



## Biogeochemistry of Nitrogen in Seagrass and Oceanic Systems

R. PURVAJA<sup>1,4</sup>, R. RAMESH<sup>1,2</sup>, A. SHALINI<sup>3</sup>, and TIM RIXEN<sup>4</sup>

<sup>1</sup> Institute for Ocean Management, Anna University, Chennai 600 025, India. Email: purvaja\_ramachandran@yahoo.com. Currently at: ZMT, Bremen, Germany, <sup>2</sup> Corresponding author: Email: ramesh\_au@yahoo.com, <sup>3</sup> Novartis, U.K.

<sup>4</sup> Center for Tropical Marine Ecology (ZMT), Bremen, Fahrenheitstr. 6, 28359 Bremen, Germany

### Abstract

The coastal and marine nitrogen cycle occupies a complex, central role within the biogeochemical cycles, and yet we have just barely begun to understand its major processes and the factors that regulate them. Spatial variations of dissolved inorganic nutrients ( $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ , and TDP) and its fluxes from different coastal ecosystems (seagrass ecosystems and brackish water lagoon) of South India to the Bay of Bengal. The results show a strong spatial variability in nutrient distribution and highlight the effects of anthropogenic land-based input. There was a consistent decline in nutrient concentration from freshwater reaches to the Bay of Bengal, displaying a strong negative correlation (-0.99) with surface water salinity. Other factors that probably influence nutrient distribution in the coastal ecosystems include: i) phytoplankton primary productivity and ii) nutrient utilization by phytoplankton (N: P ratio) and iii) dissolved oxygen ( $\text{O}_2$ ) content. Here, we review some of the major processes, transformations and fluxes of nitrogen in the coastal and marine ecosystems, occurring both naturally and as an effect of human perturbation in a seagrass ecosystem.

**Keywords:** Biogeochemistry, Nitrogen, Seagrass, Oceanic systems

### INTRODUCTION

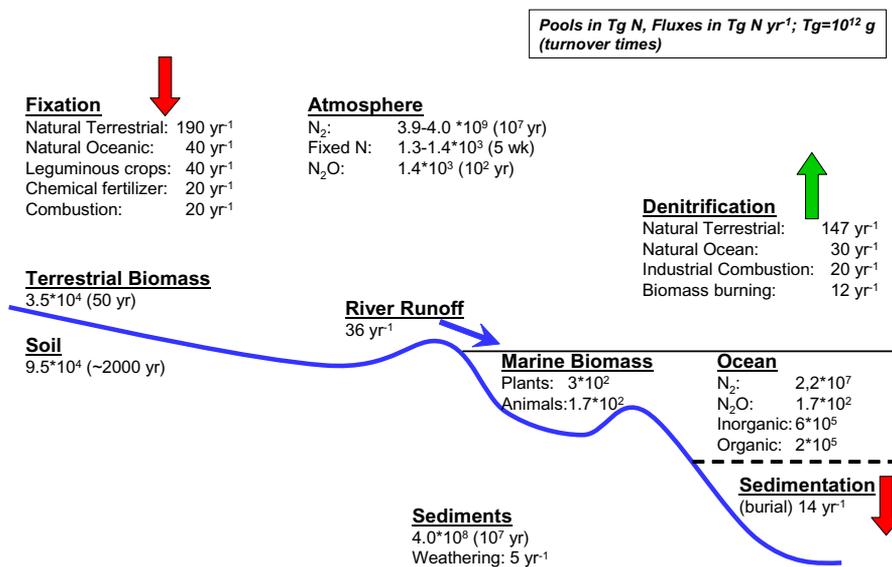
Seagrasses — a unique group of flowering plants that have adapted to exist fully submersed in the sea — profoundly influence the physical, chemical and biological environments of coastal waters. They provide critical habitat for aquatic life, alter water flow and can help mitigate the impact of nutrient and sediment pollution (Dennison, 2006). Nitrogen (N) is an extremely essential element, existing in both inorganic and organic forms as well as many different oxidation states. The movement of N between the atmosphere, biosphere, and geosphere in different forms is described by the N cycle one of the major biogeochemical cycles (Fig. 1). Similar to the carbon cycle, the N-cycle consists of various storage pools and processes, by which they exchange N. Typically five main processes cycle N



Although N is an essential element, it is sometimes a limiting nutrient in coastal and marine ecosystems, but its role in controlling productivity is well-understood. Major nitrogen sources to coastal ecosystems include: atmospheric deposition onto land, freshwaters, and estuary, fertilizers from agriculture and wastewater from sewage. Tidal exchange can introduce marine nitrogen, but this source is relatively unimportant in embayments receiving high nitrogen loads from the riverine systems and estuaries. N exists in the surface ocean mostly as dissolved organic nitrogen (DON), but despite decades of research, only a small fraction of the DON in surface ocean waters has been chemically characterized. Fig. 2 provides the global nitrogen reservoirs, fluxes and turnover times as given by Reeburgh, 1997.

Estuaries and shallow lagoons are the link between terrestrial and oceanic ecosystems and receive considerable external inputs of nutrients and organic matter. Excess inorganic nutrient loading from coastal watersheds has been directly related to increases in primary production, changes in habitat structure and trophic dynamics of the receiving waters. By comparison, little is known about the cycling and bioavailability of organic nutrients in nearshore systems, even though organic nutrient inputs to these systems can sometimes be higher than inorganic loadings. Coastal ecosystems and bays constitute a major type of land margin ecosystem on most continents, but the retention and transport of nutrients through these systems have received far less attention than in major estuaries. A major difference in the

Fig. 2: Global nitrogen reservoirs, fluxes and turnover times. Major reservoirs are underlined; pool sizes and fluxes are given in Tg ( $10^{12}$  g) N and Tg N yr<sup>-1</sup>. Turnover times (reservoir divided by largest flux to or from reservoir) are in parentheses (taken from Reeburgh, 1997)



nitrogen cycling processes between these systems is the large influence that benthic primary producers have on nutrient transformations in shallow coastal lagoons and bays. Exchanges across the sediment-water interface play a key role in nutrient cycling in coastal systems because the water column is well-mixed and small in volume relative to the large sediment surface area. It is this coastal-margin interface that makes the biogeochemical cycles very complex as also challenging our understanding of these complexities.

### COASTAL ECOSYSTEMS OF INDIA

The Indian sub-continent has an area of 3.28 million km<sup>2</sup> (329 million hectares). It is the second largest country in Asia and the seventh in the world. It measures 3214 km from north to south and 2933 km from east to west, with a total area of 3.2\*10<sup>6</sup> km<sup>2</sup>. The land frontier is 15200 km and the coastline is 7516.5 km. India, lies between latitudes 8° 4' and 37° 6' north and longitudes 68° 7' and 97° 25' east. Statistics pertaining to the extent of the Indian coast and its biodiversity is given in Table 1. The nearshore coastal waters of India are extremely rich fishing grounds and the rich biodiversity of the wetlands is seriously threatened due to human pressures. India has a very wide range of coastal ecosystems such as estuaries, lagoons, mangroves, backwaters, salt marshes, rocky coasts, sandy stretches and coral reefs, which are characterized by unique biotic and abiotic properties and processes. A network of 14 major, 44 medium and numerous minor rivers together with their tributaries cover the entire country. The total length of

**Table 1.** Estimates of Coastal and Marine ecosystems of India in comparison to the World's coastal resources: Coastal Statistics, 2000 (Data from <http://earthtrends.wri.org>)

Coastal Feature	India	World
Length of coastline (km)	7516	1634701
Percent of population within 100 km of coast	26%	39%
Area of continental shelf (km <sup>2</sup> )	372424	24285959
Territorial Sea (up to 12 nautical miles) (km <sup>2</sup> )	193834	18816919
Claimed Exclusive Economic Zone	2103415	102108403
Coastal biodiversity and protected areas (1990s)		
Area of mangrove forests (km <sup>2</sup> )	4871	169452
Area of mangrove forests (km <sup>2</sup> ) 2000 <sup>§</sup>	6100	
Percent of mangroves protected	>50%	13%
Number of mangrove species	28	70
Number of seagrass species	12	58
Area of coral reefs (km <sup>2</sup> )	2330	527000
Number of coral genera	59	X
Number of marine/ littoral protected areas (1999)	115	3636
Wetlands of national importance extent (km <sup>2</sup> ) 2000	1930	730116

<sup>§</sup>Aizpuru et al., 2000

the rivers is estimated at over 40000 km. The dissimilarities of marine biodiversity between the west and east coasts are remarkable. The west coast is generally exposed with heavy surf and rocky shores and headlands whereas the east coast is generally shelving with beaches, lagoons, deltas and marshes. The west coast is a region of intense upwelling associated with southwest monsoon (May-September) whereas the east coast experiences only a weak upwelling associated with the northeast monsoon (October-January), resulting in marked differences in hydrographic regimes, productivity patterns and qualitative and qualitative composition of fisheries. All islands on the east coast are continental islands whereas the major island formations in the west coast are oceanic atolls.

### SEAGRASS MEADOWS

Of the major coastal ecosystems of India, seagrass meadows exist along the southeast coast (Gulf of Mannar and Palk Bay) and in the lagoons of islands from Lakshadweep (Arabian Sea) and Andaman and Nicobar (Bay of Bengal). The flora comprises 15 species and is dominated by *Cymodocea rotundata*; *C. serrulata*, *Thalassia hemprichii*, *Halodule uninervis*, *H. pinifolia*, *Halophila beccarii*, *H. ovata* and *H. ovalis*. Its distribution occurs from the intertidal zone to a maximum depth of approximately 15 m. Maximum growth and biomass are restricted from the lower littoral zone to the depth of 2 to 2.5 m. Greatest species richness and biomass of seagrass occur mainly in open marine sandy habitats. Although seagrass habitats are categorized as 'ecologically sensitive' coastal areas, they are largely ignored from both scientific and management point of view (Jagtap, 1997).

