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# Biogeochemistry of Nearshore Bermuda Sediments. I. Sulfate Reduction Rates and Nutrient Generation

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ABSTRACT: Sulfate reduction rates, enumeration of sulfate-reducing bacteria, as well as pore water concentrations of $PO_4^{3-}$, $NH_4^+$ and titration alkalinity were determined for the upper 14 cm of sediments collected from 3 nearshore Bermudian environments: Coot Pond (LG), Mangrove Bay (MB) and Devil's Hole (DH). Sulfate reduction rates were rapid at LG and MB but slow at DH (~ 300 and 8.0 nmoles $ml^{-1}$ $d^{-1}$, respectively). Differences in source and deposition of organic matter caused rate variations. There was a linear relationship between sulfate reduction rates and sulfate-reducing bacteria. Pore water nutrient concentrations were low compared to clastic sediments. Nutrient regeneration rates, as calculated from organic matter C:N:P ratios, and sulfate reduction rates were used to calculate the turnover times of dissolved $PO_4^{3-}$ and $NH_4^+$. Sediments subject to active bioturbation had $NH_4^+$ turnover times 9 to 63 times less than those for non-bioturbated sediments.

## INTRODUCTION

Bacterially-mediated sulfate reduction in anoxic marine sediments is an important reaction in terms of the production of reactive byproducts (Goldhaber and Kaplan, 1974) and the regeneration of nutrients (Berner, 1977; Martens et al., 1978). A considerable portion of the photosynthetically fixed carbon which enters sediments is metabolized via sulfate-reducing bacteria (Jørgensen, 1977; Howarth and Teal, 1979; Skyring et al., 1979; Aller and Yingst, 1980).

Sulfate reduction reactions in sediments result in a buildup of dissolved reactive phosphate ($PO_4^{3-}$), ammonium ($NH_4^+$) and alkalinity in pore waters which may be orders of magnitude more concentrated than in the overlying seawater (Sholkovitz, 1973; Berner, 1974; Suess, 1976). The stoichiometry of sulfate reduction as expressed by the equation of Richards (1965):

$$(CH_2O)_{106}\ (NH_3)_{16}\ H_3PO_4 + 53\ SO_4^{=} \rightarrow 106\ CO_2 + 53\ S^{=} + 16\ NH_3 + 106\ H_2O + H_3PO_4$$

has been used, with some success, to describe sedimentary nutrient regeneration (Gaines and Pilson, 1972; Berner, 1977; Martens et al., 1978; Gaudette and Lyons, 1980). Hence sulfate concentration depth profiles can be used to calculate theoretical nutrient regeneration rates using diagenetic models (Berner, 1974, 1977; Martens et al., 1978). Difficulties in the application of these models arise from the adsorption of ions to sedimentary particles and authigenic mineral formation (Berner, 1977; Martens et al., 1978) as well as the 'straightening' of nutrient depth profiles through particle reworking and irrigation by bioturbating infauna (Aller, 1977).

Although clay-ion interactions are not important in carbonate sediments, the influence of irrigating macrofauna and inhanced removal of $PO_4^{3-}$ from pore waters (Berner, 1966; Gaudette and Lyons, 1980) impair the use of sulfate concentrations for describing nutrient regeneration in these environments.

Sulfate reduction rates as determined by $^{35}S\text{-}SO_4$ reduction have been measured in salt marsh soils (Nedwell and Abram, 1978; Howarth and Teal, 1979; Skyring et al., 1979), subtidal clastic sediments (Jørgensen, 1977) and coral reef carbonates (Skyring and Chambers, 1976). We present here sulfate reduction rates, distribution of recoverable sulfate-reducing bacteria, and pore water nutrient concentrations in carbonate sediments of Bermuda. Sulfate reduction and nutrient chemistry are discussed in terms of rates

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of nutrient regeneration during sulfate reduction and the effects of bioturbation.

