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Nutrient cycling in the water column of a subtropical seagrass meadow

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ABSTRACT: The cycling of nutrients was studied over a 16 mo period to determine how processes occurring between the water column and benthos influenced nutrient dynamics in a *Thalassia testudinum* dominated seagrass meadow. Nutrient concentrations were low and ranged from below detection to 0.59 µM ammonium (NH_4^+), 0.04 to 0.29 µM nitrate plus nitrite ($NO_3^- + NO_2^-$), and below detection to 0.22 µM soluble reactive phosphate (SRP). Water column and benthic fluxes of $NO_3^- + NO_2^-$ and SRP were usually below detection. The benthic fluxes of NH_4^+ ranged from an uptake of −228 µmol N m^{-2} d^{-1} to a release of 363 µmol N m^{-2} d^{-1}. Positive fluxes (i.e. directed out of the sediment) occurred primarily in light incubations and from seagrass-dominated sediments. Water column fluxes of NH_4^+ ranged from a net uptake of −145 µmol N m^{-2} d^{-1} to a net regeneration of 643 µmol N m^{-2} d^{-1}. The net regeneration of NH_4^+ in the water column usually exceeded the release of NH_4^+ from the benthos. There was a significant correlation between the regeneration of NH_4^+ in the water column and the light-mediated release of dissolved organic matter (DOM) from the benthos, indicating that benthic-derived DOM supported the regeneration of NH_4^+ in the water column. Bacterioplankton growth efficiencies were significantly and positively correlated to the regeneration of NH_4^+ in the water column, possibly resulting from changes in the composition of DOM released from the benthos. The C:N ratios of the organic matter remineralized in the water column were variable and ranged from 14 to 81, with lowest values occurring in late summer and highest values in spring. The results of this study indicated that temporal variations in the source and composition of DOM significantly influenced the cycling of nutrients in the water column of this seagrass meadow.

KEY WORDS: Nutrient cycling · Seagrasses · Benthic fluxes · Ammonium · Dissolved organic matter

INTRODUCTION

Seagrass-dominated estuaries are among some of the most productive ecosystems on earth, supporting and serving as nurseries for commercially important species and feeding grounds for waterfowl (Hillman et al. 1989). Worldwide degradation of seagrass meadows is well documented (Dennison et al. 1993), with losses attributed to increased human activities in coastal areas. For example, the coincidence of areas of greatest reduction in aquatic grasses with areas of greatest nutrient enrichment has been reported throughout the Chesapeake Bay (Orth & Moore 1983). Nutrient enrichment has been found to increase epiphytic growth on seagrasses and possibly trigger algal blooms, both causing dramatic reductions in seagrass populations (Kemp et al. 1983, Borum 1985, Flores-Verdugo et al. 1988, Dunton 1990). Increases in dissolved inorganic nitrogen (DIN), possibly due to increases in agricultural practices as well as a massive fish kill, may have been responsible for the onset of a brown tide in northern Laguna Madre, Texas, in June 1990 (Whitledge 1993). This brown tide has been implicated in about a 20% reduction of the seagrass *Halodule wrightii* between 1992 and 1995, and has dramatically increased the phytoplankton to seagrass production ratio in northern Laguna Madre (Stockwell et al. 1993, Onuf 1996).

To help determine the influence of environmental changes, such as increases in nutrient loading, on sea-

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grass ecosystems there is a need to understand the biogeochemical cycling of nutrients within these systems. Nutrient dynamics in seagrass meadows and other shallow environments is typically dominated by benthic processes. Because concentrations of nutrients are low in the water column, seagrasses most likely obtain their nutrients from the sediments where concentrations are considerably higher (Iizumi et al. 1982, Short & McRoy 1984, Blackburn et al. 1994). Rapid recycling of nitrogen (N) in the sediments has been documented in seagrass systems and appears to occur more rapidly in sediments dominated by seagrasses versus those that are unvegetated (Boon et al. 1986). Iizumi et al. (1982) and Short (1983) estimated that about 28 and 60%, respectively, of the ammonium (NH_4^+) regenerated in the sediment of seagrass beds was released to the overlying waters. Remineralization of nutrients and nitrogen fixation in the benthos appear to be fueled by seagrass photosynthate released through the roots (Jørgensen et al. 1981, Moriarty et al. 1986, Blackburn et al. 1994, Stapel & Hemminga 1997). The release and remineralization of seagrass photosynthate in the benthos represents a possible source of inorganic N and P in the overlying water column in these ecosystems.

A significant fraction of the carbon fixed by seagrasses is released as dissolved organic matter (DOM) into the water column through leaching and exudation and is subsequently utilized by heterotrophic bacterioplankton (Moriarty & Pollard 1982, Moriarty et al. 1986, Chin-Leo & Benner 1991, Ziegler & Benner 1999). For example, water column respiration accounts for about 60% of benthic net primary production in a *Thalassia testudinum* meadow of Laguna Madre (Ziegler & Benner 1999). The activity of benthic algae and macrophytes has been found to stimulate bacterioplankton production and nutrient cycling in shallow estuaries where dissolved organic nitrogen appears to be the major form of N released from the benthos (Moriarty et al. 1986, Middelboe et al. 1998).

The influence of the benthic release of DOM on bacterioplankton activity has been observed, however, very little is known about its influence on nutrient cycling in seagrass ecosystems. How does the coupling of processes between the water column and the benthos influence the cycling of nutrients in these ecosystems? Does the remineralization of DOM serve as a major source of inorganic nitrogen or phosphorus? If so, is this source influenced by seasonal variations in the source of DOM such as seagrass exudation and leaching? The purpose of this study was to address these questions by determining the abundance and cycling of nutrients in the water column of lower Laguna Madre. Water column concentrations were investigated, as well as benthic and water column fluxes of NH_4^+, nitrate plus nitrite ($NO_3^- + NO_2^-$), and soluble reactive phosphate (SRP) from June 1996 to June 1997. These nutrient parameters were examined in relation to measurements of phytoplankton and bacterioplankton production, benthic production, respiration, and dissolved organic carbon fluxes.

