive phosphorus in carbonate-rich sediments (Froelich et al. 1983;

Ruttenberg and Berner 1993) and reduces the availability of phosphate for benthic macrophytes and phytoplankton in the shallow overlying waters (Short et al. 1985).

Therefore, the current study examines the relationship between the size of the sedimentary phosphorus pool and the abundance of seagrass on the Bahama Bank as well as the relationship between phosphorus content and grain size in the sediments. In addition, fluoride behavior with depth in the pore waters is used to infer precipitation or dissolution of phosphate mineral phases that may occur during diagenesis. Hypotheses for the current study are that there will be a positive relationship between the size of the sedimentary phosphorus pool and the abundance of seagrass, an inverse relationship between phosphorus content and grain size in the sediments, and finally carbonate fluorapatite precipitation during diagenesis will enhance phosphorus burial in carbonate sediments. Examination of these relationships helps us to better understand the biogeochemistry of carbonate sediments and the associated sediment-seagrass interactions.

II-2. Methods

II-2 a. *Study Site and Sample Collection*

The Great Bahama Bank (GBB) is a shallow water carbonate platform populated by seagrass meadows of varying size, distribution, and density as well as unvegetated, well-sorted oolitic sands, coral gardens, and carbonate muds. Sediment, pore water, and seagrass samples were collected by divers near the Caribbean Marine Research Center (CMRC) located on Lee Stocking Island, Exuma Cays, Bahamas in May-June 2002 (LSI 6 sampling trip) as well as across a broad range of sites across the GBB from the R/V *F.G. Walton Smith* in March 2004 (WS-GBB) (Fig. 1). Previously analyzed sediment phosphorus data at the Channel Marker (CM), Ooid Shoals (OS) and Halfway sites (HW) collected near Lee Stocking Island (LSI) in January 2000 were also included (LSI 4 sampling trip).

Sediments around LSI range from fine to coarse grained carbonate sands (200-800 μm) composed mostly of skeletal debris, ooids, peloids, and grapestones (Stephens et al. 2003). The sediments contain approximately 80% aragonite and 20% high-Mg calcite (Hu and Burdige 2007). Porosities in the sediments around LSI vary from approximately 50% to 80% (Burdige and Zimmerman 2002). Finally, water depths at the study sites ranged from 2 to 10 meters.

Sediments at the WS-GBB sites ranged from fine-grained carbonate and pellet muds on the west side of Andros Island to more coarse-grained carbonate sands on the northern part of the Bank and the eastern arm (Burdige et al. 2008). Seagrasses inhabited many of the sites, the dominant species of which was *Thalassia testudinum*, with the exception of two sites (3 and 25) where *Syringodium filiforme* was also observed (Bodensteiner 2006).

Sediments from all sampling locations were collected by pushing core tubes into the sediment to a depth of approximately 20 cm. The cores were sectioned in 1-2 cm intervals over the length of the core and frozen at -20° Celsius for later analysis.

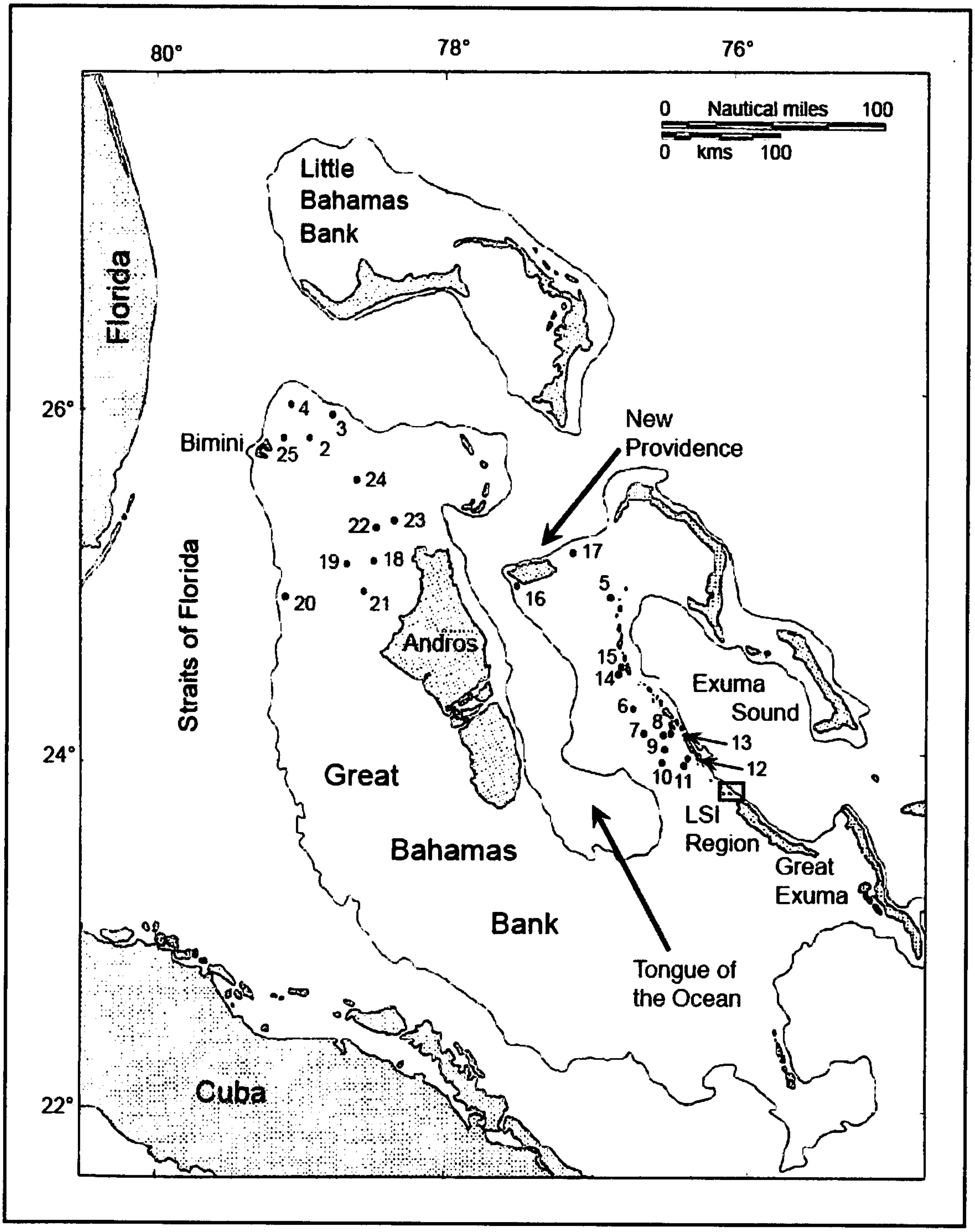

Figure 1. Map of the Bahamas displaying the GBB sample locations (map modified after Bathurst, 1974). A map of the LSI region can be found in either Burdige et al. (2008) or Hu and Burdige (2007).

II-2 b. *Analytical Methods*

The total phosphorus, inorganic phosphorus, and the organic phosphorus concentrations of sediment samples were determined in triplicate using a procedure modified from Aspila et al. (1976). For total phosphorus, approximately 1 gram of dried sediment was dried, ground to a fine powder, covered, and combusted at 500-550°C for three hours in a muffle furnace. The combusted residue was suspended in 50 ml of 1 N HCl and agitated for 12-14 h to extract the phosphate. The solution was then made up to 100 ml and total phosphorus was determined colorimetrically using the phosphomolybdate blue method (Strickland and Parsons 1968). Inorganic phosphorus was extracted from uncombusted sediments and quantified using the same procedures. Organic phosphorus was calculated by difference using the total and inorganic phosphorus measurements.

Fluoride concentrations in selected LSI 6 pore waters (Burdige et al. 2008) were determined with an ion selective electrode by a method of standard additions modified for use with small sample volumes (Rix et al. 1976). Samples were analyzed in a background matrix of total ionic strength adjusting buffer (TISAB, Orion).

II-2 c. *Phosphorus Inventory Calculations*

Phosphorus inventory calculations were performed with the goal of obtaining area-specific inventories for both the sediments and seagrass biomass. For the sediments, mean sedimentary phosphorus concentrations were integrated to a depth of 20 cm. Porosity (p) for LSI sediments was as assumed to be 50% (Burdige and Zimmerman 2002); porosity data for the WS-GBB sites (45-50) were obtained from Hu (2007). The volume fraction of sediment particles was calculated as 1-p (Burdige 2006), and the dry sediment density was calculated based on the composition of LSI sediments (Burdige and Zimmerman 2002) using values from Table 4.1 in Burdige (2006). The phosphorus inventory in the sediments for each of the sites was then calculated by multiplying the integrated sediment phosphorus concentrations, the volume fraction of sediment particles, and the dry sediment density.

The phosphorus inventory in the seagrass biomass was calculated based on the measured leaf area index (LAI) values for the LSI and WS-GBB sites. LAI is a dimensionless quantity (m^2/m^2) that represents the density of seagrass in a region. LAI values were converted to grams of leaf assuming 100 grams FW m^{-2} leaf area (Stapel et al. 1996; Fourqurean et al. 2001). Leaf dry mass was assumed to be 20% of the fresh mass (Lee and Dunton 1996). Leaf carbon was calculated by assuming a weight composition of 32.9% carbon, as observed for *T. testudinum* in the Bahamas (Capone 1979). This was converted to moles of carbon in the leaves using the atomic weight of carbon, and moles of carbon were converted to moles of phosphorus using the C:P ratio (1,070) observed by Fourqurean and Zieman (1992) for *T. testudinum* in Florida Bay. Moles of phosphorus in the leaves were finally converted to the phosphorus inventory in the total plant at each site using the biomass allocation percentages observed for *T. testudinum* by Fourqurean and Zieman (1991).

The phosphorus inventories in the overlying water column and pore water were based on previous studies which showed that in tropical and subtropical shallow coastal waters inhabited by *T. testudinum*, water-column phosphate concentrations were less than 1 μM, and pore water phosphate concentrations were less than 1.5 μM (Fourqurean et al. 1992a; McGlathery et al. 2001) or below the detection limit of 0.05 μM (Morse et al.

1985). For the water column inventory, the 1 μM value was integrated over the height of the water column to obtain mol P/m^2 of water. For the pore waters, the inventories were calculated by integrating the 0.05 μM and 1.5 μM values over the height of the sediment column (20 cm depth) and multiplying by the sediment porosity.

II-3. Results

Sedimentary phosphorus samples from LSI 6 had been previously analyzed in the Burdige lab, although it was later observed that the temperature controller on the muffle furnace was not working properly and the samples were not combusted at the correct temperature for the total phosphorus analyses. To determine whether corrections of these data were needed, a representative selection of samples covering the range of phosphorus concentrations at LSI was analyzed for total, inorganic and by difference, organic phosphorus. Property: property plots were constructed to compare the newly and previously analyzed data. A trendline was fit to the data and compared with the 1:1 line. The slope of the best-fit line through the inorganic phosphorus data showed good agreement between the two sets of analyses with a slope within 20% of 1. The data were also randomly scattered around the 1:1 line. However, the total phosphorus data all fell below the 1:1 line indicating that consistently higher concentrations were obtained in the current study versus those previously determined (Fig. 2). The former result was expected since only the total phosphorus samples were ignited in the muffle furnace, and indicated that no correction was needed for the inorganic phosphorus data. The original total phosphorus concentrations were corrected using the slope and intercept of the best fit line to the original data, and the organic phosphorus data were re-calculated by difference using the corrected total phosphorus concentrations and the original inorganic phosphorus concentrations. All of the corrected data fell within the range of total phosphorus concentrations in Fig. 2.

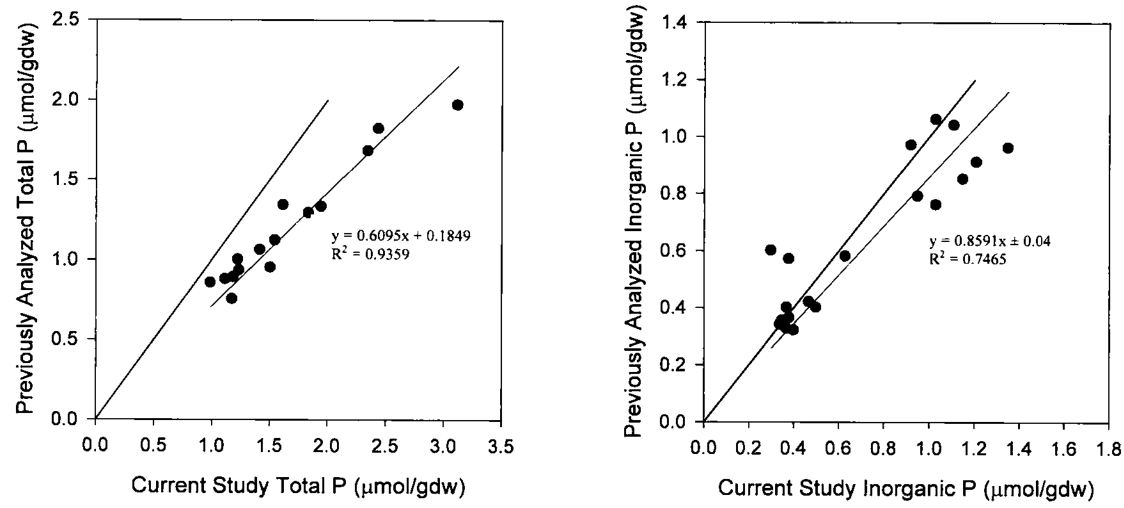

Figure 2. Property: Property plot of the previously analyzed total and inorganic phosphorus data with the current data. The slope and R^2 of the best fit line to the data are shown as well as the 1:1 line.

II-3 a. *LSI 6 Sediment P Distributions*

Once the corrections were made, the data were compiled (Table A1) and total, inorganic, and organic phosphorus concentrations were plotted with depth in the sediment. At all sites around Lee Stocking Island, solid phase phosphorus depth profiles did not show significant depth trends (Fig. 3).

Total phosphorus in the sediments of the LSI region ranged from 0.81 to 5.35 μmol g^{-1} dw with an average concentration of 2.11 ± 0.65 μmol g^{-1} dw. Inorganic phosphorus at the LSI sites ranged from 0.31-1.04 μmol g^{-1} dw with an average concentration of 0.62 ± 0.22 μmol g^{-1} dw, and organic phosphorus ranged from 0.75-2.56

μmol g^{-1} dw with an average concentration of 1.49 ± 0.45 μmol g^{-1} dw. On average organic phosphorus comprised 72% of the total sedimentary phosphorus pool and inorganic phosphorus comprised 27% of the total sedimentary phosphorus (Table 1).

Table 1. Mean total sedimentary phosphorus concentrations, % inorganic, and % organic phosphorus for the LSI 6 sites.

