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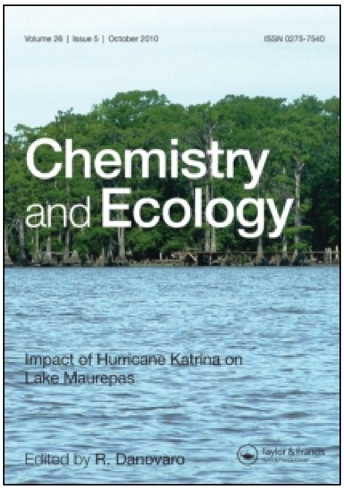

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# EXPONENTIAL COLLAPSE OF BENTHIC DEPURATIVE CAPACITY IN A EUTROPHIC TROPICAL MARINE ECOSYSTEM: A THRESHOLD RESPONSE TO ORGANIC NITROGEN LOADING

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Microbial decomposition of particulate organic matter in sediments can substantially modulate eutrophication of nearshore marine environments. Flux budgets for nitrogen compounds and quantification of rates of microbial transformation can provide important information on the process of eutrophication. This survey documents sediment nitrogen budgets for a eutrophic nearshore marine environment at La Parguera on southwest coast of Puerto Rico, including consideration of the organic fraction in addition to microbial transformations.

Sediments of the inshore channel at La Parguera denote the input of heavy organic loads with low redox potentials and high ammonium contents. Benthic fluxes of dissolved organic nitrogen are below those recorded for ammonium. These observations suggest that nearshore tropical sediments subject to heavy nitrogen loads act as a sink for organic nitrogen and that ammonification is a key process in the release of nitrogen from sediments to the water column. Nitrification and denitrification rates are low overall and inversely related to the redox potential. Depuration of excess nitrogen through denitrification is ineffective in these sediments. In contrast to more robust temperate environments, our work demonstrates that tropical marine systems are particularly susceptible to eutrophication given their limited capacity for depuration of excess nitrogen.

*Keywords:* Particulate organic matter; eutrophication; microbial transformation; La Parguera; Puerto Rico

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*Corresponding author.

## 1. INTRODUCTION

Eutrophication, the increase of nutrient concentration with increased aquatic productivity, affects coastal marine and fresh water bodies. Ocean/atmosphere exchange of greenhouse ($CO_2$, $N_2O$, $CH_4$) and ozone-active gases ($N_2O$), is enhanced as a consequence of eutrophication thus contributing to climate change. While nitrogen has been repeatedly implicated as the limiting nutrient in tropical marine environments, estimates of the magnitude of nitrogen fluxes between water, atmosphere and sediments are yet very uncertain. Nitrogen released from sediments supports a large portion of the photosynthetic nutrient demand of estuarine and coastal waters (Harrison, 1978; Nixon, 1981; Fisher *et al.*, 1982; Corredor and Morell, 1985; Corredor and Capone, 1985; Corredor and Morell, 1989). Coupled microbial nitrification and denitrification can, on the other hand, depurate excess nitrogen through release to the atmosphere in the form of gaseous products (Seitzinger, 1988; Nixon, 1981; Corredor and Morell, 1989). Benthic metabolism thus plays an important role in the regulation of water column nitrogen concentrations and consequently, the productivity of estuarine and coastal marine systems as sediments can be a source as well as a major sink in the cycling of this element. Ammonium supplement from sediments is particularly important due to its preferential assimilaltion by primary producers (Nedwell, 1975; Harrison, 1978; Aller and Benninger, 1981; Nixon, 1981).

Microbial transformations, sources and fluxes of inorganic nitrogen across the sediment/water interface have been documented in various marine environments along the south coast of Puerto Rico (Corredor and Morell, 1985; Corredor and Capone, 1985; Corredor *et al.*, 1985, 1992; Corredor and Morell, 1989; Morell and Corredor, 1993). Accumulation of reducing sediments, appearance of high concentrations of dissolved inorganic nitrogen, high phytoplankton biomass and the proliferation of the "nuisance" cyanobacterium, *Microcoleus lynbyaceus*, all indicate that the inshore waters of La Parguera are subject to eutrophication.