### Sampling Locations

Mangrove Bay (MB) is a mangrove lined, lobate embayment a few hundred meters east of the Bermuda Biological Station for Research (BBS) in Ferry Reach (Fig. 1). It measures approximately $0.6 \times 10^4$ m$^2$ with an entrance some 60 m wide and a maximum water depth of 1.2 m (Obrochta and Paisley, 1970). The tidal range is ~1.0 m and during spring low tide the area is completely exposed. The sediments have been described by Berner (1966); they consist of poorly sorted carbonate mud of which approximately the top 2 cm are oxidized.

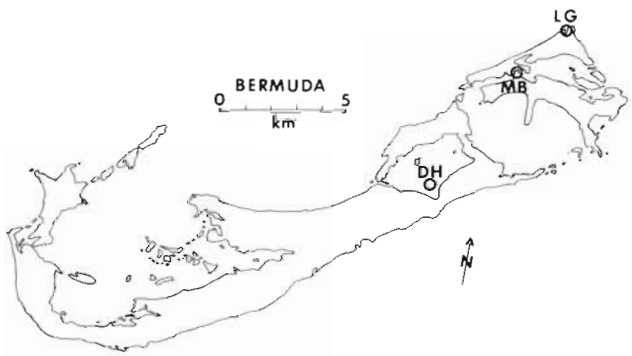


Fig. 1. Bermuda sampling locations. Coot Pond (LG), Mangrove Bay (MB), Devil's Hole (DH)

Coot Pond (LG) is a Karst feature in the northern portion of St. Georges Island (Fig. 1). This embayment is tear-drop shaped and has an area of approximately $1.3 \times 10^4$ m$^2$. It is connected to ocean by a channel which is 3 m wide and 0.5 m deep at low tide (Pavich, 1971; Wilson, 1979). Mean depth is ~1 m, with the deeper center portions of the pond reaching 2 to 3 m (Pavich, 1971). The mean tidal range is 1 m. Wilson (1979) calculated the residence time of Coot Pond water to be slightly more than 2 tidal cycles. Mangrove surrounds approximately 50% of the embayment. The sediments consist of poorly sorted silts and sands, except in the areas which are burrowed by the infaunal shrimp *Callianassa*. These sediments consist of well-sorted fine sands.

Numerous types of calcareous algae, especially *Fosliella, Penicillus* and *Cymopolia* spp., are abundant in both embayments. In Coot Pond and Mangrove Bay the turtle grass *Thalassia testudium* is found, as well as filamentous green algal colonies.

Devils' Hole (DH) is a 25 m basin in Harrington Sound (Fig. 1). A thermocline occurs at 20 m and the bottom waters become anoxic in late summer (Thorstensen and Mackenzie, 1974). Sediments are well-sorted clay size material derived primarily from the surrounding shallower water environment. DH sediments are nearly devoid of macrofauna and are not bioturbated (Thorstensen and Meckenzie, 1974).

### Sample Collection

Cores were obtained by hand using a plexiglass (25 × 10 × 30 cm) box corer (Armstrong et al., 1979). Cores at DH were obtained using SCUBA. Samples were transported to the BBS before removal of the overlying water.

### Sample Handling

After siphoning off the overlying water, cores were placed rapidly into a $N_2$-filled glove bag, 2 to 4 cm sections removed and homogenized with a spatula. Subsamples were placed in appropriate vessels for microbiological analyses. The remaining sediment was transferred to bottles and centrifuged under $N_2$ at in situ temperature at ~5000 g for ~1 h. After returning them to the $N_2$-filled glove bag, the pore fluids were filtered through precleaned 0.4 µm Nuclepore filters and subdivided into vessels for later chemical analyses. Care was taken to avoid exposure to oxygen to prevent oxidation artifacts (Lyons et al., 1979).

