BENTHIC MICROALGAL PRODUCTION AND NUTRIENT DYNAMICS IN INTERTIDAL SEDIMENTS

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Introduction

Intertidal sediments are a dynamic and important component of coastal environments that function as a reactive interface with the overlying water column at high tide and with the atmosphere at low tide. Intertidal sediments provide habitat for a variety of biota and support a plethora of biogeochemical processes which transform and redistribute nutrients and organic materials between different reservoirs. The biologically-mediated and abiotic processes that occur contemporaneously in sediments effectively regulate sediment-water column exchange of metabolic reactants and products. Because of the shallow nature of intertidal systems, the sediment surface receives ample light to support benthic photosynthesis even when sediments are submerged during high tide. Benthic primary production is a ubiquitous feature of tidal flats and creek banks around the world. The activity of benthic microalgae, in terms of oxygen production and nutrient uptake, influences the rates and magnitude of sediment metabolism. Benthic production influences whether sediments are net sources (recyclers) or sinks (consumers) of nutrients in coastal environments.

Benthic primary production has both direct and indirect effects on sediment biogeochemical cycling. Direct effects result from microalgal assimilation of nutrients and inorganic carbon into biomass, which reduces the flux from the sediment to the overlying water column. Indirect effects include: (1) increased O_2 availability which influences O_2-sensitive microbially-mediated processes (i. e. N_2 fixation and denitrification) as well as abiotically-mediated P cycling; (2) broadening or deepening of the aerobic zone which influences the degree of coupling between aerobic and anaerobic processes; and (3) altered sediment redox and pH gradients which impact authigenic mineral formation and stability, e. g. iron oxyhydroxide formation or dissolution, and drive changes in biogeochemical zonation because of thermodynamic constraints. Microbially-mediated processes are either dependent upon (e. g. aerobic respiration, nitrification) or sensitive to (e. g. denitrification, sulfate reduction) pore water O_2 concentration. By influencing the concentration and flux of O_2 through the sediment, benthic primary production can change the sediments from a site of net heterotrophy (organic C consumption) to one of net autotrophy (organic C production). In this study, we determined the distribution of benthic chlorophyll, measured benthic primary production and pore water oxygen microprofiles, and quantified sediment-water fluxes of nutrients and organic materials during laboratory incubations at several sites along the coast of Georgia and South Carolina (USA).

Study Sites

We quantified gross oxygenic photosynthesis rates and benthic fluxes at three sites in Georgia and two sites in South Carolina over two years (Fig. 1). The study sites in Georgia lie along the Satilla River and on Sapelo Island. The South Carolina study sites lie along the Okatee River. Sapelo Island is a protected area and there is little development on the island, and the area is the focus of the Georgia Coastal Ecosystems Long Term Ecological Research Program. Little anthropogenic nutrient loading impacts Sapelo Island, and it is considered a pristine coastal habitat. The study site on the Satilla River, Dover Bluff, is adjacent to a residential development, and nutrient input to the marsh and tidal creeks are elevated because of effluents derived from septic tanks located in the upland. The sites in South Carolina lie within the Okatee River estuary. The Okatee watershed is heavily developed (mainly a retirement residential complex), and is home to several golf courses. Our study sites were selected to bracket development and environmental regimes. All of our study sites are intertidal, and the average salinity ranges between 4 and 30‰. Whereas the Sapelo Island sites can be considered pristine, sites along the Satilla and Okatee estuaries receive elevated nutrient loads from adjacent developed watersheds.