Nitrogen budgets for coastal water bodies are difficult to establish due to tidal and current exchange. In aquatic environments, nitrogen is quickly recycled between consumers and producers but a significant quantity is lost from the water column by settling of detrital particulate organic nitrogen (PON). Once deposited, PON undergoes microbial decomposition, by means of which the solid nitrogen is converted to dissolved organic nitrogen (DON) which is, in turn, quickly degraded by heterotrophic bacteria. We here take the approach of establishing budgets for nitrogen exchange across the sediment-water interface and assessing the rates of pertinent sedimentary microbial transformations. The assessment of DON fluxes in this survey allows a more robust approach to the nitrogen budget and can serve as a model for similar tropical settings. In estimation diffusion rates, we use experimental laboratory core incubations. Since diffusion rates are enhanced by current and wave action (Berner, 1980), our approach serves to establish lower limits for flux estimates. However, in protected inshore waters such as those at La Parguera, current and wave action are moderate so that *in situ* fluxes are not expected to significantly exceed our experimental values.

## 2. MATERIALS AND METHODS

Six sampling stations at La Parguera, on the southwest coast of Puerto Rico, were selected (Fig. 1). Stations 2–6 are located in the inshore channel, where conditions of incipient eutrophication have been seen as a consequence of the presence of over one hundred "stilt houses" along the mangrove fringe. These were, for several years, a source of domestic waste disposal. A station at Enrique Reef, part of an extensive reef system at La Parguera, was used as a reference site free of anthropogenic influence (Station 1). At each station, replicate sediment cores were sampled using corers with removable acrylic liners (6 cm diameter, 30 cm length) in order to determine redox potential and porosity, estimate potential benthic flux rates and quantify the different processes of nitrogen transformation. Samples were sectioned at 2 cm intervals to 10 cm depth. Portions of each section were centrifuged in order to obtain interstitial water for dissolved inorganic nitrogen (DIN) and DON analyses. Nitrate was measured using the cadmium/copper column reduction method followed by diazotization; in nitrite analysis the reduction step was omitted (Strickland and Parsons, 1972). Ammonium concentration was determined using phenol/hypochlorite technique (Strickland and Parsons, 1972).

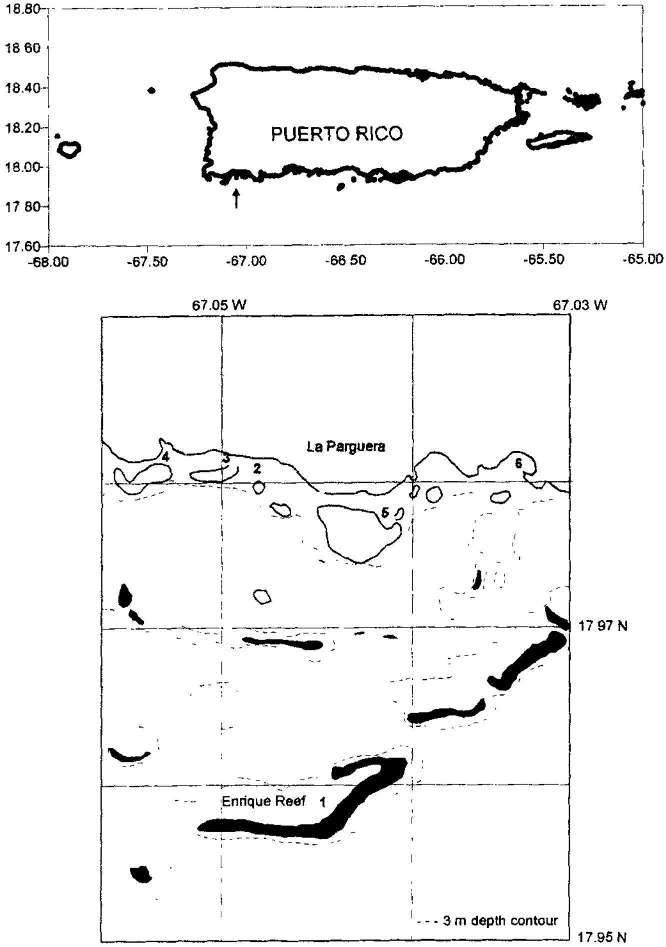

FIGURE 1 Sampling sites and locator map.