India has three large brackish water lagoons viz. (i) the Chilka Lake in Orissa State, (ii) the Pulicat Lake, extending between Andhra Pradesh and Tamil

Table 2: Mangrove wetlands of India (Based on data from Forest Survey of India, 1998)

State	Mangrove Wetland	Total area of wetland (ha)	Actual forest cover (ha)
<b>East Coast</b>			
<b>West Bengal</b>	<i>Sunderbans</i>	426000	212500
<b>Orissa</b>	<i>Mahanadi</i>	67000	21500
<b>Andhra Pradesh</b>	<i>Godavari</i>	33250	24100
	<i>Krishna</i>	25000	15600
<b>Tamil Nadu</b>	<i>Pichavaram</i>	1300	900
	<i>Muthupet</i>	13000	1200
<b>West Coast</b>			
<b>Gujarat</b>	<i>Gulf of Kutchch</i>	58200	85400
	<i>Gulf of Cambay</i>	53123	17700
<b>Other Mangroves</b>		-	11600
<b>Andaman and-</b>	<i>Andaman Islands</i>	-	92900
<b>Nicobar Island Group</b>	<i>Nicobar Islands</i>		3700
<b>Total</b>			487100

Table 3: Extent of coral reefs in India and its Islands (Adapted from DOD and SAC, 1997 "Coral reef maps of India," DOD and SAC, India)

Category	Gujarat	Tamil Nadu	Lakshadweep Islands	Andaman & Nicobar Islands
Reef flat	148.4	64.9	136.5	795.7
Sand over reef	11.8	12	7.3	73.3
Mud over reef	117.1	-	-	8.4
Coraline shelf	-	-	230.9	45
Coral heads	-	-	6.8	17.5
Live coral platform	-	-	43.3	-
Algae	53.8	0.4	0.4	-
Seaweeds	-	-	0.7	-
Seagrass	-	-	10.9	-
Reef vegetation	112.1	13.3	-	8.9
Vegetation over sand	17	3.6	0.4	10.5
Lagoon	-	0.1	322.8	-
<i>Sandy substrate</i>	-	-	67.4	-
<i>Reef patch</i>	-	-	13.4	-
<i>Deep</i>	-	-	98.5	-
<i>Uncertain</i>	-	-	143.5	-
<b>Total</b>	<b>460.2</b>	<b>94.3</b>	<b>816.1</b>	<b>959.3</b>

Nadu, located on the south east coast of India and the Vembanad Lake in Kerala on the coast of Arabian Sea. However, since nearly three decades, all these lagoons have been increasingly tending to be victims of diverse environmental tragedies, more cultural (manmade) than natural. In general, the lakes in India are being lost or altered because of the disruption of natural processes by intensification of urbanization, agriculture and pollution. Besides over-fishing and poaching of migratory birds, lakes are used as dumps for industrial effluents, runoff from agricultural fields and sewage, which leads to eutrophication. India is losing its wetlands mainly due to population pressure and lack of government control viz. The Kolleru Lake found in Andhra Pradesh is choking to death; the Chilka Lake has undergone a considerable reduction in surface area due to human activities (Panda et al 1995). The Pulicat Lake is also shrinking due to siltation caused by soil erosion (Panda, 1992).

The Pulicat Lake is the second largest brackish water lake in India with an area of 481 km<sup>2</sup> running parallel to the Bay of Bengal along the Tamil Nadu-Andhra Pradesh border. About 84% lies in Andhra Pradesh and the remaining 16% lies in Tamil Nadu (Sanjeev Raj, 1996). Situated between 13° 24', 13°43' N latitude and 80°03', 80°18' E longitude, the lake is about 60 km in length and 0.2 to 17.5 km in breadth. The lake is comparatively shallow and is connected to the Bay of Bengal on both the northern and the southern sides. The Buckingham Canal, which runs parallel to the Coromandel Coast, passes through the southern end of the lake. The Pulicat Lake is endowed with diverse natural resources, which include aquatic and terrestrial fauna and flora. The lake provides spawning and nursery grounds for migratory birds and are ideal sites for fisheries, agriculture,

tourism and accelerated urbanization leading to environmental conflicts. The lake is a home to 50 species of water birds mainly for resident and migratory waterfowl, notably pelicans, flamingoes, ducks, storks, herons, egrets, gulls, terns and other shore birds. The International Union for Conservation of Nature and Natural Resources (IUCN) and the World Wide Fund for Nature (WWF) recently declared the Pulicat lagoon system a Ramsar site of international importance and as a protected area respectively. Many natural and anthropogenic disturbances have caused significant changes in the atmospheric concentrations of several greenhouse gases contributing to the warming of the Earth.

### CONTINENTAL SHELF OF INDIA

The ocean floor can be divided into the continental margin and the deep-sea floor. The continental margin consists of the continental shelf, the continental slope, and the continental rise. The North Indian Ocean has two major submarine fans: the Bengal Fan and the Indus Fan. The basins are filled with sediments that are mostly derived from the continents through river systems. The Bengal fan in the Bay of Bengal is the largest deep-sea fan in the world. Its total area is  $\sim 3.0 \times 10^6$  km<sup>2</sup>. It is  $\sim 3000$  km in length, 1430 km at its maximum width, and 20 km at its maximum thickness. The sediments of the fan are largely eroded from the Himalayas and transported by the Ganga-Brahmaputra River system. The sediments making up this deep-sea fan at times are deposited at a rate of 35 cm 1000 yr<sup>-1</sup>, a rate comparable to that of deposition in shallow shelves (20-30 cm 1000 yr<sup>-1</sup>). The Indus fan ( $1.1 \times 10^6$  km<sup>2</sup> area, 1500 km length, 960 km maximum width, >10 km maximum thickness) in the Arabian Sea not only receives sediments from the Himalayas, but also from the alluvial soils of Pakistan and the arid soils of Arabia (NIO, 2006).

### PRODUCTIVITY OF THE INDIAN COASTAL SYSTEMS

The productivity of coastal margin waters is largely controlled by the availability of either nitrogen or phosphate nutrients. A number of anthropogenic sources can often contribute to major increases of nutrients in coastal margins. The most commonly acknowledged source is via point source pollution of streams and rivers, such as wastewater treatment facilities. However, there has also been a growing recognition that urban and agricultural runoff are important sources of nutrients (Cooper 1990). The additional nutrients have impacts well beyond just increasing net productivity. For example, increased plankton in the water can severely reduce the water depth at which light penetrates to the bottom in sufficient amounts for seagrasses and other benthic flora to grow. This can then have major consequences on other parts of the ecosystem such as fisheries that depend on seagrass beds or causes algal blooms. In this review we have made an effort to provide a concise understanding of the past and current changes in the N-cycle and how humans have impacted the various processes that affect coastal ecosystems and the adjacent oceans.

## ATMOSPHERIC SOURCES OF N TO COASTAL AND MARINE SYSTEMS

Atmospheric deposition is currently a major source of N to many aquatic and terrestrial ecosystems (Fisher et al. 1988; Howarth et al. 1996; Jaworski et al. 1997). The global nitrogen cycle has been massively perturbed by human activity (Galloway et al., 2004) and this includes the atmospheric component. Not only have total atmospheric nitrogen emissions changed over the last few hundred years associated with a doubling of overall global nitrogen fluxes (Galloway et al., 1995) but the nature of sources continue to change as global patterns of agriculture and industry evolve (e.g. Galloway et al., 2004; Paerl et al., 2002). Because N is the primary nutrient-limiting plant, algal and microbial production in many terrestrial and marine environments, as well as some freshwater environments, increases in N inputs can markedly alter those ecosystems (Ryther and Dunstan 1971; Schlesinger 1991; Vitousek and Howarth 1991).

In coastal waters, atmospheric inputs contribute significantly to overall eutrophication pressure, but evidence that they trigger algal blooms are rather limited. Management of atmospheric inputs to coastal waters to mitigate eutrophication pressures requires that emissions be managed over a wide area reflecting the efficient long range transport of atmospheric nitrogen (Jickells, 2006). The current fixed N inputs to the world's oceans (Table 4) as given by Jickells (2006) emphasizes the contribution of the atmospheric and riverine sources, which have probably doubled due to human activities. Atmospheric inputs are therefore comparable to fluvial inputs and are of the same order of magnitude as marine nitrogen fixation, so it is logical to ask what effect this input has on the marine ecosystem. In considering this question it is useful to separate the impact on the open ocean from coastal waters because the latter are subject to high nitrogen loadings in general including atmospheric inputs.

**Table 4.** Current fixed nitrogen inputs to the World's Oceans (adapted from Jickells 2006)

Source	Flux ( $10^{12}$ mol yr <sup>-1</sup> )
Atmospheric	3.1 – 7.9
Biological N <sub>2</sub> -Fixation	5.7
Rivers	5.4
Lightning	0.6

Atmospheric deposition rates of nutrients including nitrogen and contaminants are in general higher into coastal waters than to open ocean areas because these are closer to sources. However, the magnitude of atmospheric fluxes varies over at least two or- orders of magnitude (Jickells, 2005) between relatively pristine environments to areas close to major centers of habitation and industrial activity. There are some additional complications in coastal areas. The higher NH<sub>3</sub> concentrations in the atmosphere and complex ammonia cycling in the atmosphere and nutrient rich waters mean that air-sea exchange fluxes for ammonia

can be particularly complex (Walker et al., 2004; Sørensen et al., 2003). Assessing the impacts of atmospheric deposition to coastal waters is complicated by the importance of other inputs such as rivers and groundwater (Jickells, 1998, 2005; Paerl, 2002). These are not completely independent because a significant component of the fluvial nitrogen input may be derived from atmospheric inputs to the catchment. This issue is particularly important in regions with relatively small estuaries compared to their catchment area and hence where direct atmospheric deposition to the estuary is inevitably small (Valigura et al., 2001).