	Total P (μmol/gdw)	% Inorganic	% Organic
CM	2.88 ± 0.29	31	69
HW	1.31 ± 0.14	29	71
AC	2.60 ± 0.17	32	68
TB	1.86 ± 0.28	23	77
BP	4.08 ± 0.67	23	77
OS	1.67 ± 0.19	31	69

II-3 b. *WS-GBB Sediment P Distributions*

Two replicate cores were taken from each of the WS-GBB sites across the Great Bahama Bank, and the surface sedimentary phosphorus concentrations (0 - 0.5 cm) were analyzed in both cores at each site (Table A2). To examine whether surface sediment phosphorus concentrations were similar for the replicate cores, property: property plots as well as a student's t-test were employed.

On the property: property plots of the data from the replicate cores, the slopes of the best fit lines were not significantly different than 1 for the total, inorganic and organic phosphorus concentrations (Fig. 4). A student's t-test was employed comparing the total, inorganic and organic phosphorus concentrations of the replicate cores, and it was determined that the mean phosphorus concentrations in the surface samples from the two cores were not significantly different. Average total, inorganic and organic phosphorus concentrations from the replicate cores were calculated, and these data were analyzed in the context of their relationships with the environmental parameters LAI and grain size (Table 2).

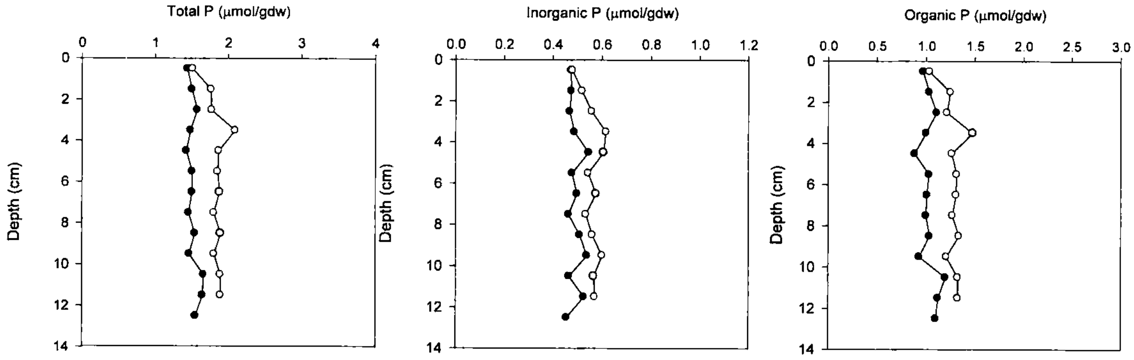

Figure 3. Total, inorganic and organic sedimentary phosphorus profiles at the Ooid Shoals site in the LSI region of the Bahamas. All other sites show similar profiles.

Results from sites 1-24 on the GBB showed that total phosphorus concentrations in the surface sediments ranged from 0.90-3.85 μmol g^{-1} dw with an average concentration of 1.77 ± 0.83 μmol g^{-1} dw. Inorganic phosphorus in the surface sediments ranged from 0.08-2.25 μmol g^{-1} dw with an average concentration of 0.63 ± 0.59 μmol g^{-1} dw, and organic phosphorus ranged from 0.49-1.76 μmol g^{-1} dw with an average concentration of 1.14 ± 0.34 μmol g^{-1} dw. Across the Bank, organic phosphorus was 41% to 93% of the total sedimentary phosphorus, and inorganic phosphorus ranges from 7% to 59% of the total sedimentary phosphorus (Table 2). On average, organic phosphorus comprises 69% of the total sedimentary phosphorus and inorganic phosphorus comprises 31% of the total sedimentary phosphorus inventory. In terms of the spatial distribution of sedimentary phosphorus on the GBB, sites on the Northwest side of Andros Island exhibited a higher mean total sedimentary phosphorus concentration of 2.05 μmol g^{-1} dry weight as compared to sites along the Exuma Sound in between Lee Stocking Island and New Providence, which exhibited a mean total phosphorus concentration of 1.58 μmol g^{-1} dry weight. In addition, sites on the margins of the Bank show larger sedimentary phosphorus concentrations than those closer to the interior of the Bank (Fig. 5).

Table 2. Mean total phosphorus concentrations, % inorganic, and % organic phosphorus for the WS-GBB sites. Grain size and leaf area index measurements are also included (Burdige and Zimmerman 2002; Xu 2007).

Site	Total P (μmol g^{-1} dw)	% Inorganic	% Organic	Grain Size (μm)	LAI
1	3.19 ± 0.54	55	46	425	3.73 ± 0.4
2	1.74 ± 0.16	26	74	409	0.96 ± 0.04
3	3.85 ± 0.01	59	41	238	1.48 ± 0.1
4	2.4 ± 0.01	33	67	587	2.24 ± 0.08
5	2.55 ± 0.02	48	52	1201	0.03 ± 0.02
6	1.05 ± 0.03	47	54	691	0 ± 0
8	1.47 ± 0.04	29	71	521	0.25 ± 0.04
9	1.36 ± 0.00	20	80	678	0 ± 0
10	1.41 ± 0.06	32	68	1319	0.02 ± 0
11	1.24 ± 0.02	15	85	374	0.09 ± 0.01
12	3.21 ± 0.09	45	55	272	1.96 ± 0.07
13	1.50 ± 0.02	22	78	406	0.75 ± 0.05
14	1.08 ± 0.03	14	86	558	0.57 ± 0.02
15	1.68 ± 0.18	17	83	340	1.2 ± 0.05
16	0.90 ± 0.04	17	83	940	0.01 ± 0
17	1.57 ± 0.03	25	75	406	0.47 ± 0.02
18	1.09 ± 0.15	26	74	458	0.24 ± 0.02
20	1.71 ± 0.04	20	80	423	1.08 ± 0.05
21	1.29 ± 0.06	62	38	306	0.1 ± 0.01
24	1.17 ± 0.04	7	93	503	0.35 ± 0.02

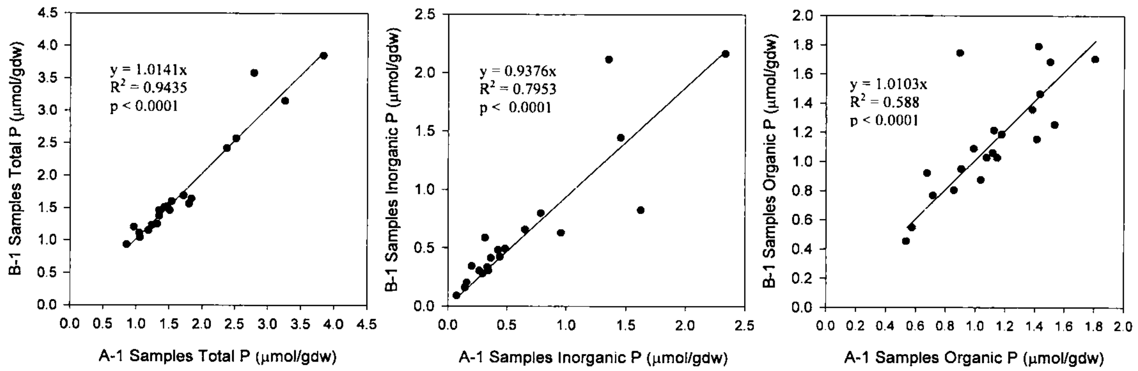

Figure 4. Property: Property plots of the surface sedimentary total, inorganic, and organic phosphorus concentrations for the replicate cores, A and B. The slope and R^2 of the best fit line to the data are shown.

II-3 c. *Sediment P vs. LAI*

Sedimentary phosphorus content was positively correlated with seagrass density (Fig. 6), supporting the idea that seagrass productivity is phosphorus-limited. If I were to reverse the axes, LAI would be positively correlated with phosphorus content suggesting phosphorus availability drives seagrass density. I will consider this point further in the discussion section. Figure 6 also includes data from the LSI 4 sampling trip. The LSI 4 (January 2000) sediment phosphorus samples were previously analyzed using the same analytical procedure used in the current study (see section II-2 b).

II-3 d. *Sediment P vs. Grain Size*

Results also indicated a weak, inverse relationship between phosphorus content and grain size (Fig. 7). Sediment surface area and grain size also exhibit an inverse relationship since the smallest grains have the largest specific surface areas (surface area normalized to particle mass). This in turn affects the sorption capacity of carbonates because grains with a higher specific surface area contain more binding sites than those with smaller specific surface areas. Thus, the negative relationship between sediment phosphorus content and grain size observed here consistent with a surface area mechanism for phosphate adsorption (Fig. 7). The inverse relationship between sediment surface area and grain size has been observed by several others: Suess (1973) in carbonate sediments from Fanning Island Lagoon, Erftemeijer and Middleberg (1993) in carbonate sediments from South Sulawesi, and finally McGlathery et al. (1994) in carbonate sediments from Bermuda.

II-3 e. *Pore Water F^- Content*

Fluoride concentrations in selected LSI 6 pore waters did not vary with depth and did not differ significantly from predicted fluoride concentrations based on measured pore water salinities (Fig. 8, Table A3). Salinity values for the respective sites were determined by titration during the LSI 6 sampling trip in May 2002 (Xu 2007). Salinity values were converted to chlorinity values and multiplied by the fluoride:chloride ratio in seawater to determine predicted fluoride concentrations.

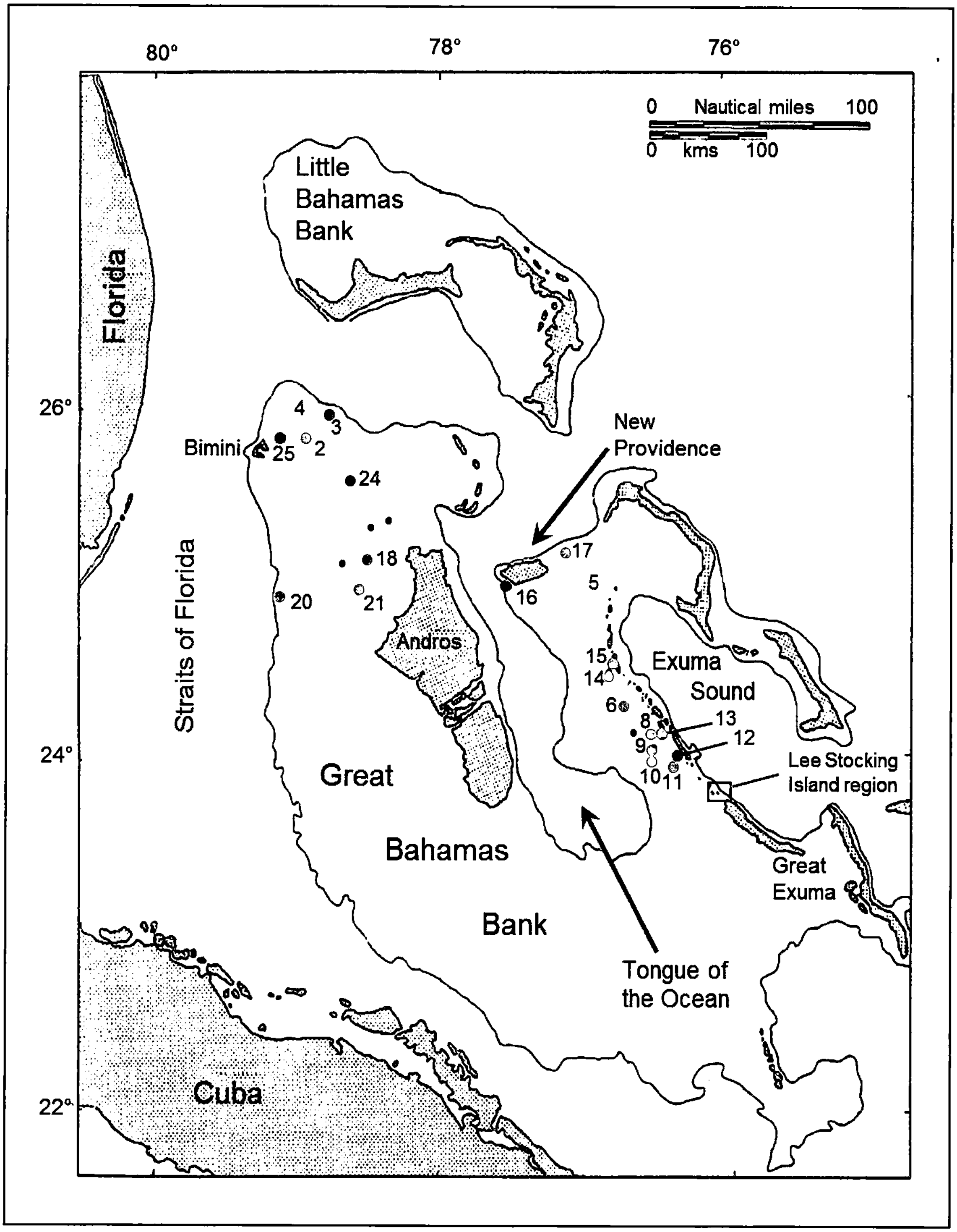

Figure 5. Map of the Great Bahama Bank displaying the WS-GBB sampling sites. The color of the circles at each of the sampling sites indicates the total sedimentary phosphorus concentration in µmol/gdw at each site; Blue = < 1.0, Green = 1.0 – 2.0, Yellow = 2.0 – 3.0, and Red = > 3.0. The black dots above Stations 18 and 9 are stations not sampled.

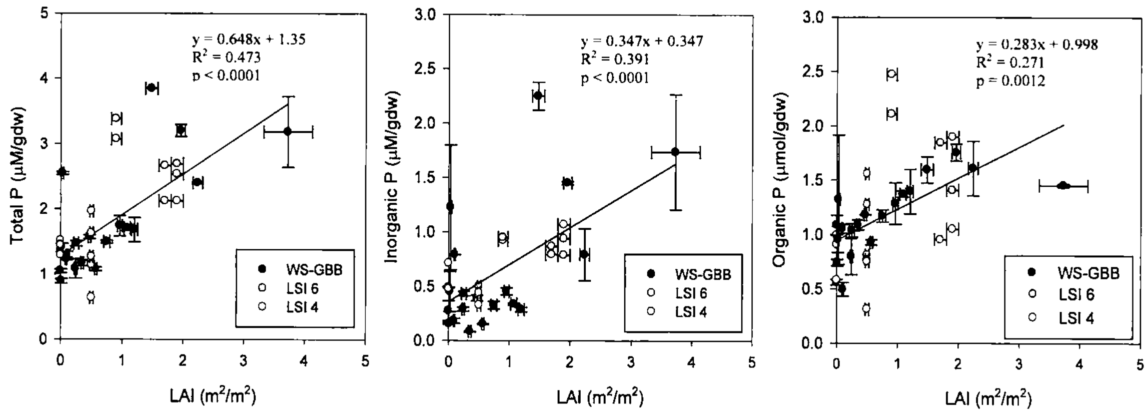

Figure 6. Solid-phase total, inorganic and organic phosphorus concentrations of Great Bahama Bank and Lee Stocking Island sediments as a function of leaf area index. Error bars are ±1 standard deviation.