Cadmium chloride (100 μl of a 0.5 M solution) was used to precipitate sulphides present in the samples which may cause interference in the analyses.

Water samples for DON analysis were filtered to eliminate particulate organic materials and biologically active particles (Sharp and Peltzer, 1993) using GF/F filters previously treated for 2–4 hours at temperatures of 450°C to eliminate organic material (Williams *et al.*, 1993). Photochemical oxidation of DON samples was carried out in 20 ml quartz tubes to which 9 ml of filtered sample were transferred. After addition of 1.5 ml 30% hydrogen peroxide, samples were irradiated with ultraviolet light for 20 hours, using a 1000 watt Hanovia lamp 189 A10 (Armstrong *et al.*, 1966; Walsh, 1989). Tubes were positioned at 7 cm from the lamp in a compartment covered with lateral and top mirrors. A fan was used to avoid excessive warming. Once oxidation was completed and samples reached ambient temperature, 1 ml concentrated ammonium chloride was added to reach a pH of 8.5, the optimum for efficient reduction in the cadmium/copper column. Differences in nitrate plus nitrate pore-water content before and after irradiation yielded the DON concentration in samples.

Rates of ammonium diffusion, nitrification, denitrification, nitrogen fixation and PON sedimentation were estimated as described previously (Corredor and Morell, 1989; Morell and Corredor, 1993). Diffusion was estimated by following ammonium accumulation in low-nutrient sea water overlying recently collected cores. Potential nitrification was estimated as nitrite accumulation under a chlorate (a nitrate reductase inhibitor) block in aerated, ammonium-amended (200 μM) surface samples. Denitrification was assessed as nitrous oxide accumulation under an acetylene block of anaerobically incubated core sections amended with nitrate at *in situ* concentrations. Nitrogen fixation (nitrogenase activity) was assessed as ethylene accumulation from an acetylene substrate in anaerobically incubated core sections and PON sedimentation was documented using Kjeldahl analysis of material captured in field-deployed Imhoff cones. In addition to experimental benthic ammonium diffusion rates, Fickian rates were calculated using a coefficient of $9.8 \times 10^{-6}\,\mathrm{cm}^2\,\mathrm{s}^{-1}$ (Berner, 1980) for ammonium and $1.55 \times 10^{-6}\,\mathrm{cm}^2\mathrm{s}^{-1}$ (Burdige *et al.*, 1992) for DON.

Cores sectioned at 2 cm intervals were used for gravimetric determination of porosity by weighing before and after 72 h drying at temperature of 70°C and estimation of total organic matter contents after 1 h ignition at 550 ± 50°C. Replicate cores were used to measure redox potential with a platinum indicating silver–silver chloride electrode pair coupled to an ACCUMET 15 mV/pH meter (Whitfield, 1969).

## 3. RESULTS

Surface core sections at station 1 were yellowish with plant and animal remains, mainly molluscs and echinoderms. Inshore channel samples were yellowish, muddy and mucilaginous in the surface section but acquired a blackish colour with the characteristic odour of hydrogen sulphide in the deeper sections. Vertical redox potential gradients were apparent at all stations but potentials were significantly higher throughout the core at station 1 (Fig. 2).