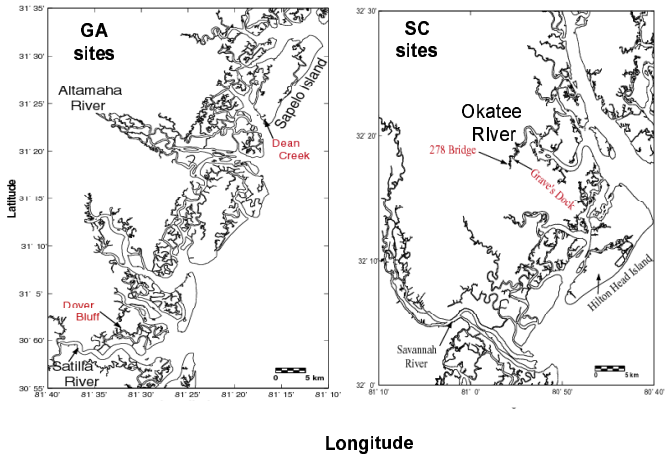

Fig. 1. Maps of study sites in coastal Georgia (GA) and South Carolina (SC).

Methods

Samples for the work described here were collected during winter and summer. Chlorophyll *a* samples were collected at 5 to 10 locations along the creek bank and from cores used in microelectrode studies. Cores for the determination of primary production rates (n=3 to 5; 5 cm deep) and flux (n=2 to 4; 20 cm deep) were collected and returned to the UGA laboratory for experimental incubations and physical analyses. Rates of gross oxygenic photosynthesis (GOP) were determined using the light-dark shift method. A Unisense® picoammeter, a fiber-optic full spectrum light source, an automated micromanipulator and a data system were used to determine GOP rates under average ambient daily *in situ* irradiance (in µmol photons m^{-2} s^{-1}). Integrated rates are presented in units of mmol O_2 m^{-2} h^{-1}. Pore water dissolved oxygen concentration profiles were obtained contemporaneously. GOP rates were standardized to sediment chlorophyll *a* concentration to obtain the chlorophyll-specific GOP rate (mmol O_2 (mg chl *a*)$^{-1}$ h^{-1}). Both GOP measurements and light and dark flux core incubations were carried out at the same irradiance. Three to five profiles for GOP and dissolved oxygen concentration were obtained for each core and data obtained for replicate cores were averaged for each site.

Flow-through core incubations were used to quantify fluxes of nutrients, dissolved gases, dissolved organics, and reduced constituents. Paired (n=2 each) light and dark cores were incubated at *in situ* temperatures and light conditions. Samples were collected every 12 hours for at least 72 hours; light and dark incubations allowed us to elucidate the impact of benthic primary production on benthic fluxes. After determining basic metabolic rates, selected flux cores (1 set each from Georgia and South Carolina) were used in $^{15}NO_3^-$ tracer studies to evaluate the fate of NO_3^- under experimental conditions. The added $^{15}NO_3^-$ was tracked into N_2 (to quantify

denitrification) and NH_4^+ (to quantify dissimilatory nitrate reduction to ammonium) pools using membrane inlet mass spectrometry and isotope ratio mass spectrometry methods, respectively.

Results and discussion

Rates of GOP and benthic chlorophyll distribution illustrated that intertidal sediments were very productive throughout the year. Oxygen penetration depths ranged between 0.9 to 3.5 mm, and GOP rates were highest between 0.2 and 0.5 mm. Chlorophyll concentration (30-200 mg m^{-2}) and GOP (8 to 50 mmol O_2 m^{-2} h^{-1}) were highest in spring at all sites (Fig. 2). In Georgia, highest average annual rates of GOP and chlorophyll *a*-specific GOP were observed at Dover Bluff, along the Satilla River. Dover Bluff sediments were reducing and enriched in inorganic and organic nutrients, possibly contributing to the high rates of benthic production observed there. In South Carolina, GOP rates were slightly lower than those observed in Georgia and the highest rates observed at Graves Dock. Microscopic observations of samples from all sites showed that sediments were inhabited largely by benthic diatoms whereas cyanobacteria were rare.

