Nitrogen cycling and anthropogenic impact in the tropical interamerican seas

JORGE E. CORREDOR[1], ROBERT W. HOWARTH[2], ROBERT R. TWILLEY[3] & JULIO M. MORELL[1]
[1]*Department of Marine Sciences, University of Puerto Rico, U.S.A.;* [2]*Section of Ecology and Systematics, Cornell University, NY, U.S.A.;* [3]*Department of Biology, University SW Louisiana, U.S.A.*

Abstract. We discuss the mechanisms leading to nutrient limitation in tropical marine systems, with particular emphasis on nitrogen cycling in Caribbean ecosystems. We then explore how accelerated nutrient cycling from human activities is affecting these systems.

Both nitrogen and phosphorus exert substantial influence on biological productivity and structure of tropical marine ecosystems. Offshore planktonic communities are largely nitrogen limited while nearshore ecosystems are largely phosphorus limited. For phosphorus, the ability of sediment to adsorb and store phosphorus is probably greater for tropical carbonate sediments than for most nearshore sediments in temperate coastal systems. However, the ability of tropical carbonate sediments to take up phosphorus can become saturated as phosphorus loading from human sources increases. The nature of the sediment, the mixing rate between nutrient-laden runoff waters and nutrient-poor oceanic waters and the degree of interaction of these water masses with the sediment will probably control the dynamics of this transition.

Nearshore tropical marine ecosystems function differently from their temperate counterparts where coupled nitrification/denitrification serves as an important mechanism for nitrogen depuration. In contrast, nearshore tropical ecosystems are more susceptible to nitrogen loading as depurative capacity of the microbial communities is limited by the fragility of the nitrification link. At the same time, accumulation of organic matter in nearshore carbonate sediments appears to impair their capacity for phosphorus immobilization. In the absence of depurative mechanisms for either phosphorus or nitrogen, limitation for both these nutrients is alleviated and continued nutrient loading fuels the proliferation of nuisance algae.

The health of marine ecosystems in the American tropics is finely constrained by nutrient availability within a narrow band separating limitation from excess. More than for temperate marine ecosystems, those of the tropics are often quite limited by nutrient availability and yet enormously vulnerable to the detrimental effects of nutrient excess. We briefly discuss the mechanisms leading to nutrient limitation in tropical systems, with particular emphasis on

nitrogen cycling in Caribbean ecosystems. We then explore how accelerated nutrient cycling from human activities is affecting these systems.

In some marine ecosystems, nitrogen is limiting to primary production, while in others, phosphorus is limiting (Smith 1984; Howarth 1988; Vitousek & Howarth 1991; Howarth et al. 1995, 1996). In oceanic systems well away from coastal and riverine influences, nitrogen and phosphorus may often be nearly co-limiting (but see Downing 1997; Tyrrell & Law 1997). While in nearshore ecosystems, the influences of terrestrial and riverine ecosystems, of human activity, and of biogeochemical processes in the coastal zone often act to make either nitrogen or phosphorus much more limiting in a particular system. Often, nitrogen is considered more limiting to primary production in coastal marine ecosystems in the temperate zone while phosphorus is thought to be more limiting in tropical coastal systems. There are however, many exceptions to these generalities (Howarth et al. 1995, 1996).

Plankton systems

Evidence for the Caribbean Sea strongly suggests nitrogen limitation for planktonic systems. Compared to the requirements of phytoplankton (Redfield molar ratio of N:P = 15), nitrogen is quite depleted relative to phosphorus in surface waters as is shown in N:P depth profiles for inorganic nitrogen and phosphorus at long-term oceanographic grids off the south coast of Puerto Rico. For example, during the CEER-OTEC project a grid of offshore stations was occupied at bimonthly interval for a period of over a year. The data set (unpublished) yields an overall N:P molar ratio of 2.41 (SD = 1.96, n = 49) for the mixed layer (above 100 m). Deeper waters have an N:P ratio more closely matching the Redfield ratio, perhaps indicating the influence of detrital material with a near-Redfield ratio sinking from the photic zone and decomposing at depth. Inorganic N:P is however only a partial proxy for nutrient limitation of phytoplankton since turnover rates in the water column are high and recent work suggests that DON and DOP may also constitute important sources of nutrients for the phytoplankton (see below).