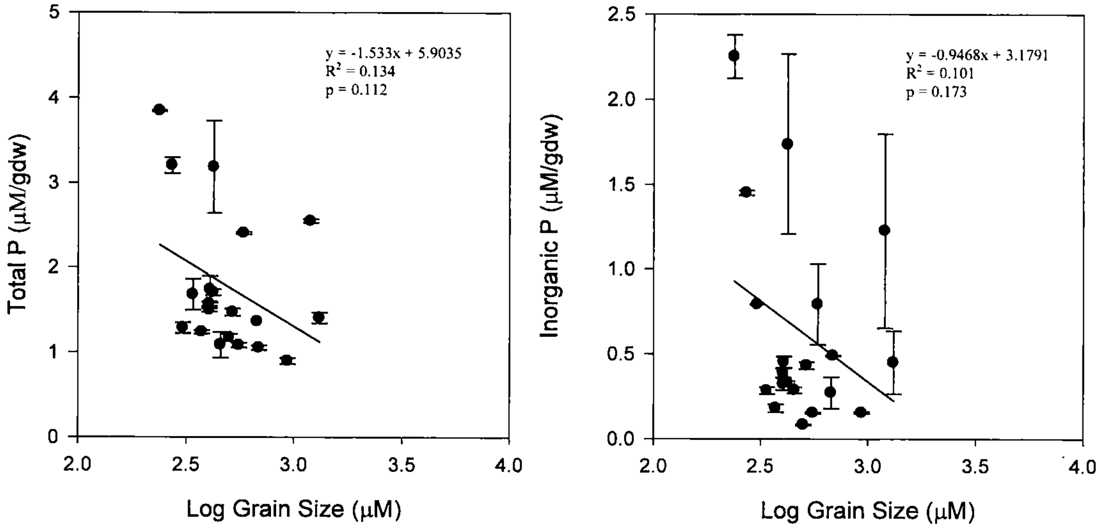

Figure 7. Log of the solid-phase total and inorganic phosphorus concentrations of Great Bahama Bank sediments as a function of grain size (Xu 2007). Vertical error bars are ±1 standard deviation.

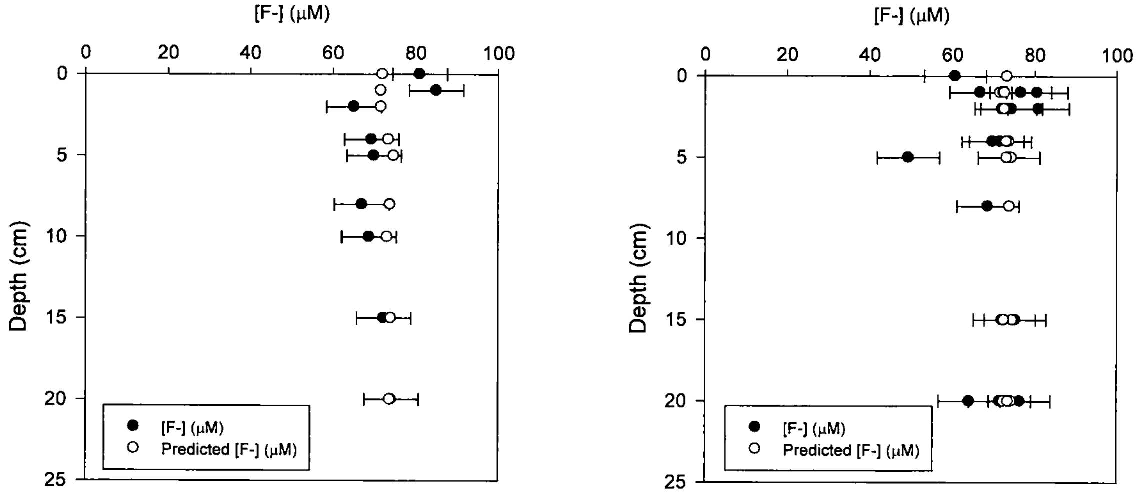

Figure 8. Profiles of measured and predicted fluoride concentrations in LSI 6 pore waters at the Adderly Cut and Channel Marker sites in the LSI region of the Bahamas. Predicted fluoride concentrations were calculated using measured pore water salinities. Error bars are ±1 standard deviation. The LAI value for this site are 1.7 m^2/m^2 and 1.9 m^2/m^2 respectively.

II-3 f. *Solid Phase Phosphorus Speciation*

To better understand the burial and diagenesis of phosphorus in carbonate sediments, it is necessary to examine not only the magnitude and distribution of total phosphorus in the sediments, but the distribution of the different sedimentary fractions (Ruttenberg 1992). The current study employed an extraction technique which separates phosphorus into its inorganic and organic fractions (Aspila et al. 1976). At sites near LSI, there was a consistent percentage of inorganic and organic phosphorus across sites (Table 1). Also around LSI, inorganic and organic phosphorus concentrations did not show significant trends with depth (Fig. 3). WS-GBB sediments exhibited more variability in the distribution of inorganic and organic phosphorus across sites although the average proportions of organic and inorganic phosphorus (31% inorganic, 69%

organic) were within 15% of the values seen at the LSI sites (Table 2). Plots of the ratios of inorganic:total P, organic:total P and inorganic:organic P as a function of LAI for LSI and WS-GBB sediments (combined data sets) revealed that the slope of each best-fit regression line was not statistically different from zero. A weak relationship apparently exists between these variables, and these plots are not shown here ($p=0.065$, 0.051, and 0.080 respectively).

The fact that phosphorus speciation is independent of LAI is an important observation here because one might expect to see differences in phosphorus speciation if LAI was controlling phosphorus content, as one might infer from Fig. 6. However, these observations suggests that more appropriate way to view the positive correlations in Fig. 6 is that the phosphorus content of the sediments drives seagrass density.

II-4. Discussion

II-4 a. *Phosphate Adsorption onto Carbonate Grains*

The weak correlation between grain size and sediment phosphorus content in Bahamian carbonate sediments ($R^2 = 0.134$ and 0.101 for total phosphorus and inorganic phosphorus respectively) indicates that phosphate adsorption is not principally a result of surface adsorption in these sediments. Other workers that have examined this problem suggest phosphate uptake via adsorption onto carbonate grains can be influenced by several chemical and physical aspects of the sediment. Specifically, organic matter content, iron content, sediment surface area, and even phosphorus content itself have all been shown to affect phosphate adsorption in carbonate sediments (Suess 1973; Krom and Berner 1980; Sherwood et al. 1987; Morse 1986; McGlathery et al. 1994).

Organic carbon content has been linked to phosphate adsorption in carbonate sediments. Typically though, the relationship observed has been a decrease in phosphate adsorption with increasing organic carbon content because organic matter competes with phosphate binding to carbonate grains (Krom and Berner 1980). The TOC content of the sediments in the current study was not measured; therefore, we are unable to correlate sedimentary phosphorus concentrations with TOC content in the sediments. Data for the TOC content of Bahamian carbonate sediments all indicate low organic carbon as measured by weight percent. For example, LSI sediments consist of <0.5 weight percent organic carbon (Dobbs unpub.). More specifically, Morse et al. (1985) measured 0.24-0.34 weight percent organic carbon at their sites in the Bahamas. Sampling locations of the Morse et al. (1985) study were similar to those of the current study extending from Little Bahama Bank, along the Abaco Islands, south to the Berry Islands, to the Joulters Cays, and finally onto the Great Bahama Bank. A more recent study using samples collected exclusively across GBB reported that total sedimentary organic carbon averages 0.10% and ranges from 0.002 to 0.97% (Oehlert et al. 2012). Comparison of the total sedimentary phosphorus distribution across the Bank in the current study (Fig. 5) with the sedimentary organic carbon distribution across the Bank (Oehlert et al. 2012; Fig. 6C) indicates a similar pattern for organic carbon and that of sedimentary total phosphorus in which higher percentages were found on the bank margins and northwest side of Andros. The exact locations of increased organic carbon, however, do not coincide with the locations of the WS-GBB sites in the current study, limiting our ability to make strong conclusions about the influence of organic carbon content on phosphate adsorption in Bahamian carbonate sediments.

In contrast, iron oxide coatings on carbonate grains have been shown to enhance phosphate adsorption (Sherwood et al. 1987). While iron concentrations were not measured for the current study, it is not likely that iron would have an effect on phosphate adsorption because these sediments are extremely low in iron (~0.004%, Morse et al. 1985).

Phosphate adsorption is also negatively related to the total phosphorus content in the sediments (McGlathery et al. (1994), suggesting a feedback mechanism that reduces the active surface sites available for adsorption as total phosphorus increases. This is consistent with the multi-step mechanism in which phosphate is rapidly adsorbed to available surface sites and then slowly moves into the near-surface carbonate matrix, most likely as calcium phosphate (DeKanel and Morse 1978; Froelich 1988; McGlathery et al. 1994). In Bermuda, high phosphorus loading and more eutrophic conditions result in higher phosphorus content and less surface area available to adsorb phosphate, whereas in the Bahamas no significant local terrestrial inputs and oligotrophic conditions result in more surface reaction sites available for phosphate adsorption. This can be evidenced in a comparison of data from the current study and that of Morse et al. (1987) from the Bahamas with data from McGlathery et al. (1994) from Bermuda (Table 3).

Sedimentary total phosphorus concentrations exhibited a decreasing trend from the eutrophic Bermuda site to the mesotrophic site in Bermuda and finally the oligotrophic sites in the Bahamas. Morse et al. (1987) reported solid-phase phosphorus concentrations of 6.5 and 5.6 nmol/g dry weight in seagrass covered and barren sediments of the Bahamas respectively. These solid phase phosphorus concentrations are significantly lower than those of the current study as well as many others from a broad range of carbonate sediments at other sites (see Table 5 in Jensen et al. 1998), and at the present time the reason(s) for this difference is unknown.

Table 3. Solid phase phosphorus, sediment slurry, and grain size data from the WS-GBB sampling sites of the current study, the Berry Islands in the Bahamas from Morse et al. (1987) and Bailey's Bay in Bermuda from McGlathery et al. (1994).

Site	Study	Tp_{sed} (µmol g^{-1} dw)	*% Removal	Grain Size
Eutrophic (Bermuda)	McGlathery et al. (1994)	4.77 ± 0.03	56%	66% > 210 µm
Mesotrophic (Bermuda)	McGlathery et al. (1994)	3.37 ± 0.20	67%	75% > 210 µm
Oligotrophic (GBB)	Current Study	1.77 ± 0.08	N/A	95% > 250 µm
	Morse et al. (1987)	0.0065	100%	100% > 250 µm
	Morse et al. (1987)	0.0056	100%	100% > 250 µm

*Indicates the magnitude of phosphate adsorption in a sediment slurry measured by % removal from solution after 6 hours.

Despite this difference, the overall trend of increasing total sedimentary phosphorus with increasing trophic status is consistent with the observed positive correlation between total phosphorus content and seagrass density. With respect to phosphate uptake, the sediment slurry data in Table 3 show an increasing trend from the eutrophic Bermuda site to the mesotrophic Bermuda site, and finally highest uptake at the oligotrophic site in the Bahamas. Although phosphate uptake increases with decreasing trophic status, grain size is consistently dominated by the large, coarse-grained size fractions. If adsorption was the predominant process controlling phosphorus content in carbonate sediments, phosphorus concentration would increase as grain size decreased and surface area increased. However, a comparison of the data reveals the opposite trend, suggesting other factors may be important. The observed increase in phosphate adsorption from eutrophic to oligotrophic sites suggests that not only does grain size influence adsorption, but the total phosphorus content as dictated by the environmental conditions plays a role as well.

II-4 b. *Mineral Transformations during Diagenesis*

Since the fluoride content of the major phosphatic mineral phases is high, dissolved fluoride concentrations during diagenesis could vary due to reactions such as precipitation and dissolution (Rude and Aller 1991). Therefore, fluoride may be useful as a tracer to infer the precipitation or dissolution of authigenic fluorapatite.

Here, because no significant changes in pore water fluoride concentrations with sediment depth were observed at Adderly Cut or Channel Marker sites, fluoride cannot be utilized as a tracer to infer the precipitation or dissolution of authigenic CFA. CFA was not measured directly in the solid phase after separation using a sequential extraction technique such as the previously mentioned SEDEX method (Ruttenberg 1992), so our results do not indicate a lack of CFA formation or dissolution in Bahamian carbonate sediments. While the current results do not directly indicate a lack of CFA formation or dissolution, additional support for that suggestion may be that solid phase phosphorus depth profiles at sites around LSI do not show significant depth trends (Fig. 3). However, Adderly Cut and Channel Marker are metabolically active as is evidenced by the LAI values for each (1.7 m^2/m^2 and 1.9 m^2/m^2, respectively). Metabolic activity is significant in this context because seagrasses facilitate carbonate dissolution by the input of photosynthetically produced oxygen from the roots and rhizomes, and the fluoride mobilized during dissolution may be incorporated into precipitating CFA (Rude and

Aller, 1991). Therefore, alternative explanations for the lack of variability in pore water fluoride profiles are that rates of CFA precipitation or dissolution are low, or that the timescale of dissolution or precipitation of CFA is much longer than the timescale of pore water advection in the sediment. If the rates of advection are fast relative to uptake or release of fluoride from the pore waters, this advection could mask the occurrence of CFA precipitation or dissolution.

II-4 c. *Ecological Significance*

The precipitation of CFA and adsorption of phosphate onto carbonate grains results in the retention of reactive phosphorus in carbonate sediments. This retention makes phosphorus the limiting nutrient in carbonate-rich sediments (Short et al. 1985; Howarth 1988; Fourqurean et al. 1992a; Fourqurean et al. 1992b; Koch et al. 2001; Zhang et al. 2004).

The observed link between the magnitude of the sedimentary phosphorus pool and leaf area index, paired with inventory calculations performed for the various reservoirs of phosphorus in the system (Table 4), may provide insight into the primary sources of phosphorus for seagrass productivity. The current study is not the first to compute phosphorus inventories in seagrass-dominated sediments. Short et al. (1985) calculated a total seagrass pool of 0.32 g P/m^2 (= 10.3 mmol P/m^2] in the *S. filiforme* biomass in Graham's Harbor at the north end of San Salvador Island, Bahamas. In the current study, total phosphorus in the seagrass biomass ranges from 0 to 13 mmol P/m^2 seafloor with an average of 2.7 ± 3.1 mmol P/m^2. Given the large range and standard deviation relative to the average, my results are in reasonable agreement with those of

Short et al. (1985), despite the fact that this comparison involves two different seagrass species with very different patterns of growth.

Table 4. Phosphorus inventories in mmol m^{-2} for the various reservoirs in the Bahama Bank. The description of the calculation for each of these values can be found in the section II-2c.