### Sulfate Reduction

Sulfate reduction rates were determined using a sediment mixing technique similar to that used by Jørgensen (1978a), Nedwell and Abram (1978) and Howarth and Teal (1979). Four ml of anoxic sediment was placed into 5 cc syringes and sealed with serum stoppers. A 25 µl solution of $^{35}S$-$SO_4$ (1.0 µ Ci; New England Nuclear) was injected, in triplicate, with a microliter syringe as the needle was withdrawn. Syringes were incubated for 24 h in the dark at in situ temperature. The reaction was stopped by freezing (−80 °C). DH samples were incubated for 72 h. All $^{35}S$-containing samples were shipped frozen (dry ice) to the University of New Hampshire for analysis.

Frozen subsamples were placed into reaction vessels containing 25 ml of deoxygenated distilled water and 4 drops of antifoam silicone emulsion. Concentrated HCl (8 ml) was added slowly to dissolve carbonate material and release acid-volatile sulfides. Vessels were bub-

bled continuously with $O_2$-free $N_2$ for 1.5 h and sulfides collected as ZnS in traps containing 3% Zn acetate. With 2 traps in series, all radioactivity was recovered in the first trap. Trapping efficiency was greater than 97% (Hines, 1981). The ZnS precipitate was counted in an Aquasol™ gel suspension using a Packard Tricarb Scintillation spectrometer. Because of the similarity between the energy spectra of $^{35}S$ and $^{14}C$ (Wang et al., 1975) counting efficiencies were determined for each sample using a $^{14}C$-toluene (New England Nuclear) internal standard (Oremland and Taylor, 1978).

Following the distillation of sulfides, the 3 replicates from each core section were pooled and centrifuged. An aliquot of the supernatant fluid was counted and the remainder was analyzed gravimetrically for its sulfate content. Replicates analyzed separately for sulfate were within 4%. The ratio of 'hot' to cold sulfate was used to calculate the rate of sulfate reduction (Jørgensen and Fenchel, 1974):

$$\text{Rate (nmoles ml}^{-1}\text{ d}^{-1}) = \frac{(\text{dpm } ^{35}S\text{–}S^{2-})\ (\text{nmoles } SO_4^{2-})\ (1.06)}{(\text{ml, sample vol.})\ (\text{dpm } ^{35}S\text{–}SO_4^{2-})\ (\text{days, incubation time})}$$

where 1.06 is the $^{35}S$ fractionation factor.

Scrubbing gas ($N_2$) was rendered $O_2$-free by passage through a vanadous chloride solution. Two grams of ammonium metavanadate was boiled in 25 ml concentrated HCl and diluted to 250 ml with distilled water. The solution was transferred to a gas washing tower and amalgamated zinc added as a reducing agent. $N_2$ was passed through the solution until a clear violet color was obtained. Amalgamated zinc was prepared by covering ~10 g of powdered zinc with distilled water and adding 2 drops of concentrated HCl followed by 2 to 4 drops of mercury.

Although the distribution of $^{35}S$ between water and acid-soluble sulfides can be determined (Jørgensen and Fenchel, 1974) only a very small quantity of $^{35}S$ was recovered prior to the addition of HCl. This was unexpected since these sediments were iron poor and contained high concentrations of dissolved sulfides (Thorstensen and Mackenzie, 1974; Lyons et al., 1980b). Apparently a large portion of the water-soluble sulfides was either trapped within carbonate grains or in some way prevented from being scrubbed out by $N_2$.

### Sulfate-Reducing Bacteria

These were enumerated using anaerobic spread plates as described previously (Lyons et al., 1980a).

### Pore Water Nutrients

Titration alkalinity was determined according to Strickland and Parsons (1972). $NH_4^+$ and $PO_4^{3-}$ samples were acidified and shipped to the University of New Hampshire for analysis. Both were determined using a Technicion autoanalyzer and the techniques outlined in Glibert and Loder (1977).

## RESULTS

Two samples each from different locations in LG and MB were analyzed (Table 1). Only 1 sample from DH was analyzed. Sediment cores were divided vertically into 2 cm sections except for the top section (0 to 4 cm). The upper 4 cm were combined to avoid difficulty in sectioning the top 2 cm of cores from LG and MB which contained large quantities of benthic algae. Although DH was devoid of algae the top 4 cm were used for comparison.