Stations along the inshore channel showed the expected behaviour for sediments receiving exogenous inputs with higher contents of organic matter in the top layers and decreasing concentration toward the deeper sections as a result of microbic mediated diagenetic

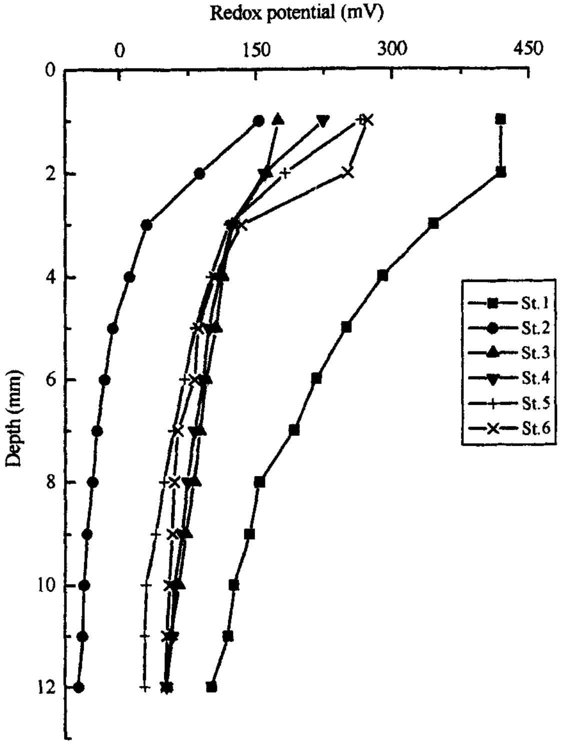

FIGURE 2 Characteristic redox potential profiles in sediments (Stations 1–6) at La Parguera.

processes (Tab. I). Organic matter content was lower at station 1 and exhibited a trend of increasing content with depth, most probably as the result of bioturbation and rapid near-surface remineralization due to oxic conditions.

The predominant DIN form in these sediments is ammonium; nitrate and nitrite concentrations are lower by several orders of magnitude (Tab. I). As is common for near-shore marine sediments, pore-water ammonium concentrations in most cases increased with depth. The prevalence of nitrite over nitrate at stations 1–4 could reflect the presence of agents such as hydrogen sulphide (Henricksen and Kemp, 1988) which can inhibit the efficient finalization of

TABLE I Vertical variation of interstitial concentration of ammonium, nitrite, nitrate and DON in sampling stations. Porosity and organic matter content are also recorded

