NOTE

Sediment denitrification in the Gulf of Mexico zone of hypoxia

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ABSTRACT: The largest zone of anthropogenic bottom water hypoxia in the Western Hemisphere occurs seasonally in the northern Gulf of Mexico between the Mississippi River delta and the coast of eastern Texas. This zone of hypoxia reaches its greatest extent in the summer months and is a consequence of seasonal stratification of the water column combined with the decomposition of organic matter derived from accelerated rates of primary production. This enhanced productivity is driven primarily by the input of inorganic nitrogen from the Mississippi River. There are 3 likely sinks for fixed nitrogen within this zone of hypoxia: sequestration in the sediment, dispersion and dilution into the Gulf of Mexico, and denitrification. We assessed potential denitrification rates at 7 stations in the zone of hypoxia during the summer of 1999. Those data are compared with bottom water nitrate, ammonium and dissolved oxygen (DO) concentrations. No denitrification was observed in the water column. Denitrification potential rates in the surface sediments were unexpectedly low and ranged between 39.8 and 108.1 µmol m^{-2} h^{-1}. The highest rates were observed at stations with bottom water DO concentrations between 1 and 3 mg l^{-1}. Denitrification activity was significantly lower at stations where DO was lower than 1 mg l^{-1} or higher than 3 mg l^{-1}. Nutrient data for these stations demonstrate that as anoxia is approached, the dominant species of nitrogen shifts from nitrate to ammonium. The shift in nitrogen species suggests competition between microbial populations in the sediment community. The lower denitrification rates at stations with bottom water DO <1 mg l^{-1} may be due to nitrate limitation or an increase in the competitive advantage of microorganisms capable of dissimilatory nitrate reduction to ammonium (DNRA). Suppression of denitrification at low DO by any mechanism will increase the residence time of bioavailable nitrogen. This trend could act as a positive feedback mechanism in the formation of hypoxic bottom waters.

KEY WORDS: Sediment · Denitrification · Gulf of Mexico · Hypoxia

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The waters of the Mississippi River plume are highly productive with annual carbon fixation estimated to be near or slightly over 320 g C m^{-2} yr^{-1} (Lohrenz et al. 1990). This high productivity is directly proportional to river-borne dissolved inorganic nutrient inputs (Justić et al. 1993, Lohrenz et al. 1997, 1999). Nutrient loading has increased substantially over the last half century in the Mississippi River plume (Turner & Rabalais 1991, Goolsby et al. 1999). In a parallel time sequence, the accumulation of marine-origin phytoplankton carbon (Eadie et al. 1994), and in particular diatoms (Turner & Rabalais 1994), as evidenced by paleoindicators from sediments beneath the Mississippi River plume, have also increased and have done so in direct proportion to the increased nutrient loads.

Nitrate discharge from the river and primary production are both at a maximum during the late spring to early summer (Lohrenz et al. 1997) and coincide with the period of maximum stratification of the water column (Dinnel & Wiseman 1985, Cochrane & Kelly 1986). This nutrient loading combined with seasonal stratification of the water column results in the formation of the largest zone of anthropogenic bottom water hypoxia (<2 mg O_2 l^{-1}) in the Western Hemisphere. Bottom water and benthic respiration rates on the Louisiana continental shelf are high enough to deplete the bottom water of oxygen within 1 mo (Dortch et al. 1994, Amon & Benner 1998). This hypoxic zone can exist from April to October.

There have been several investigations into the microbial ecology of the Mississippi River plume. However, these have focused largely on the surface waters. Chin-Leo & Benner (1992) and Cotner & Gardner (1993) both investigated bacterial production in the surface waters and found that production was highest at intermediate salinities. Pakulski et al. (1995) likewise found high rates of carbon remineralization at salinities of 18

and 27 PSU and proposed that nitrification could account for 20 to >50% of community oxygen demand. Cotner & Gardner (1993) found that ammonium regeneration rates in the plume were an order of magnitude higher during the summer than in the winter and concluded that dissolved amino acids are the likely substrate for this regeneration.