Nitrogen-fixing cyanobacteria (*Trichodesmium* species) are common in the nitrogen-depleted waters of the Caribbean Sea, as they are generally in nutrient depleted oceanic waters of the tropics and subtropics (Margalef 1971; Carpenter 1983; Carpenter & Capone 1992; Bergman et al. 1997; Capone et al. 1997). These organisms fix substantial quantities of molecular nitrogen into biologically usable forms, yet their rate of nitrogen fixation in the Caribbean Sea is probably not sufficient to alleviate nitrogen limitation as indicated by the low N:P ratio for dissolved nutrients in surface waters. The presence of

active nitrogen-fixing cyanobacteria in the plankton of the oligotrophic waters of the Caribbean Sea contrasts with the general lack of planktonic nitrogen-fixing organisms in most estuaries and coastal seas of the temperate zone which are generally mesotrophic or eutrophic (Howarth 1988; Howarth et al. 1988; Vitousek & Howarth 1991). The reason for this dichotomy between oligotrophic tropical marine systems and mesotrophic/eutrophic temperate marine systems remains unknown; see Howarth and Marino (1998) and Howarth et al. (this volume) for further discussion.

Along limited stretches of the Caribbean coast, particularly along the southern margins, wind driven upwelling of deep nutrient-rich waters brings about substantial fertilization and sustains large biological communities (Margalef 1965; Corredor 1976, 1979). When upwelling occurs in the Caribbean, the phytoplankton communities preferentially take up nitrogen (Corredor 1979), further evidence for nitrogen limitation of primary production by these planktonic systems. Tidal pumping and breaking internal waves along the oceanic margins (Garret & Munk 1972) may serve as additional mechanisms for enrichment of the photic layer of the Caribbean (Corredor et al. 1984).

The mechanism leading to nitrogen limitation of primary production by the phytoplankton communities in the Caribbean is not entirely clear. Elsewhere in the world's oceans, N:P ratios for inorganic nutrients as low as those seen in the photic zone for the Caribbean south of Puerto Rico are sometimes observed, but are not that common (Tyrrell & Law 1997). Low N:P ratios are quite rare in the world's oceans away from the coast and are mostly related to low oxygen sites in the Pacific Ocean. Tyrrell and Law (1997) suggest that when low N:P ratios are observed, denitrification is the most likely cause as the N:P ratio for most rivers in the world is high. For portions of the Caribbean Sea, however, the low N:P ratio in surface waters may be in part caused by rivers as the Caribbean Sea is influenced by rivers with unusually low N:P ratios. One such river is the Amazon, which has a surprisingly low N:P ratio, 4.8 for total nitrogen and phosphorus (Howarth et al. 1996). Although the Amazon discharges at the equator well south of the Caribbean Sea, ocean currents act to carry its plume northward (Howarth et al. 1996). Some of this plume seasonally enters the Caribbean Sea, and its influence there on nutrients and phytoplankton populations has long been recognized (Ryther et al. 1967). This hypothesis is however subject to a better understanding of the Amazon's relative contribution to the total volume of Caribbean Surface Water (CSW). Other rivers draining South America such as the Orinoco and Magdalena also influence the nutrient status of the Caribbean Sea and in fact may have a greater influence than does the Amazon. The N:P ratio for total nitrogen and phosphorus in the discharge of the Orinoco is 17 (Lewis & Saun-

ders 1989), considerably higher than that from the Amazon but far lower than average fluxes from the temperate zone of North America into the Atlantic Ocean (N:P = 42; Howarth et al. 1996) and lower than the world's average rivers (Meybeck 1993). Coastal ecosystems receiving inputs from rivers with N:P ratios as low as the Orinoco are frequently nitrogen limited since the input ratio is near the Redfield ratio of 16:1 and nitrogen is further removed in denitrification (Howarth et al. 1996). For the Orinoco River plume, there appears to be massive nitrate depletion before waters exit the Gulf of Paria and enter into the southern Caribbean (Bonilla et al. 1993; Sánchez-Suárez et al. 1995). In any event, river inputs are significantly diluted as they merge with the oceanic waters of the CSW mass. In fact, the freshwater fraction attributable to river input in surface waters at a serial observing station south of Puerto Rico (Caribbean Time Series Station at 67° W 17° 36' N) never exceeds 5% (Corredor & Morell In Review).

