



Using porewater profiles to assess nutrient availability in seagrass-vegetated carbonate sediments

KAREN J. MCGLATHERY¹, PETER BERG¹ & ROXANNE MARINO²

¹*Department of Environmental Sciences, Clark Hall, University of Virginia, Charlottesville, VA 22903, U.S.A.;* ²*Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853, U.S.A.*

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Abstract. We measured porewater profiles of inorganic (NH_4^+ , NO_3^- (+ NO_2^-), PO_4^{3-} (hereafter referred to as DIP)) and organic (DON, DOP) nutrients in seagrass-vegetated sediments at two sites in a shallow bay in Bermuda within close proximity (200 m) but subject to different nutrient loading. At both sites, total dissolved and inorganic nutrient concentrations were usually 1–2 orders of magnitude higher in the sediments than in the water column, with the exception of NO_3^- . Organic N and P were significant components of the total dissolved nutrient pools both in the sediment porewater and in the overlying water column (up to 75% for DON and 40% for DOP), and may be important in meeting plant nutrient demands. We used two approaches to examine how well porewater nutrient concentrations reflected the relative availabilities of N and P for seagrasses: (1) a simple stoichiometric nutrient regeneration model based on the N:P ratio of decomposing organic matter and porewater NH_4^+ concentrations to predict porewater DIP, and (2) fitting of the porewater profiles to estimate rates of net nutrient production (or consumption), which reflects the balance between nutrient sources and sinks in the rhizosphere. The stoichiometric model indicated that sediment porewaters were depleted in P relative to N in the low-nutrient outer bay site, and enriched in P relative to N in the higher-nutrient inner bay site. These results are consistent with the mechanism of carbonate sediments in oligotrophic tropical environments being a strong sink for dissolved inorganic P and our previous work suggesting that nutrient enrichment causes P to become disproportionately more available than N. Net nutrient production rates of porewater P at both sites and N at the inner bay site were low (typically < 2%) relative to the nutrient demands of the seagrasses. The implications of the profile interpretation are two-fold: (1) the low rates of net nutrient production indicate diffusive losses from the root zone were insignificant and that nutrient turnover rates were high, except in the P-limited outer bay where N accumulated in sediment porewaters; and (2) because standing stock nutrient concentrations often represent a small fraction of the total nutrients cycled in the sediments, they are in many cases a poor indicator of nutrient availability. Based on our estimates of losses from the root zone, decomposition, and plant uptake we have constructed a rough budget for the cycling of P and N at our two sites.

Introduction

Net primary productivity of seagrasses is commonly limited by nutrient availability in tropical and subtropical coastal waters, except in highly eutrophic environments where shading from excessive macro- and microalgal biomass reduces light availability at the leaf surface (Borum 1985; Cambridge et al. 1986; Short et al. 1995). Seagrasses may take up nutrients both through their leaves and roots, but because sediment porewater nutrient concentrations are typically one to several orders of magnitude higher than those in the water column, it is generally assumed that root uptake from the sediments is the primary source for most rooted aquatic plants (Carignan & Kalff 1980; Barko & Smart 1981). Leaf uptake is mainly important at times when water column nutrient concentrations are relatively high (Hemminga et al. 1991; Stapel et al. 1996). In addition, recent modeling efforts have indicated that internal resorption of nutrients from decaying leaves can increase the importance of leaf uptake relative to root uptake (Erfemeijer & Middelburg 1995). When compared over a range of environmental conditions, porewater nutrient concentrations can provide useful information on the relative availabilities of nitrogen (N) and phosphorus (P) for seagrasses. For example, Fourqurean et al. (1992a) found that porewater dissolved inorganic P concentrations and seagrass tissue P content were positively correlated in a broad survey of Florida Bay (Fourqurean et al. 1992a). These porewater pools, however, are transient and can be depleted rapidly by plant uptake; turnover times calculated from standing stock concentrations may be on the order of several hours to several days (Patriquin 1972; Jensen et al. 1998). Renewal of the porewater nutrient pools occurs largely by the remineralization of organic matter (Erfemeijer & Middelburg 1993). In addition, desorption of P loosely adsorbed onto the carbonate particles (Patriquin 1972; Short 1987; Delgado & Vidal 1989) and dissolution of P-bearing carbonate sediments in the seagrass rhizosphere (Jensen et al. 1998) may contribute to porewater P renewal, and nitrogen fixation can be an important source of N to sediment porewaters (Capone 1983; Howarth et al. 1988; McGlathery et al. 1998).

Correlational studies and nutrient enrichment experiments have shown a general dichotomy of P limitation of marine macrophytes in tropical/subtropical carbonate-rich ecosystems and N limitation in temperate siliclastic coastal regions (Short et al. 1990; Fourqurean et al. 1992b; Lapointe et al. 1992). The main mechanisms for P limitation are believed to be the immobilization of P by carbonate sediments (Short 1987; McGlathery et al. 1994; Howarth et al. 1995) and the high rates of nitrogen fixation relative to denitrification (Capone 1983; Howarth et al. 1988; Seitzinger 1988; Corredor & Morrell 1989). As a result of these processes, ratios of inorganic N:P in

the porewater of carbonate-dominated sediments tend to be higher than in temperate siliclastic sediments (Gaudette & Lyons 1980; Short et al. 1985; Morse et al. 1987; Fourqurean et al. 1992a). However, some exceptions have been reported of high porewater DIP concentrations and low dissolved inorganic N:P ratios in vegetated carbonate sediments (Powell et al. 1989; Fourqurean et al. 1992a; Erftemeijer & Middelburg 1993; Charpy-Roubaud et al. 1996), which suggests that P is not always rapidly removed by sediment immobilization and plant uptake (Erftemeijer & Middelburg 1993; McGlathery et al. 1994). This may partly account for the observation of N rather than P limitation in some enriched tropical systems (McGlathery et al. 1994; Larned et al. 1998). We know comparatively little about how the availability of dissolved organic P (DOP) and N (DON) in sediment porewaters influences nutrient limitation in these systems. However, given the ability of some marine plants to access P bound in organic forms using alkaline phosphatase (Lapointe 1989; Lapointe et al. 1992) and to take up and utilize some organic N compounds (Flynn & Butler 1986; Antia et al. 1991; Robaina et al. 1995), DON and DOP may be important to plant nutrition when the ratio of organic to inorganic porewater nutrients is high.

In this study we examined porewater profiles of dissolved P and N in carbonate sediments at two sites within a shallow bay in Bermuda that differed in the degree of external nutrient loading. We have included both inorganic and organic nutrient fractions in our study. We used two approaches to evaluate the relative availabilities of N and P in the sediment porewaters: (1) a simple stoichiometric model to determine the relative depletion of N or P in sediment porewaters, and (2) fitting of the porewater profiles to estimate rates of net nutrient production in the seagrass rhizosphere. These net nutrient production rates reflect the balance between all nutrient sources and sinks and provide information on the extent to which standing stock porewater concentrations are indicative of total nutrient turnover in the rhizosphere. In addition, the net nutrient production rates reflect the diffusive losses from the rhizosphere. We related these measures to our previous results on seagrass elemental (N and P) content and growth requirements to examine how well porewater nutrient concentrations reflected the relative availabilities of N and P for seagrasses at this subtropical site.