For instance, the contribution of atmospheric inputs to the total fluvial nitrogen input ranges from 7–61% (Castro et al., 2001). Thus atmospheric nitrogen sources are clearly significant compared to other terrestrial nitrogen sources, and as noted earlier these inputs have been significantly increased by human impact. In addition, responses can be anticipated from different coastal biogeochemical communities in response to nutrient loadings depending on the hydrography of each coastal area (e.g. Jickells, 1998; Paerl et al., 2002).

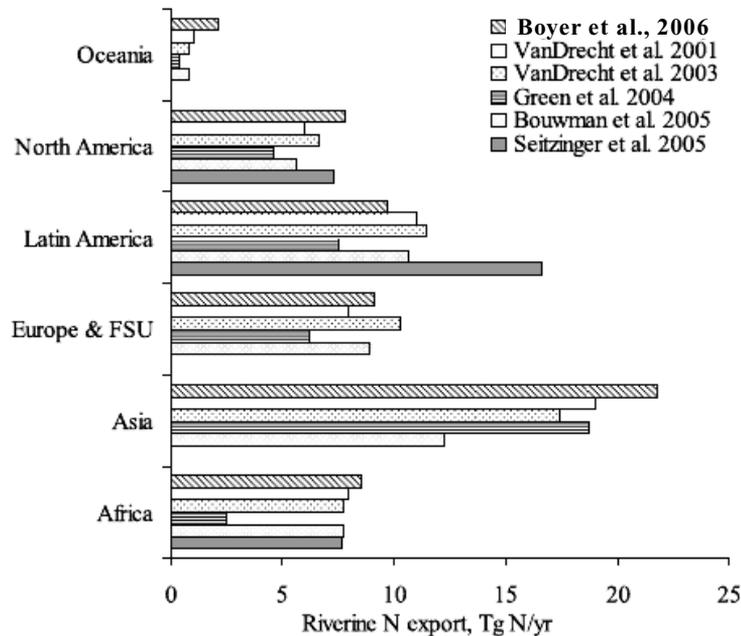
### RIVERINE NITROGEN INPUTS

River discharge is major source of nutrients to coastal waters as we have seen from the data provided in Table 4. River inputs are very important both in terms of the physical structure of the systems and as a source of N (Jickells et al., 1991). Inputs of N to rivers arise primarily from fertilizers, atmospheric deposition to the catchment, and to a lesser extent, direct discharges. Following discharge to a river system, denitrification, photosynthesis, and particle water interactions can modify N and P fluxes. The balance of inputs and river processing of nutrients is such that river fluxes have not only increased in absolute magnitude, but the N:P ratio of those inputs has increased to greater than the value required for optimal plant growth [16:1 on an atomic basis (Duce et al., 1991; Howarth et al., 1996; Billen et al., 1991 and Justic and Rabalais, 1995)]. This has led to pressure to reduce inputs, which has met with some success for P but less for N (Jickells et al., 1991, 1998). Meybeck 1982 reported that the net flux of nutrients N and P to the oceans is rather difficult to estimate because of their high reactivity in the estuarine and coastal zones, which include phytoplankton uptake, change of chemical species from soluble to gaseous forms ( $\text{CO}_2$ ,  $\text{N}_2$  and  $\text{N}_2\text{O}$ ) and flocculation of particulate matter. Classical reviews of these processes have been made by Aston (1978) and Wollast (1981). According to their data, rivers of the humid tropics, which drain about one-fifth of the exoreic drainage area and carry about half of the river water to the oceans, transport about 55% of the dissolved organic carbon, nitrogen and total dissolved phosphorus (Meybeck, 1982).

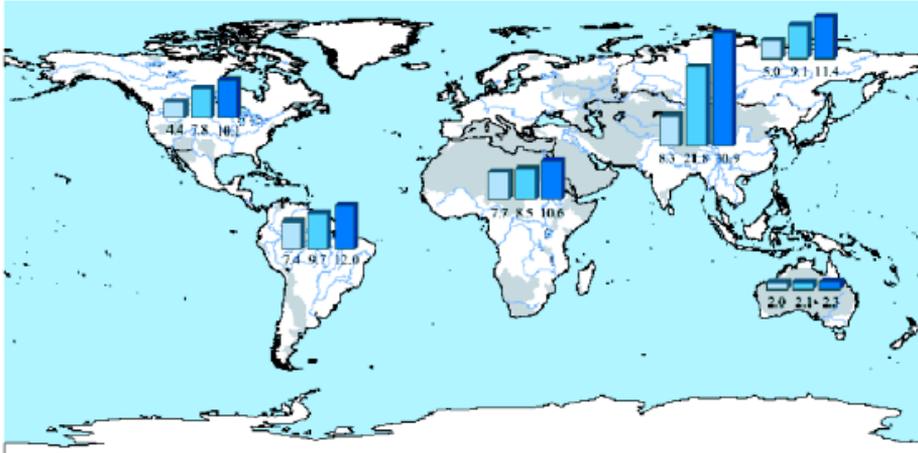
Galloway (2000) estimates that Asia is a source of N to the rest of the world as a consequence of atmospheric and riverine transport (Fig. 3a and 3b).

Riverine discharge injects both soluble and particulate N to the ocean, which have substantial impacts on the coastal regions of Asia and hence nutrient fluxes have consequently increased (Vorosmarty et al., 1998; Hu et al., 1998). Long-term data sets on N fluxes for individual Asian rivers or synoptic coverage of all Asian rivers on total N discharge are very limited. The data scarcity is compounded by the several forms of N that need to be measured to understand total N fluxes. Model studies on fate of N from Asian rivers by Seitzinger and Kroeze (1998) shows that about 12 Tg N yr<sup>-1</sup> of dissolved inorganic N are discharged annually from Asian rivers into adjacent coastal seas (Fig. 3b). This value is about 20% of the anthropogenic N mobilized within Asia (Galloway, 2000). Recently, Boyer et al. (2006) quantified anthropogenic and natural inputs of reactive nitrogen (N) to terrestrial landscapes and the associated riverine N fluxes (Fig. 3a), using empirical model relating total N inputs per landscape area to the total flux of N discharged in rivers based on watershed data from contrasting ecosystems spanning multiple spatial scales. They determined that anthropogenic N sources were greater than natural sources in Asia (74%), North America (61%), and Europe (59%). They observed a direct, linear relationship between Total Net Nitrogen Inputs (TNNI) and the total N fluxes in these watersheds, which suggests that, on average, 75% of the N inputs are retained in the landscape (that is, stored in soils and vegetation, or lost via volatilization and denitrification), while 25% of the N inputs are exported to rivers. Rates of riverine N export vary greatly among the continents, reflecting

Fig. 3a: Total riverine export by region (adapted from Boyer et al., 2006)



ig. 3b: Riverine Nr export to the coastal zone ( $\text{Tg N yr}^{-1}$ ) in the past (1860), present (1990) and future (2050). Dry and inland watershed regions that do not transmit coastal areas are shown in grey (adapted from Galloway, 2000)



the regional differences in N inputs. This significantly affects water quality, as riverine N fluxes from Asia to the coastal zone ( $16.7 \text{ Tg N yr}^{-1}$ ) and to inland waters ( $5.1 \text{ Tg N yr}^{-1}$ ) are the largest in the world.

In developing nations such as India, wastewater inputs can be an additional major source of nitrogen to an estuary or coastal system; since the watershed is heavily populated and small, relative to the surface area of the estuary itself (Nixon and Pilson 1983). Even in some estuaries fed by larger watersheds, wastewater can be the largest source of nitrogen if the watershed is heavily populated. Human sewage and wastewaters are obvious sources of nitrogen to rivers. In an analysis of 42 major world rivers, Cole et al. (1993) concluded that sewage inputs alone are sufficient to account for the increased flux of nitrate observed in rivers whose watersheds have a higher population density. Although they acknowledged that deforestation, atmospheric deposition, and fertilizer application can all contribute significantly to nitrogen export from rivers, they stated that “watersheds with moderate to high human population will likely be dominated by sewage” rather than other inputs.

### NITROGEN CYCLE IN A SEAGRASS BED ECOSYSTEM

Seagrasses are a conspicuous and often dominant feature of coastal subtidal and intertidal environments (den Hartog 1970; McRoy and Helfferich 1977; Phillips and McRoy 1980). There is abundant evidence that substrates underlying seagrass have substantially larger amounts of fine textured sediments, organic matter, and both total and intermediate pools of nitrogen. The correlation between sediment texture and the total pool of nitrogen suggests that the process of trapping

and stabilizing fine textured inorganics is accompanied by an enlargement in the nitrogen pool. Decomposition and retention of organic matter from animal and plant detritus makes a substantial contribution to the sedimentary nitrogen pool in such ecosystems. Table 5 provides an overall estimate of the various N-cycling processes in seagrass beds.

### SOURCES OF N IN SEAGRASS SYSTEMS

In contrast to terrestrial plants, aquatic vascular plants, including seagrasses, can take up inorganic N through both leaf and root tissues (Short and McRoy 1984; Stapel et al. 1996; Pedersen et al. 1997; Terrados and Williams 1997). The major N sources for seagrasses are  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in the water column for leaves and  $\text{NH}_4^+$  in sediment pore waters for roots. With the exception of areas characterized by high river inflow, water-column  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations in seagrass beds are usually  $<3$  mM (Dunton 1996; Terrados and Williams 1997). By contrast, pore-water  $\text{NH}_4^+$  concentrations range from  $<20$  mM to well over 200 mM, significantly higher than that of the water column (Iizumi et al. 1982; Fourqurean et al. 1992; Dunton 1996). Thus, sediment pore waters are often considered the main source of N for seagrass growth (Short and McRoy 1984; Zimmerman et al. 1987). Lee and Dunton (1999) developed a whole plant nitrogen budget for *Thalassia testudinum* and reported that seagrass root and leaf tissues contributed equally to the N budget.