Reservoir	Range	Mean
Mean Total P_{sed}	280.51 - 1184.02	561.11 ± 247.11
Mean Inorganic P_{sed}	25.86 - 412.87	183.03 ± 143.31
Mean Organic P_{sed}	120.54 - 917.02	378.06 ± 152.36
Mean Seagrass Total P	0 - 13	2.74 ± 3.08
Water Column P	$1 \times 10^{-11} - 2 \times 10^{-12}$	N/A
Pore Water P	0.005 - 0.15	N/A

The seagrass phosphorus inventory calculations performed using LAI values from the current study allow for a direct comparison between the abundance of phosphorus in the biomass relative to that in the sediments (Table A4) as well as the water column and the pore waters. Results indicate that the largest pool of phosphorus in these environments resides in the sediment, as is evidenced by the 2 order of magnitude difference between total phosphorus in the sediment and seagrass biomass, the 3 order of magnitude difference between the sediments and pore waters, and finally the >10 order of magnitude difference between the sediments and the water column.

Solid phase phosphorus is unavailable to seagrass as a nutrient for growth, but studies show that seagrass thrive in the Bahamas, producing 292 g C m^{-2} y^{-1}, roughly 32 times the phytoplankton production across the same region (Dierrsen et al. 2010; Behrenfield and Falkowski 1997). The positive relationship observed between leaf area index and sedimentary phosphorus content along with the phosphorus inventory in the system suggests that seagrass growth occurs through utilization of nutrient resources in the sediment. This has been suggested for *T. testudinum* in Florida Bay, Caribbean, and Bermuda as well as *S. filiforme* in the Bahamas (Patriquin 1972; Short 1987; Fourqurean et al. 1992a; Jensen et al. 1998).

A likely mechanism for mobilization of solid phase phosphorus to the pore waters where seagrass root uptake can occur is metabolic carbonate dissolution (Fig. 9). Seagrasses facilitate carbonate dissolution by transporting photosynthetically produced oxygen from the roots and rhizomes (Bodensteiner 2006). This input drives the production of the respiratory acid which dissolves carbonate minerals (Burdige and Zimmerman 2002). As a result of the dissolution of the carbonate matrix in the rhizosphere, phosphate is released to the pore waters where it is then taken up by seagrass roots, supporting further plant growth (Jensen et al. 1998).

Sulfide oxidation, organic acid exudates and aerobic respiration have been suggested as sources of acid to create dissolution of the carbonate matrix (Ku et al. 1999; Long et al. 2008; Burdige et al. 2008). Previously published pore water sulfate profiles for the GBB (including LSI) showed no downcore gradients, suggesting little to no net sulfate reduction is occurring in these environments, therefore discounting sulfide oxidation as a source of acid for dissolution (Burdige et al. 2008). Furthermore, carbonate dissolution resulting from acidification by sulfate reduction is merely a transient effect, and reversed by sulfide oxidation – this represents a "shuttle" process – not a stable end-result. Burdige et al. (2008) also showed a strong positive correlation between dissolution rates and LAI because seagrass O_2 pumping is the major source of oxygen to the sediments. The correlation suggests that aerobic respiration is the source of acid for seagrass-mediated carbonate dissolution in the GBB and LSI sediments.

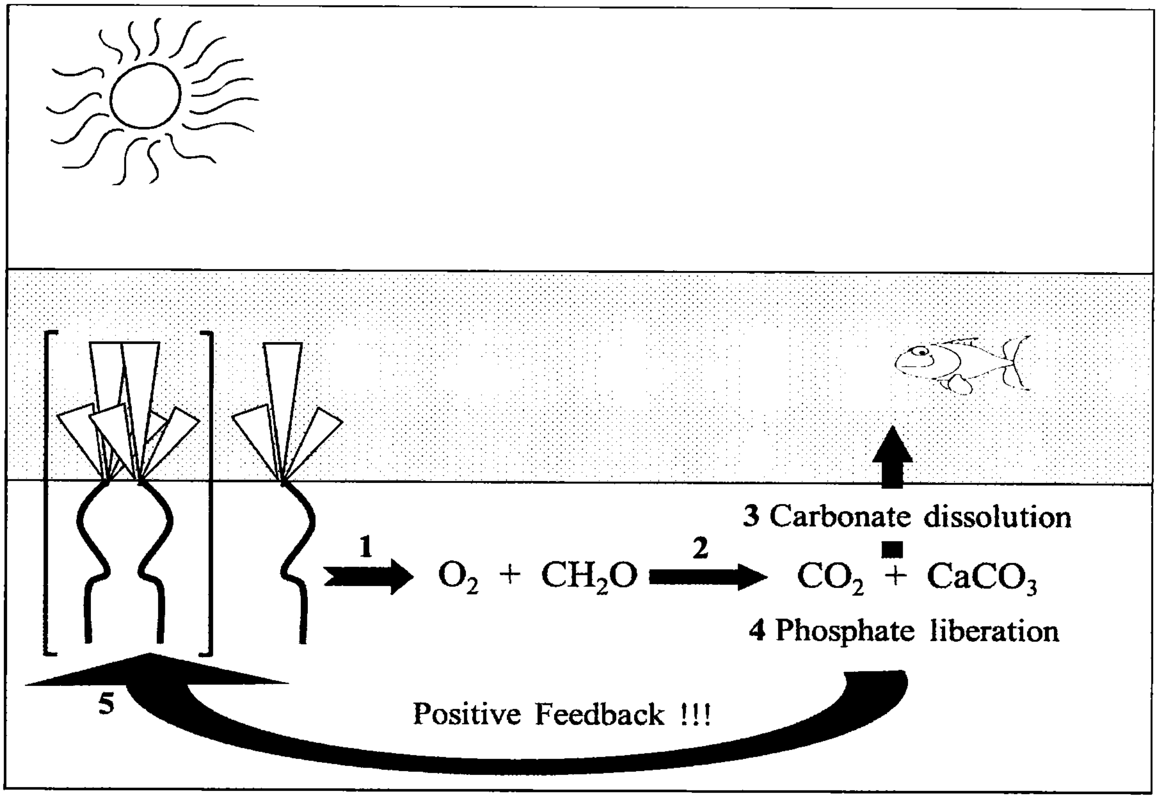

Figure 9. Schematic of acid-mediated carbonate dissolution and its possible role in phosphorus acquisition by seagrasses.

Although metabolic carbonate dissolution provides a mechanism for seagrasses to access phosphorus for growth, phosphorus limitation of primary productivity still occurs. Examination of the timescale over which release occurs may provide clarity. Jensen et al. (1998) concluded that although most of the adsorbed phosphorus in sediments can become available to the seagrass as a result of dissolution of the carbonate matrix in the rhizosphere, such phosphorus release may be too slow to support maximum growth rates at more oligotrophic sites such as the GBB. Another explanation for phosphorus limitation in carbonate sediments is that once phosphorus is released from the sediments as a result of metabolic carbonate dissolution, competition exists between uptake onto new mineral grains and uptake by seagrass, and perhaps seagrass uptake is slower (Short et al. 1985). In addition, there is some loss (export) of seagrass biomass (as detritus) to the surrounding waters, leading eventually to phosphorus depletion unless there is phosphorus input to the sediments to balance this loss. This will be discussed further in Chapter 3.

II-5. Conclusions

Phosphate adsorption onto carbonate grains is inversely related to sediment grain size, suggesting a surface area control of phosphate uptake occurs, but it is not the principal factor behind phosphate uptake (Fig. 7). No evidence exists for CFA precipitation (Fig. 8); however, this may be due to low precipitation rates or long timescales of these transformations relative to pore water advection.

A predictive relationship between the magnitude of the sedimentary phosphorus pool and leaf area index was observed (Fig. 6). This relationship, along with the phosphorus inventory calculations performed for the various reservoirs in the system (Table 4), suggests that seagrass growth occurs through utilization of nutrient resources in the sediment. A likely mechanism to access these resources is based on metabolic carbonate dissolution (Fig. 9), where seagrass respiration produces CO_2 that dissolves carbonate grains, releasing adsorbed phosphate to the pore waters for uptake by seagrass roots.

CHAPTER III

PHOSPHORUS FLUXES TO CARBONATE SEDIMENTS AS DETERMINED USING SEDIMENT TRAPS

III-1. Introduction

Sediments in shallow tropical and subtropical environments such as the Bahamas are primarily composed of calcium carbonate. Phosphate, an essential nutrient for growth, adsorbs to the surfaces of both calcite and aragonite (deKanel and Morse 1978; Millero 2001) which results in low concentrations of phosphate in pore waters (Gaudette and Lyons 1980; Short et al. 1985; Morse et al. 1987). Phosphate is initially rapidly adsorbed to available surface sites and then is more slowly transformed into the near-surface carbonate matrix, most likely as apatite (DeKanel and Morse 1978; Froelich 1988; McGlathery et al. 1994). Of the apatites, fluorapatite has been described as the dominant sink for phosphorus in carbonate-rich sediments (Gaudette and Lyons 1980; Ruttenberg and Berner 1993). As a result of adsorption and precipitation reactions, phosphorus is the limiting nutrient in these calcium carbonate-rich shallow marine environments.

Seagrasses are important primary producers in the shallow oligotrophic waters of the Great Bahama Bank, in part because they are able to exploit phosphate sources in the sediment (Short et al. 1987). However few studies of seagrass density and distribution in carbonate environments have examined these topics in the context of phosphate delivery and deposition. Satellite imagery of seagrass density across GBB shows that seagrass distribution is greatest near the bank margins and decreases toward the center of the bank, particularly behind the islands, possibly due to low exchange of nutrients (Dierssen et al. 2003). Further investigation into seagrass density at the margin reveals that seagrass density appears to be highest in areas of high flow, consistent with Kindler and Hine's (2009) observation that tidal exchange provides a persistent set-up by which water is piled up against the bank margin and flows through the inter-island gaps, preferentially augmenting the daily flood-tidal currents over the ebb-tidal currents.

This study quantified the flux of phosphorus from the water column to the sediments, elucidated the source of the phosphorus associated with particle deposition, and examined the fate of the phosphorus that was deposited. My hypothesis is that seagrass distribution on the GBB is controlled by the pattern of oceanic nutrient, particularly phosphorus, deposition to the sediments. Because there are no significant local terrestrial inputs, the waters are clear and oligotrophic, and the sediments are composed of calcium carbonate which results in phosphorus limitation, these regions of high flow and exchange should promote phosphate delivery and deposition to the sediments where they become available to the seagrass. The work was performed to answer two questions: How does flow affect the distribution and density of seagrass across the Bahama Bank, and how does biogeochemistry interact with geography to determine the large-scale pattern of seagrass distribution? Answers to these questions will provide new information about the physical/chemical controls on productivity and maintenance of important coastal ecosystems as well as about carbon and nutrient dynamics in productive coastal environments.

III-2. Methods

III-2 a. *Study Site and Sample Collection*

Sediment and seagrass samples were collected by divers in May-June 2002 and 2003 at various sites near the Caribbean Marine Research Center (CMRC) located on Lee Stocking Island (LSI), Exuma Cays, Bahamas (Fig. 2). The environment around LSI is described in section II-2a.

The seagrass studies carried out at each site in parallel with geochemical studies included the analysis of shoot density (shoots m^{-2}seafloor) and shoot-specific one-sided leaf area (m^2 leaf shoot^{-1}) in 20 to 40 randomly located 0.1 m^2 quadrats at each site. These procedures are described in detail elsewhere (Burdige and Zimmerman 2002; Bodensteiner 2006). Leaf area index (LAI) was calculated as the product of mean shoot density and mean shoot-specific, one-sided leaf area, and is therefore defined as the one-sided leaf area per square meter of seafloor (m^2leaf m^{-2}seafloor).

Tidal current flow velocities were determined by first measuring the current velocities (cm s^{-1}) over several tidal cycles at each of the sites using a Marsh-McBirney electromagnetic flow meter. Tidal height velocities (cm h^{-1}) were determined by calculating the time derivatives of a 3rd order polynomial fit to short segments of tidal height predictions (N. Smith HBOI pers. comm.) each day over the period May 27 to June 18, 2003. Vertical tidal velocities and the horizontal current velocities at each site were positively correlated with varying slopes at the different sites. The slopes of these curves were used to compute an amplitude index of the horizontal tidal current velocity for each of the sites on LSI.

Small sediment traps were designed to measure particle deposition, minimizing interference with the water flow and the plant canopy. Cylindrical plastic 15 mL centrifuge tubes with an aspect ratio of 8.3 were chosen to maximize trap capture efficiency (Hardgrave and Burns 1979; Blomquist and Hakanson 1989; Gacia et al. 1999). The tubes were attached to a PVC frame with arms arranged in a helical pattern so that upper traps were not situated immediately above lower traps. Three replicate tubes were placed on each arm at heights of 20, 40, 60, 80, and 100 cm above the bottom to correct for the effects of near-bottom resuspension on the sediment trap data (Fig. 9). The tubes were filled with 3.7% formaldehyde solution in seawater (pH 8.2) prior to deployment and traps were deployed by divers at each of the sites for two one-week Material collected in the traps was pelleted by centrifugation (~1,000 g), washed briefly in deionized water, and dried at 60°C to constant weight in preparation for phosphorus analysis.

III-2 b. *Analytical Methods*

Total phosphorus, inorganic phosphorus, and the organic phosphorus content of sediment and sediment trap samples were determined in triplicate using a procedure modified from Aspila et al. (1976). Sediment trap total phosphorus analyses were performed at Moss Landing Marine Laboratory in Moss Landing, California by Laura Bodensteiner from December 2002 to January 2003. Sediment trap inorganic phosphorus analyses were performed at Old Dominion University in Norfolk, Virginia by Mandy Stoughton in November 2006. For total phosphorus, approximately 1 gram of dried sediment was weighed, covered, and ignited at 500-550° C for three hours in a muffle furnace. Phosphorus was extracted from the ignited sediments in 50 mL of 1 N HCl followed by gentle shaking overnight (12-14 hours). Total phosphorus was determined colorimetrically using the phosphomolybdate blue method described by Strickland and Parsons (1968). The same procedure was used to obtain the concentration of inorganic phosphorus with the exception that the sample was not ignited. Organic phosphorus was calculated as the difference between the total and inorganic phosphorus concentrations.

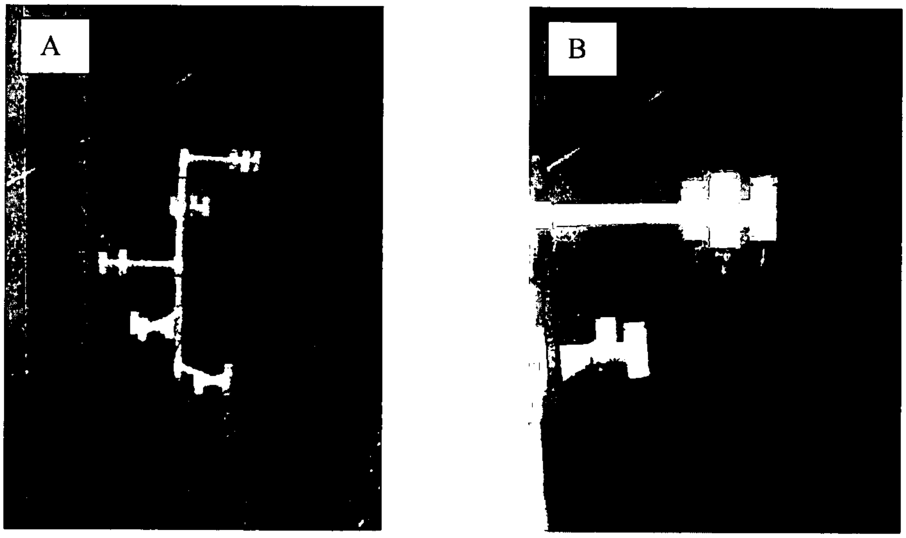

Figure 10. Photographs of sediment trap setup. A. The total height of the trap is 100 cm, and the arms are 20, 40, 60, 80, and 100 cm above the seafloor respectively. B. Close-up of one of the trap arms, with 3 centrifuge tubes in place.