| *Station* | *Core interval cm* | *Porosity %* | *Nitrite (μM)* | *Nitrate (μM)* | *Ammonium (μM)* | *DON (μM)* | *Organic matter %* |
|---|---|---|---|---|---|---|---|
| 1 | 0–1 | 36 | 12.18 | 5.46 | 7.1 | 171.0 | 9.7 |
| | 1–2 | 36 | 12.18 | 5.46 | 19.1 | 180.0 | 10.8 |
| | 2–4 | 40 | 12.18 | 5.46 | 37.2 | 191.0 | 11.9 |
| | 4–6 | 40 | 22.40 | N.D. | 67.2 | 103.8 | 15.0 |
| | 6–8 | 41 | 19.88 | 0.70 | 73.3 | 136.1 | 9.9 |
| 2 | 0–1 | 76 | 2.39 | 0.17 | 381.1 | 132.1 | 16.3 |
| | 1–2 | 74 | 2.23 | 0.43 | 555.5 | 138.4 | 15.4 |
| | 2–4 | 70 | 2.14 | 0.89 | 636.8 | 147.0 | 14.6 |
| | 4–6 | 64 | 2.06 | 1.07 | 898.4 | 165.1 | 12.2 |
| | 6–8 | 59 | 1.98 | 1.25 | 603.7 | 128.3 | 12.6 |
| 3 | 0–1 | 63 | 2.23 | 0.81 | 1.1 | 113.7 | 9.3 |
| | 1–2 | 60 | 2.14 | 1.09 | 16.1 | 120.8 | 9.3 |
| | 2–4 | 54 | 2.23 | 1.10 | 14.6 | 130.2 | 8.6 |
| | 4–6 | 48 | 2.06 | 1.07 | 38.7 | 137.6 | 9.4 |
| | 6–8 | 49 | 2.95 | 0.76 | 52.2 | 119.0 | 8.3 |
| 4 | 0–1 | 76 | 1.98 | 0.96 | 43.2 | 116.0 | 13.9 |
| | 1–2 | 71 | 2.31 | 0.54 | 73.3 | 119.6 | 13.9 |
| | 2–4 | 68 | 2.47 | 0.19 | 83.8 | 122.8 | 16.3 |
| | 4–6 | 61 | 2.71 | N.D. | 106.4 | 116.9 | 14.4 |
| | 6–8 | 59 | 2.31 | 0.83 | 127.4 | 171.3 | 20.6 |
| 5 | 0–1 | 69 | 0.23 | 0.72 | N.D. | 96.8 | 14.6 |
| | 1–2 | 69 | 0.32 | 0.63 | 58.7 | 68.4 | 13.6 |
| | 2–4 | 69 | 0.32 | 0.63 | 58.7 | 49.0 | 13.6 |
| | 4–6 | 70 | 0.37 | 0.69 | 79.0 | 93.2 | 16.3 |
| | 6–8 | 68 | 0.37 | 0.69 | 307.8 | 103.5 | 18.1 |
| 6 | 0–1 | 60 | 0.04 | 0.60 | 44.0 | 112.6 | 9.8 |
| | 1–2 | 54 | N.D. | 0.48 | 102.9 | 126.1 | 9.8 |
| | 2–4 | 54 | N.D. | 0.59 | 122.5 | 135.5 | 8.0 |
| | 4–6 | 49 | N.D | 0.43 | 128.7 | 164.8 | 8.5 |

denitrification in sedimentary layers. DON was the main dissolved nitrogen species except for station 2 where ammonium concentrations were greater by a factor of four. There is no apparent trend in pore-water DON concentration (Tab. I) except for station 6 where a moderate increase with depth is apparent, and station 1 where a maximum interstitial DON content near 3 cm depth appeared, below which there is a progressive decrease. Remarkably, the strong difference in DIN concentration between the control and the inshore stations is not reflected in pore-water DON concentrations which exhibit no significant differences between stations. Reproducibility of the hydrogen peroxide photo-oxidation method, calculated from three replicates of different standard concentrations was ± 0.30 μM (1–2%), at low concentrations (5–50 μM), and ± 1.3 μM (1–2%) at high concentrations (< 80 μM). Standards (30 and 80 μM) measured in several oxidation periods were reproducible at ± 0.33 μM (1%) for the first and ± 7.0 μM (5–8%) for the second concentration.

PON sedimentation rates (Tab. II) were higher by up to two orders of magnitude at the inshore stations compared to the control. Despite the higher DON pore-water concentrations, calculated DON diffusion rates were generally lower than those reported for ammonium (Tab. II). Only at station 3 did DON diffusion exceed ammonium diffusion. Higher fluxes of both ammonium and DON were recorded at stations with highly reducing, organic-laden sediments. Greatest ammonium diffusion rate were recorded at station 2. Ammonium diffusion was overall the most significant source of nitrogen to the water column.

Sediments of the inshore channel at La Parguera exhibit low rates of nitrification and dinitrification (Tab. II) in comparison with values