### Sulfate Reduction

Sulfate reduction rates and numbers of sulfate-reducing bacteria decreased with depth (Table 1). There was a significant linear relationship ($P < 0.05$) between these parameters. The bacterial counts at LG and MB may have been low because of bacteria trapped in fissured and course carbonate grains.

Sulfate reduction rates are similar to those reported for other nearshore sediments (Skyring and Chambers, 1976; Jørgensen, 1977; Nedwell and Abram, 1978; Howarth and Teal, 1979; Skyring et al., 1979). At LG-1 sulfate reduction in the top 4 cm was considerably faster than at LG-2. Sulfate-reducing bacteria were more abundant in this region as well. In deeper sediments, rates at both locations were similar. Rates and numbers of sulfate reducers were higher at MB-2 than at MB-1 and at the former remained higher down to 10 cm. Sulfate reduction rates and the population size of recoverable sulfate-reducing bacteria were relatively low at DH and only detectable in the top 8 cm of sediment.

### Pore Water Nutrient Concentrations

$PO_4^{3-}$, $NH_4^+$, and titration alkalinity concentrations were higher at LG than at MB (Table 1) by an average of 12, 2.9 and 1.6 respectively. However, sulfate reduction rates at MB were 1.4 times faster that at LG. Nutrients at MB did not vary greatly with depth, whereas at LG-2 an increase in depth was noted. Except for $PO_4^{3-}$ values at MB-1, pore water nutrient concentrations were higher than in overlying water.

Table 1. Sulfate reduction and nutrient data in Bermudian sediments

| Depth (cm) | $SO_4^=$ red. rate (n moles $ml^{-1}$ $d^{-1}$) | $SO_4^=$ red. bact. (CFU $ml^{-1}$ $10^3$) | $PO_4^{3-}$ (μM) | $NH_4^+$ (μM) | Alkalinity (meq $l^{-1}$) |
|---|---|---|---|---|---|
| | | LG–1 | | | |
| overlying | – | – | 0.8 | <10 | 2.33 |
| 0–4 | 498 (46)* | 81 | 9.3 | 186 | 3.87 |
| 4–6 | 88 (38) | 91 | 13.0 | 114 | 6.30 |
| 6–8 | 49 (42) | 13 | 13.6 | 96 | 5.09 |
| 8–10 | 30 (13) | 2.8 | 12.9 | 87 | 4.95 |
| 10–12 | 11 (1.2) | 3.9 | 13.3 | 123 | 6.26 |
| 12–14 | 17 (1.7) | 2.9 | 13.1 | 141 | 4.95 |
| | | LG–2 | | | |
| overlying | – | – | 0.4 | <10 | 2.38 |
| 0–4 | 205 (13) | 19 | 6.1 | 69 | 3.47 |
| 4–6 | 91 (26) | 11 | 12.5 | 123 | 5.77 |
| 6–8 | 45 (12) | 1.5 | 12.4 | 186 | 7.43 |
| 8–10 | 67 (18) | 5.0 | 12.4 | 195 | 7.04 |
| 10–12 | 47 (11) | 9.1 | 15.0 | 231 | 7.99 |
| 12–14 | 19 (2.4) | 1.6 | 13.3 | 285 | 8.67 |
| | | DH | | | |
| overlying | – | – | 0.9 | – | – |
| 0–4 | 8.5 (3.9) | 3.8 | 6.1 | 42 | 3.14 |
| 4–6 | 2.5 (1.2) | 1.5 | 4.8 | 42 | 3.11 |
| 6–8 | 0.8 (0.3) | 0.9 | 4.1 | 42 | 2.95 |
| 8–10 | <0.05 | <0.1 | 3.3 | 42 | 2.75 |
| 10–12 | <0.05 | <0.1 | 3.3 | 42 | 2.71 |
| 12–14 | <0.05 | <0.1 | 2.9 | 51 | 2.77 |
| | | MB–1 | | | |
| overlying | – | – | 0.5 | <10 | 2.38 |
| 0–4 | 230 (41) | 12 | 0.4 | 114 | 3.18 |
| 4–6 | 150 (26) | 20 | 0.5 | 60 | 4.11 |
| 6–8 | 84 (23) | 12 | 0.4 | 51 | 4.12 |
| 8–10 | 85 (10) | 0.99 | 0.5 | 42 | 4.11 |
| 10–12 | 65 (20) | 0.20 | 0.5 | 42 | 5.02 |
| 12–14 | 38 (10) | 0.40 | 0.7 | 51 | 4.69 |
| | | MB–2 | | | |
| overlying | – | – | 0.2 | <10 | 2.45 |
| 0–4 | 383 (101) | 74 | 1.6 | 33 | 4.00 |
| 4–6 | 125 (34) | 35 | 2.1 | 60 | 3.58 |
| 6–8 | 129 (62) | 18 | 1.8 | 51 | 3.09 |
| 8–10 | 222 (71) | 84 | 1.8 | 51 | 3.16 |
| 10–12 | 51 (12) | 10 | 1.1 | 42 | 2.98 |
| 12–14 | 82 (8.6) | 5.9 | 1.1 | 42 | 2.82 |