The microbial ecology of the sediments and hypoxic bottom water has not been as well documented as surface processes and investigations of anaerobic microbial processes on the Louisiana Continental Shelf are particularly lacking. The fluxes of organic matter combined with low dissolved oxygen (DO) and high nitrate concentrations suggest that anaerobic processes and denitrification rates, in particular, should be quite high in the Louisiana Shelf zone of hypoxia. Gardner et al. (1993) has been the only study to report denitrification rates for this area. They estimated denitrification rates at 4 stations using benthic flux chambers on the Louisiana Shelf in July of 1990 and reported rates between 21.0 and 69.6 μg atom N m^{-2} h^{-1}.

Denitrification is a form of anaerobic microbial respiration in which nitrate or nitrite is reduced to nitrous oxide or dinitrogen. It is a major sink for bioavailable nitrogen. All known denitrifying bacteria are facultative anaerobes, i.e. they are capable of using either the nitrogen oxides or oxygen in respiration. These bacteria only begin to denitrify when the nitrogen oxides are present and oxygen concentration is low (Zumft 1997). However, low oxygen concentrations can also limit denitrification by inhibiting nitrification — the oxidation of ammonium to nitrate — thus, increasing ammonium regeneration. Tiedje et al. (1982) also proposed that very low oxygen concentrations could favor dissimilatory nitrate reduction to ammonia (DNRA) over denitrification. DNRA is another form of anaerobic respiration in which nitrate or nitrite is reduced completely to ammonium.

The input of fixed nitrogen is one of the defining characteristics of the ecology of the Louisiana Shelf. Understanding the local dynamics of denitrification is critical to developing a more complete understanding of this system. In this paper, we report potential sediment denitrification rates measured at 7 different stations on the Louisiana Shelf during the peak of the hypoxic season in 1999. These data are compared with contemporaneous water quality data. The role of DO and the concentration of nitrogenous species in regulating denitrification are examined, and the relationship between various pathways of nitrate reduction is discussed. Potential denitrification rates in the Louisiana Shelf zone of hypoxia are compared with reported rates from other systems.

MATERIALS AND METHODS

Study site and hydrographic data. In July 1999, the zone of seasonal bottom water hypoxia in the northern Gulf of Mexico was surveyed on a transect cruise aboard the RV 'Pelican'. The cruise covered an area of more than 20 000 km^2 with 83 stations along 13 transects between 29° 08' N, 89° 28' W and 29° 17' N, 92° 48' W (Fig. 1). Hydrographic data and water samples were collected at each station. Hydrographic data were obtained using a SeaBird 911+ CTD system and a Hydrolab Surveyor 3. Data collected included temperature, pH, DO, conductivity, salinity, fluorescence, % light transmission and depth. Oxygen sensor end point calibrations were made prior to the cruise and Winkler titrations were conducted aboard ship to confirm the accuracy of instrumental values for DO.
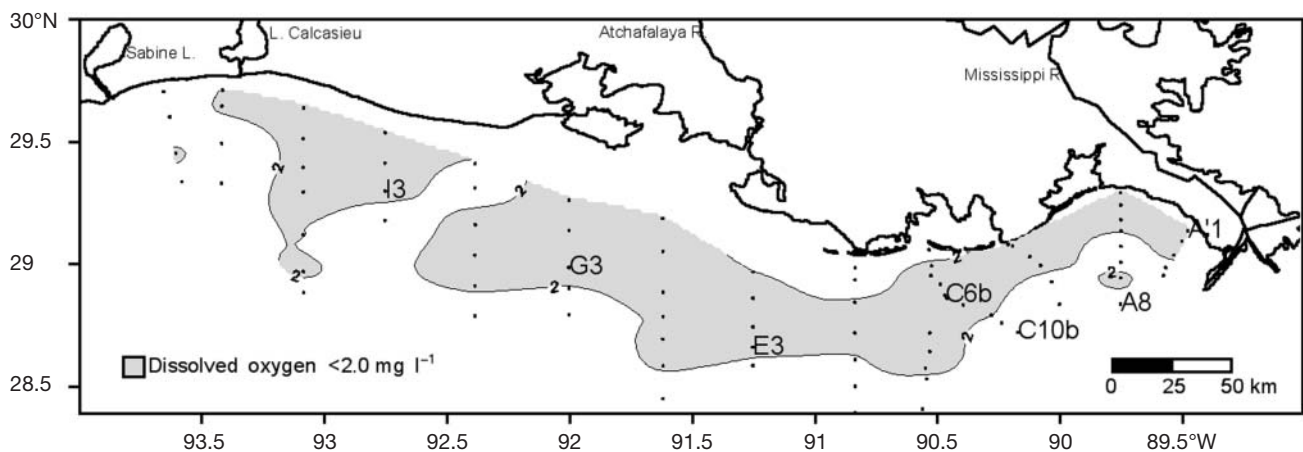