MATERIALS AND METHODS

Site description. Laguna Madre is the southernmost estuary located on the Texas coast, and it is separated from the Gulf of Mexico by Padre Island. Our study was conducted in a *Thalassia testudinum* dominated seagrass meadow in the southern portion of Laguna Madre. Beds of *Syringodium filiforme* and *Halodule wrightii* as well as drift algal species such as *Digenia simplex* and *Laurencia poitei* also occur in southern Laguna Madre (Humm & Hildebrand 1962, Onuf 1996). The study site was located east of the Gulf Intracoastal Waterway at about 26° 10' N 97° 12' W. (For map see Herzka & Dunton 1996.) A total of ten 5 day trips were made to southern Laguna Madre approximately every 6 to 8 wk from February 1996 to June 1997. Data from 2 of these 10 trips are not presented here due to brown tide blooms which interfered with the collection of nutrient data.

Water column parameters. Water temperature and depth were recorded using a data logging system (YSI6000, YSI Inc.) secured at mid-depth (~0.5 m) for the duration of each trip. Average NH_4^+, $NO_3^- + NO_2^-$, and SRP concentrations were determined from 12 to 24 samples collected over a 24 h period using an autosampler (see Ziegler & Benner 1998) Samples were collected in 45 ml glass bulbs (acid washed) at 60, 70 or 120 min intervals from about 0.6 m depth. Sample bulbs were kept in the dark and collected from the sampler every 12 h around sunrise and sunset. The 45 ml samples were transferred from the bulbs into 125 ml high-density polyethylene bottles (acid washed) and immediately placed on ice. Samples were frozen within 4 h of collection. All nutrient samples were analyzed within 4 wk of collection.

Seagrass carbon and nitrogen. Whole live plants were collected using a 15 cm diameter corer at the study site in July, September, and November. The cores were sieved with water to remove live plants from the sediment. The plants were rinsed with seawater and then kept on ice until they were brought back to the lab. The tissues were rinsed with distilled water and separated into above-(blades) and below-ground (roots and rhizomes) tissues. Once separated, the tissues were placed in a drying oven at 45°C for 48 h. The dried tissues were milled, and carbon and nitrogen content were determined on a Carlo Erba EA 1108 elemental analyzer.

Water column production, respiration, and nutrient fluxes. Water was collected around dawn and incubated in light and dark bottles (300 ml biological oxygen demand bottles or 90 ml quartz bottles) for about 12 h during the day to estimate primary production, respiration, and net fluxes of nutrients in the water column. Another water sample was collected around sunset and incubated overnight in dark bottles to estimate respiration and nutrient fluxes at night. Dark bottles were wrapped in aluminum foil, and all bottles were incubated *in situ* on racks set at mid-depth (~0.5 m) in the water column. To estimate primary production and respiration, changes in dissolved oxygen were determined in light and dark incubations using Winkler titrations with an automated titrator and potentiometric endpoint detection (Biddanda et al. 1994). Rates of net O_2 production or consumption were determined from the slope of the least-square linear regression ($n \geq 6$) of the dissolved oxygen data versus time. Consumption of dissolved oxygen in dark incubations during the daytime were added to the value for light incubations to obtain estimates of gross primary production. Water column gross primary production and respiration rates based on O_2 were converted to units of carbon using photosynthesis and respiration quotients of 1.2 and 1.0, respectively (Oviatt et al. 1986).

Rates of net nutrient production or consumption were determined from the slope of the least-square linear regression analysis of nutrient concentration versus time ($n \geq 6$). Initial and final samples were dispensed into clean 125 ml polyethylene bottles, immediately placed on ice and frozen within 4 h of collection. The daily net flux of nutrients occurring in the light was based on the number of daylight hours. The number of hours of light for each day was based on the number of hours of saturating PAR light for seagrasses (~300 $\mu E\ m^{-2}\ s^{-1}$; Herzka & Dunton 1996) determined from underwater continuous PAR light data collected close to the study site (K. Dunton, J. Kaldy & J. Kowalski unpubl. data). The daily net dark flux was calculated from the number of hours below saturating light levels. Daily net regeneration of NH_4^+ in the water column (dark incubations) was calculated from the sum of the water column fluxes estimated for daytime and nighttime. Positive fluxes indicated net regeneration and negative fluxes indicated the net uptake of the nutrient.

Bacterioplankton production. Bacterioplankton production was estimated from protein synthesis using ^{3}H-leucine (Kirchman et al. 1985). Triplicate 20 ml samples were incubated in the dark with ^{3}H-leucine (20 nM final concentration, specific activity of 50 Ci $mmol^{-1}$, New England Nuclear) for 1 h in a circulating bath of Laguna Madre water. One formaldehyde (4% final concentration) killed control was run with each triplicate live sample set to determine abiotic sorption of the labeled leucine. Incubations were terminated by filtration through a 0.2 µm pore-sized MF Nucleopore membrane filter. Filters were immediately extracted with ice cold 5% trichloroacetic acid for 5 min, followed by a 5 ml rinse with ice-cold trichloroacetic acid, stored in scintillation vials and refrigerated until measurement of radioactivity within 7 d of collection. Prior to scintillation counting samples were extracted at 50°C for 1 h using the tissue solubilizer Solvable (Dupont, New England Nuclear Inc.) as described by Amon & Benner (1998). Rates of bacterial carbon production were estimated from leucine incorporation rates using conversion factors of 4.3×10^{16} cells mol^{-1}, derived from experiments using Laguna Madre water (Chin-Leo & Benner 1991), and 20 fg C $cell^{-1}$ (Lee & Fuhrman 1987).