III-3. Results

Upon examination of the total phosphorus concentrations in the sediment trap samples, it was discovered that a mistake had been made in the initial input of the data. Once this error was corrected, it was also discovered that for many samples the total phosphorus concentration (μmol P g^{-1} dw) was smaller than the inorganic phosphorus concentration. Since inorganic phosphorus is a component of total phosphorus, this is physically impossible. Further examination of the data analysis revealed no issues in the inorganic phosphorus analysis; however, a problem was discovered in the analysis of total phosphorus that resulted in the abnormally low concentrations being determined.

This analytical problem dealt with the volume of acid relative to water used in the dilution of HCl extracts that underwent colorimetric phosphate analysis. In the total phosphorus extracts, the volume of acid used to extract the phosphate from the ignited sediments was too large relative to the volume of water used for dilution, resulting in the pH being too low for the phosphate analysis. To correct the data for this observed pH effect, a study was performed using a 3 mM phosphate standard and varying amounts of acid and water. A 10 mL mixture of acid and water in varying concentrations was spiked with either 0.1 mL or 0.05 mL of a 3 mM phosphate standard. Each of these solutions of known phosphate concentration were analyzed colorimetrically in triplicate and percent recoveries were calculated (Table A5). Percent recoveries varied with the fraction of water in the solution according to a sigmoid function (Fig. 11).

Experimental results were fit to a sigmoid function using cftool in Matlab (The MathWorks, Inc., 1994-2012). The resulting fit to the data in Fig. 11 ($y=0.1439 +$ $(97.47/ (1 + 51.34^{-17.01x})$) was then used to calculate the corrected total phosphorus concentrations. The correction worked very well for those samples in which little to no water was added for dilution but absorbances were still obtained; however, it could not correct those samples in which negative absorbances were obtained, so these samples were excluded from data analysis and interpretation.

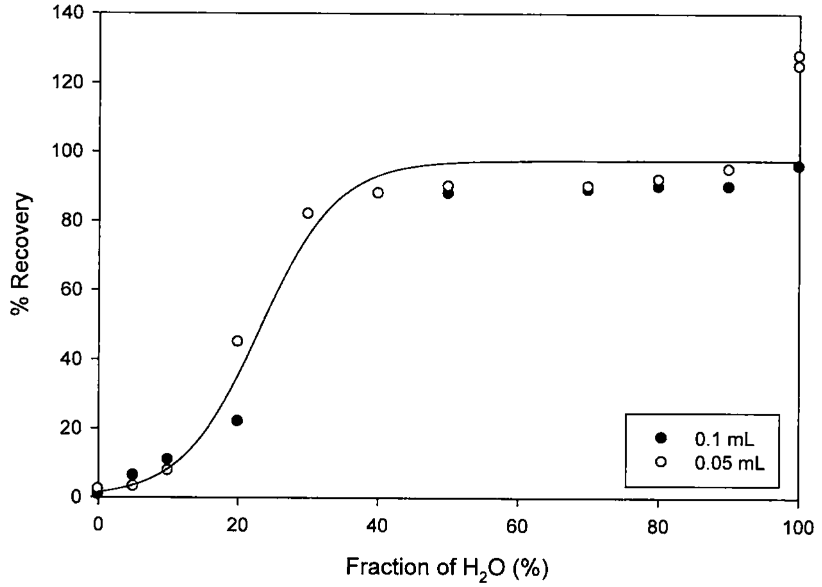

Figure 11. Results of an experiment performed to correct for the pH effect on the phosphate analysis of the sediment trap total phosphorus samples.

After this correction of the phosphorus concentrations in the sediment particles, complete profiles of the resulting phosphorus fluxes existed for only a few of the LSI sites. Where complete profiles existed, the structure of the profiles exhibited an exponential behavior (see, for example, results from the Ooid Shoals site in Fig. 12). At the same time though, the mass flux data for each deployment (Table A6) also decreased exponentially with height above the seafloor. Such profiles therefore suggest that in the sediment traps there was a mixture of newly deposited and resuspended phosphorus, and that the flux of the latter decreased in magnitude with height above the seafloor until the profile reached an asymptote and the true (primary) particle flux was attained (Valeur 1994; Perjup et al. 1996; Gacia et al. 1999). Because the profiles all reached an asymptote at one meter above the seafloor, the phosphorus flux at one meter above the seafloor was assumed to be the primary sediment flux.

Based on the available data, it was also assumed that the phosphorus content of the primary flux particles (i.e., in the 1 m trap samples) was constant across all sites, and was taken to be the mean concentration of total, inorganic and organic phosphorus in the 1 m flux particles (Table 5). Mass fluxes (Table A6) were then used with the mean values in Table 5 to calculate a complete set of phosphorus fluxes to the sediment (Table A7). These fluxes varied by more than two orders of magnitude across the sites (Table 6).

Tidal current velocity (TCV) index values at the same sites in the LSI region also showed spatial variation (Table 6). Regression analysis revealed slopes at each of the sites that, with the exception of Twin Beaches, were statistically different from zero (Fig. 13). The magnitude of the tidal current velocity index at Twin Beaches was taken as zero for data analysis and interpretation.

A positive exponential relationship was observed between the total phosphorus fluxes and the TCV index values (Fig. 14). The site which exhibited the largest tidal current velocity and largest phosphorus fluxes, Ooid Shoals, is a site with an LAI value of 0 indicating no seagrass in this region of LSI.

Table 5. Corrected phosphorus concentration data. The resulting means were used with the mass fluxes to calculate a complete data set of phosphorus fluxes. CM=Channel Marker, HW=Halfway, AC=Adderly Cut, OS=Ooid Shoals, BB=Before Brigantines, TB=Twin Beaches, NC=New Cay.

		[P] in Flux (μmol g^{-1} DW)			
Site	Year	Deployment	TP	IP	OP
CM	2002	1	1.5		
	2002	2	1.9		
HW	2002	2	0.13		
AC	2002	2	0.85		
OS	2002	1	6.5*		
	2002	2	8.8*		
CM	2003	1	0.95	0.38	0.57
	2003	2	0.37*	1.06*	
HW	2003	1	0.31*	4.33*	
	2003	2	26.8*	0.14*	
AC	2003	1	3.8	0.32	3.48
		2	2.85	0.76	2.09
BB	2003	1	0.67	0.65	0.02
		2	2.1	0.61	1.49
OS	2003	1	0.48	0.35	0.13
TB	2003	1	1.57	1.51	0.06
TB	2003	2	1.77	0.35	1.42
NC	2003	1	0.25*	0.63*	
	2003	2	0.74	0.38	0.36
		Mean	1.5	0.6	0.9
		St Dev	1	0.4	1.2
		Std Error	0.3	0.1	0.4

* These data were not used in calculation of the mean values because the values were anomalously high or the inorganic P concentrations were larger than the total P concentrations.

** Organic P mean was calculated by difference of the mean total and inorganic P concentrations, so the standard deviation and standard error were not calculated.

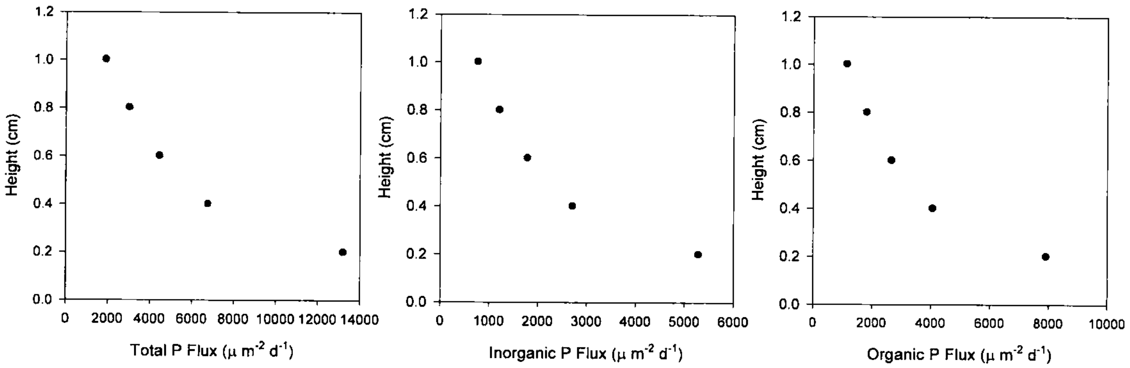

Figure 12. Total, inorganic, and organic phosphorus fluxes as a function of height above the bottom of the seafloor at Ooid Shoals for the first week's deployment.

Table 6. Total, inorganic, and organic mean phosphorus primary sediment fluxes at the LSI sites. AC = Adderly Cut, OS = Ooid Shoals, TB = Twin Beaches, CM = Channel Marker, HW = Halfway, BP = Briar Patch, NC = New Cay.

		Mean Phosphorus Deposition Rates (µmol m^{-2} d^{-1})					
Year	Station	Total P	St Dev TP	Inorganic P	St Dev IP	Organic P	St Dev Op
2003	AC	11.6	7.22	4.64	2.89	6.96	4.33
2003	BB	12.73	6.51	5.09	2.61	7.64	3.91
2003	CM	14.43	1.96	5.77	0.78	8.66	1.18
2003	HW	5.66	2.45	2.26	0.98	3.4	1.47
2003	NC	373.48	7.7	149.39	3.08	224.09	4.62
2003	OS	390.46	15.09	156.18	6.04	234.28	9.05
2003	TB	1.98	0.49	0.79	0.2	1.19	0.29
2002	CM	59.11	2.6	23.64	1.04	35.46	1.56
2002	AC	22.78	0.9	9.11	0.36	13.67	0.54
2002	HW	5.48	2.51	2.19	1	3.29	1.51
2002	TB	4.96	0.12	1.98	0.05	2.97	0.07

Table 7. Tidal current velocity slopes and the resulting tidal current velocity index values for the sites on LSI. Calculation of the TCV index from using the slope involved cancelling out the time and distance units in the slope values. Tidal current velocity data was taken in 2003 only, so it was assumed the measurements were the same in 2002.

Tidal Current Velocity (TCV) Index Values				
Year	2002			
Site	Slope	Std Error	TCV Index	Std Error
AC	2.28	0.21	6.34	0.58
BB	1.22	0.14	3.38	0.38
CM	1.68	0.19	4.66	0.53
HW	1.26	0.11	3.51	0.31
NC	1.94	0.19	5.4	0.52
OS	3.21	0.2	8.91	0.55
TB	-0.12	0.09	-0.32	0.25

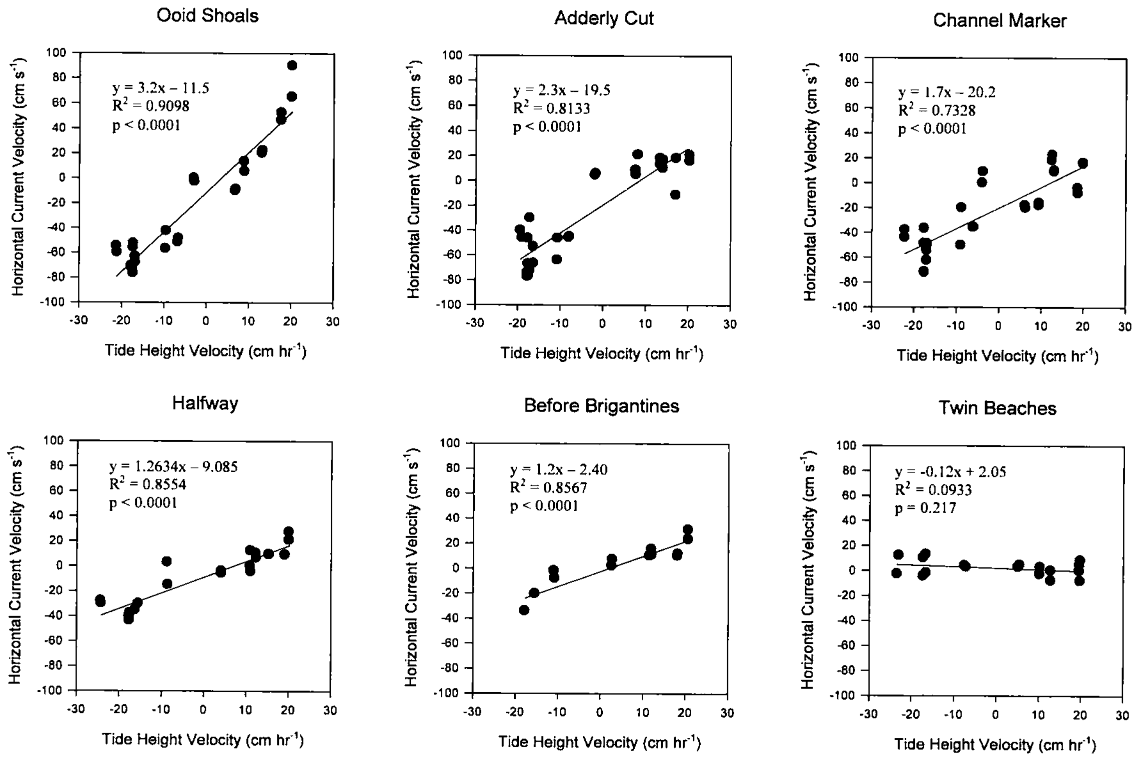

Figure 13. Horizontal current velocity plotted as a function of tide height velocity for each of the LSI sites in 2003. The slopes of these curves were used to compute an amplitude index of the horizontal tidal current velocity for each of the sites on LSI.

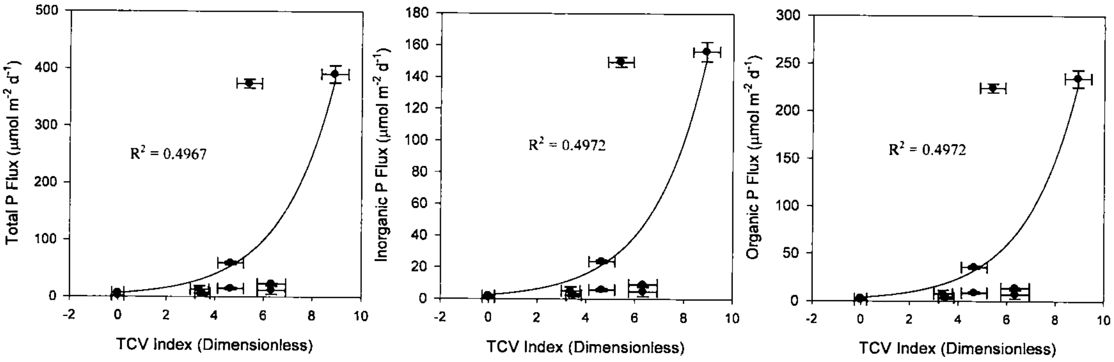

Figure 14. TCV index as a function of the total, inorganic, and organic phosphorus fluxes at the LSI sites.