* Standard deviation of triplicates

$PO_4^{3-}$ concentrations decreased with depth at DH, wehreas $NH_4^+$ and alkalinity showed little variation with depth. $PO_4^{3-}$ levels at DH were intermediate between those at LG and MB while $NH_4^+$ and alkalinity were lower.

## DISCUSSION

A significant linear relationship was noted between sulfate reduction rates and sulfate-reducing bacteria in these Bermudian sediments. Jørgensen (1978b) reported a similar relationship in subtidal clastic sediments, whereas Nedwell and Abram (1978) did not for salt marsh soils. Skyring and Chambers (1976) found similar sulfate-reducing bacterial population sizes in coral reef carbonate sediments exhibiting widely different sulfate reduction rates. Although Jørgensen (1978b) showed that viable counts of sulfate-reducing bacteria may be up to 1000-fold too low, changes in population sizes reported here yielded reasonable estimates of changes in sulfate reduction rates in the Bermudian sediments examined.

Sulfate reduction rates decreased with depth by more than an order of magnitude. The metabolizable organic matter available for sulfate reduction at LG and MB is produced in situ at the sediment surface by benthic algae. Because of the shallow nature of these coves and lack of significant freshwater runoff, the pelagic and terrestrial contributions probably are negligible. In this regard, LG and MB sediments resemble salt marsh soils. However, in many areas in salt marshes rapid anaerobic processes occur throughout much of the upper 30 to 50 cm of sediment because of the subsurface contribution of organic matter by *Spartina* roots (Howarth and Teal, 1979; Skyring et al., 1979). In the Bermudian sediments, primary production and anaerobic remineralization are restricted largely to the upper 2 to 4 cm. An analogous situation exists in cyano-bacterial mats (Jørgensen and Cohen, 1977). No primary productivity data are available for LG and MB which prevents calculations of the percentage of photosynthetically-fixed carbon which is metabolized via sulfate reduction. Others (Jørgensen, 1977; Howarth and Teal, 1979; Skyring et al., 1979; Aller and Yingst, 1980) have shown that 36 to 100% of near-shore primary produced and deposited carbon can be metabolized via sulfate reduction in anoxic marine sediments and salt marsh soils. A similar situation probably exists in the shallow sediments at LG and MB.