Bacterial growth efficiencies were calculated as the ratio of bacterial production to bacterial production plus water column respiration, except in March 1997. During March 1997 primary production was relatively high due to the presence of a brown tide. Respiration due to bacterioplankton, at this time, was assumed to be 70% of the total plankton respiration. This assumption was based on previous measurements of bacterial respiration ranging from 40 to 100% of plankton respiration for different marine environments (Williams 1981, Chin-Leo & Benner 1992, Biddanda et al. 1994).

Benthic nutrient fluxes. Net fluxes of NH_4^+, NO_3^- + NO_2^- and SRP into and out of the benthos were determined by measuring changes in nutrient concentrations in light and dark chambers. Chambers were constructed from 20 l Nalgene polycarbonate carboys by removing the bottoms and adding a sampling port at the shoulder. Caps of the chambers were fitted with a current-driven stirring mechanism to mimic *in situ* water movement (see Ziegler & Benner 1998). Covers for the chambers were constructed of dark-gray plastic and used for the dark incubations. Four chambers were placed carefully about 8 cm into the sediment at 3 seagrass-dominated sites (primarily *Thalassia testudinum*) and 1 unvegetated area (void of all macrophytes) adjacent to the other chambers. An average of the 4 chambers was used to estimate net benthic nutrient fluxes in lower Laguna Madre. The distribution of chambers was based on estimates of the aerial coverage of seagrass-dominated (75%) and unvegetated (25%) sediments in lower Laguna Madre (Quammen & Onuf 1993). Positive flux values indicated a net flux from the sediments to the water column, and negative fluxes indicated a net flux from the water column into the sediments.

Benthic chambers were carefully deployed without caps the day prior to the benthic measurements. At

dawn, water in the chambers was exchanged with overlying water using a hand-held pump. Dark incubations were conducted early in the morning and late in the afternoon to avoid dramatic shifts in light levels. Incubations lasted for 1.5 to 4 h depending upon level of activity (i.e. incubations were the longest in winter and shortest in summer). Samples were collected for nutrient analysis through the sampling port using a 60 ml syringe, dispensed into 125 ml high-density polyethylene bottles and treated as described for the diel water column samples. After completion of all benthic incubations, volumes for all 4 chambers were determined by injecting each with 15 ml of 30 mM $NaNO_3$. Each chamber was stirred for 2 min before a sample was collected and later frozen. The concentration of NO_3^- in these samples was used to estimate the volume of each chamber during every trip. Nutrient fluxes measured in the water column were used to correct the benthic nutrient fluxes for changes in nutrient concentrations due to processes occurring in the water contained in each chamber. The daily net benthic flux of nutrients occurring in the light was based on the number of hours of saturating PAR light levels for seagrasses, and the daily net fluxes occurring at night were calculated from the number of hours below saturating light levels.

Nutrient analyses. All samples collected for nutrient analyses were unfiltered to avoid additional steps that could have caused contamination in these samples with low concentrations of nutrients. In March, however, all samples were passed through a GF/F filter immediately after collection because of the unusually high phytoplankton production caused by a brown tide bloom that occurred in the previous months. There was no difference between 0.2 µm (polycarbonate) filtered water and whole water collected in April, June, July, September and November with respect to NH_4^+, NO_3^- + NO_2^- concentrations (Table 1). There was a difference in SRP concentration between the 0.2 µm filtered water and whole water collected in April; however, SRP was usually below detection in both the filtered and unfiltered water (Table 1).

Concentrations of NH_4^+ were determined using the phenol-hypochlorite method (Solorzano 1969). The detection limit was 0.30 µM at a confidence level ≥89%. The precision of the NH_4^+ analysis at 0.3 µM was 15% (expressed as coefficient of variance). Concentrations of NO_3^- + NO_2^- were determined for 10 ml samples using the standard cadmium reduction method modified for small samples (Gardner et al. 1976). Imidazole buffer was used in place of the NH_4Cl in both the additions to the sample (0.05 M, pH = 7.5) and through the column itself (0.1 M, pH = 7.5) in order to avoid NO_3^- contamination often found in reagent grade NH_4Cl. Standards of KNO_3 and $NaNO_3$ were analyzed before and after every set of samples. The detection limit for NO_3^- + NO_2^- was 0.02 µM, and precision was 40 and 4% at 0.02 and 1.00 µM, respectively. Samples collected in June 1997 were analyzed for NO_3^- + NO_2^- using an Antek Model 745 Nitrate/Nitrite Reduction Assembly and Antek Model 7020 nitric oxide chemiluminescence detector. The precision for 1 nM NO_3^- + NO_2^- was <6% using chemiluminescence detection. SRP was determined using the standard colormetric method (Strickland & Parsons 1972). The detection limit was 70 nM and the precision was 1% at 70 nM.

RESULTS

Water column nutrient concentrations

Nutrient concentrations in the water column of southern Laguna Madre were low throughout the year as compared with most estuarine systems, and relative to most seagrass systems (Fig. 1) Considerably higher nutrient concentrations have been reported in other tropical and temperate seagrass meadows (Pederson & Borum 1993, Johnson & Johnstone 1995, Stapel et al. 1997). NH_4^+ concentrations in lower Laguna Madre ranged from <0.30 to 0.59 µM and were highest in the late summer (Table 2, Fig. 1). NO_3^- + NO_2^- concentrations ranged from 0.04 to 0.18 µM, with the lowest concentrations in the sum-

Table 1. Average nutrient concentrations (µM) of whole and filtered (0.2 µm) water samples. Each value is reported as the mean (n ≤ 3) ± 1 SD. SRP: soluble reactive phosphorus