Methods

Site characteristics

The two sites were located approximately 200 m apart in Bailey's Bay, a shallow subtropical lagoon on Bermuda's north shore (32° N, 64° W).

The inner bay site was most strongly affected by nutrient loading, probably from seepage of enriched groundwater or surface runoff during storms (Simmons et al. 1985; McGlathery 1992). This was evident in the higher N and P contents of seagrass tissue (McGlathery 1995; Jensen et al. 1998) and in the more P-enriched sediments (McGlathery et al. 1994). Both sites were colonized by mixed seagrass-macroalgal communities dominated by the seagrass *Thalassia testudinum*; bloom-forming filamentous macroalgae (*Spyridea hypnoides*) were present only at the nutrient-enriched inner bay site (McGlathery 1995).

Characteristics of the carbonate sediments at the two sites were summarized in McGlathery et al. (1994) and Jensen et al. (1998). The main difference between the sites was the amount of solid-phase P of the bulk sediments; the inner bay sediments had higher P concentrations (5.5 vs. 3.2 $\mu\text{mol P g}^{-1}$ dw) primarily due to a larger pool of inorganic P. Sediment organic carbon content was similar at both sites and was low (< 0.5% of dry weight). Iron content was higher at the inner bay site probably due to terrestrial influence, but at both sites concentrations were low (representing < 0.02% of sediment dry weight), which is typical of tropical carbonate sediments. The sediments were only slightly different in grain size distributions, and the difference was not sufficient to account for the higher P content or the lower P adsorption capacity of the inner bay sediments (McGlathery et al. 1994). The sediments at both sites were dominated by the large, coarse-grained size fractions. Approximately 55% (by weight) of the outer bay sediments and 50% of the inner bay sediments were in the 210–710 μm size fraction. For both sites, the largest size fractions (> 710 μm) accounted for ~20% and the finest fraction (< 52 μm) accounted for < 2% of the sediments.

Sampling and nutrient analyses

Porewater was collected in August from 4 depths (5, 10, 20, 30 cm) at each site using sediment sippers. The sippers were constructed of PVC and nylon and resembled a stake with a sampling chamber fitted with 1 μm ceramic filters located 5 cm above the sipper base. A piece of Tygon tubing connected the sampling chamber with a luer-lock sampling port above the sediment surface. The sippers were placed at the desired depth in the sediment with N_2 -bubbled, anoxic 0.2 μm filtered Sargasso seawater in the chamber, and allowed to equilibrate for 24 hr. The lysimeters were placed in 5 clusters to achieve 5 separate sets of porewater profiles at both sites. Water samples were withdrawn by syringe from the sampling port; the first 10 ml were discarded, then 25 ml were sampled and immediately filtered through 0.45 μm Millipore filters into vacutainers and placed on ice until analysis. At the same time, water column samples were taken in triplicate at 0.5 m above the

sediment surface. Samples were kept on ice in the dark until they were filtered through 0.45 μm Millipore filters and analyzed for dissolved nutrients. For the porewater dissolved inorganic P (DIP, as PO_4^{3-}) and ammonium (NH_4^+), samples were acidified with 1.2 N HCl to pH = 2, sparged with N_2 to drive off H_2S , and readjusted to the original pH with 0.5 N NaHCO_3 prior to the colorimetric analyses. DIP and NH_4^+ concentrations were determined immediately using standard colorimetric methods; DIP was measured as soluble reactive phosphorus following reaction with molybdate-antimony (Stainton et al. 1974), and NH_4^+ was measured using the indophenol blue method modified from Strickland and Parsons (1972). The remaining sample was frozen for later analysis of nitrate (+nitrite), total dissolved phosphorus (TDP) and total dissolved nitrogen (TDN). Nitrate (NO_3^-) was determined following cadmium reduction on an autoanalyzer (Grasshoff et al. 1983). TDP and TDN were measured spectrophotometrically as DIP and NO_3^- , respectively, after persulfate digestion modified for small sample sizes (Koroleff 1983). For all analyses, analytical replicates ($n = 2$) were run for each individual sample.

Interpretation of porewater profiles

Since porewater nutrient profiles only provide immediate information on standing stock nutrient concentrations, we used a simple fitting methodology to estimate the rates of net nutrient production (or consumption) of N and P in the root zone. These net rates are defined as the total nutrient (N or P) production in the sediments (from decomposition, release of P from sediment dissolution (Jensen et al. 1998), nitrogen fixation) minus total nutrient consumption (due to plant uptake, sediment immobilization of P, denitrification). The measured concentration profiles of DIP, NH_4^+ , TDP and TDN in the top 30 cm of the sediment (Figures 1, 2) show a clear parabolic shape with a pronounced maximum at 10 to 20 cm depth. The parabolic shape appears to occur over the entire 0 to 30 cm depth interval, suggesting that if steady-state conditions are present, the net production occurs in this whole interval, and perhaps slightly below it. Furthermore, the maximum in the 10 to 20 depth interval for each profile indicates that there is a downward directed diffusive flux below this maximum and that there is net nutrient consumption at some depth below 30 cm. The individual profiles ($n = 5$) for each nutrient were fitted separately in the 0 to 30 cm depth interval, and the rates of net nutrient production were calculated from each fit. Given the relatively few depths (0, 5, 10, 20 and 30 cm) where nutrient concentrations were measured and the somewhat uncertain location of the lower boundary for the net nutrient production, the net production rate derived from each individual fit represents only a first-order estimate. However, by using the mean of all rates in our further calculations we believe that our net nutrient production rates have