The concentration of  $\text{NO}_3^-$  and  $\text{NO}_2^-$  in the Pulicat Lake waters were at least twice higher than in the mangroves of Pichavaram (Figures. 4 and 5 respectively - data shown only for Pulicat and not for other coastal ecosystems). Vegetation in the Pulicat Lake is sparse and is restricted to mangrove shrubs such

Fig. 4: Mean  $\text{NO}_3^-$  versus mean  $\text{PO}_4^{3-}$  concentrations for the unpolluted (Pichavaram), polluted (Adyar and Ennore Creek mangroves) and the brackish water lake (Pulicat). Diagonals represent lines of equal N/P ratio (in mol/mol). Grey area represents the unpolluted range

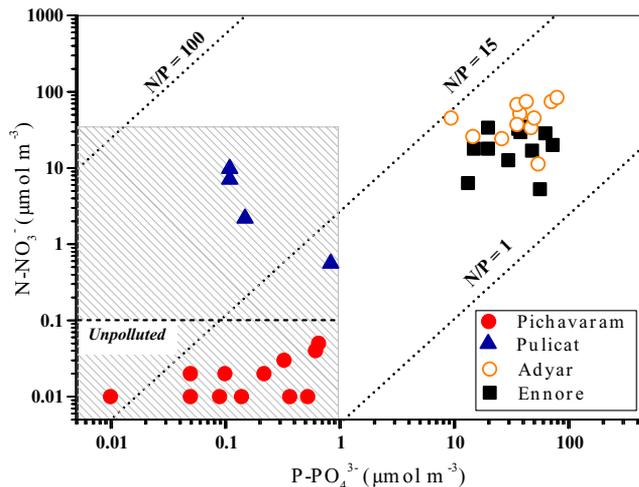
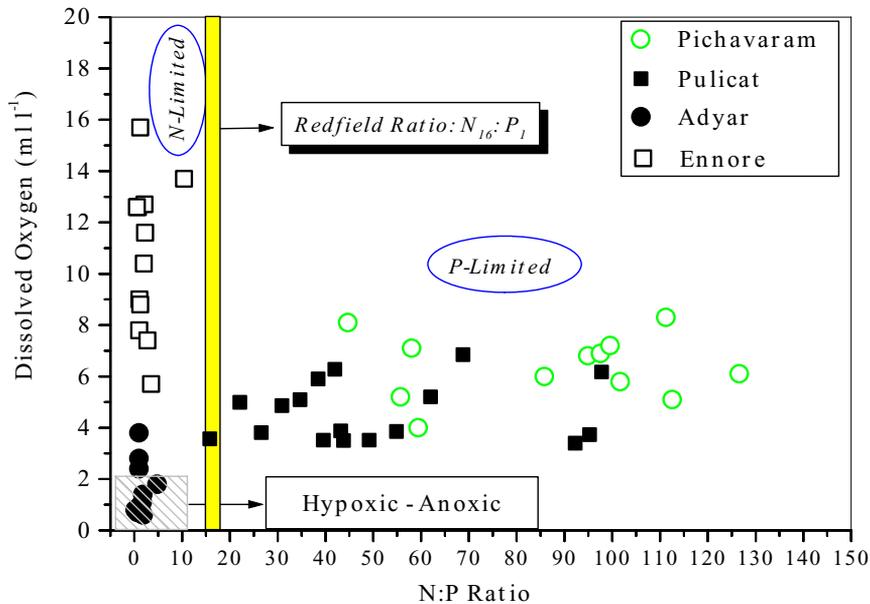


Fig. 5: Spatial variations of dissolved oxygen versus N:P ratio in the unpolluted (Pichavaram), polluted (Adyar and Ennore Creek mangroves) and the brackish water lake (Pulicat). Shaded area represents the hypoxic-anoxic areas while the vertical bar denotes the idealized phytoplankton Redfield ratio of N16:P1.



as *Suaeda maritima*. Additionally, green algae such as *Enteromorpha*, and *Chaetomorpha*, seagrasses such as *Halophila ovalis* exist covering a large extent of the inter-tidal zone of the lake, making the surface waters eutrophic.

Our observations show that the lake waters are murky with suspended plankton, and algae, causing occasional decline in the dissolved O<sub>2</sub> concentration (ca. 4.0 ml l<sup>-1</sup>) of the surface waters. The green color in the surface waters at several locations with abrupt increases in primary productivity (2.54 to 16.37 g C m<sup>-2</sup> d<sup>-1</sup>) (Ramesh, 2000) is a result of localized nutrient input from non-point sources of pollution viz., from the land-derived sewage and runoff from adjacent agricultural areas. Pulicat Lake has a high NO<sub>3</sub><sup>-</sup> (average 0.97±0.6 μmol m<sup>-3</sup>) and NH<sub>4</sub><sup>+</sup> (52.25±41 μmol m<sup>-3</sup>) content reacting to “cultural” eutrophication. Mats of green algae were present throughout the inter-tidal stretches of the lake ecosystem, typical of a eutrophic lake.

Primary production by phytoplankton whether N or P limited is a function of the relative availabilities of N and P in the surface coastal waters. Based on the high N and P concentration in the coastal waters, the spatial variation in N:P ratio was calculated (Table 3) and was found to be “P-limited”. This has occurred due to a sediment process termed “phosphorus adsorption” which counteracts the influence of denitrification. Sediments potentially can absorb and store large

quantities of phosphorus, making it unavailable to phytoplankton, tending to drive the system towards P-limitation. The N:P ratios are discussed in detail later in this paper, along with intra-annual variations for certain locations.

Seasonal variations in the N:P ratio were less marked, being P-limited almost through the annual cycle in the Pulicat Lake. However, N-limitation was predominant during the pre-monsoon season. We attribute this to denitrification, the process of bacterial reduction of  $\text{NO}_3$  to molecular N, removing N and making these ecosystems more N-limited. It specifically implies that a higher percentage of N mineralized during decomposition is denitrified from the sediments (Seitzinger, 1988; Gardner et al., 1991). Howarth (1988) state that although the evidence for limitation of production by phytoplankton is not entirely clear in tropical systems and, production by seagrasses and attached macro algae is sometimes N-limited, primary productivity by seagrasses in tropical estuaries is clearly limited by phosphorus (Powell et al., 1989). The vegetation in the Pulicat Lake is dominated by seagrasses and macro algae (as mentioned in the description of the study area) tend to drive the surface waters towards N or P-limitation, depending also on the external sources of nutrient input from land-based sources. The N:P ratio in the coral reef ecosystem was N50 : P1 similar to the other P-limited coastal ecosystems in this study. In general, P-limitation is obvious in all the coastal ecosystems with the exception of Ennore Creek, which is N-limited.

Although N and P primarily control eutrophication in coastal waters, other elements can have a major influence on the community structure of aquatic ecosystems and can influence the nature of the response to nutrients. A key element in this regard is silica, which is required by diatoms.

### **$\text{N}_2$ -FIXATION IN SEAGRASS BEDS**

In contrast to other marine ecosystems, high rates of heterotrophic nitrogen fixation are often observed in seagrass colonized sediments with reported rates ranging between 0.03 and 140  $\text{mg N m}^{-2} \text{d}^{-1}$ , dependent upon the seagrass species and the locality (Welsh, 2000). Rates of nitrogen fixation in temperate seagrass meadows (Table 5; Fig. 6) are generally considerably lower than those in tropical and subtropical systems (0.1–7.3 compared with 0.03–140  $\text{mg N m}^{-2} \text{d}^{-1}$ ) and as would be expected, show a much larger degree of seasonal variation. Similarly, the few studies that have attempted to quantify the contribution of nitrogen fixation to the productivity of the seagrasses indicate that this contribution is substantially greater in tropical and subtropical compared with temperate seagrass meadows. In temperate systems, nitrogen fixation was estimated to provide 6.3%–12% of the total annual nitrogen requirement (Welsh et al. 1996). In contrast, in tropical and subtropical seagrass meadows 50% or more of the plant's nitrogen requirements may be furnished by nitrogen fixation in the sediments (Patriquin and Knowles 1972; Capone 1983; O'Donohue et al. 1991). Seagrass meadows

account for less than 0.1% of the total surface area of the marine sediment environment, but have been calculated to account for 10% of total inputs of nitrogen from nitrogen fixation (Capone, 1983). Indeed, if salt marsh ecosystems that show similar characteristics to seagrass meadows in terms of nitrogen fixation rates and the regulation of this process are also taken into consideration, more than 50% of the nitrogen inputs to marine sediments can be accounted for (Capone, 1983). Thus, although the areas of the marine environment colonized by rooted angiosperms are insignificant, the contribution of these ecosystems to nitrogen fixation in the marine environment is far from insignificant (Welsh, 2000).

### COUPLED NITRIFICATION AND DENITRIFICATION AND N<sub>2</sub>O EMISSIONS

Only a few studies have addressed nitrification and denitrification in seagrass beds, but the processes mentioned above undoubtedly operate in these marine meadows. Nitrate and nitrite are present in tropical (Boon, 1986) and in temperate sediments of seagrass beds, even below 30 cm depth (Iizumi et al. 1982), indicating nitrification in the root zone. The latter authors measured in situ rates of denitrification in the upper 7 cm of the sediments equivalent to a daily loss of 0.3 to 3 mg N m<sup>-2</sup>. As denitrification was also found below 20 cm depth, this most probably is a conservative estimate. In situ denitrification rates in the top 10.5 cm of the sediment of a *Zostera novazelandica* bed varied between 1.2 and 6.0 mg N m<sup>-2</sup> d<sup>-1</sup> (Kaspar 1983). The denitrification rates reported for seagrass beds thus are on the low end of the range of activities measured in coastal bays and estuarine sediments (0 to 130 mg N m<sup>-2</sup> d<sup>-1</sup>). However, the potential denitrification rates in the sediment of seagrass meadows (measured in nitrate-saturated soil slurries), are much higher (Kaspar, 1983, Caffrey and Kemp, 1990; Hemminga et al., 1991). It is possible, therefore, that under favourable conditions of high nitrate availability higher in situ denitrification rates do occur (Hemminga et al., 1991).