Month	NH_4^+		NO_3^- + NO_2^-		SRP	
	Whole water	0.2 µm	Whole water	0.2 µm	Whole water	0.2 µm
April	0.22 ± 0.08	0.23 ± 0.05	0.07 ± 0.01	0.04 ± 0.02	0.10 ± 0.02	<0.07
June	0.21 ± 0.03	0.26 ± 0.03	0.12 ± 0.03	0.14 ± 0.02	<0.07	<0.07
July	0.45 ± 0.10	0.43 ± 0.02	<0.02	<0.02	<0.07	<0.07
September	0.28 ± 0.07	0.29 ± 0.04	0.02 ± 0.02	0.05 ± 0.05	<0.07	<0.07
November	0.31 ± 0.08	0.25 ± 0.02	0.06 ± 0.01	0.08 ± 0.00	<0.07	<0.07

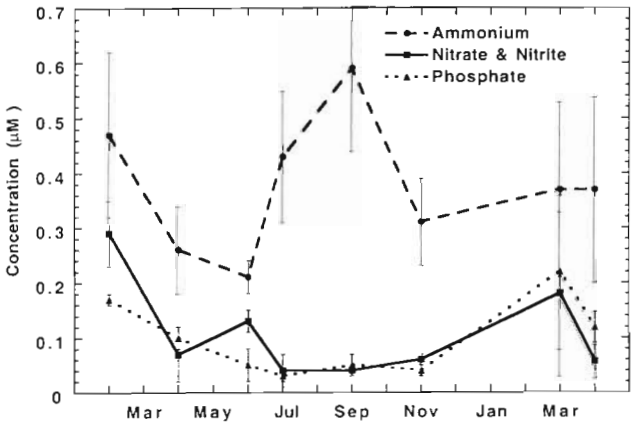

Fig. 1. Mean ammonium, nitrate + nitrite, and soluble reactive phosphate concentrations in the water column at the study site from February 1996 through June 1997. Error bars represent ±1 SD

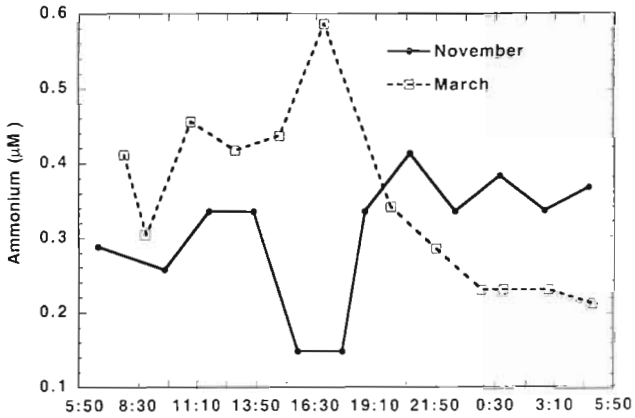

Fig. 2. Diel water column ammonium concentrations collected at the study site on November 5–6, 1996 and March 8–9, 1997

mer and fall. SRP was generally below detection limit and ranged from <0.07 to 0.17 µM. NO_3^- + NO_2^-, and SRP concentrations peaked in March when phytoplankton production was the highest due to a brown tide. The concentration of SRP remained high in June 1997 when phytoplankton production remained higher than normal. There was no apparent diel pattern in water column nutrient concentrations except in March 1997, when NH_4^+ concentrations increased during the day and decreased at night (Fig. 2). Concentrations of SRP in Florida Bay (annual average of 0.03 µM) were similar to those in lower Laguna Madre, whereas DIN concentrations (annual average of 2.7 µM) were generally higher (Fourqurean et al. 1993). The ratios of DIN to SRP in lower Laguna Madre were below the Redfield ratio of 16:1 (Redfield 1958) during the spring and winter (Table 2). From April through November 1996, SRP was not detectable and thus only minimal values for the ratio of DIN to SRP could be calculated.

Table 2. Mean water temperature, ammonium (NH_4^+), nitrate plus nitrite (NO_3^- + NO_2^-), and soluble reactive phosphorus (SRP) concentrations, and the ratio of dissolved inorganic nitrogen (DIN) to SRP. All errors are reported as ±1 SD

Month	Temperature (°C)	NH_4^+ (µM)	NO_3^- + NO_2^- (µM)	SRP (µM)	DIN:SRP Ratio
February	22.1 ± 1.6	0.41 ± 0.09	0.29 ± 0.04	0.17 ± 0.01	4.11
April	22.7 ± 1.4	<0.30	0.07 ± 0.05	<0.07	>5.29
June	30.2 ± 0.6	<0.30	0.13 ± 0.02	<0.07	>4.86
July	30.7 ± 0.1	0.43 ± 0.12	0.04 ± 0.03	<0.07	>6.71
September	30.5 ± 0.1	0.59 ± 0.15	0.04 ± 0.00	<0.07	>9.00
November	23.9 ± 1.7	0.31 ± 0.08	0.06 ± 0.01	<0.07	>5.29
March	20.7 ± 1.5	0.37 ± 0.16	0.18 ± 0.15	0.13 ± 0.07	4.23
June	27.3 ± 1.5	0.37 ± 0.17	0.06 ± 0.03	0.12 ± 0.03	3.58

Seagrass carbon and nitrogen content

The C and N content of above- and below-ground *Thalassia testudinum* tissues collected in July, September, and November indicated that there were large differences in the N content of the seagrass tissues between the summer and fall (Table 3). The C and N content decreased slightly from July to September in both the above- and below-ground tissues. Molar C:N ratios of the above- and below-ground tissues collected in July and September were similar. The C:N ratios were much lower in November due to a higher N content in both the above- and below-ground tissues. The N content of the seagrasses collected in November were 28 and 111% higher in the above- and below-ground tissues, respectively, than those collected in September. The higher N content of the tissues in November suggests that N storage in the fall could help support rapid growth in the spring (Pedersen & Borum 1993).