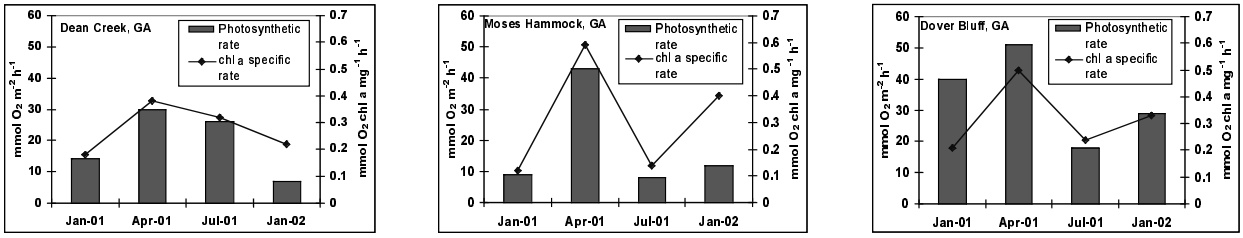

Fig. 2. Rates of GOP (left y-axis) and chlorophyll *a*-specific GOP (right y-axis) during winter, spring and summer for Dean Creek, Moses Hammock, and Dover Bluff (left to right) sites.

The activity and distribution of benthic phototrophs exerted a strong influence on sediment-water nutrient exchange. Inorganic nutrients, including dissolved inorganic nitrogen, DIN, dissolved inorganic phosphorus, DIP, and dissolved silicate, DSi, were depleted from the overlying water column in cores incubated under fluctuating light-dark conditions. Though we observed day-night variability in dissolved oxygen and inorganic carbon concentrations, nutrients did not accumulate in the overlying water during the dark part of the day-night cycle. Fig. 3 provides an example of the temporal variability in water column nutrient concentrations during a summer incubation (September 2002) of sediments from the Dover Bluff site. These data are from triplicate cores incubated under a natural day-night cycle. At the initiation of the flux experiments, both NO_3^- and NH_4^+ were rapidly depleted from the overlying water column; DIP was also taken up from the water column (Fig. 3, days 1 to 3). Between days 3 and 6, sampling was infrequent because we were allowing the water column in continuously dark-incubated cores to go anoxic. Around day 6.5, the dark cores were completely anoxic, and the overlying water of all cores was amended with $^{15}NO_3^-$ tracer (final concentration ~100 µM). Following $^{15}NO_3^-$ addition, light-dark incubated sediments illustrated immediate uptake of NO_3^- and PO_4^{3-}. After approximately 24 hours, $H_2SiO_4^{2-}$ uptake from the water column increased rapidly, drawing water column $H_2SiO_4^{2-}$ concentrations down to 20 µM (from about 100 µM) over a 2-day period. The temporal lag between DIN/DIP uptake and DSi uptake may suggest that the benthic diatom community was originally DIN, and to some extent DIP, limited. When the overlying water column was enriched in NO_3^-, the benthic diatoms became DSi limited; to overcome DSi limitation, benthic phototrophs increased DSi uptake from the water column. These data illustrate that benthic microalgae can be significant sink for nutrients in the overlying water column, as well as for nutrients regenerated within the sediments (see below).

Three replicate cores were incubated in parallel to the cores described above, but these cores were incubated under continuous darkness. Nutrient fluxes in these “dark” cores are shown in Fig. 4. Nutrients (DIN, DIP and DSi) were low as long as the water column was oxygenated, illustrating continued uptake by benthic microalgae even without exposure to sunlight. Nutrient concentrations in the overlying water column did not increase significantly until water column oxygen concentrations reached zero (data not shown; but this occurred at day 2.5 in Fig. 4). At this time, fluxes increased