Fig. 1. Location of sample stations and the extent of hypoxia in the summer of 1999. Number-letter combinations designate the stations where sediment cores were collected

Nutrient analysis. Water samples for chlorophyll (chl *a*), nutrients, oxygen and salinity analyses were collected from the surface, midwater and bottom water. Surface water samples were collected by bucket, and midwater and bottom water samples were collected with 5 l Niskin bottles. Water samples for nutrient analysis were frozen on board at –20°C for later analysis at Louisiana State University. Nitrogen species were analyzed according to methods described in EPA Publication EPA 600/4-79-020 (1979), Method 350.1 for ammonia-N and Method 353.2 for nitrate/nitrite-N.

Denitrification potential assays. Denitrification potential was assessed in the surface water, bottom water and sediments. Intact sediment cores were collected at 7 different stations (Fig. 1) using a box-coring device. The denitrification potential was assessed using a modification of the acetylene inhibition technique described by Sorensen (1978). Sediment samples were collected using a box-coring device. The box core was subcored using 5 cm diameter butyrate cores. Maintaining a layer of water over the sediment surface reduced oxygenation of the sediment. The top 1 cm of sediment was incubated anaerobically in 160 ml serum bottles in a medium containing 50 ml of aged, filtered seawater amended to 100 µM KNO_3^- and a head space containing 90% UZ grade (ultra high purity) N_2 (g) and 10% C_2H_2 (g). Water samples from above and below the pycnocline were collected in Niskin bottles. Water samples of 50 ml were incubated anaerobically in 160 ml serum bottles with a head space space containing 90% UZ grade N_2 (g) and 10% C_2H_2 (g). After incubation, samples of the headspace gas from the water and the sediment incubations were transferred to 10 ml Vacutainers™. The gas samples were refrigerated and returned to Florida State University for analysis. The gas samples were assayed for N_2O concentration using a Shimadzu GC-8A gas chromatograph (Porpak Q column) equipped with an electron capture detector (350°C). The linearity of N_2O production over varying incubation periods was confirmed in 2 time course experiments conducted on board with incubation times of 1, 2 and 4 h.

RESULTS

The areal extent of the Gulf of Mexico zone of hypoxia in the summer of 1999 was over 20 000 km^2. This was the largest recorded area of bottom water hypoxia in this region since regular cruises began charting this phenomenon in 1985.

Bottom water dissolved inorganic nitrogen (DIN) (nitrate + nitrite + ammonium) concentrations ranged between 11.5 and 41.0 µM at all stations where sediment cores were collected (Table 1). The species composition of this nitrogen pool was closely correlated with DO concentration. As oxygen concentrations increased, the percentage of DIN in higher oxidation states increased. The lowest levels of total DIN occurred at stations where DO was between 1 and 3 mg l^{-1}.

Nitrate concentrations ranged between 1.9 and 26.8 µM with peak concentrations at stations with a DO of 0.4 mg l^{-1} or greater. Ammonium concentrations displayed the greatest range, with concentrations between 0.1 and 37.4 µM. Ammonium concentrations were significantly higher at stations where DO was below 0.4 mg l^{-1} (Fig. 2).