Water column production and respiration

Water column gross primary production was generally low, ranging from 0.4 to 9.2 mmol C m^{-2} d^{-1}, except during January 1997, when it was as high as 35.5 mmol C m^{-2} d^{-1} due to a brown tide bloom (Table 4). The water column was almost always net heterotrophic, with respiration ranging from 6.6 to 27.0 mmol C m^{-2} d^{-1} (Table 4). Bacterioplankton production in the water column ranged from 1.8 to 9.1 mmol C

Table 3. Carbon (C) and nitrogen (N) content of live seagrass blades and roots and rhizomes. The carbon to nitrogen ratios (C:N) are reported as the molar ratio. Total plant C:N is calculated assuming 85% of the total plant biomass is in below-ground tissues (Kaldy 1997)

Month	Tissue type	C (wt%)	N (wt%)	C:N	Total plant C:N
July	Blades	34.97	2.08	19.62	39.06
	Roots/rhizome	36.06	0.89	47.03	
September	Blades	32.45	1.89	20.03	42.06
	Roots/rhizome	33.30	0.75	51.87	
November	Blades	33.57	2.41	16.27	22.63
	Roots/rhizome	32.89	1.58	24.35	

m^{-2} d^{-1} and was similar to bacterial production rates measured in the water column over other subtropical seagrass meadows, including upper Laguna Madre (Moriarty & Pollard 1982, Moriarty et al. 1990, Chin-Leo & Benner 1991). The estimated bacterioplankton growth efficiencies ranged from 21 to 38% and fell within the range of most aquatic ecosystems studied (del Giorgio et al. 1997).

Water column and benthic nutrient fluxes

Net regeneration of NH_4^+ in the water column occurred primarily in the dark and ranged from 45 to 643 µmol N m^{-2} d^{-1} or 0.04 to 0.55 µmol N l^{-1} d^{-1} (Table 5). Water column regeneration of NH_4^+ measured in the dark increased through the summer and decreased in the fall (Fig. 3). However, regeneration was greatest in March possibly due to the presence of a brown tide which may have provided additional dissolved organic nitrogen for remineralization. NH_4^+ was primarily taken up in the water column in the light, and net fluxes ranged from −145 to −45 µmol N m^{-2} d^{-1} or −0.13 to −0.04 µmol N l^{-1} d^{-1}, except in June 1997, when net regeneration of NH_4^+ (76 µmol N m^{-2} d^{-1} or 0.10 µmol N l^{-1} d^{-1}) was measured in the light (Table 3, Fig. 3). Bacterioplankton N demand, calculated from bacterioplankton production and C:N = 4.3, ranged from 450 to 2110 µmol N m^{-2} d^{-1} and far exceeded the estimated NH_4^+ regeneration, which may indicate that uptake of dissolved organic nitrogen was important. Phytoplankton N demand, calculated from gross primary production and C:N ratio of 6.6, ranged from <10 to 700 µmol N m^{-2} d^{-1}, indicating that the net uptake (in the light) was usually an underestimate of total uptake (Table 4). In the water column, net uptake of NH_4^+ in the light was generally much lower than net regeneration measured in the dark, and there was no seasonal pattern to the variability in fluxes measured in the light (Fig. 3).

The rates of water column NH_4^+ regeneration, calculated as the sum of NH_4^+ release in dark incubations conducted during the day and night, ranged from 124 to 652 µmol N m^{-2} d^{-1} or 0.10 to 0.59 µmol N l^{-1} d^{-1} (Table 4). On 25 June 1997, potential rates of NH_4^+ uptake and regeneration were estimated using the ^{15}N isotopic dilution technique in incubations amended with 4 µM $^{15}NH_4Cl$ (Gardener et al. 1991, 1995). Potential regeneration rates were similar in both light (0.10 µM h^{-1}) and dark (0.11 µM h^{-1}) incubations (Gardner unpubl. data), and were about 3 times the rate estimated from the net change in NH_4^+ measured in the water column during the same period (0.03 µM h^{-1}). This suggested that the absence of light and use of net changes in NH_4^+ did not grossly underestimate the regeneration of NH_4^+ in the water column. The presence of light has been reported to increase rates of remineralization in systems with a greater proportion of phytoplankton production (Gardner et al. 1996).

Water column fluxes of NO_3^- + NO_2^- were almost always undetectable, except in June 1997, when samples were analyzed using chemiluminescence detection (Table 5). The more sensitive and precise chemiluminescence method served to verify that the NO_3^- +

Table 4. Average water column estimates of respiration (R), gross primary production (GPP), bacterioplankton production (BP), bacterioplankton growth efficiency (BGE), phytoplankton nitrogen demand (Phyto. N demand) based on C:N = 6.7, and bacterioplankton N demand (Bacterio. N demand) based on C:N = 4.3, ammonium (NH_4^+) regeneration, and molar C:N radio of dissolved organic matter (DOM) remineralized. All rates are in units of mmol C m^{-2} d^{-1} or mmol N m^{-2} d^{-1}. Errors are reported as ±1 SD

Month	R	GPP	BP	BGE (%)	Phyto. N demand	Bacterio. N demand	NH_4^+ regeneration	C:N of DOM remineralized
June	27 ± 2	3 ± 2	6 ± 0.7	19	<0.01	1.20	0.33 ± 0.06	81 ± 0.2
July	14 ± 6	0.4 ± 3	6 ± 0.4	30	<0.01	1.08	0.55 ± 0.17	26 ± 0.7
September	9 ± 1	3 ± 1	6 ± 1.9	38	0.10	1.35	0.65 ± 0.10	14 ± 0.2
November	7 ± 2	1 ± 1	2 ± 1.0	21	0.04	0.45	0.12 ± 0.07	55 ± 0.6
March	17 ± 7	9 ± 3	9 ± 1.6	36	0.35	2.11	0.65 ± 0.46	26 ± 0.8
June	15 ± 3	6 ± 2	6 ± 2.2	28	0.70	1.37	0.28 ± 0.13	54 ± 0.5