Following the late summer peak in river flow, the influence of the Orinoco River extends throughout the Eastern Caribbean Basin (Muller Karger et al. 1981; Yoshioka et al. 1985). As noted above, despite enhanced phytoplankton biomass within the river plume, input of inorganic nutrients to CSW by the Orinoco River plume is low (Bonilla et al. 1993). Recent evidence from this (Morell & Corredor, In Review) and other riverine systems (Carlsson et al. 1993; Moran & Hodson 1994; Bushaw et al. 1996) indicates that organically bound nitrogen in the form of humic acids dissolved in river water may constitute a major source of nutrient enrichment to marine waters. Given the refractive nature of these compounds, nutrients are only slowly released as the molecules are broken down by a combination of UV-aided oxidation and bacterial activity. Little is known regarding the release of phosphorus from these organic matrices. Clark et al. (1998) have recently demonstrated the selective remineralization of phosphate over nitrogen from marine dissolved organic matter but it remains unclear whether river-borne humic acids display such selectivity as well.

Benthic systems

In shallow-water systems, benthic processes and exchange of water with sediments become increasingly important in both the nitrogen and phosphorus cycles (Corredor & Morell 1985; Corredor & Morell 1989; Aller 1988; Howarth et al. 1988, 1995). One such important process in many tropical marine sediments is nitrogen fixation. While nitrogen fixation rates within the sediments of temperate estuaries are generally lower than are rates of denitrification (Howarth et al. 1988; Seitzinger 1988), this may not be true in tropical sediments because of lower denitrification potentials (discussed below). Rates

of nitrogen fixation by heterotrophic bacteria within tropical sediments are generally rather low, but porewater ammonium can accumulate to levels of up to $ca.$ 200 μM before rate reductions are apparent, thus favoring accumulation of reduced nitrogen (Nieves & Corredor 1984). Rates of nitrogen fixation by mats of photosynthetic cyanobacteria and by epiphytes on seagrasses are far higher than are those of heterotrophic bacteria in sediments and in tropical lagoons with high water clarity. Such nitrogen fixation by benthic and epiphytic photosynthetic cyanophytes can be quite important (Howarth et al. 1988; Morell & Corredor 1993). In some cases, area-specific rates of fixation by $Microcoleus$ $lyngbyaceus$ as high as 200 umole $N.m^{-2}.h^{-1}$ have been found (Díaz et al. 1990). In contrast to nitrogen fixation by heterotrophic bacteria in sediments, $M.$ $lyngbyaceus$ responds rapidly to ammonium and nitrate additions (Díaz et al. 1990; Corredor et al. 1994) by suppressing nitrogenase activity; an adaptation which optimizes the use of energy resources by this species. On coral reefs and seagrass beds, a significant fraction of the nitrogen cycled is fixed by $Calothrix$ $crustacea$ (Capone 1983), an epiphytic cyanophyte. In contrast to tropical systems, nitrogen fixation by benthic and epiphytic cyanobacteria in temperate systems tends to be fairly unimportant (Capone 1983; Howarth et al. 1988), in part because the temperate systems are often turbid resulting in light limitation of benthic cyanophytes.

Bacteria living symbiotically with sponges in coral reefs (Corredor et al. 1988) and in algal mats of coral reefs and in fringe mangroves oxidize significant amounts of ammonium to nitrate. In contrast to that of sedimentary nitrification, this process is not coupled to denitrification, resulting in the net release of nitrate to the water column. Elevated concentrations of nitrate are common in reef environments and are considered one of the sources of nitrogen export from these tropical ecosystems.

Intertidal systems

Mangrove ecosystems dominate the intertidal zone of diverse environmental settings in the Caribbean from carbonate platforms to terrigenous deltas that exhibit different patterns of nutrient cycling (Twilley 1997). Phosphorus has been implicated more than nitrogen as the nutrients most likely limiting primary productivity of mangrove wetlands. The enhanced productivity of mangrove islands off the coast of Florida was associated with presence of bird guano and leaf tissue analyses indicated there was more enrichment with added P than N (Onuf et al. 1977). Growth of scrub mangroves on a carbonate island off the coast of Belize was stimulated when fertilized with mixtures of nitrogen and phosphorus (Twilley 1995), however more specific studies showed that phosphorus was more important than nitrogen in limiting

mangrove growth (Feller 1995). Both studies showed that mangroves in these sites are also influenced by a combination of fertility and hydroperiod. Fertilization studies of scrub mangroves in south Florida have also shown that phosphorus rather than nitrogen can stimulate growth in red mangroves (Koch 1996). A Monod model (Bridgham et al. 1995) of forest biomass along the estuarine gradient of the Shark River estuary has a stronger correlation with soil concentrations of P than N (Chen 1996), with a half-saturation constant of 29.3 g/m^2 (to a depth of 40 cm).