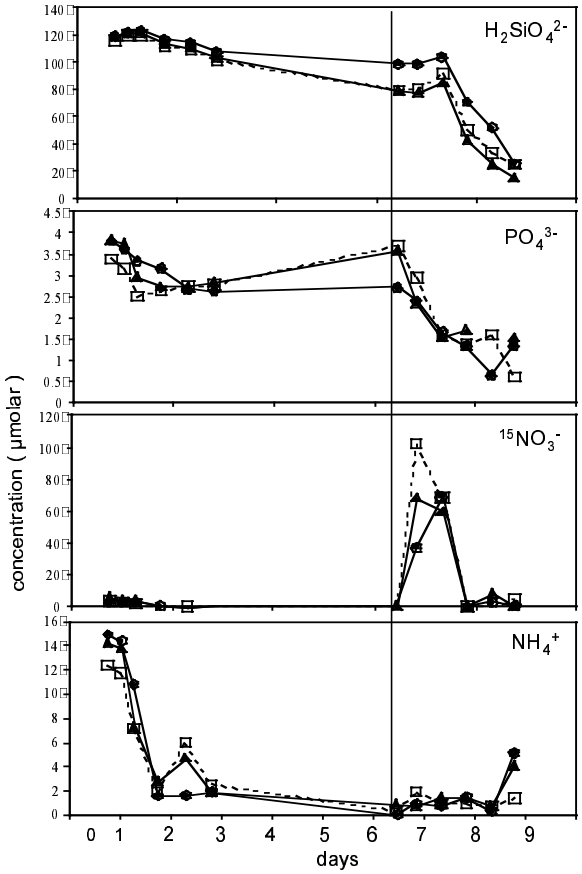

Fig. 3. Nutrient uptake during light-dark core incubations before and after $^{15}NO_3^-$ addition (horizontal line, day 6.5). Data from replicate (n = 3) cores are shown.

significantly, and water column NH_4^+ concentrations reached 100 µM (about 100X higher than observed in light-dark cores), PO_4^{3-} concentrations reached 70 µM (about 17X higher than observed in light-dark cores), and $H_2SiO_4^{2-}$ concentrations reached 225 µM (about 2X higher than

observed in light-dark cores). The large increase in NH_4^+ fluxes, relative to DIP and DSi fluxes may reflect the cessation of coupled nitrification-denitrification (which requires O_2) in addition to reductions in uptake by benthic primary production. Both of these processes would impact NH_4^+ fluxes and could explain why NH_4^+ fluxes increased more so than PO_4^{3-} and $H_2SiO_4^{2-}$ fluxes. Generally speaking, during flux core incubations, fluxes of PO_4^{3-}, Fe^{2+}, and NO_3^-, in particular, exhibited a strong correlation to water column O_2 concentration.