Table 5. Water column and benthic net nutrient fluxes (μmol N or P m^{-2} d^{-1}) measured in light and dark incubations. Daily rates for light and dark incubations were calculated from the number of hours of daylight or night, respectively. All rates are reported as mean (n ≥ 3) ± 1 SD. –: not detectable, na: not available due to contamination

Date	NH_4^+		$NO_3^- + NO_2^-$		SRP	
	Light	Dark	Light	Dark	Light	Dark
Water column						
12–13 Jun 1996	–99 ± 382	182 ± 35	–	–	–	–
23–24 Jun 1996	–	314 ± 102	–	–	–	–
10–11 Sep 1996	–145 ± 56	421 ± 60	–	–	–	–
6–7 Nov 1996	–45 ± 40	45 ± 32	–	–	–	–
8–9 Mar 1997	–114 ± 111	643 ± 619	–	–	–116 ± 0	101 ± 155
24–25 Jun 1997	76 ± 41	277 ± 130	9 ± 10	5 ± 4	–	–
Benthos						
13 Jun 1996	253 ± 136	na	–	–	–	–
25 Jul 1996	187 ± 0.2	–107 ± 255	–	–	–	–
12 Sep 1996	310 ± 327	28 ± 333	–	–	–	76 ± 77
5 Nov 1996	112 ± 233	296 ± 213	–	–	–	–
8 Mar 1997	363 ± 293	–228 ± 101	–	–	–	–
24 Jun 1997	123 ± 220	306 ± 295	–1 ± 9	6 ± 23	–	–

NO_2^- fluxes were small and variable (9 ± 5 μmol N m^{-2} d^{-1}). Water column fluxes of SRP were usually below detection, except in March, when fluxes in the water column were –116 and 101 μmol N m^{-2} d^{-1} in the light and dark, respectively (Table 5).

Net benthic NH_4^+ fluxes were always positive in the light and ranged from 112 to 363 μmol N m^{-2} d^{-1} (Table 5, Fig. 3). Net fluxes in the dark were more variable and ranged from –228 to 306 μmol N m^{-2} d^{-1}. The large standard deviation was in part a result of the major differences in fluxes between vegetated and unvegetated sites. The net flux of NH_4^+ in the light was usually much lower in the unvegetated versus the vegetated site (Fig. 4). The magnitude of the benthic release of NH_4^+ was often lower than NH_4^+ regeneration in the water column (Fig. 5). The NH_4^+ released from the seagrass-dominated sediments on 25 June 1997 (a clear day) was more than double the flux measured on the previous day when light levels were much lower (Table 6). The net fluxes of both $NO_3^- + NO_2^-$ and SRP were almost always undetectable. The samples

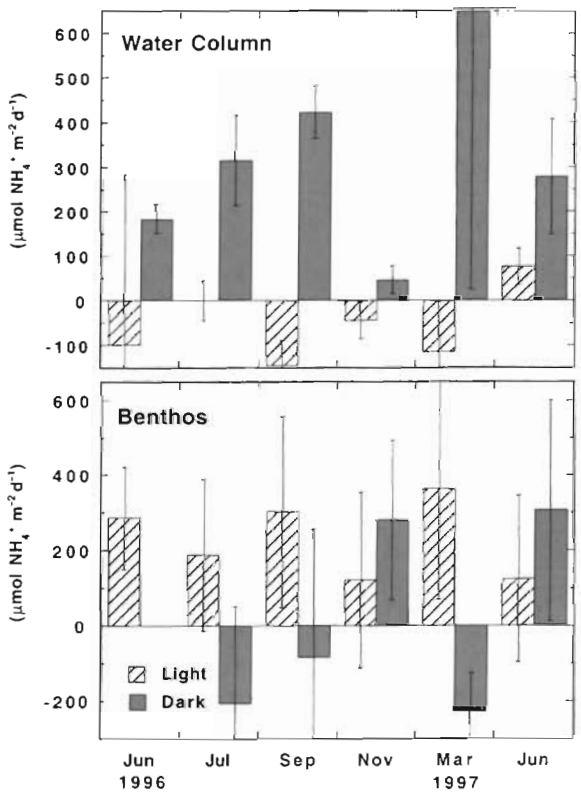

Fig. 3. Average ammonium (NH_4^+) fluxes in the water column (n ≥ 3) and benthos (n = 4) measured in light and dark incubations. Rates are reported as daily rates based on the number of hours of saturating PAR light (for seagrasses) and the number of hours below saturation for light and dark rates, respectively. Error bars represent ±1 SD

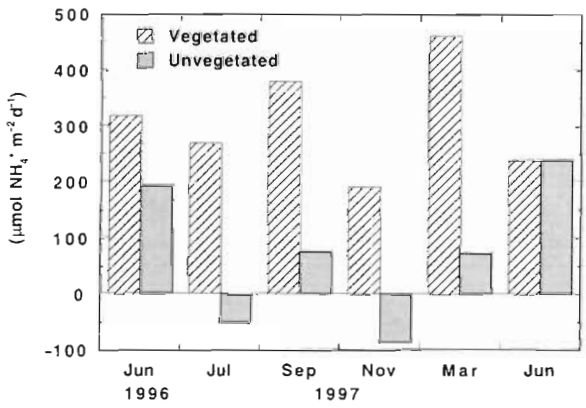

Fig. 4. Benthic ammonium (NH_4^+) fluxes measured in the light from vegetated and unvegetated sediments

Table 6. Total underwater PAR irradiance, benthic net primary production (NPP), dissolved organic carbon (DOC) and ammonium (NH_4^+) fluxes measured in the light for seagrass-dominated sediments on 24 June and 25 June 1997. Benthic rates are reported as the mean (n = 4) ±1 SD

Date	PAR[a] (E m^{-2} d^{-1})	NPP[b] (mmol C m^{-2} d^{-1})	DOC flux[b] (mmol C m^{-2} d^{-1})	NH_4^+ flux (µmol C m^{-2} d^{-1})
24 Jun 1997	14	7.7 ± 1.5	1142 ± 219	2 ± 9
25 Jun 1997	36	15.6 ± 2.4	2260 ± 1298	21 ± 26

[a]K. Dunton (unpubl. data); [b]Ziegler & Benner (1999)

collected in June and analyzed for $NO_3^- + NO_2^-$ using chemiluminescence detection verified that, in fact, the benthic fluxes of $NO_3^- + NO_2^-$ were extremely small and variable (Table 5).