The lack of nitrogen limitation may be associated with the accumulation of this nutrient in leaf litter supplied either from the atmosphere and/or from tidal waters. It is a general pattern to observe a net increase in nitrogen during the initial two months of decomposing leaf litter that reduces the C:N ratio of this material to nearly half the ratios of litter falling from the canopy (Twilley et al. 1986; Twilley et al. 1997). Nitrogenase activity has been observed in decomposing leaves, root surfaces (prop roots and pneumatophores) and sediment, but few studies have interpreted areal fixation rates that can be compared to nitrogen demand by annual net production of mangrove biomass (Kimball & Teas 1975; Gotto & Taylor 1976; Zuberer & Silver 1978; Potts 1979; Gotto et al. 1981). Results from mangrove sediments in south Florida indicate that nitrogen fixation rates range from 0.4 to 3.2 g N.m^{-2}.y^{-1} (Kimball & Teas 1975; Zuberer & Silver 1978), similar to the natural rates of denitrification. These studies have shown that decaying mangrove leaves are sites of particularly high rates of fixation, and thus may account for some of the nitrogen immobilization in leaf litter on the forest floor (Gotto et al. 1981; Van der Valk & Attiwill 1984). In addition, there seems to be a pulse of nitrogen fixation in mangrove leaf litter with a 20 day lag following the initiation of decomposition on the forest floor (Pelegri et al. 1997). This may result from a combination of factors including organic matter source, time for microbial colonization, and inhibition by phenolics (Pelegri and Twilley 1998). However, the spatial and temporal analysis of nitrogen fixation is still inadequate to provide a clear estimate of this contribution to the nitrogen budget of mangrove wetlands.

While a substantial capacity has been documented for denitrification of nitrate-laden secondary effluents in mangrove sediments (Corredor & Morell 1994), doubt exists as to the capacity of microbial communities in these sediments to oxidize reduced nitrogen. Rivera-Monroy and Twilley (1996), documented only minimal losses of ^{15}N-labeled reduced organic substrates when added to mangrove sediments of Laguna de Terminos on the Gulf of Mexico. These data thus indicate minimal transformation to gaseous products of the added substrate and consequently of a lack of coupled nitrification/denitrification. Competitive advantage in reduced nitrogen uptake of

heterotrophic bacterial communities over the nitrifiers, or the inhibition of nitrifying activity by phenolic compounds or reduced sulfur may in part explain these results. In mangrove sediments devoid of sulfide, nitrification can proceed at rates of *ca.* 250 μmole N.m^{-2}.h^{-1} (Corredor et al. In Press) among the highest values recorded for this process throughout the marine environment (Kaplan 1983). It must be held in mind however that in these particular environments, the mangroves themselves can compete vigorously for both the reduced and oxidized species of available nitrogen. The lack of ^{15}N$_2$ gas production indicates that much of the net DIN exchange at the boundary of mangroves (Rivera-Monroy et al. 1995; Twilley 1997) may not be lost to the atmosphere via denitrification, but accumulated in the litter on the forest floor due to the high demand associated with C:N ratios that can exceed 70 in senescent leaf litter (Twilley et al. 1986).

The relative availability of nitrogen and phosphorus to mangrove production is recorded in the concentration and burial of these two nutrients in mangrove sediments. Mangroves in river-dominated estuaries have higher sedimentation rates of inorganic matter with N:P ratios <10 compared to mangroves in reef environments with little terrigenous input and N:P ratios >60 (Twilley 1995, 1997). The availability of P associated with the deposition of terrigenous sediments can be linked to the litter productivity of mangrove wetlands. Nitrogen concentrations vary directly with organic content of mangrove sediments and exhibit less variation among sites than concentrations of P. Thus in nearshore oligotrophic waters of the Caribbean, there seems to be less phosphorus that nitrogen due to the relative availability of terrigenous *vs* atmospheric sources for these two nutrients. A more thorough examination of these unique ecosystems is certainly due.