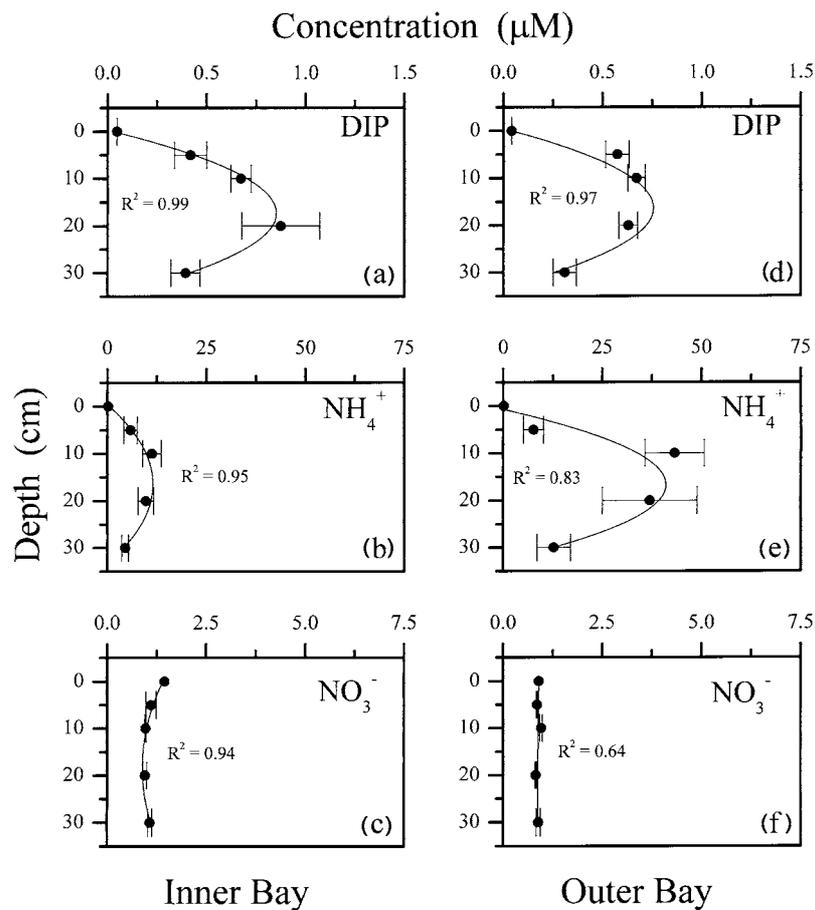


Figure 1. Porewater profiles of dissolved inorganic phosphorus (a, d), ammonium (b, e) and nitrate (c, f) at the two sites in Bailey's Bay. Five replicate porewater profiles were measured at each site, and the error bars reflect standard errors of average concentrations ($n = 5$) measured at each depth interval. The zero depth interval represents the overlying water column concentration ($n = 3$). Each of the 5 individual profiles was fit with a parabola to calculate a rate of net nutrient production in the sediment. Shown here are the parabolic fits of the average nutrient concentrations.

reasonable accuracy as reflected in our error estimates. The depth resolution of our porewater sampling was restricted by the methods available for coarse-grained sandy sediments. Suction sampling with lysimeters, as used in the present study, is the standard technique for porewater sampling in vegetated carbonate sediments, which are typically coarse-grained (Montgomery et al. 1979; Short et al. 1985; Powell et al. 1991; Fourqurean et al. 1992a; McGlathery et al. 1992; Jensen et al. 1998). The two techniques that work

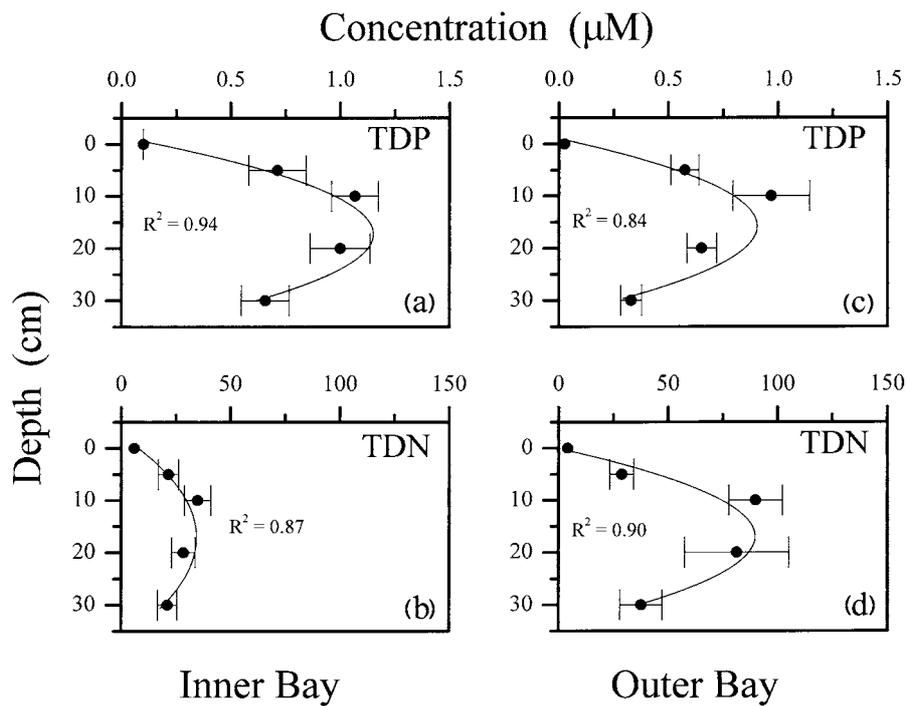


Figure 2. Porewater profiles of total dissolved phosphorus (a, c) and nitrogen (b, d) at the two sites in Bailey's Bay ($n = 5 \pm \text{SE}$). Five replicate porewater profiles were measured at each site, and the error bars reflect standard errors of average concentrations ($n = 5$) measured at each depth interval. The zero depth interval represents the overlying water column concentration ($n = 3$). Each of the 5 individual profiles was fit with a parabola to calculate a rate of net nutrient production in the sediment. Shown here are the parabolic fits of the average nutrient concentrations. Concentrations of dissolved organic N and P can be calculated as the difference between TDP and DIP and between TDN and DIN.

well in fine-grained, muddy sediments (core sectioning and porewater extraction by centrifugation or squeezing, diffusion equilibration using peepers) to produce finer depth resolution profiles are difficult, or impossible, to use in vegetated coarse carbonate sands (Berg & McGlathery 2001).

Our fitting methodology assumes that molecular diffusion is the most important transport process in our sediments (see discussion later) and that steady-state conditions are present, thus the mass conservation equation for a nutrient yields (Berner 1980; Boudreau 1997)

$$\varphi D_s \frac{d^2 C}{dz^2} + R = 0 \quad (1)$$

where C is the pore water concentration, z is the depth, φ is the porosity, D_s is the molecular diffusivity corrected for tortuosity, and R is the net rate

of nutrient production (or consumption if R is negative) per unit volume of sediment. In Eq. (1) φ and D_s are assumed to be constant with depth. One of the many analytical solutions to Eq. (1) is a parabola, which assumes that R also is constant with depth. With the parabolic shape of our measured concentration profiles (Figures 1, 2), it is appropriate to fit the profiles with a parabola. In doing this, we implicitly assume that R is constant with depth and the analytical solution yields

$$C = -\frac{R}{2\varphi D_s} z^2 + Az + B \quad (2)$$

Where A and B are constants. To make more refined estimates, including any depth variation of R , we would need a more detailed depth resolution in our measured profiles. In other words, using parabolic fitting functions appears to be a well-balanced match between the depth resolution of our data and the level of detail at which the profiles are interpreted. Such interpretation gives estimates of depth-averaged net nutrient production rates. One additional advantage of using fitting functions compared to any direct solutions of Eq. (1) is that no boundary conditions for the solution of Eq. (1) are needed. Fitting each of the measured concentrations profiles with a parabola gives us the three coefficients $R/(2\varphi D_s)$, A , and B in Eq. (2). After the coefficient $R/(2\varphi D_s)$ is known, it is straightforward to calculate R for known values of φ and D_s .

Porosities of 0.62 and 0.72 were used for the inner and outer bay sediments (Jensen et al. 1998). The sediment diffusivity (D_s) was calculated from the molecular diffusivity for the relevant nutrient in free water (D) and the porosity as $D_s = D/(1 + 2(1 - \varphi))$ (Iversen & Jørgensen 1993). The diffusivities in free water of PO_4^{3-} (DIP; used also for TDP), NH_4^+ (used also for TDN), and NO_3^- were calculated to be $6.62 \cdot 10^{-6} \text{ cm}^2 \text{ s}^{-1}$, $21.6 \cdot 10^{-6} \text{ cm}^2 \text{ s}^{-1}$, and $20.4 \cdot 10^{-6} \text{ cm}^2 \text{ s}^{-1}$ respectively, from the measured water temperature (28 °C) and the temperature correlations given by Boudreau (1997).