DISCUSSION

Nutrient limitation of phytoplankton production

The close proximity of the seagrasses to high concentrations of nutrients and bacterial activity in the benthos can provide them with an advantage over phytoplankton where nutrients are in much lower concentrations (Wetzel 1975, Sandjensen & Borum 1991). In lower Laguna Madre, low inorganic nutrient concentrations and the release of DOC from the benthos fueling heterotrophic activity (Ziegler & Benner 1999) limit primary production in the water column. The degree to which phytoplankton are nutrient limited may depend upon the magnitude of allochthonous as well as the macrophytic input of DOC (del Giorgio & Peters 1994). Bacterioplankton have been found to outcompete phytoplankton for available DIN at times when nutrients are in very low concentrations and carbon substrate is readily available (Rhee 1972). In Laguna Madre, water column net uptake of NH_4^+ in the light was always small relative to net regeneration of NH_4^+ in the dark. Phytoplankton demand for N represented only about 0.8 to 34% of the total N demand in the water column, indicating that heterotrophic uptake was probably responsible for most of the utilization of NH_4^+ in the water column. Furthermore, potential NH_4^+ uptake rates, measured at the study site on 25 June 1997 using the ^{15}N isotope dilution approach, were essentially the same in light and dark incubations (W. Gardner unpubl. data).

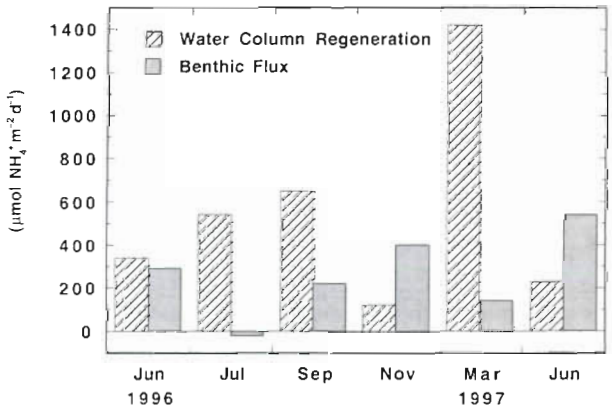

Fig. 5. A comparison of the rates of ammonium (NH_4^+) regeneration in the water column and total daily benthic flux of ammonium

Benthic source of water column nutrients

Release of nutrients from the benthos is often important for the growth of phytoplankton in the overlying water (Rowe et al. 1975). In various types of estuaries, benthic nutrient fluxes have been reported to range from −1 to 37 mmol NH_4^+ m^{-2} d^{-1}, −16 to 15 mmol $NO_3^- + NO_2^-$ m^{-2} d^{-1}, and −1 to 9 mmol SRP m^{-2} d^{-1} (Cowan et al. 1996 and references cited within). In most shallow estuarine systems studied, the availability of labile organic matter ultimately regulates benthic nutrient regeneration rates (Nixon 1981, Kemp et al. 1992). Net NH_4^+ regeneration rates estimated for temperate seagrass beds ranged from 7 to 106 mmol N m^{-2} d^{-1} for shallow and deeper sites during different times of the year, suggesting that remineralization in the benthos acts as a major source of nutrients (Dennison et al. 1987). Fluxes of nutrients in shallow tropical environments, such as mangroves, suggest that efficient bacterial activity is responsible for tight recycling of the regenerated nutrients within the sediments (Alongi 1994). The tight recycling of nutrients within the sediments of shallow aquatic ecosystems may prevent benthic remineralization from providing nutrients to the overlying water column.

In subtropical, southern Laguna Madre fluxes of NH_4^+, $NO_3^- + NO_2^-$, and SRP were all much smaller then those reported for many other estuaries, suggesting extremely efficient recycling of nutrients within the sediments in this ecosystem. NH_4^+ was the major form of inorganic N exchanged between the water column and the benthos. Rates of benthic NH_4^+ release were in the range of those calculated from measurements of NH_4^+ regeneration and seagrass assimilation for a *Zostera marina* bed in Alaska

(88 µmol N m^{-2} d^{-1}; Short 1983). However they were much lower than fluxes reported for Puttalam Lagoon (–14 to 7 mmol N m^{-2} d^{-1}), a more eutrophic tropical seagrass community in Sri Lanka that receives effluent from local shrimp farming facilities (Johnson & Johnstone 1995). The low nutrient fluxes and high respiration in the benthos (Ziegler & Benner 1999) indicated rapid and tight recycling of N and P within the sediments in Laguna Madre. NH_4^+ regeneration in the sediments of seagrass beds have been found to approximately equal utilization by seagrasses, suggesting that N is often tightly recycled within seagrass sediments (Boon et al. 1986) and not a major source of nutrients for the overlying water column. The relatively high nutrient fluxes in Puttalam Lagoon may be indicative of a perturbed seagrass community (Johnson & Johnstone 1995). The large inputs of nutrients and subsequent reduction in the productivity of the seagrasses in Puttalam Lagoon may have destroyed the tight recycling of nutrients evident and potentially important in southern Laguna Madre where allochthonous input is very small.