Anthropogenic impact

Human activity is causing large imbalances in the nitrogen and phosphorus cycles of coastal marine waters as a consequence of increased fertilizer use, of wetland reclamation for aquaculture ponds, of poor land management practices leading to topsoil erosion, and of large inputs of treated and untreated sewage. Abnormal nitrogen and phosphorus inputs to otherwise nutrient limited coastal waters can bring about rapid changes in algal communities disrupting existing ecological structure. Opportunistic algal species, particularly the filamentous cyanophytes and several members of the Chlorophyta may come to dominate the benthos excluding both other macrophytes and the macroinfauna as well. In Puerto Rico, Diaz et al. (1990) and Corredor et al. (1992) have documented the course of environmental degradation brought about by the filamentous cyanophyte *M. lyngbyaceus* in response to anthro-

pogenic eutrophication. Monospecific mats of this species cover large areas of the shallow benthos in affected areas displacing the previously predominant marine grasses (mainly *Thalassia testudinum*). *M. lyngbyaceus* mats are buoyed during the daytime by oxygen entrapped within the dense mat and sink to the bottom during the night when the entrapped oxygen is consumed by the microbial and faunal populations of the mat community. When the mats sinks to a depth below the euphotic zone, already narrowed by the proliferation of planktonic algae, decomposition of the mats brings about severe anoxia of the sediments with the consequent exclusion the natural infaunal communities.

In coral reef environments, fleshy green algae and can rapidly overwhelm the coral population in response to excessive anthropogenic nutrient inputs as was demonstrated for Hawaiian reefs by Smith (1984). In coral reefs of the tropical Intra-American seas, proliferation of fleshy and filamentous macroalgae have also been reported. Littler et al. (1992) found significant growth of *Sargassum sp* and *Enteromorpha sp.* associated to anthropogenic nutrient inputs off Fort-de France, Martinique while Lapointe et al. (1992) reported extensive populations of *Ulva, Chaetomorpha* and others along the Belize barrier reef associated with natural eutrophication from bird rookeries. While in both cases, alleviation of phosphorus limitation was implicated, increased nitrogen inputs were reported and concurrent alleviation of nitrogen limitation may not be ruled out. Healthy coral reef ecosystems, set in clear oligotrophic waters experience low sedimentation of detrital organic material and diffusion of remineralized nutrients from the sediments is moderate (Corredor & Morell 1985). Nevertheless, sessile organisms of these ecosystems filter or capture large volumes of plankton representing a large input of reduced nitrogen. While ammonium release from the reef framework is low, Corredor et al. (1988) have shown that sponges, the principal filtering organisms on the reef, excrete nitrate rather than ammonium; presumably as a result of the activity of symbiotic populations of nitrifying bacteria within the sponges. As planktonic and macrobenthic algae exhibit a marked preference for reduced nitrogenous species over the oxidized forms this mechanism might serve to maintain algal populations in check. When water quality deteriorates, however, and increased inputs of dissolved and detrital nutrients appear, coral reefs rapidly succumb to the competition of the fleshy algae.

Nitrification and denitrification are other benthic process which may function differently in nearshore subtidal tropical marine ecosystems than in their temperate counterparts. In temperate estuaries, denitrification plays a major role in reducing the effects of increased nitrogen loading from human activity, with much of the denitrification resulting from close coupling to nitrification (Seitzinger 1988; Nixon et al. 1996). In contrast, microbial oxidation of

ammonium (nitrification) in tropical coastal sediments appears to be more severely constrained than in comparative temperate environments (Morell & Corredor 1993). Oxygen requirements of nitrifying bacteria (whose activity peaks in microaerophyllic, environments) and strong inhibition by light may explain the fragility of these communities in tropical marine environments. Susceptibility to light limits nitrification to the lower sediment layers below the limits of light penetration (Vanzella et al. 1989); light is less of a problem in most temperate estuaries because of the greater turbidity. Oxygen depletion of subsurface sediments poses a lower limit for active nitrification in tropical sediments. Hydrogen sulfide can aggravate this lower limit, both by consuming oxygen and by inhibiting the enzyme responsible nitrification (Richardson 1985). Given comparable levels of respiration, hydrogen sulfide concentrations will build up more quickly in tropical carbonate sediments than in temperate estuarine sediments because of the much lower concentrations of iron available for precipitating the sulfides. Thus, in comparison to temperate estuarine sediments, the realm available to nitrifying bacteria in many tropical lagoons is reduced to a thin and vulnerable veneer where light does not penetrate and yet where oxygen is present and sulfides are absent (Morell & Corredor 1993). In coral reef sands, nitrification and denitrification proceed at comparable rates (Corredor & Capone 1985), thus maintaining low levels of ammonium in the sediments. However, eutrophication will increase oxygen consumption in the sediment, increase the production of sulfides through sulfate reduction, and thereby decrease the zone in the sediment where nitrification can occur (Morell & Corredor 1993). Given sufficient input of organic matter to the sediment, nitrification and denitrification both cease. As a result, interstitial ammonium concentrations may increase to very high levels (millimolar range), and the ammonium flux from sediment to overlying water column can be high (Mosquera et al. 1998).