No nitrous oxide production was observed in any of the water samples. Denitrification potential rates in the sediment ranged between 39.7 and 108.1 µmol N m^{-2} h^{-1} (Table 1). The highest rates were observed at stations where the bottom water DO concentration was between 1 and 3 mg l^{-1} (Fig. 2). The lowest rates were observed at Stn C10b where the DO concentration was 5.18 mg l^{-1}. Denitrification rates at the stations where DO was below 1 mg l^{-1} were approximately $^1/_2$ the rates found at stations where the DO was between 1 and 3 mg l^{-1}. This decline in denitrification rates at low DO was unexpected.

The time course assays showed that N_2O production in our experiments was linear (R^2 = 0.93) over the duration of our incubations (data not shown). Thus, we feel confident in inferring denitrification rates from endpoint incubations. Variability among replicate cores was slight at most stations, with an average coefficient of variation of 0.18.

Table 1. Station location, bottom water concentrations for dissolved oxygen (DO), salinity, nitrate, nitrite and ammonium, and surface sediment denitrification potential (µmol N m^{-2} h^{-1}) ± SD, from 7 stations on the Louisiana Continental Shelf in July 1999

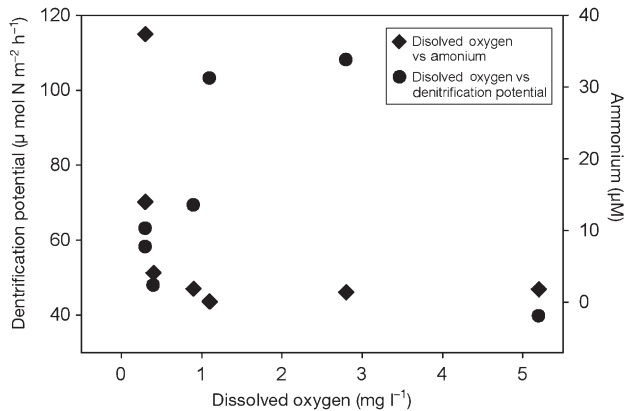| Stn	Location	DO (mg l^{-1})	Salinity (PSU)	NO$_3^-$ (µM)	NO$_2^-$ (µM)	NH$_4^+$ (µM)	Denitrification (±SD) (µmol N m^{-2} h^{-1})
A'1	29.1° N, 89.3° W	0.3	32.3	2.9	0.7	37.4	58.2 (±9.5)
A8	28.8° N, 89.75° W	2.8	36.2	9.3	1.8	1.4	108.1 (±13.8)
C6b	28.85° N, 90.3° W	0.4	35.2	10.9	6.2	4.1	47.9 (±6.9)
C10b	28.75° N, 90.2° W	5.2	36.1	26.8	1.2	1.8	39.8 (±14.5)
E3	28.75° N, 91.25° W	1.6	35.2	10.7	0.7	0.1	103.3 (±14.5)
G3	28.6° N, 92.0° W	0.9	34.7	13.1	2.4	1.9	69.3 (±12.6)
I3	29.0° N, 92.75° W	0.3	34.3	1.9	0.6	14.0	63.1 (±9.6)

Fig. 2. Bottom water ammonium concentration (µM) and surface sediment denitrification potential (µmol N m^{-2} h^{-1}) as a function of bottom water dissolved oxygen concentration (mg l^{-1}). There is a pronounced accumulation of ammonium and decrease in denitrification potential as anoxic conditions are approached

DISCUSSION

The potential denitrification rates we measured are consistent with the earlier estimates made by Gardner et al. (1993). These rates are at the low end of denitrification rates reported from other systems (Herbert 1999). This was unexpected because the current paradigm for denitrification suggests that the conditions in the hypoxic zone (high carbon, low oxygen and high nitrate) should be ideal for denitrification. However, reported denitrification rates show a wide range of values with the highest rates found in fresh water environments or in shallow nearshore marine waters (Herbert 1999). Additionally, *in situ* denitrification rates could be somewhat lower because our method measures the maximum potential denitrification capability of the sediment. Such problems are typical of denitrification measurements because there is no consensus method for measuring this process (Seitzinger et al. 1993). Our data presented here are a reasonable estimate of the enzymatic potential for denitrification in the microbial community.