Differences in benthic fluxes measured in Laguna Madre on 24 and 25 June 1997 demonstrated that a link may exist between seagrass exudation of DOC and the benthic release of NH_4^+ (Table 6). This difference between 24 and 25 June was not observed in the unvegetated sediments, where fluxes of NH_4^+ were the same on the 2 consecutive days. Throughout the year, most of the release of NH_4^+ from the benthos occurred in the light and from the seagrass-dominated sediments, indicating that the source of NH_4^+ was often related to seagrass exudation and its subsequent remineralization. The greatest light-mediated benthic release of NH_4^+ occurred in March and coincided with the highest rate of benthic net primary production (Ziegler & Benner 1999) and seagrass tissue N content (Kaldy 1997). In November, when benthic net primary production was lowest (Ziegler & Benner 1999), the release of NH_4^+ did not appear to be related to any light-mediated process. There is some evidence that amino acids, released by the roots of seagrasses during active photosynthesis, are degraded by bacteria thereby generating NH_4^+ (Jørgensen et al. 1981, Wood & Hayasaka 1981, Smith et al. 1984). Porewater NH_4^+ concentrations have been observed to increase diurnally in the sediments of some seagrass beds, suggesting that remineralization of N in root exudates could be a major source of NH_4^+ (Moriarty et al. 1986, Blackburn et al. 1994, Stapel et al. 1997). Some proportion of this regenerated NH_4^+ in the benthos may be released into the overlying water column and could account for the small light-mediated release of NH_4^+ measured in Laguna Madre.

Water column remineralization of DOM as a source of nutrients

Remineralization of DOM was a major source of water column NH_4^+ in lower Laguna Madre. The magnitude of NH_4^+ regeneration in the water column was usually larger than the net release of NH_4^+ from the benthos. NH_4^+ regeneration in the water column was significantly correlated to the release of DOC from the benthos ($r^2 = 0.91$, $p < 0.05$, $n = 4$; Ziegler & Benner 1999), suggesting that benthic release of DOM was fueling the regeneration of NH_4^+ in the water column. The correlation between NH_4^+ regeneration in the water column and water temperature was not significant, indicating that temperature was not as important as the benthic supply of DOM in regulating NH_4^+ regeneration.

Phytoplankton N demand was always met by the sum of the NH_4^+ regeneration in the water column and the benthic release of NH_4^+. Bacterioplankton N demand generally exceeded the supply of NH_4^+ from water column regeneration and the benthic fluxes. The sum of water column NH_4^+ regeneration and benthic release of NH_4^+ represented 37 to 73% of bacterioplankton N demand, except in November, when it was about 117% of bacterioplankton N demand. This indicated that dissolved organic nitrogen was probably a major source of N for bacterioplankton during most of the year.

Relationship between the source of DOM and nutrient cycling

Changes in the availability and composition of benthic-derived DOM in Laguna Madre significantly influenced the cycling of N in the water column. Bacterioplankton growth efficiencies were significantly correlated to water column NH_4^+ regeneration, with the highest growth efficiencies occurring in March and September (Fig. 6). The C:N ratio of organic matter remineralized in the water column, calculated from water column respiration and NH_4^+ regeneration, varied temporally and ranged from 14 to 81 (Table 4). Because there is no net accumulation of bacterioplankton biomass in Laguna Madre during the day (Chin-Leo & Benner 1991) these C:N values are representative of the DOM utilized by heterotrophic bacterioplankton. The temporal variability in the C:N of the bioreactive DOM and bacterioplankton growth efficiency indicated that the DOM released from the benthos and utilized in the water column was seasonally variable in composition. The C:N of the organic matter remineralized in the water column was lowest in September and highest in June, indicating that bio-

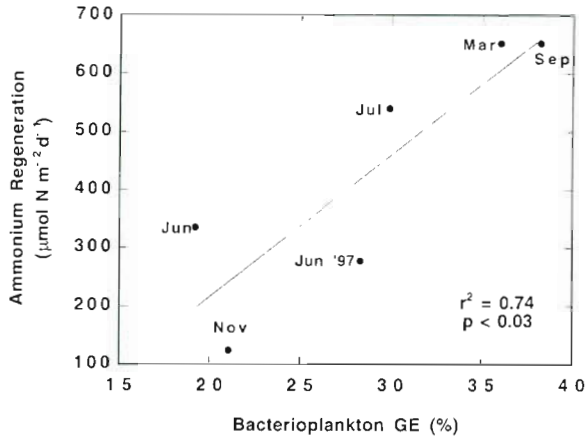

Fig. 6. Linear regression analysis of water column ammonium regeneration versus bacterioplankton growth efficiency (GE)

reactive DOM was enriched in N during the late summer and relatively depleted in N during early summer. Processes responsible for the release of DOM, namely exudation and leaching, were probably quite different during these times of the year. During June, benthic net primary production was relatively high and seagrass exudation would be expected to be greatest. Leaching, however, was probably more predominant in September, when seagrasses were beginning to senesce and benthic net primary production was low (Ziegler & Benner 1999).

Bacterial processes and N cycling have been found to be closely coupled to photosynthetic production of organic matter in other aquatic environments (Cole et al. 1982, 1988, Coffin et al. 1994). In Laguna Madre, release of DOM from the benthos was found to enhance regeneration of NH_4^+ in the water column. Studies have indicated that efficient regeneration of nutrients by bacterioplankton may only occur when available substrates have a C:N < 10 (Fenchel & Blackburn 1979, Billen 1984, Goldman et al. 1987). Therefore, bacterial regeneration of NH_4^+ in Laguna Madre may have been due to remineralization of a fraction of DOM with a C:N < 10 or a combination of C-rich and N-rich compounds. Previous studies in seagrass beds have demonstrated that DON constituted the majority of interstitial N (Boon et al. 1986) and the dominant form of N released from the sediments. Seasonal variations in bacterioplankton growth efficiencies and the C:N of bioreactive DOM in Laguna Madre suggest that the regeneration of NH_4^+ in the water column is directly linked to the chemical composition of the DOM released from the benthos.

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