Nitrification activity is enhanced in seagrass beds, probably as a result of release of oxygen from plant roots (Iizumi et al. 1982; Caffrey and Kemp, 1990). Coupled nitrification-denitrification rates in the rhizosphere of 4 different aquatic macrophytes, *Zostera marina*, *Lobelia dortmanna*, *Littorella uniflora* and *Potamogeton pectinatus*, were measured by means of both an indirect and a direct <sup>15</sup>N technique by Ottosen et al., 1999. Their study indicates that denitrification activity in the rhizosphere of *Z. marina* and *P. pectinatus* was low (1.5 to 5 μmol N m<sup>-2</sup> h<sup>-1</sup>) compared to the activity measured in *L. dortmanna* and *L. uniflora* vegetated sediments (24 and 30 μmol N m<sup>-2</sup> h<sup>-1</sup>). This variability in denitrification activity (Table 5) was due to differences in the ability of the plants to oxidize the rhizosphere, and difference in the character of sediment O<sub>2</sub> and NO<sub>3</sub><sup>-</sup> consumption. Their study demonstrated how rooted aquatic vegetation affects the sediment nitrogen cycle via oxygen excretion from the roots. Thus, rhizosphere associated

nitrogen transformations (coupled nitrification-denitrification- Fig. 6) are central to the understanding of nutrient cycling in shallow aquatic ecosystems. Welsh et al., 2001 report that the rates of denitrification in seagrass were highly dependent on the nitrate concentration in the water column and to the specific features of the rhizosphere sediments. High denitrification activities were reported for seagrass beds by Iizumi et al. (1982) with much greater rates in vegetated than in bare sediments (Blotnick et al. 1980; Caffrey and Kemp, 1990).

### AMMONIFICATION IN SEAGRASS SYSTEMS

Ammonification in both tropical and temperate seagrass beds can supply  $\text{NH}_4^+$  in excess of that required for plant growth (Short et al. 1993; Dennison et al. 1993), except in some organic-poor sediments (Iizumi et al. 1982; Short 1993). Ammonification rates (Table 5) in the vegetated sediments of *Potamogeton perfoliatus* (380-570  $\mu\text{mol N m}^{-2} \text{ h}^{-1}$ ) were similar to rates measured in other seagrass beds, where  $\text{NH}_4^+$  regeneration varied from 50 to 3500  $\mu\text{mol N m}^{-2} \text{ h}^{-1}$  (Dennison, 1987; Caffrey and Kemp 1990). Regeneration of  $\text{NH}_4^+$  in bare sediments (361-1280  $\mu\text{mol N m}^{-2} \text{ h}^{-1}$ ) had a greater range than previously reported (22-246  $\mu\text{mol N m}^{-2} \text{ h}^{-1}$ , Blackburn and Henriksen 1983; Kaspar et al. 1985) and rates were highly variable. Depletion of  $\text{NH}_4^+$  in porewater suggested that the demand for  $\text{NH}_4^+$  was greater than its supply (Caffrey and Kemp, 1990).

Table 5: Comparison of various N-cycle processes in seagrass-dominated sediment systems (modified from Miyajima et al., 2001)

Process	Location	Nitrogen flux ( $\mu\text{mol m}^{-2} \text{ h}^{-1}$ )	Depth of integration (cm)	Source
Nitrogen fixation	Ishigaki Island	7.1 - 13.1	0 - 15	Miyajima et al., 2001
	Australia	16 - 166	-	Perry, 1998
	Jamaica	40	0 - 8	Blackburn et al., 1994
	Bahamas	14 - 41	-	Oremland et al., 1976
	Hog Island	15.3	-	Windham and Ehrenfeld, 2003
	Florida	0.15 - 0.75	0 - 20	Perry, 1997
	Florida Bay	0.1 - 0.9	-	Plus et al., 2003
Nitrification	Hog Island	0.001	-	Windham and Ehrenfeld, 2003
Denitrification	Ishigaki Island	2.7 - 11.8	0 - 15	Miyajima et al., 2001
	Jamaica	80 - 170	0 - 8	Blackburn et al., 1994
$\text{NO}_3^-$ (+ $\text{NO}_2^-$ ) flux to sediment	Ishigaki Island	64 - 79	-	Miyajima et al., 2001
	Texas Coast	0.00 - 0.04	-	Ziegler and Berner, 1999
	Hog Island	2.5	-	Windham and Ehrenfeld, 2003
$\text{NH}_4^+$ flux to sediment	Ishigaki Island	-4.7 - +2.3	0 - 15	Miyajima et al., 2001
	Texas Coast	-15.3 - +9.5	-	Ziegler and Berner, 1999
	Sulawesi Island	-12.7 - +4.3	-	Ertfmeijer and Middleburg, 1993
Ammonification	Hog Island	0.0023	-	Windham and Ehrenfeld, 2003
Microalgal DIN Uptake	Ishigaki Island	80 - 800	0 - 15	Miyajima et al., 2001
	New Caledonia	85 - 382	-	Boucher et al., 1994
	Hog Island	15.3	-	Windham and Ehrenfeld, 2003
Litter Immobilization	Hog Island	12	-	2003

### SOURCES AND SINKS OF $\text{NH}_4^+$

Nitrogen is supplied to the sediment as particulate organic nitrogen (PON) and through nitrogen fixation. In addition, dissolved inorganic nitrogen (DIN) is taken up from the water column by seagrass leaves and by benthic microalgae. A schematic of the rates of N-transformations in a seagrass bed is given in Fig. 6. Average urea turnover rate in the vegetated sediment was  $18 \text{ mmol N m}^{-2} \text{ d}^{-1}$  and nitrogen fixation was  $4 \text{ mmol N m}^{-2} \text{ d}^{-1}$ , leading to a gross ammonium production of at least  $22 \text{ mmol N m}^{-2} \text{ d}^{-1}$  (Hansen et al., 2000). Denitrification accounted for  $1.5$  to  $5.0 \mu\text{mol m}^{-2} \text{ d}^{-1}$  in the and nitrification was The net requirement of nitrogen for growth of *Zostera capricorni* was  $\sim 3 \text{ mmol N m}^{-2} \text{ d}^{-1}$ . Uptake of nitrogen by seagrasses is assumed to occur both from the water column and the sediment with a maximum of  $2/3^{\text{rd}}$  of the demand supplied from one of the sources (Zimmerman et al. 1987, Pedersen and Borum 1992). The plant uptake of nitrogen was relatively low compared to the gross ammonium production, which suggests, as there was no net ammonium production, a high rate of nitrogen incorporation into the bacteria (Hansen et al., 2000). Nitrogen incorporation into aerobic bacteria in the present study was  $7$  to  $21 \text{ mmol N m}^{-2} \text{ d}^{-1}$ , assuming that the aerobic respiration was responsible for  $25$  to  $50\%$  of carbon oxidation.

Hansen et al., also suggest that nitrogen was presumably incorporated into benthic microalgae. Together with the observation that there was no net ammonium production, the estimates on nitrogen incorporation into the microbial biomass demonstrate high rates of internal nitrogen cycling in the sediment. They propose that mineralization within the sediment, was through an almost closed cycle of alternate organic nitrogen degradation and resynthesis, driven by carbon oxidation as also suggested by Lomstein et al. (1989, 1998). The seagrass *Z. capricorni* functioned as a temporary storage of nitrogen supplied, partly as leakage from root-rhizomes, some of the carbon that fuelled the recycling of nitrogen. The rapid recycling of nitrogen in an almost closed cycle within the sediment implies that porewater concentrations of nitrogen was kept low and that most of the nitrogen, at least temporarily, was unavailable to phytoplankton. Thereby, high microbial activity in the sediment and relatively high growth rates of seagrasses was sustained even in low nutrient environments (Hansen et al., 2000).

### PRIMARY PRODUCTIVITY IN SEAGRASS ECOSYSTEMS

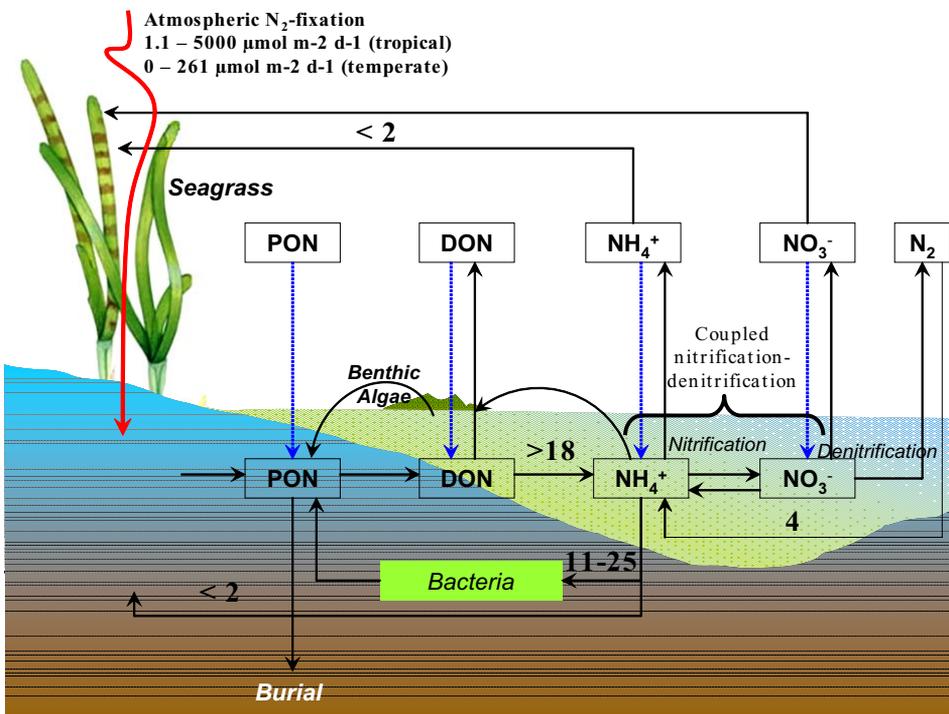
Coastal regions often receive large anthropogenic inputs of nitrogen and phosphorus that cause eutrophication, promoting the growth of phytoplankton and fast growing floating macroalgae. Growth of benthic rooted plants (seagrasses) and benthic microalgae on the other are suppressed due to reduced light availability (Duarte, 1995). This shift from benthic to pelagic primary production introduces large diurnal variations in oxygen conditions from high rates of photosynthesis during day followed by high respiration rates at night. In addition, oxygen consumption within the sediment increases following the deposition of easy

degradable algal material on the sediment. Accompanying and enhancing these shifts in the primary producers are changes in benthic metabolism, benthic nitrogen fluxes and sediment denitrification. For example, lagoons dominated by phytoplankton and macroalgae often show large diurnal changes in oxygen concentrations associated with high sediment production and respiration rates (Sand-Jensen and Borum 1991, Viaroli et al. 1995). These rapid changes in benthic metabolism are enhanced by the composition of the primary producers.