There was a nonlinear relationship between the TCV index values and LAI (Fig. 15), as well as a quadratic relationship between TCV index values and above ground productivity (Fig. 16). Exclusion of the TB site from figure 15 (TCV=0 and for which there is no above ground productivity data in Fig. 16) results in a similar quadratic relationship between the TCV index and LAI.

Results indicated an initial increase in sedimentary phosphorus with increasing phosphorus flux at all sites except Ooid Shoals, where sediment P was lower than predicted by P flux. (Fig. 17).

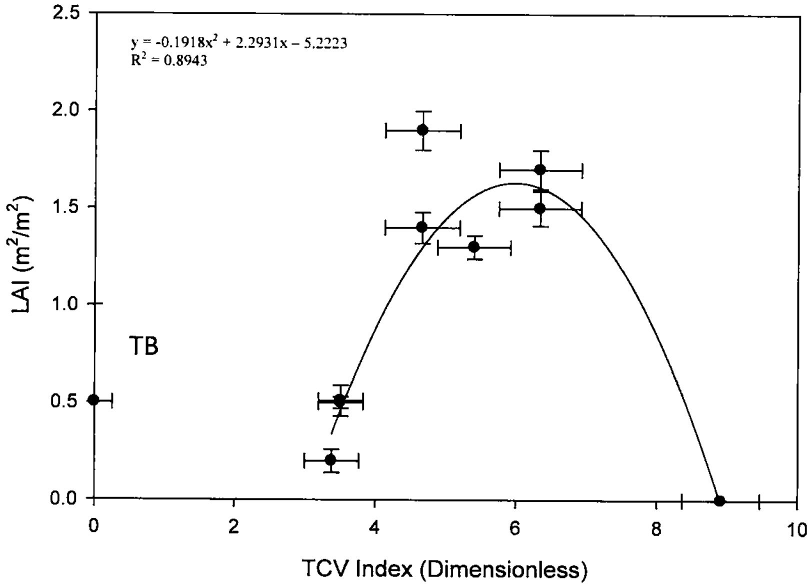

Figure 15. Relationship between the TCV index values and seagrass density at sites on Lee Stocking Island. The quadratic fit to the data excludes the Twin Beaches site.

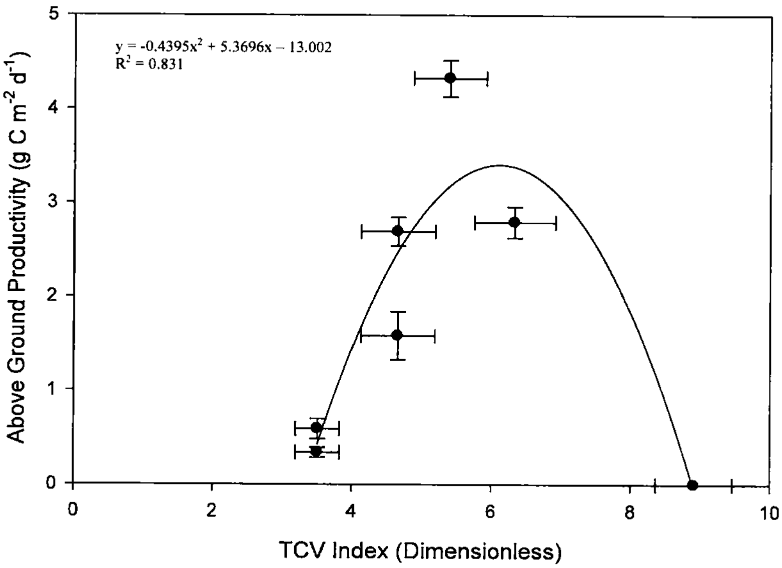

Figure 16. Quadratic relationship between the TCV index values and above ground productivity.

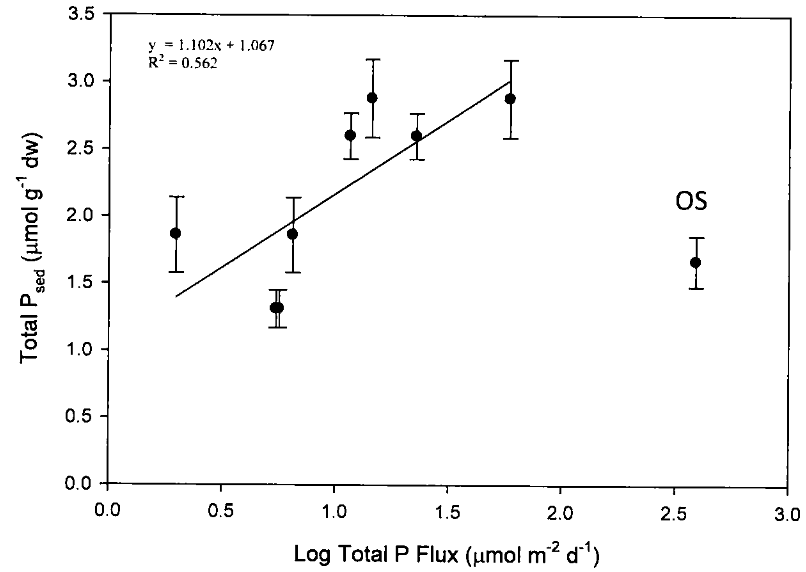

Figure 17. Relationship between the log of the total phosphorus flux and total phosphorus in the sediment at sites on Lee Stocking Island. The best fit line to the data excludes the Ooid Shoals site.

III-4. Discussion

Spatial variation in the magnitude of the fluxes, sediment phosphorus concentrations, and seagrass densities is evident, especially between the seagrass sites and Ooid Shoals. Much of this spatial variation stems from the pattern of flow in the region (Reijmer et al. 2009). Tidal current velocities are largest at Ooid Shoals, resulting in the highest phosphorus fluxes to the sediment (Fig. 14), but tidal velocities may be too large for mechanical stabilization of seagrass and the sediments (Fig. 15, 16). This then results in the highest resuspension flux (results not shown here) as well as lower sediment phosphorus concentrations (Fig. 17). Figure 16 suggests that when tidal current velocities are low, there is still enough phosphorus available locally to support low seagrass densities.

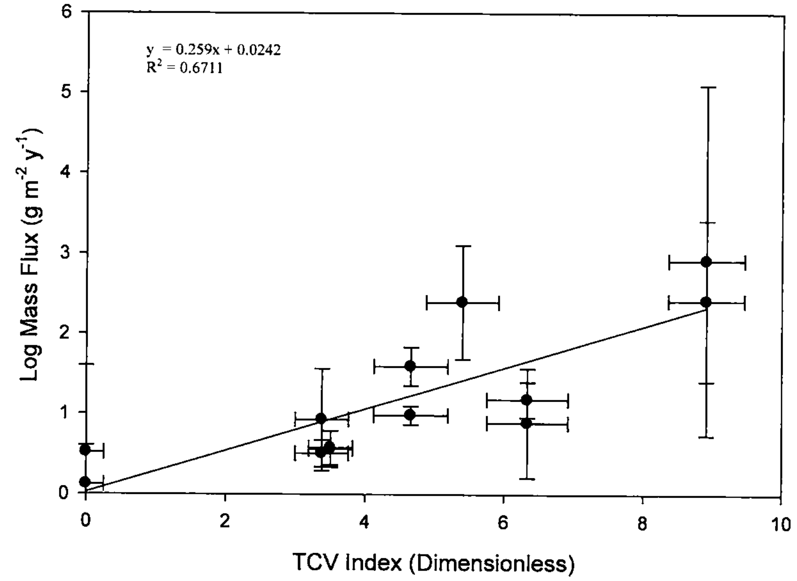

Figure 18. Exponential relationship between magnitude of the tidal current velocity and the mass flux to the sediment.

Ooid Shoals is an outlier among the LSI sites because it is a migrating dune field (Gonzalez and Eberli 1997). Further evidence of this can be seen by calculating the mass accumulation rate at this site and comparing it with accumulation rates at the other LSI sites as well as those from previous studies on GBB. Mass accumulation rates were calculated as the primary flux of all material and exhibit an exponential increase with tidal current velocity (Fig. 18). This relationship is similar to that observed by Brand et al. (2010) in a study of resuspension in the shallow waters of South San Francisco Bay. They observed exponential increases in sediment fluxes due to the nonlinear interaction between wind waves and tidal currents, but also observed smaller exponential increases in the sediment flux when sites were examined solely for the influence of tidal currents.

The mass accumulation rate calculated in the current study for Ooid Shoals was 1749 g m^{-2} y^{-1}, whereas the average for the remaining LSI sites was 24 g m^{-2} y^{-1}. These accumulation rates for the ooid sands around LSI can be compared with literature values from the GBB banktop where aragonitic muds accumulate at rates of 300-500 g m^{-2} y^{-1} (Broeker and Takahashi 1966; Milliman et al. 1993). In contrast, Steinen et al. (1988) estimated algal lime-mud production across the banktop at 20 g m^{-2} y^{-1}, more than an order of magnitude lower. The accumulation rates calculated in the current study are gross accumulation rates at a particular time (i.e., "snapshot" rates), and are not necessarily representative of the long-term net accumulation in the LSI region. Gross accumulation rates are different from net accumulation rates because they do not take into account export or dissolution rates. Further evidence of spatial heterogeneity in sediment deposition in the LSI region comes from the 1-2 order of magnitude difference between measured accumulation rates at Ooid Shoals versus other sites in this region, as well as the difference of a factor of three between accumulation rates at Ooid Shoals and previously calculated rates for aragonitic muds on the bank that should accumulate faster than ooid sands. The important point here is that this is not random variability. These differences are due to flow.

In comparison to Ooid Shoals, tidal flow velocities at the seagrass sites are lower, resulting in smaller fluxes to the sediment (Fig. 14), but these sites also have lower resuspension fluxes (results not shown) and higher sedimentary phosphorus concentrations (Fig. 6). Among the seagrass sites, the two with the highest tidal flow velocities, sediment fluxes, and seagrass densities are Channel Marker and Adderly Cut, which are geographically positioned on the bank margin at the edges of the tidal flow channel near the northern end of LSI (Fig. 1). The remaining seagrass sites are geographically positioned on the bank margin behind LSI where low flow and exchange brings fewer particles with nutrients needed for growth. This conclusion that tidal flow and exchange bring nutrients onto the Banks can also be seen in the WS-GBB data since sites on the margins of the Banks show larger sedimentary phosphorus concentrations than those closer to the interior of the Banks (Fig. 5).

III-5. Conclusions and Future Work

Tidal current flow is highest at sites at the margins of the Banks around LSI and lowest at those directly behind the islands (Fig. 13), resulting in exponential increases in the total phosphorus fluxes to the sediment (Fig. 14). It also suggests that seagrass density and productivity are controlled by hydrodynamics and nutrient delivery (Fig. 15, 16). These observations suggest that tidal flow and exchange bring nutrients onto the Banks, a conclusion consistent with the WS-GBB data, where it can be seen that sites on the margins of the Banks show larger sedimentary phosphorus concentrations than those closer to the interior of the Banks (Fig. 5). With the exception of Ooid Shoals, which is a migrating dune field, phosphorus content in the sediments appears to increase linearly with the phosphorus flux to the sediments (Fig. 17). Phosphorus is delivered in the flux primarily as organic phosphorus (Table 5) to be regenerated in the sediments as inorganic phosphorus, and then either taken up by seagrasses or adsorbed onto carbonate grains. The latter is related to the specific surface area (Fig. 7) and total phosphorus content (Table 3) of sediment particles, consistent with a multi-step mechanism in which phosphorus is initially rapidly adsorbed to available surface sites and then is more slowly transformed into the carbonate matrix. Finally, a link between the magnitude of the sediment phosphorus pool and LAI (Fig. 6) suggests seagrass growth occurs through utilization of nutrient resources in the sediment, a likely mechanism for which is metabolic carbonate dissolution (Fig. 9).

Maintenance of Bahamian seagrass meadows therefore requires carbonate dissolution to mobilize the sedimentary phosphorus as well phosphorus associated with the organic matter retention and in situ decomposition of seagrass detritus (Fig. 19). Future work on this topic should include quantifying rates of sediment phosphorus mobilization, especially organic matter decomposition, as well as rates of uptake by carbonate sediments and seagrasses.

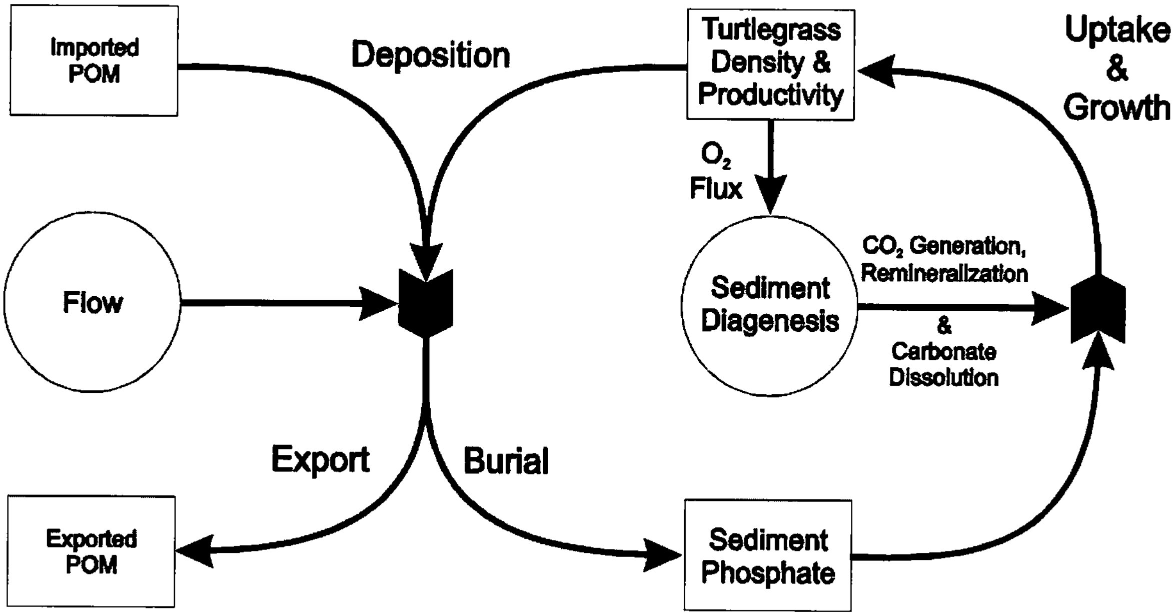

Figure 19. Conceptual diagram demonstrating the maintenance of Bahamian seagrass meadows.

CHAPTER IV

SUMMARY

This thesis presented two related studies focusing on phosphorus cycling in calcium carbonate sediments-seagrass systems. This chapter summarizes the major conclusions drawn from these studies.