Integrating Eq. (1) over the root zone, from the sediment-water interface ($z = 0$) to the bottom of the root zone ($z = L$), gives

$$\int_0^L \left(\varphi D_s \frac{d^2 C}{dz^2} \right) dz + \int_0^L R dz = 0 \quad (3)$$

Since R is assumed to be constant with depth, the integral gives

$$-\varphi D_s \frac{dC}{dz} \Big|_{z=L} + \varphi D_s \frac{dC}{dz} \Big|_{z=0} = RL \quad (4)$$

which expresses that the difference between the diffusive fluxes at $z = L$ and $z = 0$ equals the depth-integrated net nutrient production rate (RL). With the

typical parabolic shape of our measured porewater profiles (Figures 1, 2), the fluxes at $z = 0$ are directed from the root zone up into the water column (a loss) while the fluxes at $z = L$ are directed from the root zone down to sediment layers below (also a loss). Thus the depth-integrated net nutrient production rate (RL) formulated in Eq. (4) is equal to the sum of diffusive losses from the root zone.

An important consideration in our analyses is the assumption that molecular diffusion was the major active transport process in the sediment. Other transport processes caused by faunal activity, wave action, and/or groundwater flow also may have been present, but we considered each of these processes and believe that they had a relatively minor effect on solute transport over the 30 cm depth profiles described in our study.

Bioturbation, the bulk sediment mixing caused by random movements of fauna, is commonly described as a diffusive process (Berner 1980; Boudreau 1997) where the intensity is expressed through the biodiffusivity (D_B), and the effects of bioturbation vs. molecular diffusion is reflected in the ratio between D_B and the sediment diffusivity (D_s). From the regression of Middelburg et al. (1997) for D_B vs. water depth we estimate a D_B value of $0.8 \cdot 10^{-6} \text{ cm}^2 \text{ s}^{-1}$ for our two sites, which is considerably smaller than our D_s values; a factor of 5 for DIP and a factor of 16 for NH_4^+ . In addition, since D_B , unlike D_s , decreases rapidly with sediment depth (Boudreau 1997), and often is reduced significantly just a few cm below the sediment surface, we believe that bioturbation is relatively insignificant compared to molecular diffusion in our 30 cm profiles.

Irrigation, the non-local transport of porewater due to the pumping activity of tube-dwelling animals, can enhance the transport of solutes in sediments significantly (Aller 1983; Pelegri et al. 1994; Wang & Van Cappellen 1996), and it is not uncommon that irrigation is the dominant transport process in the upper 10–15 cm of the sediment. To our knowledge, no published data exist on the abundance of tube-building fauna at our sites or in areas nearby. However, we have worked extensively in these sediments (McGlathery et al. 1992, 1994; McGlathery 1995; Jensen et al. 1998), and have never found such animals in core sediment samples. Occasionally, we have found shrimp mounds in the field. But the density is so low that they probably only have a marginal effect on the total transport. There were no shrimp mounds in the vicinity of our lysimeters.

Experiments with dissolved tracers (Aller & Aller 1992) have shown that the natural abundance of meiofauna in marine sediments can increase the transport of solutes by a factor of two relative to molecular diffusion. Similar results were obtained by Berg et al. (2001) for fine-grained sediments. In both studies, the enhanced solute transport appears to exceed the

anticipated effects of bioturbation (bulk sediment mixing) and is probably the result of a locally-induced and small-scale advective porewater transport caused by the movement of meiofauna. Since the flow directions are random, the resulting mixing can be described as a diffusive process. Berg et al. (2001) suggested that this transport be described as enhanced bioturbation simply by defining two biodiffusivities: one for solid mixing and a larger one for the mixing of solutes. To our knowledge, no similar studies have been done in seagrass-vegetated coarse-grained sediments. However, based on the meiofaunal density determined in coarse-grained carbonate sediments by Decho et al. (1985), this advective transport is likely to be considerable only in the top 2–4 cm of the sediment. Below this depth interval, the advective transport contribution is probably insignificant relative to molecular diffusion due to a rapid decrease in meiofaunal density.

Wave action also can induce a transport of porewater in the upper sediment layers of coarse-grained sediments in shallow systems (Rutgers van der Loeff 1981). On average, this mixing results in a diffusive-like transport process and Rutgers van der Loeff (1981) has suggested an expression for calculating order-of-magnitude values for the resulting diffusivity. The expression has variables that are difficult to assign values, but it contains an exponential decrease with sediment depth of $\exp(-4\pi z/\lambda)$, where z is the sediment depth and λ is the wavelength of the surface waves. This decline with sediment depth is rather steep. At a wavelength, for example, of 30 cm, the diffusivity resulting from wave action is reduced by a factor of 10 only 5 cm below the sediment surface. Since our two sites were relatively well protected and our porewater samples were collected during a calm period, we believe that wave action only had a minor effect on the overall transport in the sediments during our sampling.

Finally, the characteristic parabolic shape of the porewater profiles indicates that there was not a strong, steady transport of nutrients via groundwater, in which case we would expect to observe higher nutrient concentrations with depth. There also were no differences in the shape of the profiles between the inner and outer bay site, even though there was evidence of significant external nutrient input to the inner bay. Since external nutrient inputs via groundwater likely represents a small fraction of nutrient turnover relative to internal recycling in these sediments, we would not expect large differences in porewater standing stock concentrations due to groundwater inputs. Also, the delivery of nutrients by groundwater intrusion likely occurs periodically during and after heavy rain events.

Statistical analysis

Means and standard errors are reported for each depth interval for the 5 replicate porewater profiles measured at each site. Differences between depths, or between sites, were determined by one-way analysis of variance (ANOVA).

Results

Porewater nutrient profiles

With the exception of NO_3^- , all nutrient concentration profiles in the vegetated sediment showed significant depth variation from 0–30 cm ($P < 0.01$). There was a subsurface peak at 10 to 20 cm depth for all profiles except for NO_3^- (Figure 1). DIP concentrations were similar at both sites ($P > 0.05$), and were always below $1.5 \mu\text{M}$ (Figures 1(a), (d)). Ammonium concentrations throughout the depth profile were higher at the inner bay site (Figures 1(b), (e); $P < 0.01$). The subsurface peak in NH_4^+ at 10–20 cm depth also was more pronounced in the outer bay, with concentrations ranging from $14\text{--}67 \mu\text{M}$, some 3-fold higher than at the inner bay site. Porewater nitrate concentrations always were low ($< 1 \mu\text{M}$) and showed little depth variation at either site or any significant differences in concentrations between the sites (Figures 1(c), (f); $P > 0.05$). Largely because of the differences in NH_4^+ concentration, DIN:DIP ratios based on individual samples from the 10–30 cm depth sippers were higher in the outer bay sediments (44:1–66:1) than in the inner bay sediments (12:1–18:1) (Table 1).