### BENTHIC N-FLUXES

According to Hansen et al. (2000) benthic nutrient fluxes (Table 5; Fig. 6) are typically low in macrophyte systems ( $<2 \text{ mmol m}^{-2} \text{ d}^{-1}$ ) due to the low nitrogen and phosphorus content of the decomposing organic matter and efficient recycling within the plant-sediment system. In contrast, macroalgae can reduce denitrification by physically separating the denitrifiers from water-column nitrate, by efficient assimilation of water-column nitrate, and by suppression of nitrification through anoxia below the algal mats (Krause-Jensen et al. 1999). Deposition of large quantities of phytoplankton detritus may also result in sediment anoxia. A combination of reduced denitrification and decomposition of large quantities of organic matter enhances benthic ammonium fluxes (Owens and Stewart 1983,

Fig. 6: Conceptual diagram of the seagrass model



Sfriso et al. 1987). Increased benthic nitrogen and phosphorus fluxes in turn stimulate further primary production in the lagoon (Sfriso et al. 1987). Information on how changes in benthic metabolism, benthic nutrient fluxes and sediment denitrification accompany and enhance shifts in the primary producers is important for understanding how shallow coastal lagoons respond to nutrient enrichment.

There have been a number of field and laboratory studies that have examined the effect of production and decomposition of individual plant-sediment systems representing different stages of eutrophication on benthic nutrient fluxes and denitrification, including seagrasses (Johnson and Johnstone, 1995, Risgaard-Petersen et al. 1998, Pedersen et al. 1993, Hansen et al. 2000), benthic microalgae (Christensen et al. 1990, Enoksson 1993, Risgaard-Petersen et al. 1994), and macroalgae (Owens and Stewart, 1983). Eyre and Ferguson (2002) measured carbon decomposition and production, benthic nutrient fluxes and sediment denitrification in four shallow warm-temperate Australian lagoons. They determined that differences in carbon production and decomposition across the lagoons were the main regulators of the quantity and quality of benthic nutrient fluxes and the relative proportion of nitrogen lost through denitrification. For example, the efficiency with which the lagoon sediments recycled nitrogen as  $N_2$ , (i.e. denitrification efficiency:  $N_2-N/(N_2-N + DIN)$ ), decreased as carbon decomposition rates increased. Their study demonstrated that production by plants had a significant influence on benthic nutrient fluxes, with a typical pattern of an efflux during the dark cycle and an uptake during the light cycle. As such, the sediment productivity/respiration ( $p/r$ ) ratio was one of the major controls on net benthic inorganic and organic nutrient fluxes and appears to be one of the key changes which occur in shallow coastal lagoons as these become eutrophic.

More recently, Plus et al. (2003) modeled seasonal dynamics of biomasses and nitrogen contents in a seagrass meadow in the Thau lagoon of the French Mediterranean coast. They report that, in such shallow ecosystems, seagrasses remain the most productive compartment when compared with epiphytes or phytoplankton productions, and that seagrasses, probably due to their ability in taking nutrients in the sediment, have a lower impact on nutrient concentration in the water column than the phytoplankton.

#### **NITROGEN RECYCLING/MINERALIZATION IN SEAGRASS BEDS**

Seagrasses are also known to be quite well adapted to poor nutrient environments (Zimmerman et al., 1987, Hemminga et al., 1991, Pedersen and Borum, 1992). Then, internal nitrogen redistribution (from belowground parts to leaves and vice versa) and reclamation (from old to young tissues) seem to play an important role in the plant nitrogen budget. Pedersen and Borum (1992) have estimated the contribution of internal recycling to meet 27% of the annual nitrogen requirements for *Zostera marina*. Mineralization processes, benthic mineralization

**Table 6:** Contribution of coastal systems to the global N<sub>2</sub>O production

Coastal/ System	Marine	% of World's Ocean Area <sup>a</sup>	N <sub>2</sub> O Emission (Tg year <sup>-1</sup> )	% of global oceanic N <sub>2</sub> O emission <sup>s</sup>	Source
Estuaries		0.4	0.2 <sup>b</sup> – 1.5 <sup>c</sup>	<b>10</b>	<sup>b</sup> Seitzinger and Kroeze (1998) <sup>c</sup> Wilde and De Bie (2000)
Coastal Upwelling		0.2	3.0 <sup>a</sup> – 4.7 <sup>d</sup>	<b>35</b>	<sup>a</sup> Bange et al (1996) <sup>d</sup> Capone et al., (1997)
Continental Shelves		17.9	0.6 <sup>b</sup> – 2.7 <sup>a</sup>	<b>15<sup>b</sup></b>	<sup>b</sup> Seitzinger and Kroeze (1998) <sup>a</sup> Bange et al (1996)
Open Ocean		81.5	4.2 <sup>a</sup> – 5.8 <sup>d</sup>	40	<sup>a</sup> Bange et al (1996) <sup>d</sup> Capone (1996)

<sup>s</sup>*Note:* % global oceanic N<sub>2</sub>O emission from Estuaries + Coastal Upwelling + Continental Shelves = 60%, demonstrate high production per unit area related to the Open Ocean

processes, nitrification and denitrification processes at the sea surface are described in Chapelle et al. (2000). Results for the nitrogen budget seem to indicate that the seagrass growth could suffer from nitrogen limitation during summer period in spite of effective mechanisms of nitrogen redistribution and reclamation (Plus et al., 2003). They concluded that the ability of seagrasses in taking nitrogen from the sediment and the internal nitrogen recycling processes make their impact on dissolved inorganic nitrogen in the water column smaller than the phytoplankton. Table 5; Fig. 6 provides a comparison of various N-cycle processes in seagrass-dominated sediment systems, which suggests the domination of processes such as N<sub>2</sub>-fixation and N-uptake in seagrass ecosystems. The above review clearly suggests a distinct lacuna in the availability of data from tropical areas, particularly from the extensive seagrass ecosystems of India.

Pulicat Lake which has an extensive seagrass bed is found to export on an average < 40% of its nutrients to the Bay of Bengal. The formation of a sand bar across the estuarine-marine transition has resulted in a lower flux from the system to the Bay of Bengal (Shalini, 2002). This is because the sedimentation rate of the Pulicat Lake is between 5.5 and 10 mm yr<sup>-1</sup> and is constantly on the rise due to low fresh water inflow from the rivers. The flux of materials and nutrients from the lake to the Bay of Bengal occurs mainly due to the semi-diurnal tides (tidal range: 1 m) and for a short duration during the monsoon season (October – December). For a major part of the year, the lake remains only partially connected with the sea, thereby retaining much of the anthropogenically derived nutrients in its sediments. This creates eutrophic conditions, resulting in algal bloom formation along the fringes of the lake.

#### ACKNOWLEDGEMENTS

The authors thank the various researchers whose works have been mentioned here and those whose references have not been cited by oversight; for their valuable contribution in understanding the Nitrogen cycling in coastal and marine ecosystems. RR and PR thank the Department of Science and Technology, Government of India for the financial support for a part of the nitrogen work

carried out in India. PR thanks the Hanse-Wissenschafts Kolleg, Delmenhorst, Germany for supporting her research at ZMT, Bremen. We gratefully acknowledge the support and encouragement given by Venu Ittekkot, Director, ZMT, Bremen, Germany.