Gaudette and Lyons (1980) reported that sulfate was not significantly depleted from the upper 60 to 70 cm of sediment at LG and MB and suggested that little sulfate reduction had occurred. The $^{35}S$ results of the present study demonstrated the occurrence of sulfate reduction. The rates were more than sufficient to significantly deplete sulfate from these pore waters (Goldhaber et al., 1977; Rosenfeld, 1981). The lack of sulfate depletion is probably due to the exchange of pore waters with overlying waters by bioturbating infauna (Rhoads, 1967, 1974; Aller, 1977; Hylleberg and Henriksen, 1980). Although not abundant, infaunal organisms are present in these sediments (Zajac, Dobbs, Lyons, and Hines, in unpubl. prep.).

Unlike MB and LG, sedimentary organic matter at DH is derived from primary production in the overlying water column. Using Beers and Herman's (1969) average primary productivity data for Harrington Sound (50 mg C $m^{-3}$ $d^{-1}$), a 20 m water depth, and the relationship of 2 moles carbon metabolized per mole sulfate reduced (Richards, 1965; Jørgensen, 1977; Howarth and Teal, 1979) we calculated that less than 0.3% of the pelagically produced organic carbon is metabolized via sulfate reduction in DH sediments. Since DH bottom waters annually become anoxic, pelagic sulfate reduction may increase this percentage. Although 0.3% is low compared to other nearshore sediments (Jørgensen, 1977; Howarth and Teal, 1979; Skyring et al., 1979; Aller and Yingst, 1980), sedimentation at DH is hampered by a thermocline and we observed the accumulation of particulate material in this region. Pelagically-produced organic matter is probably highly degraded prior to deposition. In addition, the lack of bioturbating infauna at DH prevented the premature burial of organic matter into anoxic sediments.

Pore water nutrient concentrations were similar to those reported by Gaudette and Lyons (1980) for Bermudian nearshore sediments and lower than those reported for clastic estuarine sediments (Matisoff et al., 1975; Aller, 1977; Goldhaber et al., 1977; Lyons and Fitzgerald, 1978; Martens et al., 1978; McCaffrey et al., 1980).

The occurrence of rapid sulfate reduction in the LG and MB sediments, the role of sulfate reduction processes in nutrient regeneration and the low nutrient concentrations indicated that nutrients were rapidly removed from these pore waters by advection, adsorption or precipitation. A major nutrient removal mechanism in these sediments was undoubtedly irrigation due to bioturbation.

Stoichiometric models based on sulfate depletion with depth and the C:N:P ratios of sedimentary organic matter have been used to describe nutrient regeneration in sediments (Sholkovitz, 1973; Berner, 1977; Martens et al., 1978; Gaudette and Lyons, 1980; Rosenfeld, 1981). Such types of models are not applicable to these sediments because sulfate depletion in the pore waters was not observed. However, theoretical nutrient regeneration rates can be calculated using sulfate reduction rate data.

Nutrient regeneration rates were calculated assuming sedimentary organic matter C:N:P ratios similar to marine plankton (106:16:1), a sediment porosity of 50% and the relationship proposed by Richards (1965) for oxidation of organic matter via sulfate reduction reactions. Therefore, for every 53 moles of sulfate reduced, 106, 16, and one mole of $CO_2$, $NH_4^+$, and $PO_4^{3-}$ are produced respectively. Others (Berner, 1977; Martens et al., 1978) have used pore water nutrient concentrations and diagenetic models in a somewhat similar manner to explain nutrient concentrations and calculate sedimentary organic C:N:P ratios. However, here we have used sulfate reduction rate measurements to calculate gross nutrient regeneration rates which are independent of removal mechanisms. The calculated regeneration rates at MB and LG (Table 2) are very similar to those obtained from jar experiments using Long Island Sound sediments (Rosenfeld, 1981). These rates are useful for a comparison with actual pore water nutrient concentrations. The in situ nutrient concentrations divided by regeneration rates yield the