The depth variation in porewater TDP and TDN at both sites was similar to that observed for NH_4^+ and DIP (Figures 2(a), (c)). There were significant differences between the sites; across all sediment depths, TDP concentrations were higher in the inner bay sediments (Figures 2(a), (c); $P < 0.01$), while TDN concentrations were about 3-fold greater in the outer bay sediment (Figures 2(b), (d); $P < 0.01$). DOP and DON concentrations were calculated as the difference between total dissolved and dissolved inorganic pools for each sample. Except for the 10 cm depth interval, DOP contributed little to the TDP pool in the outer bay sediments (Table 1). At the more enriched inner bay site, however, DOP was 13–14% of the TDP pool. It should be noted, however, that there are considerable uncertainties in the absolute values for DOP since the concentrations of both TDP and DIP were small at both sites. A more precise method would be to determine porewater and water column DIP using the MAGIC method, which concentrates DIP by coprecipitation with $\text{Mg}(\text{OH})_2$ and thus has a lower detection limit (30 nM, Karl & Tien

Table 1. Average ratios of total dissolved and inorganic nitrogen and phosphorus in the water column and in sediment porewaters, and percentage of total dissolved nitrogen and phosphorus as organic nitrogen and phosphorus. Ratios were calculated as the average of nitrogen and phosphorus concentrations at each sampling interval and the percentages were based on depth averages

Depth (cm)	DIN:DIP		TDN:TDP		%DON		%DOP	
	Outer bay	Inner bay	Outer bay	Inner bay	Outer bay	Inner bay	Outer bay	Inner bay
0	20:1	30:1	84:1	60:1	75	72	0	50
5	15:1	17:1	50:1	30:1	71	68	< 1	41
10	66:1	18:1	93:1	33:1	51	65	31	37
20	60:1	12:1	125:1	28:1	54	63	3	13
30	44:1	14:1	114:1	32:1	64	74	6	40

1992; Jensen et al. 1998). DON comprised 50–75% of the dissolved N pool in the porewaters at both sites (Table 1), with a slightly higher proportion of DON in the 10–30 cm depth intervals at the inner bay site. As with the DIN:DIP ratios, TDN:TDP was more variable and always higher at the outer bay site (50:1–125:1) than at the inner bay site (28:1–32:1).

For all nutrients measured, except NO_3^- , the fits of the porewater concentration profiles indicated net nutrient production in the sediments (Figure 3). The average of the 5 profile fits for each nutrient are shown in Figures 1 and 2, and have R^2 values of 0.84–0.99. The net nutrient production rates for DIP and TDP were small ($0.3\text{--}0.5 \mu\text{mol P m}^{-2} \text{d}^{-1}$), as would be expected from the low porewater concentrations, and were similar at both sites. There were significant differences in net nutrient production rates between TDN and DIN at the outer bay site ($P < 0.05$), but not at the inner bay site ($P > 0.05$), reflecting the larger DON pool in the outer bay sediments. There also was a significant difference between sites, with release of TDN and NH_4^+ both about 4x higher in the outer bay ($P < 0.01$). Net nutrient production of NO_3^- in the sediments was insignificant at both sites (Figure 3).

Several studies have used simple stoichiometric nutrient regeneration models in carbonate sediments to indicate the relative depletion of N or P, either based on process measurements (e.g. sulfate reduction) and the C:N:P of sediment organic matter, or on the N:P ratio of decomposing organic matter and porewater NH_4^+ concentrations (Gaudette & Lyons 1980; Hines & Lyons 1982; Erftemeijer & Middelburg 1993). We used the latter approach to predict the DIP concentrations expected in the sediment porewaters at the different depth intervals, and compared these with our observed values. We

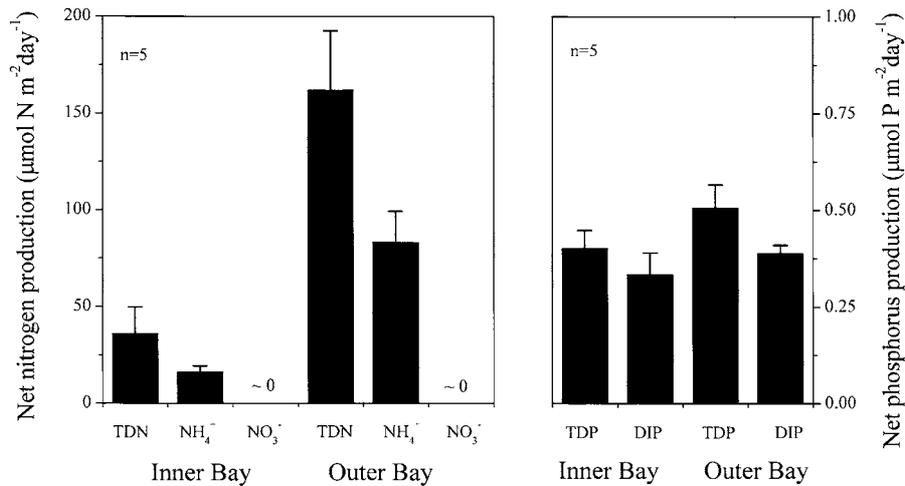


Figure 3. Average rates of net nutrient production (= sources – sinks) calculated from parabolic fits of porewater profiles ($n = 5 \pm \text{SE}$). Net nutrient production rates equal diffusive losses from the sediments.

assumed that the dominant source of nutrients to the sediment porewaters was the decomposition of seagrass material (roots, rhizomes, leaves, sheaths). Decomposition of algal material (macroalgae and phytoplankton) and particulate matter trapped by the seagrass meadows also can contribute to nutrient concentrations in the uppermost sediment layers. However, in oligotrophic tropical waters seston content (phytoplankton and water column particulates) is low and thus sedimentation rates also are likely to be low. For the calculation, we used a N:P for *T. testudinum* biomass of 20:1. This corresponds to a ratio of 20:1 for belowground biomass reported by Short et al. (1985) from a site in the Bahamas, and to a value of 19:1 for living seagrass material (leaves, sheaths, roots and rhizomes) used by Erftemeijer and Middelburg (1993) to calculate the enrichment of porewater NH_4^+ and DIP from decomposition at a site in Indonesia. Predicted DIP concentrations were calculated by dividing the measured NH_4^+ concentration for each sample by this N:P ratio, and then were plotted against the measured DIP concentration for that sample (Figure 4). The 1:1 line indicates where the predicted DIP concentrations exactly match the measured values. This calculation shows a clear distinction between the two sites: in the inner bay sediments, the predicted DIP concentrations were consistently below the measured values, whereas in the outer bay sediments, predicted DIP was typically higher than measured concentrations. This suggests different source-sink relationships for DIP and NH_4^+ at the two sites.