#### References

- ASTON SR (1978) Estuarine chemistry. In: Riley JP and Chester R (Eds) *Chemical Oceanography*, 7: pp. 361–440. Academic Press, New York
- BANGE, H. W., RAPSOMANIKIS, S. and ANDREAE, M. O. (1996) Nitrous oxide in coastal waters. *Global Biogeochemical Cycles*, v. 10, pp. 197–207.
- BILLEN G, LANCELOT C, and MEYBECK M. (1991) N, P and Si retention along the aquatic continuum from land to ocean. In: Mantoura RFC, Xlartin JM. Wollast R (eds) *Ocean margin processes in global change*. Dahlem Workshop Reports, Wiley, pp. 19-44
- BLACKBURN, T. H., and HENRIKSEN, K. (1983) Nitrogen cycling in different types of sediments from Danish Waters. *Limnol. Oceanogr.*, v. 28, pp. 477-93.
- BLOTNICK, J. R., RHO, J, and GUNNER, H. B. (1980) Ecological characteristics of the rhizosphere microflora of *Myriophyllum heterophyllum*. *J. Environ. Qual.*, v. 9, pp. 207-2 10.
- BOON, P. I. (1986a) Uptake and release of nitrogen compounds in coral reef and seagrass, *Thalassia hemprichii* (Ehrenb.) Aschers., bed sedvments at Lzard Island, Queensland. *Aust. J. Freshwat. Res.*, v. 37, pp. 11-19
- BOUCHER G, CLAVIER J, and GARRIGUE C. (1994) Estimation of bottom ammonium affinity in the New Caledonia lagoon. *Coral Reefs* , v. 13, pp. 13–19
- BOYER, E. W., R. B. ALEXANDER, and W. J. PARTON, C. (2006) Li, K. Butterbach-Bahl, S. D. Donner, R. W. Skaggs, and S. J. Del Grosso.. Modeling denitrification in terrestrial and aquatic ecosystems at regional scales. *Ecological Applications*, v. 16, pp. 2123–2142.
- CAFFREY J.M., and KEMP W.M. (1990) Nitrogen cycling in sediments with estuarine populations of *Potamogeton perfoliatus* and *Zostera marina*. *Mar Ecol Prog Ser*, v. 66, pp. 147-160
- CAPONE, D.G. (1988) Benthic nitrogen fixation. In *Nitrogen Cycling in Coastal Marine Environments* ed. T.H. Blackburn and J.Sørensen. John Wiley, Chichester, pp. 85–123.
- CAPONE, D.G., ZEHR, J.P., PAERL, H.W., BERGMAN, B. and CARPENTER, E.J. (1997) *Science* 276 (5316), 1221. [DOI: 10.1126/science.276.5316.1221]
- CAPONE, D.G. (1983) Benthic nitrogen fixation. In *Nitrogen in the Marine Environment* ed. E.J. Carpenter & D.G. Capone. Academic Press, New York, pp. 105–137.
- CHAPELLE A., MENESGUEN A., DESLOUS-PAOLI J. M., SOUCHU P., MAZOUNI N., VAQUER A., and MILLET B. (2000) *Ecological Modelling*, v. 127 (2-3), pp. 161-181.
- CHRISTENSEN PB, NIELSEN LP, SØRENSEN J, and REVSBECK N.P (1990) Denitrification in nitrate-rich streams: diurnal and seasonal variation related to benthic oxygen metabolism. *Limnol Oceanogr*, v. 35, pp. 640–651
- Coastal Statistics, 2000 (Data from <http://earthtrends.wri.org>)
- COLE, J.E., D. RIND, and R.G. FAIRBANKS (1993) Isotopic responses to interannual climate variability simulated by an atmospheric general circulation model. *Quaternary Sci. Rev.*, v. 12, pp. 387-406.

- COOPER, A.B. (1990) Nitrate depletion in the riparian zone and stream channel of a small headwater catchment. *Hydrobiologia.*, v. 202, pp. 13-26.
- DEN HARTOG, C. (1970) The Sea-grasses of the World. *Verhandl. der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde*, No. 59(1).
- DENNISON, W.C. (1987) Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquat Bot.*, v. 27, pp. 15-26
- DENNISON W.C, R.J, MOORE K.A, STEVENSON J.C., CARTER V, KOLLAR S, BERGSTROM P.W., and BATIUK R.A. (1993) Assessing water quality with submersed aquatic vegetation. *Bioscience*, v. 43, pp. 86-94.
- DUARTE, C.M. (1995) Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia*, v. 41, pp. 87-112.
- DUCE (1991) *Global Biogeochem. Cycles*, v. 5, 193p.
- DUNTON K.H. (1996) Photosynthetic production and biomass of the subtropical seagrass *Halodule wrightii* along an estuarine gradient. *Estuaries*, v. 19, pp. 436-447
- ENOKSSON, V. (1993) Nutrient cycling by coastal sediments: effect of added algal material. *Mar Ecol Prog Ser*, v. 92, pp. 245-254
- ERFTEMEIJER, P.L.A., and MIDDLEBURG, J.J. (1993) Sediment nutrient interactions
- EYRE, B.D. and FERGUSON, A.J.P. (2002) Comparison of carbon production and decomposition, benthic nutrient fluxes and denitrification in seagrass, phytoplankton, benthic microalgae- and macroalgae-dominated warm-temperate Australian lagoons. *Mar Ecol Prog Ser.*, v. 229, pp. 43-59
- FISHER, D.C., J. CERASO, T. MATHEW, and M. OPPENHEIMER (1988) *Polluted coastal waters: The role of acid rain*. Environ. Defense Fund, New York.
- Forest Survey of India. 1998. The State of Forest Report 1997
- FOURQUREAN, J. W., ZIEMAN, J.C., and POWELL, G.V.N. (1992) Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. *Mar. Biol.*, v. 114, pp. 57-63
- GALLOWAY JN, DENTENER FJ and CAPONE DG (2004) Nitrogen cycles: past, present, and future. *Biogeochemistry*, v. 70, pp. 153-226.
- GALLOWAY JN, SCHLESINGER WH and LEVY H. (1995) Nitrogen fixation: atmospheric enhancement – environmental response. *Global Biogeochem Cycles*, v. 9, pp. 235-252.
- GALLOWAY, J.N. (2000) Nitrogen mobilization in Asia; *Nutrient Cycling in Agroecosystems*; v. 57(1), pp. 1385-1314
- GALLOWAY, J.N. (1998) The global nitrogen cycle: changes and consequences. *Environmental Pollution*, v. 102, pp. 15-24.
- HANSEN J.W, UDY J.W, PERRY C.J, DENNISON W.C, and LOMSTEIN B.A. (2000) Effect of the seagrass *Zostera capricorni* on sediment microbial processes. *Mar Ecol Prog Ser*, v. 199, pp. 183-196.
- HARRISON, J.A. (1998) The Nitrogen Cycle of Microbes and Men. In: *Vision Learning*; [http://www.visionlearning.com/library/module\\_viewer.php?mid=98](http://www.visionlearning.com/library/module_viewer.php?mid=98).
- HEMMINGA M.A, HARRISON P.G, and VAN LENT, F. (1991) The balance of nutrient losses and gains in seagrass meadows. *Mar. Ecol. Prog. Ser.*, v. 71, pp. 85-96
- HOWARTH, R. W., G. BILLEN, D. SWANEY, A. TOWNSEND, N. JAWORSKI, K. LAJTHA, A. DOWNING, R.

- ELMGREEN, N. CARACO, T. JORDAN, F. BERENDSE, J. FRENEY, V. KUDEYAROV, P. MURDOCH, and Z. ZHAO-LIANG (1996) Regional nitrogen budgets and riverine N and P fluxes for the drainages to the North Atlantic Ocean: Natural and human influences. *Biogeochemistry*, v. 35, pp. 181-226.
- HU D, SAITO Y and KEMPE S. (1998) Sediment and nutrient transport to the coastal zone. In: Galloway JN & Melillo JM (eds) *Asian Change in the Context of Global Change*. Cambridge University Press, Cambridge, UK
- IZUMI, H., HATTORI, A., and McROY, C. P. (1982) Ammonium regeneration and assimilation in eelgrass (*Zostera marina*) beds. *Mar. Biol.*, v. 66, pp.59-65.
- JAGTAP, S.S. (Guest Editor) (1997) Mitigating Effects of Climatic Variability on Food Production: Special Issue, *The Nigerian Meteorological Society Journal*, 2:1.
- JAWORSKI, N.A., HOWARTH, R.W. and HETLING, L.I. (1997) Atmospheric deposition of nitrogen oxides onto the landscape contributes to coastal eutrophication in the northeast United States. *Environ. Sci. Technol.*, 31p.
- JICKELLS, T. (2006) The role of air-sea exchange in the marine nitrogen cycle. *Biogeosciences Discuss*, v. 3, pp. 183–210.
- JICKELLS, T. (2005) External inputs as a contributor to eutrophication problems. *Journal of Sea Research*, v. 54, pp. 58-69.
- JICKELLS, T. (1998) Nutrient Biogeochemistry of the Coastal Zone, *Science*, v. 281. no. 5374, pp. 217–222.
- JICKELLS, T.D., YAAQUB, R.R., KANE, M.M., RENDELL, A., DAVIES, T.D. (1991) Atmospheric inputs to the North Sea: a progress report. In: *Proc. EUROTRAC Symp. 90* (Eds. P. Burrell et al.), pp.85-86 SPB Academic Publishing bv., The Hague, Netherlands.
- JOHNSON P, AND JOHNSTONE R. (1995) Productivity and nutrient dynamics of tropical sea-grass communities in Puttalam Lagoon, Sri Lanka. *Ambio*, v. 24, pp. 411–417.
- JUSTIC, D., and N. N. RABALAIS (1995) “Changes in nutrient structure of river-dominated coastal waters: Stoichiometric nutrient balance and its consequences.” *Estuarine, Coastal and Shelf Science*, v. 40, pp. 339-356.
- KASPAR, H. F. (1983) Denitrification, nitrate reduction to ammonium, and inorganic nitrogen pools in intertidal sediments. *Mar. Biol.*, v. 74, pp. 133-139.
- KASPAR, H. F., ASHER, R. A., and BOYER, I. C. (1985) Microbial nitrogen transformations in sediments and inorganic nitrogen fluxes across the sediment-water interface on the South Island west coast, New Zealand. *Estuar coast. Shelf Sci.*, v. 21, pp. 245-255.
- KRAUSE-JENSEN D, CHRISTENSEN PB, and RYSGAARD S. (1999) Oxygen and nutrient dynamics within mats of the filamentous macroalga *Chaetomorpha linum*. *Estuaries*, v. 22, pp. 31–38.
- LEE K.S. and K.H. DUNTON. (1999) Inorganic nitrogen acquisition in the seagrass *Thalassia testudinum*: development of a whole-plant nitrogen budget. *Limnology and Oceanography*, v. 44(5), pp. 1204-1215.
- LOMSTEIN B.A, BLACKBURN T.H, and HENRIKSEN K. (1989) Aspects of nitrogen and carbon cycling in the northern Bering Shelf sediment. I. The significance of urea turnover in the mineralization of  $\text{NH}_4^+$ . *Mar Ecol Prog Ser*, v. 57, pp. 237-247.
- LOMSTEIN BA, JENSEN AGU, HANSEN JW, ANDREASEN JB, HANSEN LS, BERNTSEN J, and KUNZENDORF H. (1998) Budgets of sediment nitrogen and carbon cycling in the shallow water of Knebel