TABLE II Potential rates of nitrification, denitrification, ammonium diffusion, nitrogen fixation, sedimentation and dissolved organic nitrogen diffusion recorded in sediment cores. ($\mu$mol m$^{-2}$ h$^{-1}$)

| *Station* | *Nitrification* | *Denitrification* | *$NH_4^+$ Diffusion* | *$N_2$ Fixation* | *Sedimentation* | *Fickian DON Diffusion* |
|---|---|---|---|---|---|---|
| 1 | 10.01 | 2.30 | 1.53 | 1.48 | 80 | 0.85 |
| 2 | 3.15 | 0.03 | 316.30 | 7.14 | 1478 | 6.05 |
| 3 | 1.96 | 0.29 | 2.59 | 3.56 | 588 | 2.83 |
| 4 | 2.04 | 0.02 | 35.10 | 2.90 | 590 | 5.06 |
| 5 | 0.44 | 0.35 | 8.67 | 6.54 | 1046 | 3.23 |
| 6 | 0.71 | 0.13 | 22.41 | 6.53 | 872 | 2.23 |

reported in other coastal ecosystems (Capone *et al.*, 1992; Morell and Corredor, 1993; Zimmerman and Benner, 1994). Coinciding with reports by Capone *et al.* (1992), higher rates of nitrification and denitrification occur at station 1, characterized by sediments with greater particle size. Coarse-grained sediments generally occur in areas of greater turbulence and higher wave action which provide relatively well-aerated conditions near the water/sediment interface. Patriquin and Knowles (1975) note that the coarse skeletal particles of reef sands may favour the existence of anoxic microzones where oxygen concentration is reduced sufficiently for the induction of denitrifying enzymes so that both processes may co-occur in close proximity.

Nitrogenase activity was detected in all sediments with greater activity in the top 2 cm section. There was a small difference relative to particle size, with higher values in fine-grained reducing sediments. Nitrogen fixation rates (Tab. II) in these sediments were lower than those reported by Morell and Corredor (1993) in sediments of Laguna Joyuda in Puerto Rico.

## 4. DISCUSSION

The overall balance of the several pathways of nitrogen transformation can be established by constructing benthic budgets. Assuming no subsequent erosion or migration, once deposited, organic material suffers one of two fates. It is remineralized and released back into overlying water either as DON, as DIN, or as a gaseous product, or it is permanently incorporated into sedimentary deposits. Nitrogen sources are detrital contributions and nitrogen fixation.

PON inputs ranged from a low of 80 $\mu$mol $m^{-2}h^{-1}$ at station 1 to a high of 1478 $\mu$mol $m^{-2}h^{-1}$ at station 2 and averaged $776 \pm 475$ $\mu$mol $m^{-2}h^{-1}$ for the inshore stations combined. Assuming a steady state between DON mineralization (ammonification) and ammonium flux and between ammonification and nitrification/denitrification, we calculate remineralization rates as the sum of ammonium diffusion and denitrification. Our remineralization values range from less than 1% (station 4) to 21% (station 2). However, at station 1, 60% of the ammonified nitrogen is eventually denitrified (6% of the total input) and less than 10% of the ammonified fraction is denitrified at the more eutrophic inshore stations.

In this study benthic nitrogen fluxes were dominated by ammonium. Although DON pore-water concentrations are similar to or greater than those for ammonium, DON diffusion as calculated using the Fickian model and experimentally derived diffusion coefficients for dissolved organic matter (Burdige *et al.*, 1992) contributes substantially less to sediment nitrogen losses. When the anomalously high ammonium diffusion values for station 2 are included, the relationship between ammonium and DON diffusion takes on a hyperbolic form. However, upon exclusion of this station, a linear relationship is apparent indicating that, on the average, one molecule of DON diffuses to the water column for every twelve molecules of ammonium (Fig. 3). Nitrate uptake by sediments was not quantified, but previous work (Corredor and Morell, 1993) indicates that there is low sediment uptake in such environments. As our estimates for diffusive flux are based upon Fickian computations (DON) or laboratory incubations in the dark (ammonium), our results do not take into account uptake by benthic alga. Our interest is, however, in assessing transfer rates between the sedimentary compartment and the phototrophic water column/surface sediment community.