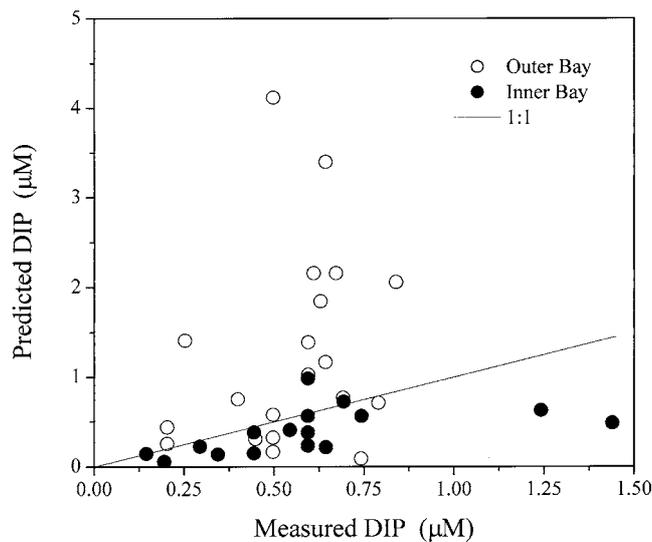


Figure 4. Comparison of measured porewater DIP concentrations in sediment porewaters and expected DIP concentrations calculated from measured ammonium concentrations and a N:P ratio of 20:1 for decomposing seagrass material. The line represents the 1:1 relationship where the predicted concentrations exactly match the measured values.

Discussion

The subsurface concentration peak for all porewater nutrient profiles, with the exception of NO_3^- indicates that N and P regeneration from decomposition of seagrass material and other organic matter exceeded assimilatory uptake by the roots at this depth in the sediments. Others also have shown elevated nutrient concentrations where seagrass roots and rhizomes were dense compared to deeper sediments or to nearby unvegetated sediments, and have attributed this to organic matter decomposition (Montgomery et al. 1979; Short et al. 1985; Erfteimeijer & Middelburg 1993; Jensen et al. 1998). Another indication of a subsurface input of organic matter, either from decomposing organic matter or the release of labile organic carbon from seagrass roots, are the high sulfate reduction rates that typically occur at depth in seagrass beds (Barnes 1993; Blackburn et al. 1994; Welsh et al. 1996). In some cases, porewater nutrient concentrations have been found to increase with depth in vegetated sediments or to show no pattern due to the large variability in porewater nutrient concentrations (Williams 1990; Fourqurean et al. 1992a).

Overall, the ratios of DIN:DIP in our Bermuda sediment porewaters were significantly lower in the inner bay (depth-averaged: 15:1 vs. 46:1). In addition, the lower TDN:TDP ratios of sediment porewater in the inner bay

(depth-averaged: 31:1 vs. 96:1) and the faster recycling rate of DOP relative to that of DON (Jackson & Williams 1985; Smith et al. 1985) suggest a lower relative availability of N in the inner bay. This agrees with our previous work showing that while seagrass tissue N and P contents both were higher in the more enriched inner bay, by 10% and 32% respectively, the N:P ratios were significantly lower in the inner bay seagrass (25:1 vs. 32:1, McGlathery 1995). These data, combined with our evidence of higher nutrient loading to the inner bay (McGlathery et al. 1994), indicate that nutrient enrichment has caused P to become disproportionately more available at this subtropical site. Other studies have shown variation in N and/or P availability for benthic macrophytes in broad surveys over much larger spatial scales (e.g. Florida Bay, Fourqurean et al. 1992b), between sites in close proximity but with different sediment composition (carbonate vs. siliclastic; Erftemeijer & Middelburg 1993), or in seagrass tissue P but not N within a short distance from a point source of nutrients (Fourqurean et al. 1992a). We have suggested previously that the difference in seagrass nutrient content at our study site in Bermuda was partly due to the sediments becoming a weaker sink for DIP in the more enriched inner bay (McGlathery et al. 1994), and to greater dissolution of P-bearing carbonate sediments in the seagrass rhizosphere in the enriched site (Jensen et al. 1998). Both processes would increase the relative availability of P to the inner bay plants. In the present study, we show that this difference also may be partly due to a relative depletion of DIN in the porewaters of the inner bay site. We currently do not know the degree to which DOP and DON can meet plant nutrient demands, but given the ability of some plants to use dissolved organic compounds (Flynn & Butler 1986; Antia et al. 1991; Lapointe et al. 1992; Robaina et al. 1995) and the high ratio of organic to inorganic nutrients in sediment porewaters at both sites, we believe that these also may be important nutrient sources in this system.

Several studies have used the stoichiometry of inorganic nutrients in sediment porewaters to indicate the preferential removal of N or P released from decomposing organic matter (Gaudette & Lyons 1980; Hines & Lyons 1982; Erftemeijer & Middelburg 1993). Using this approach, we found that predicted porewater DIP concentrations from the stoichiometric nutrient regeneration model were usually higher than measured concentrations in the outer bay sediments, indicating a depletion of P relative to N at this site. In contrast, there was a relative enrichment of DIP in sediment porewaters in the inner bay since predicted DIP concentrations were typically lower than measured concentrations. There are four possible mechanisms that could account for this difference. First, we have shown in previous short-term adsorption experiments that the outer bay sediments were a stronger sink for DIP, with uptake significantly faster than by the more P-enriched

inner bay sediments (McGlathery et al. 1994). Rapid surface adsorption of DIP and subsequent incorporation of P into carbonate fluorapatite or other carbonate minerals is typical of tropical/subtropical systems where external nutrient loading is low (Short et al. 1990; McGlathery et al. 1994; Jensen et al. 1998). As the P-enriched sediments lose their capacity to adsorb and store P, this alters the exchange of P between the porewater and sediment and results in increased P availability for primary producers (McGlathery et al. 1994). Second, the high DIP concentrations relative to predicted values in the inner bay indicate there was either a source of P in addition to decomposition or a greater relative loss of NH_4^+ . It is evident from the high seagrass tissue P content (0.19% dw) and the total sediment P concentration, that there was a significant source of P (as well as N) to this nearshore site (McGlathery et al. 1994; Jensen et al. 1998). In addition, liberation of carbonate-bound P by dissolution of sediments in the seagrass rhizosphere was found to be greater at the inner bay site (Jensen et al. 1998). However, despite the P enrichment of both sediments and seagrasses in the inner bay, we found no significant differences in actual porewater DIP concentrations, probably because turnover of DIP was rapid at both sites. This suggests a third mechanism, that the higher DIP concentrations relative to NH_4^+ measured in the standing stock concentrations of inner bay porewaters reflected greater removal of NH_4^+ at this site. High root assimilation of NH_4^+ by productive P-rich plants could account for this depletion of porewater N, as has been shown for N in seagrasses in siliclastic sediments (Caffrey & Kemp 1990; Short et al. 1993). Seagrass production in the inner bay was nearly double that of the outer bay ($1.18 \text{ gdw m}^{-2} \text{ d}^{-1}$ vs. $0.63 \text{ gdw m}^{-2} \text{ d}^{-1}$), resulting in a 2-fold higher N demand than for the more strongly P-limited (0.13% dw P) outer bay seagrasses (Table 2). Finally, there may have been differences in rates of nitrogen fixation relative to denitrification at the two sites. The low NH_4^+ concentrations in the inner bay sediments may be the result of higher rates of coupled nitrification-denitrification stimulated by greater root release of oxygen and dissolved organic carbon from the more productive plants (Reddy et al. 1989; Caffrey & Kemp 1990; Blackburn et al. 1994). However, if this were the case, we would expect porewater NO_3^- concentrations to be higher, since NO_3^- concentrations and denitrification rates have been shown to be positively correlated in vegetated temperate sediments (Caffrey & Kemp 1990). It is also possible that zones of nitrification and denitrification were in close enough proximity and NO_3^- turnover rates were rapid enough that no elevated NO_3^- concentrations could be observed at the time and space resolution we used. Whatever the specific mechanism, it is clear that N fixation did not make up the deficit of N relative to P in sediment porewaters at the inner bay site. This consistent with the P enrichment study of Short et al. (1990) where there was an apparent