- Vig, Denmark. *Aquat Microb Ecol*, v. 14, pp. 69-80.
- LZUMI H, HATTON A, and McROY C.P (1980) Nitrate and nitrite in interstitial waters of eelgrass beds in relation to the rhizosphere. *J Exp Mar Biol Ecol*, v. 47, pp. 191-201.
- McROY CP, and HELFFERICH, C. (1977) *Seagrass ecosystems: a scientific perspective*. Mareel Dekker, Inc., New York, 314p.
- MEYBECK, M. (1982) Carbon, nitrogen, and phosphorus transport by world rivers. *Amer. J. Sci*, v. 282, pp. 401-250.
- MİYAJIMA, T., SUZUMURA, M., UMEZAWA, Y. and KOIKE, I. (2001) Microbiological nitrogen transformation in carbonate sediments of a coral-reef lagoon and associated seagrass beds. *Mar Ecol Prog Ser.*, v. 217, pp. 273–286.
- National Institute of Oceanography (NIO), Goa, Sagar: A pocketbook on the ocean with special reference to the waters around India 2006 [http://www.nio.org/aroundus/Sagar/sagar\\_rev.pdf](http://www.nio.org/aroundus/Sagar/sagar_rev.pdf)
- NIXON S.W., and PILSON M.E. (1983) Nitrogen in estuarine and coastal marine ecosystems, In Carpenter EJ and Capone DG (eds) *Nitrogen in the Marine Environment*, Academic Press., pp. 565-648.
- O'DONOHUE, M.J., MORIARTY, D.J.W. and McRAE, I.C. (1991) Nitrogen fixation in sediments and the rhizosphere of the seagrass *Zostera capricornia*. *Microbial Ecol.*, v. 22, pp. 53–64.
- OREMLAND, R.S., GOTTO J.W., and TAYLOR B.F. (1976)  $N_2(C_2H_2)$  fixation associated with the rhizosphere communities of the seagrass *Thalassia testudinum*. *Am Soc Microbiol Abstr*, 171p.
- OWENS N.J.P, and STEWART W.D.P. (1983) Enteromorpha and the cycling of nitrogen in a small estuary. *Estuar Coast Shelf Sci*, v. 14, pp. 237–249.
- PAERL, H. W. (2002) Connecting atmospheric nitrogen deposition to coastal eutrophication. *Environ. Sci. Technol.*, v. 36, pp. 323A–326A.
- PATRIQUIN, D.G. and KNOWLES, R. (1972) Nitrogen fixation in the rhizosphere of marine angiosperms. *Mar. Biol.*, v. 16, pp. 49–58.
- PEDERSEN MF and BORUM J. (1993) An annual nitrogen budget for a seagrass *Zostera marina* population. *Mar. Ecol. Prog. Ser.*, v. 101, pp. 169-177.
- PEDERSEN MF, and BORUM J. (1992) Nitrogen dynamics of eelgrass *Zostera marina* during a late summer period of high growth and low nutrient availability. *Mar Ecol Prog Ser*, v. 80, pp. 65-73.
- PEDERSEN, M.F., PALING, E.I. and WALKER, D.I. (1997) Nitrogen uptake and allocation in the seagrass *Amphibolis antarctica*. *Aquat. Bot.*, v. 56, pp.105–117.
- PERRY C.J. (1998) *Microbial processes in seagrass sediments*. PhD thesis, University of Queensland. Brisbane.
- PHILLIPS RC, and McROY C.P. (1980) *Handbook of seagrass biology: an ecosystem perspective*. Garland STPM Press New York, 353p.
- PLUS, M., CHAPELLEB, A., MÉNESGUENB, A., DESLOUS-PAOLIC, J. and AUBY, I. (2003) Modelling seasonal dynamics of biomasses and nitrogen contents in a seagrass meadow (*Zostera noltii* Hornem.): application to the Thau lagoon (French Mediterranean coast). *Ecological Modelling*, v. 161(3), pp. 211-236.

- REEBURGH, W. S. (1997) Figures Summarizing the Global cycles of biogeochemically important elements. *Bull. Ecol. Society of America*, v. 78(4), pp. 260-267.
- RISGAARD-PETERSEN N, RYSGAARD S, NIELSEN L.P, and REVSBECK N.P. (1994) Diurnal variation of denitrification and nitrification in sediment colonized by benthic microphytes. *Limnol Oceanogr*, v. 39, pp. 573-579.
- RYTHER J.H., and DUNSTAN W.M. (1971) Nitrogen, phosphorus and eutrophication in the coastal marine environment. *Science* v. 171, pp. 1008-1013.
- SAND-JENSEN K, and BORUM J. (1991) Photosynthetic responses of *Ulva lactuca* at very low light. *Mar Ecol Prog Ser*, v. 50, pp. 195-201.
- SCHLESINGER, W. H. (1991) *Biogeochemistry: An Analysis of Global Change*. Academic Press, San Diego.
- SEITZINGER SP and KROEZE C. (1998) Global distribution of nitrous oxide production and N inputs in freshwater and coastal marine ecosystems. *Global Biogeochemical Cycles*, v. 12, pp. 93-113.
- SEITZINGER SP, KROEZE C, and STYLES RV. (2000) Global distribution of N<sub>2</sub>O emissions from aquatic systems: Natural emissions and anthropogenic effects. *Chemosphere: Global Change Science*, v. 2, pp. 267-279.
- SFRISO A, MARCOMINI A, and PAVONI B. (1987) Relationships between macroalgal biomass and nutrient concentrations in a hypertrophic area of the Venice Lagoon. *Mar Environ Res*, v. 22, pp. 297-312.
- SHALINI, A. ( ) *Biogeochemical cycling of methane in natural wetland: Pulicat Lake, A case study*. PhD Thesis, Anna University, Chennai, India 220 pp.
- SHORT F.T., MONTGOMERY J, ZIMMERMAN C.F., and SHORT C.A. (1993) Production and nutrient dynamics of a *Syringodium filiforme* Kütz. seagrass bed in Indian River Lagoon, Florida. *Estuaries*, v. 16, pp. 323-334.
- SHORT, F.T., and McROY, C. P. (1984) Nitrogen uptake by leaves and roots of the seagrass *Zostera marina* L. and its epiphytes. *Mar. Bot.*, v. 27, pp. 547-555.
- SØRENSEN, L. L., HERTEL, O., SKJØTH, C. A., LUND, M., and PEDERSEN, B. (2003) Fluxes of ammonia in the coastal marine boundary layer. *Atmos. Environ.*, v. 37, Supplement No. 1, pp. S167-177.
- STAPEL, J., AARTS, T.L., VAN DUYNHOVEN, B.H.M., DE GROOT, J.D., VAN DEN HOOGEN, P.H.W. AND HEMMINGA, M.A. (1996) Nutrient uptake by leaves and roots of the seagrass *Thalassia hemprichii* in the Spermonde Archipelago, Indonesia. *Mar. Ecol. Prog. Ser.*, v. 134, pp. 195-206.
- TERRADOS, J., and WILLIAMS, S. L. (1997) Leaf versus root uptake by the surfgrass *Phyllospadix torreyi*. *Mar. Ecol. Prog. Ser.*, v. 149, pp. 267-277.
- VALIGURA, R. A., ALEXANDER, R. B., CASTRO, M. S., MEYERS, T. P., PAERL, H. W., STACEY, P. E., and TURNER, R. E. (Eds.). (2001) *Nitrogen Loading in Coastal Water Bodies: An atmospheric Perspective*, Am. Geophysical Union, 254p.
- VIAROLI P, BARTOLI M, BONDAVALLI C, and NALDI M. (1995) Oxygen fluxes and dystrophy in a coastal lagoon colonised by *Ulva rigida* (Sacca Di Goro, Po River Delta, Northern Italy). *Fresenius Envir Bull*, v. 4, pp. 381-386

- VITOUSEK P.M., and R.W. HOWARTH (1991) Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry*, v. 13, pp. 87-115.
- VOROSMARTY CJ, LI C, SUN J and DAILN Z. (1998) Drainage basins, river systems, and anthropogenic change: the Chinese example. In: Galloway JN & Melillo JM (eds) *Asian Change in the Context of Global Change*. Cambridge University Press, Cambridge, UK.
- WALKER, J. T., WHITALL, D. R., ROBARGE, W., and PAERL, H. W. (2004) Ambient ammonia and ammonium aerosol across a region of variable emission density, *Atmos. Environ.*, v. 38, pp. 1235–1246.
- WELSH, D.T. (2000) Nitrogen fixation in seagrass meadows: Regulation, plant-bacteria interactions and significance to primary productivity. *Ecology Letters*, v. 3(1), pp. 58–71.
- WELSH, D.T., BOURGUÈS, S., DE WIT, R. and HERBERT, R.A. (1996a) Seasonal variations in nitrogen fixation (acetylene reduction) and sulphate-reduction rates in the rhizosphere of *Zostera noltii*: nitrogen fixation by sulphate-reducing bacteria. *Mar. Biol.*, v. 125, pp. 619–628.
- WILDE, H.P.J. and DE BIE, M.J.M. (2000) Nitrous oxide in the Schelde estuary: production by nitrification and emission to the atmosphere. *Mar. Chem.*, v. 69, pp. 203-216.
- WINDHAM, L. and EHRENFELD, J.G. (2003) Net impact of a plant invasion on nitrogen cycling processes within a brackish tidal marsh. *Ecological Applications*, v. 13(4), pp. 883–896.
- WOLLAST, R. (1981) Degradation mechanism of organic nitrogen in surficial sediments and its mathematical modeling, pp. 155-166 In: *Matiere organique a l'interface eau-sediment marin*.
- ZIEGLER S, and BENNER R. (1999) Nutrient cycling in the water column of a subtropical seagrass meadow. *Mar Ecol Prog Ser*, v. 188, pp. 51–62.
- ZIMMERMAN RC, SMITH RD, and ALBERTE R.S. (1987) Is growth of eelgrass nitrogen limited? A numerical simulation of the effects of light and nitrogen on the growth dynamics of *Zostera marina*. *Mar Ecol Prog Ser*, v. 41, pp. 167-176.