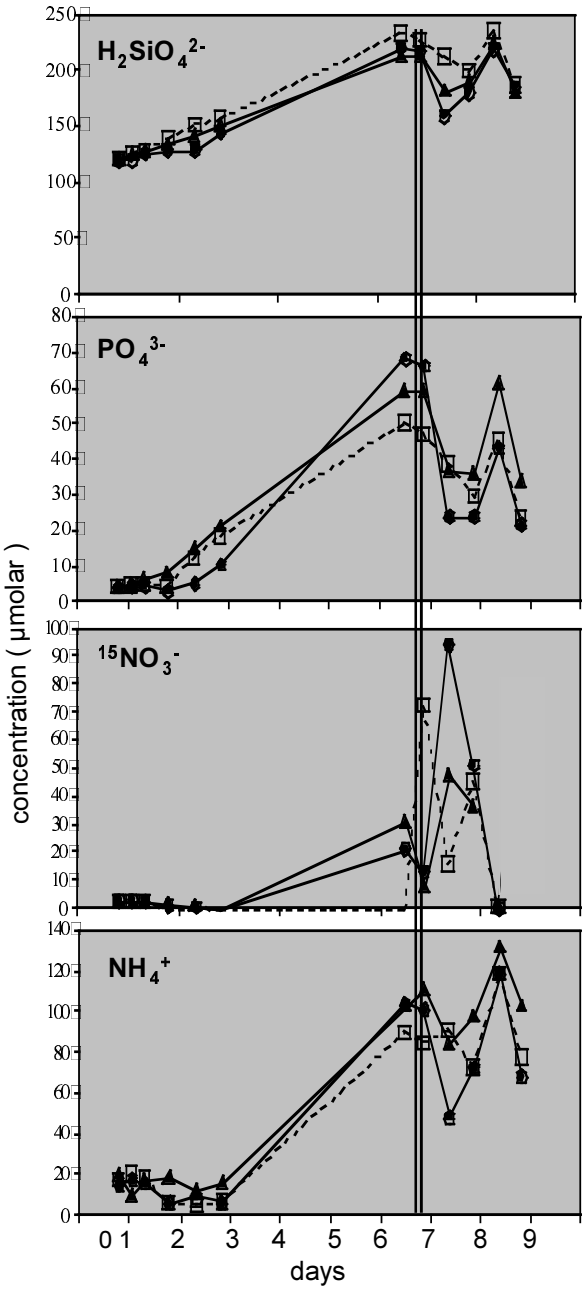

Fig. 4. Nutrient uptake during continuously dark incubations before and after $^{15}NO_3^-$ addition (double horizontal line, day 6.5). Data from replicate (n=3) cores are shown.

To examine specific nitrogen cycling processes in detail, we carried out $^{15}NO_3^-$ tracer experiments during winter and summer. We observed high rates of denitrification at all sites and some sites exhibited significant rates of N_2O production. Fluxes of N_2 and N_2O showed that high denitrification rates (up to 28 mmol m^{-2} d^{-1}) were correlated with both photosynthetic activity and redox (oxic *versus* anoxic) conditions. As discussed above, during light-dark incubations, both denitrification and benthic primary production rates were limited by nitrate availability. Following the addition of $^{15}NO_3^-$, denitrification rates increased dramatically. Benthic diatoms also appeared to be limited by nitrogen availability as benthic primary production rates increased following $^{15}NO_3^-$ addition (Fig. 3) and sediment fluxes of DSi changed direction: sediments were a source of silicate to the water column prior to $^{15}NO_3^-$ addition, but were a large sink of water column silicate (uptake up to 8 mmol m^{-2} d^{-1}) following $^{15}NO_3^-$ amendment. Denitrification rates in cores incubated under a fluctuating light-dark regime were lower than rates in continuously dark incubations. Denitrifying bacteria in light incubations may have been inhibited by increased oxygen concentrations or out-competed for NO_3^- by benthic phototrophs. Benthic microalgal production of oxygen can stimulate denitrification *via* increasing the rates of nitrification, an important NO_3^- source for denitrifying bacteria. Under nitrogen-replete conditions, it is likely that stimulation of coupled nitrification-denitrification results from benthic primary production. However, under nitrogen-limited conditions, benthic microalgae probably compete directly with denitrifiers for DIN and may thereby limit denitrification rates.