Table 2. Summary of *T. testudinum* characteristics in Bailey's Bay, Bermuda

	Outer bay	Inner bay
Biomass (gdw m ⁻²)	17.5 ± 1.5	28 ± 2.5
Leaf-specific growth (gdw gdw ⁻¹ d ⁻¹)	0.036 ± 0.004	0.042 ± 0.006
%C leaf	34.1 ± 0.24	33.4 ± 0.27
%N leaf	1.89 ± 0.05	2.11 ± 0.05
%P leaf	0.13 ± 0.003	0.19 ± 0.005
C:N	21:1	19:1
C:P	670:1	464:1
N:P	32:1	25:1
N demand $\mu\text{mol N m}^{-2} \text{d}^{-1}$	899	1770
P demand $\mu\text{mol P m}^{-2} \text{d}^{-1}$	28	72

shift from P to N limitation in the tropical seagrass *S. filiforme* after 7 months, despite increased N fixation rates.

We can obtain additional information about the availabilities of N and P by interpreting the porewater nutrient profiles to obtain estimates of net nutrient production (= sources – sinks) in the sediments. First, the low net nutrient production rates relative to the estimated plant demand show that standing stock porewater concentrations reflect only a small fraction of the total nutrient production in the sediments and therefore should be interpreted with some caution as they do not necessarily reflect availability. Assuming steady-state conditions, the total amount of N and P that must be produced from all sources (internal and external) to maintain seagrass tissue levels is reflected in the nutrient demand of the plants at each site. This can be calculated from the tissue leaf-specific growth rates, aboveground biomass, and tissue N and P contents, although it does not consider belowground production. These requirements are approximately 1770 $\mu\text{mol N m}^{-2} \text{d}^{-1}$ and 72 $\mu\text{mol P m}^{-2} \text{d}^{-1}$ for seagrasses in the inner bay, and 900 $\mu\text{mol N m}^{-2} \text{d}^{-1}$ and 28 $\mu\text{mol P m}^{-2} \text{d}^{-1}$ for the outer bay seagrasses (Table 2). When we compare the net nutrient production rates calculated from the porewater profiles with this plant demand, net nutrient production was less than 2% of the total nutrient production needed to maintain tissue contents of P at both sites and N at the inner bay site. It was only for N at the lower-nutrient outer bay site, where seagrass growth was lower, that net nutrient production was a sizeable fraction (20%) of total nutrient production. This indicates, that with the exception of N in the outer bay, nutrient turnover rates were high in the sediment porewater.

A second important point that comes out of the profile interpretation is that the gradients in the profiles, both above and below the subsurface peak concentration, resulted in two diffusive fluxes pointing away from the root zone. The sum of the fluxes equals the depth-integrated net nutrient production rates as expressed in Eq. (4), and represents a loss from the rhizosphere. At both sites these losses were insignificant relative to the demand of the plants, except for N in the outer bay where approximately 20% of the total nutrient production was lost from the sediments. This also indicates that there was rapid turnover of P at both sites and of N in the inner bay. Where plant growth was more P-limited in the outer bay, N accumulated in the sediment porewaters as a result of lower plant production and uptake. This P limitation was probably the result of greater sediment P immobilization and lower external supply at this site (McGlathery et al. 1994), and possibly also of lower sediment dissolution (Jensen et al. 1998). Thus with the exception of N in the outer bay, inorganic N and P generally did not occur in great excess in the sediment porewaters despite high total rates of total nutrient production. Blackburn et al. (1994) also found that NH_4^+ concentrations in the porewater of a tropical seagrass (*Halodule* sp.) bed did not indicate large diffusive losses, and Jensen et al. (1998) reported insignificant DIP fluxes from the sediments to the overlying water at our study sites. This is in contrast to temperate vegetated sediments where NH_4^+ production typically exceeds plant N demand (Iizumi et al. 1982; Shore 1983; Dennison et al. 1987; Caffrey & Kemp 1990), and diffusive fluxes to the water column can be high. In addition, high porewater DON concentrations often result in significant fluxes to the water column from temperate marine sediments (Lomstein et al. 1989; Bartoli et al. 1996; Tyler et al. 2001). In these temperate communities, light rather than nutrients more often limits plant production and nutrients can accumulate in sediment porewaters (Borum 1996).

Using the information from the profile interpretations and estimates of decomposition and plant uptake we can construct a rough budget for N and P at the two sites (Figure 5). We estimate mineralization rates to be about $680 \mu\text{mol N M}^{-2} \text{d}^{-1}$ and $34 \mu\text{mol P M}^{-2} \text{d}^{-1}$ for the inner bay, and $520 \mu\text{mol N M}^{-2} \text{d}^{-1}$ and $26 \mu\text{mol P M}^{-2} \text{d}^{-1}$ for the outer bay. This is based on sediment oxygen consumption measurements from Jensen et al. (1998) of 34 and $26 \text{ mmol O}_2 \text{ m}^{-2} \text{d}^{-1}$ for the inner and outer bay sites, respectively, and a C:N:P ratio of 1000:20:1 for *T. testudinum* (Short et al. 1985; Erftemeijer & Herman 1994), assuming that seagrass material (roots, rhizomes, leaves) is the main source of decomposing organic matter in the sediments. In tropical seagrass meadows, a significant proportion of sloughed *T. testudinum* leaves sink and decompose in place, while the remainder is exported from the meadow as drift material (Zieman et al. 1979, 1989). These values do not include decom-