The carbonate sands (calcite and aragonite) which often dominate tropical lagoons provide a major sink for phosphorus. Phosphate readily adsorbs onto these sediments, which contributes to phosphorus limitation in many tropical seagrass systems (Morse et al. 1985, 1987; Short et al. 1990; McGlathery et al. 1994; Howarth et al. 1995). Although the affinity of phosphate for carbonate minerals is in fact less than that for iron minerals found in the surface layers of temperate estuarine sediments (Krom & Berner 1980), the huge mass of carbonates in tropical lagoons provides a substantial sink for phosphate. However, the rate of phosphate uptake by carbonate sands appears to be slower in more eutrophic sites than in oligotrophic sites. Thus, as more phosphorus is added into a tropical lagoon, the phosphorus becomes proportionally more available as the rate of sorption onto the sediment slows (McGlathery et al. 1994; Howarth et al. 1995). This can result in a conversion

from phosphorus to nitrogen limitation in the ecosystem (McGlathery et al. 1992, 1994; Howarth et al. 1995). The mechanism for the slower uptake of phosphate in eutrophied tropical systems is still not entirely understood (McGlathery et al. 1994). Most of the phosphorus in carbonate sands is present as carbonate-fluoro-apatite (Jensen et al. 1997). Apparently, once phosphate adsorbs onto the surface of the sands, it is slowly transformed into the apatite mineral, and this conversion may replenish the active sites for phosphate adsorption. If so, during eutrophication as the apatite content of the sediment increases, the rate of new apatite formation and therefore the rate of replenishment of surface-sorption sites for phosphate may slow (McGlathery et al. 1994; Jensen et al. 1997).

In summary, nitrogen and phosphorus both exert substantial influence on biological productivity and structure of tropical marine ecosystems. As offshore waters are nitrogen limited, the transition to phosphorus limitation in nearshore environments would appear to be a function of the residence time of water masses and their consequent exposure to sediments capable of immobilizing phosphorus. The nature of the sediment, the mixing rate between nutrient-laden runoff waters and nutrient-poor oceanic waters and the degree of interaction of these water masses with the sediment will probably control the dynamics of this transition.

Nearshore tropical marine ecosystems function differently from their temperate counterparts where coupled nitrification/denitrification serves as an important mechanism for nitrogen depuration. In contrast, nearshore tropical ecosystems are more susceptible to nitrogen loading as depurative capacity of the microbial communities is limited by the fragility of the nitrification link. At the same time, accumulation of organic matter in nearshore carbonate sediments appears to impair their capacity for phosphorus immobilization. In the absence of depurative mechanisms for either phosphorus or nitrogen, limitation for both these nutrients is alleviated and continued nutrient loading fuels the proliferation of nuisance algae.

Disruption of the marine nitrogen cycle can bring about not only deterioration of the aquatic environment but extends to the atmosphere when these imbalances favor the emission of gaseous products. Nitrous oxide, an intermediate of both nitrification and denitrification, is a potent green house gas and is, moreover, active in the destruction of stratospheric ozone (Delwiche 1981). Marine environments are normally a source rather than a sink for nitrous oxide but tropical waters, with the notable exception of upwelling ecosystems (Law & Owens 1980; Naqvi & Noronha 1991), exhibit the lowest rates of emission (Weiss 1981; Nevisson et al. 1995); in large part due to the depletion of available nitrogen in surface waters and the barrier to diffusion from the supersaturated lower layers posed by the well stratified surface layer.

Coastal and intertidal waters, particularly those subject to eutrophication, can however emit nitrous oxide to the atmosphere at rates significantly above those of the open ocean. Relatively pristine mangrove sediments normally emit nitrous oxide at rates up to 10 times those observed offshore. These emissions may in turn increase dramatically as allochthonous nitrogen is provided. Corredor et al. (In Press) have demonstrated enhanced nitrous oxide emissions from mangrove sediments subject to well nitrified sewage releases and greater rates yet in mangrove sediments receiving reduced nitrogenous inputs. Large scale modification of mangrove ecosystems in the neotropics thus has the potential for contributing further to global climate change.

Evidently, our knowledge of nitrogen cycling in tropical marine ecosystems is but a loosely interconnected mosaic. A sustained and concerted effort is required if we are to acquire a well rounded understanding of these important processes.

Acknowledgements

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