Rates of nitrogen regeneration in sediments are controlled by the rates at which the several remineralization reactions occur within the sediment and at the sediment-water interface. Potential nitrification rates at the sediment/water interface in all cases exceed denitrification rates integrated throughout the sediment column. Nitrification is affected by benthic fauna and turbulent flow, both of which increase advective flow simultaneously carrying oxygen and ammonium to deeper strata thus expanding the nitrification zone (Jorgensen, 1996). This is readily apparent in the redox profile for station 1 (Fig. 2). As denitrification is, for the most part, dependent on nitrate produced by nitrification and as nitrification rates are low at the inshore stations, denitrification is also prevented, removing less nitrogenous nutrients from the ecosystem. This mechanism tends to increase the effects of eutrophication. Blackburn and Blackburn (1992) note that nitrification is sensitive to eutrophication through alteration of flux balances of oxygen and ammonium and can, therefore, result in direct ammonium release to the water column.

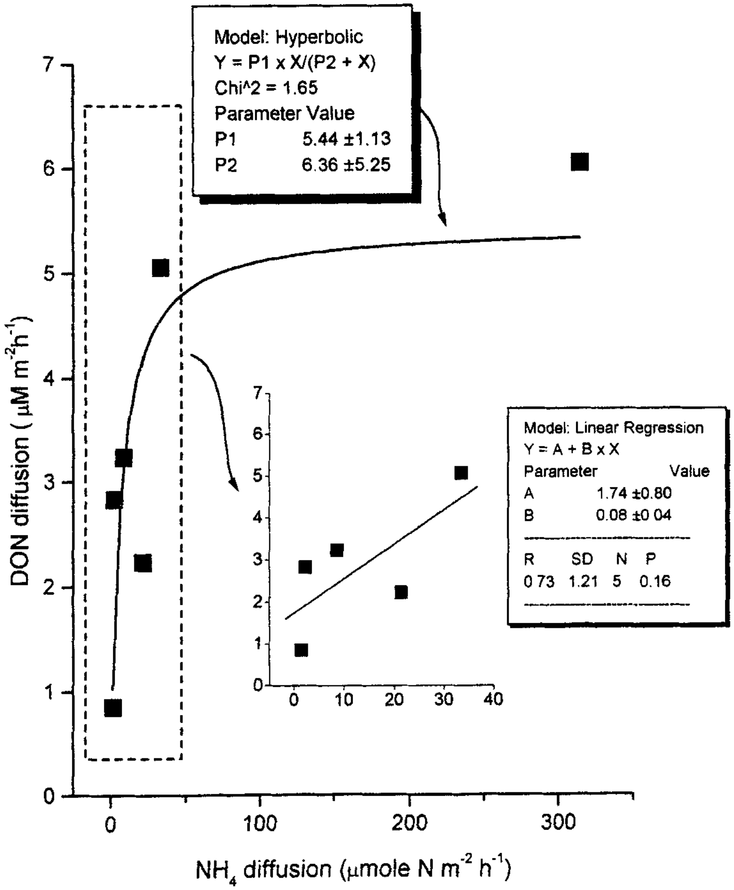

FIGURE 3 Relationship between ammonium and DON diffusion rates from the sediment to the water column.

Both potential nitrification and apparent *in situ* denitrification at our study sites decreased dramatically with increased PON inputs; a relationship which can be predicted using exponential decay models (Fig. 4). Our nitrification values reflect the potential for ammonium oxidation under aeration with added substrate and may overestimate *in situ* rates. The model for denitrification thus more accurately reflects the limited capacity for nitrogen depuration of these benthic systems.