Table 2. Comparison of actual pore water nutrient concentrations with calculated rates of nutrient regeneration in Bermudian sediments. Values for top 14 cm of sediment

| Location | $PO_4^{3-}$ Conc. (n moles 14 $cm^{-3}$) | $PO_4^{3-}$ Rate (n moles 14 $cm^{-3}$ $d^{-1}$) | $PO_4^{3-}$ Turnover time (d) | $NH_4^+$ Conc. (n moles 14 $cm^{-3}$) | $NH_4^+$ Rate (n moles 14 $cm^{-3}$ $d^{-1}$) | $NH_4^+$ Turnover time (d) |
|---|---|---|---|---|---|---|
| MB–1 | 3 | 33 | 0.1 | 470 | 530 | 0.9 |
| MB–2 | 11 | 50 | 0.2 | 310 | 800 | 0.4 |
| LG–1 | 85 | 45 | 2 | 930 | 710 | 1 |
| LG–2 | 78 | 26 | 3 | 1,200 | 410 | 3 |
| DH | 31 | 0.8 | 40 | 300 | 12 | 25 |

time necessary to regenerate a quantity of N or P equal to that present in the pore water. If steady state conditions are approached, this quotient equals the turnover or residence time of the dissolved $NH_4^+$ and $PO_4^{3-}$ pools. These pools were turned over most rapidly at MB where the $PO_4^{3-}$ pool was replaced 10 times daily. Because of the absence of additional constraints, inferences made from these regeneration rate calculations probably should be restricted to instances where at least 2 to 3 fold differences are noted.

The fact that $PO_4^{3-}$ was turned over more rapidly than $NH_4^+$ at MB demonstrated preferential removal of $PO_4^{3-}$ from these pore waters. Pore water $NH_4^+/PO_4^{3-}$ ratios witness this as well (Gaudette and Lyons, 1980) but do not yield turnover time data. $PO_4^{3-}$ removal mechanisms in carbonate environments include: (1) authigenic formation of apatite (Berner, 1974; Kitano et al., 1978; Gaudette and Lyons, 1980); (2) removal of P as organic coatings on carbonate grains (Suess, 1973; Wilson, 1979); (3) the direct precipitation of amorphous calcium phosphate (Martens and Harriss, 1970; Nathan and Lucus, 1976); (4) apatite replacement of calcium carbonate (Ames, 1959; Manheim et al., 1975). The sediments studied here were enriched in sedimentary P (Gaudette and Lyons, 1980).

The fact that the LG and DH turnover times for $NH_4^+$ were less than or equal to $PO_4^{3-}$ suggested that $PO_4^{3-}$ was not preferentially removed in those sediments. This unexpected result may have been due to underestimates of the true $NH_4^+$ concentrations. Orem (1981) found that even acidified and frozen pore water samples lose $NH_4^+$ over time.

The possible importance of bioturbation in the removal of nutrients from pore water is seen by a comparison of the nutrient turnover times in the non-bioturbated sediments at DH with those at LG and MB. If the factors affecting nutrient concentrations other than bioturbation were similar for these locations, then bioturbation may have been responsible for decreasing the turnover time of pore water nutrients by a factor of 9 to 63 (calculated for $NH_4^+$). A similarly analyzed non-bioturbated sediment in Great Bay Estuary, New Hampshire, had nutrient turnover times nearly identical to those at DH (Hines, 1981).

In conclusion, nutrient regeneration rates in anoxic sediments as calculated from sulfate reduction rates and organic matter C:N:P ratios can be applied to sediments in which stoichiometric models do not apply. The present results indirectly demonstrate the quantitative importance of bioturbation in the removal of nutrients from pore waters. It must be emphasized that gross nutrient regeneration rates, calculated in this manner may vary from true rates, depending upon (1) C:N:P ratios of organic matter; (2) variations in C:N:P ratios of easily metabolized organic matter versus the bulk, more refractory organics; and (3) preferential release of N or P over carbon (Grill and Richards, 1964; Adams, 1973). However, rates calculated in this way offer an advantage over other stoichiometric methods because they circumvent complications due to bioturbation, differential diffusion, adsorption, and precipitation of authigenic minerals.

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