In chapter II, a link between the magnitude of the sedimentary phosphorus pool and seagrass density was observed. This association, along with phosphorus inventory calculations, suggested that seagrasses maintain high productivity through utilization of nutrient resources in the sediment. Metabolic carbonate dissolution provides a likely mechanism for seagasses to access these resources. Seagrass respiration produces CO_2 which dissolves carbonate grains releasing the adsorbed phosphate to the pore waters and seagrass roots supporting seagrass growth. Additional conclusions were that a surface area control of phosphate is evident but not the primary factor behind phosphate adsorption. While results provide no evidence for CFA precipitation, this may be due to low rates of this transformation relative to the time scales of other sediment processes such pore water advection.

In chapter III, observations suggest tidal current flow in the LSI region strongly controls nutrient delivery and deposition in the LSI region. Since growth is phosphorus limited and delivery and deposition provide phosphorus to the sediments, tidal flow dynamics play a crucial role in regulating the distribution and productivity of seagrass meadows. Once in the sediments, seagrasses access those nutrient resources for growth by metabolic carbonate dissolution. Finally, it is the competition between biotic and abiotic uptake that results in the phosphorus limitation observed for seagrasses growing in calcareous sediments. Therefore, further investigations of the rates of sediment phosphorus mobilization are necessary to better understand the biogeochemistry of carbonate sediments and the associated sediment-seagrass interactions. Such investigations would provide important new information about the impacts of these sedimentary processes on the regional and global carbon cycle as well as about the maintenance of shallow water tropical and subtropical carbonate ecosystems.

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APPENDIX

LSI 6 PHOSPHORUS DATA

Table A1. Solid phase phosphorus data from the LSI 6 sampling trip. AC = Adderly Cut, OS = Ooid Shoals, TB = Twin Beaches, CM = Channel Marker, HW = Halfway, BP = Briar Patch.

Site	Depth (cm)	Total P (μmol g^{-1} dw)	Inorganic (μmol g^{-1} dw)	Organic (μmol g^{-1} dw)
AC 2-1	0.5	2.66	0.79	1.87
AC 2-2	1.5	2.49	0.83	1.67
AC 2-3	2.5	2.59	0.83	1.76
AC 2-4	3.5	2.66	0.85	1.82
AC 2-5	4.5	2.75	0.96	1.79
AC 2-6	5.5	2.99	0.93	2.06
AC 2-7	6.5	2.76	0.84	1.92
AC 2-8	7.5	2.76	0.84	1.92
AC 2-9	8.5	2.71	0.87	1.84
AC 2-10	9.5	2.78	0.83	1.94
AC 2-11	10.5	2.51	0.73	1.78
AC 2-12	11.5	2.62	0.86	1.77
AC 2-13	12.5	2.57	0.70	1.87
AC 2-14	13.5	2.59	0.81	1.78
AC 1-1	0.5	2.12	0.87	1.25
AC 1-2	1.5	2.31	0.83	1.48
AC 1-3	2.5	2.59	0.93	1.66
AC 1-4	3.5	2.58	0.84	1.74
AC 1-5	4.5	2.56	0.74	1.82
AC 1-6	5.5	2.47	0.73	1.74
AC 1-7	6.5	2.55	0.83	1.72
AC 1-8	7.5	2.73	0.85	1.88
AC 1-9	8.5	2.59	0.82	1.77
AC 1-10	9.5	2.78	0.82	1.95
AC 1-11	10.5	2.54	0.78	1.76
AC 1-12	11.5	2.59	0.79	1.80
AC 1-13	12.5	2.49	0.77	1.72
AC 1-14	13.5	2.31	0.84	1.47
AC 1-15	14.5	2.79	0.82	1.97

Table A1. Continued.

Site	Depth (cm)	Total P (μmol g^{-1} dw)	Inorganic P (μmol g^{-1} dw)	Organic P (μmol g^{-1} dw)
OS 1-1	0.5	1.51	0.48	1.03
OS 1-2	1.5	1.77	0.52	1.25
OS 1-3	2.5	1.77	0.56	1.21
OS 1-4	3.5	2.10	0.62	1.48
OS 1-5	4.5	1.87	0.61	1.26
OS 1-6	5.5	1.86	0.54	1.31
OS 1-7	6.5	1.89	0.58	1.31
OS 1-8	7.5	1.81	0.53	1.27
OS 1-9	8.5	1.90	0.56	1.34
OS 1-10	9.5	1.81	0.60	1.21
OS 1-11	10.5	1.89	0.57	1.33
OS 1-12	11.5	1.90	0.57	1.33
OS 2-1	0.5	1.44	0.47	0.97
OS 2-2	1.5	1.50	0.47	1.03
OS 2-3	2.5	1.58	0.47	1.11
OS 2-4	3.5	1.49	0.49	1.00
OS 2-5	4.5	1.43	0.55	0.88
OS 2-6	5.5	1.51	0.48	1.03
OS 2-7	6.5	1.51	0.50	1.01
OS 2-8	7.5	1.46	0.46	1.00
OS 2-9	8.5	1.54	0.51	1.03
OS 2-10	9.5	1.47	0.54	0.93
OS 2-11	10.5	1.66	0.47	1.20
OS 2-12	11.5	1.65	0.53	1.12
OS 2-13	12.5	1.55	0.46	1.10
TB 1-1	0.5	1.62	0.42	1.21
TB 1-2	1.5	1.61	0.38	1.23
TB 1-3	2.5	1.64	0.34	1.31
TB 1-4	3.5	1.65	0.37	1.28
TB 1-5	4.5	1.59	0.36	1.23
TB 1-6	5.5	1.75	0.34	1.41
TB 1-7	6.5	1.80	0.31	1.49
TB 1-8	7.5	1.94	0.37	1.57
TB 1-9	8.5	1.99	0.39	1.60
TB 1-10	9.5	1.93	0.41	1.53
TB 1-11	10.5	2.14	0.40	1.74
TB 1-12	11.5	2.20	0.44	1.76
TB 1-13	12.5	2.08	0.38	1.69

Table A1. Continued.

Site	Depth (cm)	Total P (µmol g^{-1} dw)	Inorganic P (µmol g^{-1} dw)	Organic P (µmol g^{-1} dw)
TB 1-14	13.5	2.18	0.39	1.79
TB 2-1	0.5	1.96	0.50	1.47
TB 2-2	1.5	1.81	0.42	1.38
TB 2-3	2.5	1.79	0.44	1.34
TB 2-4	3.5	1.79	0.42	1.37
TB 2-5	4.5	1.80	0.39	1.41
TB 2-6	5.5	1.73	0.42	1.32
TB 2-7	6.5	0.81	0.44	0.37
TB 2-8	7.5	1.85	0.43	1.42
TB 2-9	8.5	1.96	0.43	1.53
TB 2-10	9.5	1.93	0.55	1.38
TB 2-11	10.5	2.04	0.50	1.54
TB 2-12	11.5	2.11	0.57	1.54
TB 2-13	12.5	2.16	0.50	1.66
TB 2-14	13.5	2.12	0.54	1.57
TB 2-15	14.5	2.08	0.51	1.57
CM 11-1	0.5	2.57	0.94	1.64
CM 11-2	1.5	2.45	0.76	1.69
CM 11-3	2.5	2.59	0.79	1.80
CM 11-4	3.5	2.45	0.91	1.54
CM 11-5	4.5	2.59	1.04	1.54
CM 11-6	5.5	2.72	0.97	1.75
CM 11-7	6.5	3.61	1.06	2.54
CM 11-8	7.5	2.80	0.85	1.95
CM 11-9	8.5	3.03	0.94	2.09
CM 11-10	9.5	2.93	0.90	2.03
CM 11-11	10.5	3.05	0.86	2.19
CM 11-12	11.5	3.09	0.86	2.23
CM 11-13	12.5	2.58	0.79	1.80
CM 11-14	13.5	2.79	0.88	1.91
CM 11-15	14.5	3.04	0.96	2.08
CM 11-16	15.5	3.03	1.04	1.99
CM 11-17	16.5	3.01	0.96	2.05
CM 11-18	17.5	3.18	1.02	2.16
CM 12-1	0.5	2.69	0.79	1.90
CM 12-2	1.5	2.39	0.71	1.68
CM 12-3	2.5	2.40	0.78	1.62
CM 12-4	3.5	2.51	0.80	1.72
CM 12-5	4.5	2.56	0.84	1.73

Table A1. Continued.

Site	Depth (cm)	Total P (μmol g^{-1} dw)	Inorganic P (μmol g^{-1} dw)	Organic P (μmol g^{-1} dw)
CM 12-6	5.5	2.92	0.83	2.09
CM 12-7	6.5	2.95	0.85	2.10
CM 12-8	7.5	2.98	0.85	2.13
CM 12-9	8.5	3.00	0.82	2.17
CM 12-10	9.5	2.73	0.77	1.95
CM 12-11	10.5	2.98	0.76	2.22
CM 12-12	11.5	3.36	0.80	2.56
CM 12-13	12.5	2.73	0.88	1.86
CM 12-14	13.5	2.82	0.84	1.98
CM 12-15	14.5	2.89	0.93	1.96
CM 12-16	15.5	3.05	0.93	2.12
CM 12-17	16.5	3.13	0.95	2.18
CM 12-18	17.5	3.36	0.93	2.43
CM 12-19	18.5	3.27	0.88	2.39
CM 12-20	19.5	3.03	0.92	2.11
HW 1	0.5	1.15	0.36	0.79
HW 2	1.5	1.13	0.34	0.80
HW 3	2.5	1.10	0.33	0.77
HW 4	3.5	1.22	0.35	0.87
HW 5	4.5	1.30	0.40	0.90
HW 6	5.5	1.36	0.36	1.00
HW 7	6.5	1.53	0.42	1.10
HW 8	7.5	1.55	0.42	1.13
HW 9	8.5	1.43	0.41	1.03
HW 10	9.5	1.42	0.34	1.09
HW 11	10.5	1.43	0.32	1.11
HW 12	11.5	1.49	0.38	1.11
HW 13	12.5	1.42	0.40	1.01
HW 14	13.5	1.33	0.34	0.99
HW 15	14.5	1.29	0.37	0.92
HW 16	15.5	1.33	0.40	0.93
HW 17	16.5	1.26	0.40	0.86
HW 2-1	0.5	1.27	0.44	0.83
HW 2-2	1.5	1.03	0.37	0.66
HW 2-3	2.5	0.93	0.34	0.59
HW 2-4	3.5	1.17	0.39	0.79
HW 2-5	4.5	1.15	0.40	0.75
HW 2-6	5.5	1.26	0.39	0.86
HW 2-7	6.5	1.40	0.37	1.03

Table A1. Continued.

Site	Depth (cm)	Total P (μmol g^{-1} dw)	Inorganic P (μmol g^{-1} dw)	Organic P (μmol g^{-1} dw)
HW 2-8	7.5	1.38	0.43	0.94
HW 2-9	8.5	1.31	0.41	0.89
HW 2-10	9.5	1.29	0.35	0.94
HW 2-11	10.5	1.34	0.35	0.99
HW 2-12	11.5	1.39	0.38	1.01
HW 2-13	12.5	1.46	0.38	1.08
HW 2-14	13.5	1.36	0.34	1.02
HW 2-15	14.5	1.32	0.36	0.96
BP 1-1	0.5	3.07	0.92	2.15
BP 1-2	1.5	2.73	0.72	2.00
BP 1-3	2.5	3.65	0.98	2.67
BP 1-4	3.5	3.70	1.37	2.33
BP 1-5	4.5	4.16	0.92	3.24
BP 1-6	5.5	4.42	0.88	3.54
BP 1-7	6.5	4.27	1.00	3.27
BP 1-8	7.5	4.23	0.95	3.27
BP 1-9	8.5	4.60	0.95	3.65
BP 1-10	9.5	4.18	0.86	3.32
BP 1-11	10.5	4.17	1.44	2.73
BP 1-12	11.5	3.95	0.82	3.13
BP 1-13	12.5	4.10	1.07	3.03
BP 1-14	13.5	3.70	0.83	2.87
BP 1-15	14.5	3.09	0.65	2.44
BP 1-16	15.5	3.59	0.69	2.90
BP 1-17	16.5	3.62	0.70	2.91
BP 1-18	17.5	3.75	0.71	3.04
BP 2-1	0.5	3.38	0.95	2.43
BP 2-2	1.5	3.25	0.77	2.49
BP 2-3	2.5	3.43	0.96	2.47
BP 2-4	3.5	3.84	0.99	2.84
BP 2-5	4.5	4.27	1.06	3.21
BP 2-6	5.5	4.87	1.14	3.73
BP 2-7	6.5	5.35	1.07	4.28
BP 2-8	7.5	5.00	0.91	4.08
BP 2-9	8.5	5.07	1.12	3.95
BP 2-10	9.5	5.30	0.96	4.34
BP 2-11	10.5	4.78	0.93	3.85
BP 2-12	11.5	5.10	0.85	4.24
BP 2-13	12.5	4.45	0.85	3.60

Table A1. Continued.

Site	Depth (cm)	Total P (μmol g^{-1} dw)	Inorganic P (μmol g^{-1} dw)	Organic P (μmol g^{-1} dw)
BP 2-14	13.5	4.08	0.76	3.32
BP 2-15	14.5	3.60	0.66	2.94

WS-GBB PHOSPHORUS DATA

Table A2. Solid phase phosphorus data from the WS-GBB sampling trip. Surface sedimentary phosphorus concentrations (0 - 0.5 cm) were analyzed at each site for both of the cores, A and B.

Site	Total P (μmol g^{-1} dw)	Inorganic P (μmol g^{-1} dw)	Organic P (μmol g^{-1} dw)
1A-1	2.8	1.36	1.44
2A-1	1.85	0.43	1.42
3A-1	3.85	2.34	1.51
4A-1	2.39	0.96	1.43
5A-1	2.53	1.63	0.9
6A-1	1.07	0.49	0.58
8A-1	1.44	0.446	0.994
9A-1	1.36	0.207	1.15
10A-1	1.36	0.32	1.04
11A-1	1.25	0.164	1.08
12A-1	3.27	1.46	1.81
13A-1	1.48	0.35	1.13
14A-1	1.06	0.15	0.91
15A-1	1.81	0.27	1.54
16A-1	0.87	0.15	0.72
17A-1	1.55	0.371	1.18
18A-1	0.98	0.3	0.68
19A-1	1.52	0.659	0.861
20A-1	1.73	0.34	1.39
21A-1	1.33	0.79	0.54
24A-1	1.2	0.08	1.12
1B-1	3.57	2.11	1.46
2B-1	1.63	0.476	1.15
3B-1	3.84	2.16	1.68
4B-1	2.41	0.623	1.787
5B-1	2.56	0.819	1.741
6B-1	1.03	0.487	0.543
8B-1	1.5	0.417	1.083
9B-1	1.36	0.338	1.022
10B-1	1.45	0.58	0.87
11B-1	1.22	0.197	1.023
12B-1	3.14	1.44	1.7
13B-1	1.51	0.3	1.21
14B-1	1.1	0.155	0.945

Table A2. Continued.