Table III summarizes sediment inputs and losses of nitrogen at each station. Our results indicate that sediments at La Parguera act more as

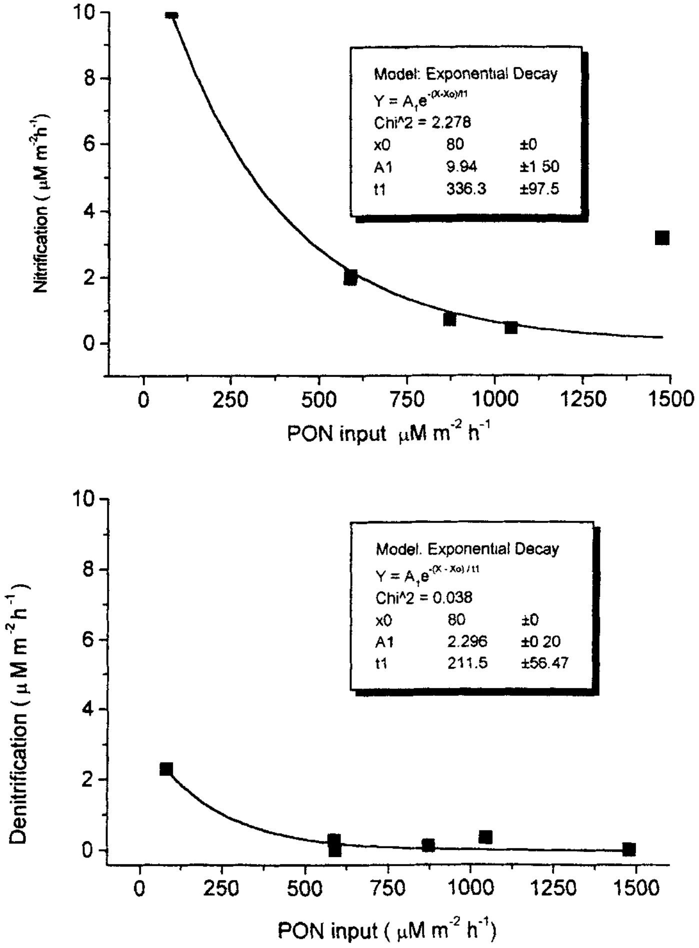

FIGURE 4 Exponential decay models for nitrification and denitrification as a function of sediment PON loading.

a sink than a source of organic nitrogen. When mineralization processes are oxygen-mediated, as in the case of station 1, a trend towards greater balance with a healthier appearance throughout the core is apparent. While the fraction of incoming nitrogen subsequently removed from the sediment through the processes at stations 2 and 4 is greater than that at the reference station (1), net inputs to the sediment are still orders of magnitude greater than the inshore stations.

TABLE III Summary of input and removal values based on estimated benthic budgets for each sampling station, showing their main removal mechanism

| *Station* | *Input* ($\mu mol\, m^{-2} h^{-1}$) | *Total removed* ($\mu mol\, m^{-2} h^{-1}$) | *Removal percentage* | *Main removal mechanism** |
|---|---|---|---|---|
| 1 | 81.5 | 4.7 | 5.74 | 3, 2 |
| 2 | 1485 | 322.4 | 21.7 | 1 |
| 3 | 591.6 | 5.71 | 0.96 | 1, 2 |
| 4 | 592.9 | 40.2 | 6.78 | 1, 2 |
| 5 | 1052.5 | 12.3 | 1.16 | 1, 2 |
| 6 | 878.5 | 24.8 | 2.82 | 1, 2 |

*Removal mechanisms: 1 = Ammonium diffusion 2 = DON diffusion 3 = Denitrification.

Although a major fraction of the PON deposited is permanently sequestered in sediments, substantial fluxes of both ammonium and DON are observed. These fluxes further contribute to the maintenance of eutrophic conditions in the water column. It has been estimated that the fraction of total input of nitrogen removed by denitrification in temperate and subtropical estuaries varies from 10% to more than 60% (Mantoura *et al.*, 1991; Seitzinger, 1988). Consequently, denitrification is considered to be one of the main pathways for the depuration of benthic regenerated nitrogen. This process plays a minimal role in inshore channel stations at La Parguera where coupled nitrification/denitrification is severely inhibited under conditions of high PON flux. In contrast to temperate environments, tropical marine systems are thus particularly susceptible to eutrophication given their limited capacity for depuration of excess nitrogen.

## *Acknowledgements*

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