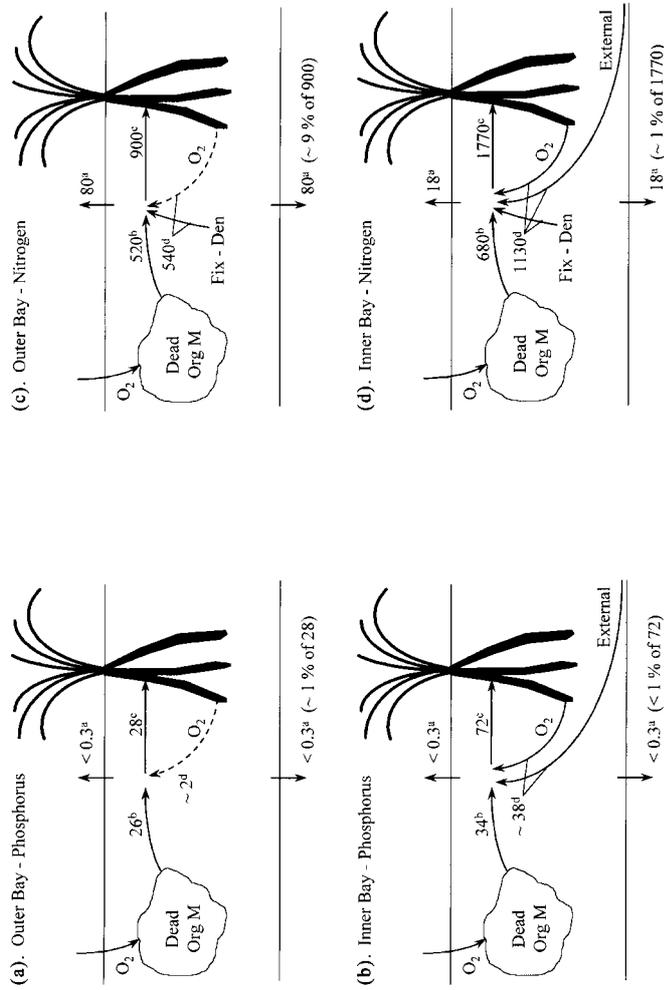


Figure 5. Rough budgets constructed for P and N at the two sites in Bailey's Bay: (a) P, outer bay; (b) P, inner bay; (c) N, outer bay; (d) N, inner bay. Units are $\mu\text{mol m}^{-2} \text{d}^{-1}$ for all processes, which are denoted by the superscripts: (a) fluxes out of the rhizosphere calculated as net nutrient production rates from the fits of the porewater profiles of total dissolved N and total dissolved P; (b) sediment mineralization rates, estimated based on oxygen consumption measurements of Jensen et al. (1998) and a C:N:P ratio of decomposing organic matter of 1000:20:1; (c) plant nutrient demand calculated from leaf-specific growth rates, aboveground biomass and tissue N and P contents reported in McGlathery (1995); this reflects the total nutrient production that is necessary to maintain tissue nutrient levels; (d) all other sources and sinks, including decomposition related to root release of oxygen and dissolved organics, direct uptake of DON and DOP, nitrogen fixation and denitrification, P liberation from sediment dissolution, and external nutrient supply. At the inner bay site, an external source of nutrients was needed to satisfy plant requirements of N and P.

position stimulated in the rhizosphere by root release of oxygen since the measurements were made on sediment cores that did not include intact plants. They also do not reflect the potential contribution of macroalgae, epiphytes, and water column particulates as sources of decomposing organic matter, that would provide 'new' N and P to seagrasses with a higher N and P content than the seagrass material. However, as we have noted previously, water column seston in oligotrophic tropical systems tends to be low and is likely not to contribute significantly to organic matter decomposition in the seagrass rhizosphere. We assume in our calculations that root uptake is the primary source of nutrients for seagrasses due to the higher concentrations of nutrients in sediment porewaters than in the water column. It is known that seagrasses also may obtain nutrients from the water column by leaf uptake and that there may be considerable resorption of nutrients before leaf senescence (Hemminga et al. 1991; Stapel et al. 1996). In this case, the contribution of organic matter mineralization in the sediments to plant nutrient demand would be lower than our calculated value.

For P, decomposition nearly balanced plant demand in the outer bay, but an additional source was needed to satisfy P requirements in the inner bay (Figures 5(a), (b)). We have previously suggested that this is likely to be external P inputs since the sediments and plant tissue were rich in P at this nearshore site (McGlathery et al. 1994). Some of the P demand in the inner bay also could be met by leaf uptake, by decomposition stimulated by root release of oxygen that is not included in our calculation, by uptake of DOP directly from sediment porewaters, or by P liberation from localized dissolution of carbonate sediments in the rhizosphere (Jensen et al. 1998). Metabolism in the rhizosphere (release of oxygen and dissolved organics, root and microbial respiration) probably was higher at the inner bay site due to the greater plant production. For N, NH_4^+ production calculated from the decomposition rates was insufficient to meet the requirements of *T. testudinum* at both sites, suggesting that additional sources were necessary (Figures 5(c), (d)). As with P, we believe that external inputs were an important source of N at the inner bay site, and that these could be obtained either by root or leaf uptake of DIN or DON. Decomposition directly associated with the seagrass roots and not measured in our study also may have contributed some of the missing N to our inner bay site. Since our calculations for P in the outer bay suggest that the decomposition of sediment organic matter was sufficient to meet plant demand, there must be a source other than mineralization that provided the N necessary to satisfy plant growth requirements. Nitrogen fixation in excess of denitrification likely was important as a new source of N. If all of the 'missing' N at both sites was supplied by nitrogen fixation, this would give rates of 0.6–1.1 $\text{mmol N m}^{-2} \text{d}^{-1}$, which are well within the range reported

for tropical and subtropical seagrass-vegetated sediments (McGlathery et al. 1998). The combined effect of these N sources/sinks in addition to our calculated decomposition rates accounted for an input of about 60% of the required N at both sites.

Conclusion

Porewater profile interpretation provides valuable information on nutrient production rates in the sediments that supplement the N:P ratios of sediment porewaters and plant tissue C:N:P to assess the relative availabilities of N and P to rooted macrophytes. Even though the ratios of porewater DIN:DIP and TDN:TDP suggested a relative deficit of P at the outer bay site and N at the nutrient-enriched inner bay site, standing stock nutrient concentrations generally were a small fraction of the total nutrients cycled in the sediments and porewater nutrients did not necessarily reflect nutrient supply. For example, the stoichiometric nutrient regeneration model indicated a relative surplus of P at the inner bay site, but we observed no differences in porewater DIP concentrations between the two sites. The seagrass tissue P was nearly 50% higher at the inner bay site and clearly indicated greater P availability. High turnover of both P and N in the sediments indicated rapid recycling such that DIP and DIN concentrations remained relatively low and there were insignificant diffusive losses from the sediments, except in the outer bay where the seagrasses were more strongly P-limited and N accumulated in the rhizosphere. DON comprised 50–75% of porewater TDN at both sites and DOP represented a significant fraction (13–40%) of TDP at the more enriched inner bay site; both probably supplemented inorganic nutrients to meet plant growth demands.

We have demonstrated that because standing stock nutrient concentrations often represent a small fraction of the total nutrients cycled in the sediments, they are in many cases poor indicators of nutrient availability. This is in agreement with others who have cautioned against using ratios of standing stock N and P concentrations in the water column to infer nutrient availability because they do not reflect variations in turnover rates (and hence supply) (Jackson & Williams 1985; Howarth 1988). Our data suggest that standing stock nutrient concentrations in sediment porewaters are most useful in inferring patterns of nutrient limitation in cases where one nutrient is strongly limiting and excess amounts of the other have built up in the sediments due to reduced uptake of saturated plants. Also, if surveys of porewater N:P and tissue N:P are sufficiently broad to encompass a range from strong nutrient limitation to saturation, porewater nutrient ratios across the gradient can give an indication of relative nutrient availabilities because the relationship is highly influenced

by these endmembers (Fourqurean et al. 1992a). Generally, however, one should not expect to find a simple relationship between porewater nutrient concentration and tissue nutrient levels unless such extremes are included.

Our data also indicate a trend toward N limitation in the nutrient-enriched site. If this result can be generalized, it suggests that a consequence of external nutrient loading may be a switch from P to N limitation in tropical seagrass beds until light becomes limiting from excessive algal growth (McGlathery et al. 1994; Howarth et al. 1995). The exact mechanisms driving these ecosystems toward N limitation with increased eutrophication are not fully known, but are likely to include the N:P of external nutrient inputs, enhanced denitrification relative to N fixation, and decreased immobilization of P by carbonate sediments.

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