Site	Total P (μmol g^{-1} dw)	Inorganic P (μmol g^{-1} dw)	Organic P (μmol g^{-1} dw)
15B-1	1.55	0.3	1.25
16B-1	0.92	0.157	0.763
17B-1	1.59	0.408	1.182
18B-1	1.19	0.274	0.916
19B-1	1.45	0.65	0.8
20B-1	1.68	0.328	1.352
21B-1	1.24	0.791	0.449
24B-1	1.14	0.085	1.055

PORE WATER FLUORIDE DATA

Table A3. Pore water fluoride concentrations at the Adderly Cut and Channel Marker sites in the LSI region of the Bahamas. Additions in the sample column indicate when different samples from the same depths were combined to resolve sample limitation.

Sample	Depth (cm)	[F-] (µM)
AC1BW1	0	80.99
AC11+21+31	1	84.97
AC12+22+32	2	65.09
AC14+24+34	4	69.33
AC35+35I	5	69.92
AC18+38	8	67.03
AC110+310	10	68.75
AC115+215+315	15	72.32
AC120+220+320	20	74.17
CM181+191	1	66.76
CM182+192	2	72.94
CM1815+1915	15	72.62
CM1820+1920	20	76.40
CM1BW1	0	60.66
CM111+121+131	1	80.61
CM112+122+132	2	80.95
CM114+124+134	4	69.80
CM125+135	5	73.74
CM118+128	8	68.63
CM1115+1215+1315	15	75.32
CM1220+1320	20	71.59
CM151+161	1	76.60
CM152+162	2	74.36
CM154+164	4	71.59
CM155+165	5	49.31
CM1515+1615	15	75.32
CM1520+1620	20	64.16

SEDIMENT AND SEAGRASS PHOSPHORUS INVENTORY

Table A4. Phosphorus abundance in seagrass and sediments of LSI and WS-GBB sampling sites.

Site	Seagrass Total P (mmol m^{-2})	Total P_{sed} (mmol m^{-2})	Inorganic P_{sed} (mmol m^{-2})	Organic P_{sed} (mmol m^{-2})
CM	6.43	836 ± 84	255 ± 25	579 ± 75
HW	1.69	381 ± 41	109 ± 10	270 ± 39
AC	5.75	755 ± 49	240 ± 17	515 ± 47
TB	1.69	540 ± 81	124 ± 19	417 ± 76
BP	3.04	1184 ± 194	268 ± 53	917 ± 182
OS	0.00	485 ± 55	153 ± 14	333 ± 45
1	12.62	924 ± 158	504 ± 154	421 ± 4
2	3.25	515 ± 46	134 ± 10	380 ± 57
3	5.01	982 ± 2	575 ± 33	407 ± 31
4	7.58	752 ± 4	248 ± 75	504 ± 79
5	0.10	798 ± 7	384 ± 180	414 ± 186
6	0.00	335 ± 9	156 ± 1	179 ± 8
8	0.85	444 ± 13	130 ± 6	313 ± 19
9	0.00	434 ± 0	87 ± 30	347 ± 29
10	0.07	424 ± 19	136 ± 55	288 ± 36
11	0.30	394 ± 6.7	58 ± 7.5	336 ± 13
12	6.63	911 ± 26	412 ± 4	499 ± 22
13	2.54	443 ± 6.3	96 ± 11	346 ± 17
14	1.93	338 ± 9	48 ± 1	291 ± 8
15	4.06	458 ± 50	78 ± 6	381 ± 56
16	0.03	281 ± 11	48 ± 1.6	232 ± 10
17	1.59	492 ± 9	122 ± 8	370 ± 0.4
18	0.81	290 ± 40	77 ± 5	213 ± 45
20	3.65	515 ± 11	101 ± 3	414 ± 8
21	0.34	313 ± 16	193 ± 0.2	121 ± 16
24	1.18	367 ± 13	26 ± 1	341 ± 14

ACID EFFECT CORRECTION DATA

Table A5. Data from the experiment performed to correct for the pH effect on the phosphate analysis of the sediment trap total phosphorus samples.

$[PO_4]$ (µmol L^{-1})	Volume $[PO_4]$ std added (mL)	Volume H_2O (mL)	Total Volume (mL)	% Recovery
29.01	0.1	10	10	97
28.9	0.1	10	10	96
26.89	0.1	9	10	90
26.97	0.1	8	10	90
26.6	0.1	7	10	89
26.44	0.1	5	10	88
6.63	0.1	2	10	22
3.26	0.1	1	10	10.9
1.9	0.1	0.5	10	6.3
0.194	0.1	0	10	0.65
19.13	0.05	10	10	128
18.79	0.05	10	10	125
14.17	0.05	9	10	95
13.8	0.05	8	10	92
13.6	0.05	7	10	90
13.6	0.05	5	10	90
13.22	0.05	4	10	88
12.37	0.05	3	10	82
6.75	0.05	2	10	45
1.16	0.05	1	10	7.7
0.465	0.05	0.5	10	3.1
0.349	0.05	0	10	2.3

MASS FLUX DATA

Table A6. Mass fluxes with height above the bottom of the seafloor at the LSI sites for the first and second week's deployments with associated standard deviations (SD) and standard errors (SE).

			Mass Deposition Rates (g dw m^{-2} d^{-1})			
Year	Deployment	Sample	Mean Mass	SD Mass	SE Mass	height (m)
2002	1	CM1	62.14	2.19	1.27	1.00
2002	1	CM2	64.90	1.05	0.61	0.80
2002	1	CM3	67.97	2.91	1.68	0.60
2002	1	CM4	80.58	2.12	1.23	0.40
2002	1	CM5	93.28	2.19	1.26	0.20
2002	1	HW1	3.92	0.33	0.19	1.00
2002	1	HW2	3.73	0.57	0.33	0.80
2002	1	HW3	4.32	0.56	0.32	0.60
2002	1	HW4	4.77	0.55	0.32	0.40
2002	1	HW5	4.41	1.47	0.85	0.20
2002	1	OS1	1278.13	291.75	168.44	1.00
2002	1	OS2	2028.65	36.99	21.36	0.80
2002	1	OS3	2982.78	243.49	140.58	0.60
2002	1	OS4	4528.81	254.10	146.71	0.40
2002	1	OS5	8820.26	329.77	233.18	0.20
2002	1	TB1	2.28	0.10	0.06	1.00
2002	1	TB2	1.94	0.91	0.52	0.80
2002	1	TB3	2.27	0.38	0.22	0.60
2002	1	TB4	3.13	0.44	0.25	0.40
2002	1	TB5	3.89	0.36	0.21	0.20
2002	1	BP1	3.22	0.68	0.39	1.00
2002	1	BP2	3.86	1.11	0.64	0.80
2002	1	BP3	3.79	0.34	0.19	0.60
2002	1	BP4	4.66	0.47	0.27	0.40
2002	1	BP5	6.08	1.16	0.67	0.20
2002	2	CM1	16.67	1.28	0.74	1.00
2002	2	CM2	18.71	0.42	0.24	0.80
2002	2	CM3	21.76	0.87	0.50	0.60
2002	2	CM4	25.44	1.98	1.14	0.40
2002	2	CM5	29.95	29.63	0.89	0.20
2002	2	HW1	3.38	3.02	0.32	1.00
2002	2	HW2	2.57	2.93	0.33	0.80
2002	2	HW3	3.44	3.43	0.15	0.60

Table A6. Continued.

Year	Deployment	Sample	Mean Mass	SD Mass	SE Mass	height (m)
2002	2	HW4	4.03	3.97	0.19	0.40
2002	2	HW5	4.98	4.61	0.62	0.20
2002	2	OS1	386.59	13.90	8.02	1.00
2002	2	OS2	551.76	63.14	36.45	0.80
2002	2	OS3	906.29	87.04	50.25	0.60
2002	2	OS4	1562.14	111.40	64.32	0.40
2002	2	OS5	3037.21	183.03	105.68	0.20
2002	2	TB1	4.33	0.06	0.04	1.00
2002	2	TB2	5.28	0.41	0.24	0.80
2002	2	TB3	6.13	0.43	0.25	0.60
2002	2	TB4	8.08	0.74	0.43	0.40
2002	2	TB5	16.74	2.28	1.32	0.20
2002	2	AC1	15.18	0.60	0.35	1.00
2002	2	AC2	16.63	0.77	0.45	0.80
2002	2	AC3	14.72	2.93	1.69	0.60
2002	2	AC4	16.33	2.03	1.17	0.40
2002	2	AC5	24.33	1.80	1.04	0.20
2003	2	CM1	13.20	1.31	0.75	1.00
2003	2	CM2	15.47	3.27	1.89	0.80
2003	2	CM3	16.98	2.99	1.73	0.60
2003	2	CM4	23.01	1.73	1.00	0.40
2003	2	CM5	32.44	1.73	1.00	0.20
2003	2	HW1	5.28	1.31	0.75	1.00
2003	2	HW2	3.77	0.65	0.38	0.80
2003	2	HW3	2.64	1.73	1.00	0.60
2003	2	HW4	2.26	1.13	0.65	0.40
2003	2	HW5	3.02	1.31	0.75	0.20
2003	2	TB1	1.51	0.65	0.38	1.00
2003	2	TB2	1.89	0.65	0.38	0.80
2003	2	TB3	1.51	0.65	0.38	0.60
2003	2	TB4	3.02	1.73	1.00	0.40
2003	2	TB5	1.51	0.65	0.38	0.20
2003	2	AC1	9.81	8.49	4.90	1.00
2003	2	AC2	15.47	2.36	1.36	0.80
2003	2	AC3	6.04	3.64	2.10	0.60
2003	2	AC4	13.20	8.49	4.90	0.40
2003	2	AC5	18.11	13.72	7.92	0.20
2003	2	NC1	179.20	4.57	2.64	1.00
2003	2	NC2	243.71	8.34	4.82	0.80

Table A6. Continued.

Year	Deployment	Sample	Mean Mass	SD Mass	SE Mass	height (m)
2003	2	NC3	297.28	1.73	1.00	0.60
2003	2	NC4	408.19	6.44	3.72	0.40
2003	2	NC5	479.12	413.00	238.45	0.20
2003	2	BB1	9.43	3.97	2.29	1.00
2003	2	BB2	13.96	0.65	0.38	0.80
2003	2	BB3	6.04	2.85	1.64	0.60
2003	2	BB4	11.32	7.42	4.28	0.40
2003	2	BB5	22.26	18.61	10.74	0.20
2003	1	CM1	6.04	1.31	0.75	1.00
2003	1	CM2	8.68	3.64	2.10	0.80
2003	1	CM3	8.68	3.46	2.00	0.60
2003	1	CM4	5.28	4.28	2.47	0.40
2003	1	CM5	32.07	28.12	16.24	0.20
2003	1	HW1	2.26	1.96	1.13	1.00
2003	1	HW2	3.77	0.65	0.38	0.80
2003	1	HW3	1.89	1.31	0.75	0.60
2003	1	HW4	5.28	2.85	1.64	0.40
2003	1	HW5	3.40	1.96	1.13	0.20
2003	1	OS1	260.31	10.06	5.81	1.00
2003	1	OS2	346.32	23.77	13.72	0.80
2003	1	OS3	474.21	36.90	21.30	0.60
2003	1	OS4	660.95	22.72	13.12	0.40
2003	1	OS5	1246.83	131.81	76.10	0.20
2003	1	TB1	1.13	0.00	0.00	1.00
2003	1	TB2	23.01	29.52	17.04	0.80
2003	1	TB3	3.02	2.36	1.36	0.60
2003	1	TB4	16.98	26.47	15.28	0.40
2003	1	TB5	5.28	5.35	3.09	0.20
2003	1	AC1	5.66	1.13	0.65	1.00
2003	1	AC2	4.53	1.60	0.92	0.80
2003	1	AC3	5.28	5.35	3.09	0.60
2003	1	AC4	10.94	0.65	0.38	0.40
2003	1	AC5	13.58	0.00	0.00	0.20
2003	1	NC1	318.78	5.70	3.29	1.00
2003	1	NC2	383.29	8.03	4.64	0.80
2003	1	NC3	482.13	10.80	6.23	0.60
2003	1	NC4	701.70	10.80	6.23	0.40
2003	1	NC5	1402.83	74.43	42.97	0.20
2003	1	BB1	7.55	4.71	2.72	1.00

Table A6. Continued.

Year	Deployment	Sample	Mean Mass	SD Mass	SE Mass	height (m)
2003	1	BB2	12.07	5.35	3.09	0.80
2003	1	BB3	11.88	0.80	0.46	0.60
2003	1	BB4	21.50	24.14	2.36	0.40
2003	1	BB5	52.06	50.18	6.44	0.20

PHOSPHORUS FLUX DATA

Table A7. Phosphorus fluxes with height above the bottom of the seafloor at the LSI sites for the first and second week's deployments. SD indicates standard deviations.

Mean Phosphorus Fluxes (µmol m^{-2} d^{-1})

Year	Deployment	Sample	height (m)	Total P	SD P	Inorganic P	SD P	Organic P
2002	1	CM1	1.00	93.21	3.29	37.28	1.32	55.92
2002	1	HW1	1.00	5.88	0.49	2.35	0.20	3.53
2002	1	OS1	1.00	1917.19	437.63	766.88	175.05	1150.32
2002	1	TB1	1.00	3.42	0.15	1.37	0.06	2.05
2002	1	BP1	1.00	4.83	1.02	1.93	0.41	2.90
2002	2	CM1	1.00	25.01	1.92	10.00	0.77	15.00
2002	2	HW1	1.00	5.08	4.53	2.03	1.81	3.05
2002	2	OS1	1.00	579.88	20.85	231.95	8.34	347.93
2002	2	TB1	1.00	6.49	0.09	2.60	0.04	3.89
2002	2	AC1	1.00	22.78	0.90	9.11	0.36	13.67
2003	2	CM1	1.00	19.81	1.96	7.92	0.78	11.88
2003	2	HW1	1.00	7.92	1.96	3.17	0.78	4.75
2003	2	TB1	1.00	2.26	0.98	0.91	0.39	1.36
2003	2	AC1	1.00	14.71	12.74	5.89	5.10	8.83
2003	2	NC1	1.00	268.80	6.86	107.52	2.74	161.28
2003	2	BB1	1.00	14.15	5.96	5.66	2.38	8.49
2003	1	CM1	1.00	9.05	1.96	3.62	0.78	5.43
2003	1	HW1	1.00	3.40	2.94	1.36	1.18	2.04
2003	1	OS1	1.00	390.46	15.09	156.18	6.04	234.28
2003	1	TB1	1.00	1.70	0.00	0.68	0.00	1.02
2003	1	AC1	1.00	8.49	1.70	3.40	0.68	5.09
2003	1	NC1	1.00	478.17	8.54	191.27	3.42	286.90
2003	1	BB1	1.00	11.32	7.07	4.53	2.83	6.79

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