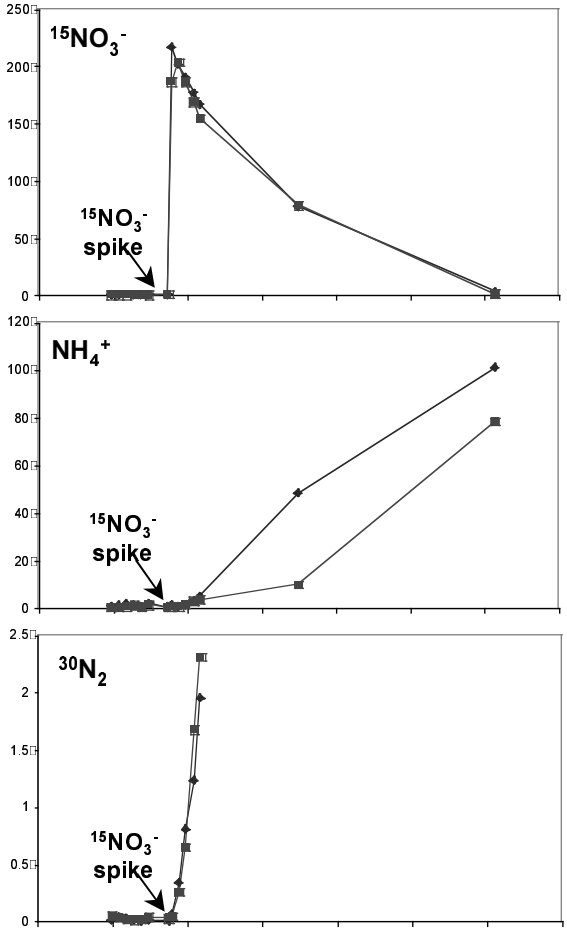

Fig. 5. ^{15}N distribution in NO_3^-, NH_4^+, and N_2 before and after $^{15}NO_3^-$ addition (noted by arrows). Data from replicate (n=2) cores are shown.

In dark incubations, $^{15}NO_3^-$ was utilized both by denitrifiers (DNF) and by microorganisms carrying out dissimilatory NO_3^- reduction to NH_4^+ (DNRA). The relative importance of DNF versus DNRA varied between sites. Fig. 5 shows the distribution of ^{15}N in the three major dissolved inorganic N pools in the overlying water column (winter incubation, Graves Dock, Okatee River, SC).

Following $^{15}NO_3^-$ addition, immediate increases in production and efflux of NH_4^+ (and in $^{15}NH^{4+}$, see Table 1) and $^{30}N_2$ were observed. At Graves Dock, between 39-50% of the added $^{15}NO_3^-$ ended up in the ammonium pool via DNRA whereas about 30% was denitrified. At Dover Bluff, in contrast, about 65% of the added $^{15}NO_3^-$ was denitrified

whereas less than 1% was processed via DNRA. To verify that the NH_4^+ fluxing from sediments was derived from the added $^{15}NO_3^-$, we determined the atom percent enrichment of ^{15}N in the NH_4^+ following the August 2002 $^{15}NO_3^-$ tracer incubation (Table 1).

Table 1. Production of $^{15}NH_4^+$ following $^{15}NO_3^-$ addition to the overlying water column in dark-incubated cores from Graves Dock and Dover Bluff.

Site	Treatment	Atom% ^{15}N in NH_4^+
Graves Dock	Dark-1	10.9
	Dark-2	20.5
	Dark-3	14.8
		Average: 15.4 ± 4.8
Dover Bluff	Dark-1	10
	Dark-2	4.8
	Dark-3	5.5
		Average: 6.8 ± 2.9

The atom percent enrichment in dissolved NH_4^+ was two times higher at Graves Dock than at Dover Bluff, supporting the idea that DNRA is more important at this site. These results corroborate the conclusions based on changes in DIN fluxes observed during the winter tracer incubations, mainly that site-specific differences in the importance of DNF versus DNRA exist. Increases in the relative percentage of DNRA were positively correlated with sediment H_2S inventories (higher at Grave's Dock than at Dover Bluff), suggesting that sediment H_2S concentrations may alter the importance of DNF versus DNRA. Interestingly, we observed higher rates of benthic photosynthesis at Dover Bluff and believe this may help establish and maintain conditions more favourable for DNF: higher GOP rates could support higher rates of H_2S oxidation, which would favor DNF over DNRA.

Benthic phototrophs are clearly an important component of tidal flat ecosystems. Our results demonstrate the dynamic nature of materials fluxes on seasonal and daily (diel) scales and underscore the importance of benthic phototrophs in influencing benthic nutrient exchange in intertidal sediments. Benthic photosynthesis may also alter the relative importance of various N cycling processes, such as DNF and DNRA, by altering redox gradients and competing with nitrogen cycling bacteria for available substrates.

Acknowledgements

We thank the National Science Foundation's Long-Term Ecological Research program and by the National Oceanic and Atmospheric Administration Sea Grant programs in Georgia and South Carolina for funding our work; Wade Sheldon for assistance with Fig. 1; and Matthew Erickson for assistance with flux core experiments.

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