There are several factors that might explain why denitrification potential would be lower than expected in the hypoxic zone. Reduced metabolic activity in the hypoxic zone has also been found in other studies (Dortch et al. 1994). They found that aerobic respiration rates for both the bottom water and the benthos were lower than rates compiled for other estuaries. There may also be factors that act to specifically restrict denitrification on the Louisiana Shelf. Other more obligatory anaerobic organisms, such as sulfate reducers, may dominate this system. Indeed, sulfate reduction has been shown to play a major role in the

bottom water biogeochemistry during summer hypoxia in the Chesapeake Bay (Kemp et al. 1990). Additionally, hydrogen sulfide, the product of sulfate reduction, is a respiratory poison (Wang & Chapman 1999) and has been shown to specifically inhibit nitrification, the oxidation of ammonium to nitrate (Joye & Hollibaugh 1995). The DNRA may also be competing with denitrification for nitrate (Tiedje 1988). However, ammonium concentrations at our sampling stations and thermodynamic considerations suggest that DNRA does not occur until DO approaches anoxia (Tiedje 1982).

In addition to finding that potential denitrification rates were lower than expected throughout the hypoxic zone, there were significant differences in denitrification potential among the 7 stations sampled. It is unclear why denitrification potential would be lower at stations where DO concentrations were below 1 mg l^{-1} than at stations where DO was higher. It is possible that the low oxygen concentration limits nitrification and thus, indirectly limits denitrification. However, limitation of denitrification by this path is likely to be restricted to environments with little to no ambient nitrate (Sloth et al. 1995). The nitrate concentration at Stn C6b, a station with one of the lowest denitrification rates in our study, was 10.9 µM, well above the nitrate concentrations reported to limit denitrification by Sloth et al. (1995). Thus, nitrate limitation does not seem to be a complete explanation for the observed changes in denitrification potential. Lower denitrification rates at stations with DO <1 mg l^{-1} could be the result of an increase in the competitive advantage of DNRA (Tiedje et al. 1982). DNRA becomes favored as the concentration of electron acceptors becomes increasingly limited because DNRA accommodates more electrons per molecule of nitrate (8) than denitrification (5). The significant increase in ammonium concentrations at stations with nearly anoxic conditions supports the proposition that DNRA could be a significant process at these stations. Additional investigations are necessary to assess the significance of DNRA in this region.

It is now recognized that impacted coastal marine ecosystems are characterized by increases in the numbers and activities of microbial populations, the so-called 'microbialization of the coastal ocean' (Jackson et al. 2001). In our study, we demonstrate that the microbial communities in impacted systems do not only increase in numbers and activity, but also increase in the complex interactions between microbial populations, with unexpected consequences. In the Louisiana shelf hypoxic zone, competing microbial processes led to the inhibition of some microbial pathways and the stimulation of others, promoting further retention of bioavailable N in the system. Understanding these microbial interactions will be important for mitigation of these impacted systems.

The Louisiana shelf has one of the most productive fisheries in the United States with an annual harvest exceeding $270 million (CAST 1999). This industry could be dramatically impacted by hypoxia. Similar processes of anthropogenic hypoxia have been observed in the Baltic Sea, the Black Sea, the Mediterranean Sea, and numerous smaller bays and estuaries. Frequently, the reduction or complete collapse of local fisheries follows the formation of these hypoxic zones (Diaz & Rosenberg 1995). The Louisiana Shelf zone of hypoxia is a consequence of anthropogenic nutrient loading. Determining the fate of fixed nitrogen on the Louisiana Shelf will be critical to remediating this problem.

The data presented here suggest the possibility of a positive feedback loop between the severity of hypoxia and the residence time of fixed nitrogen. In this study, it was observed that denitrification was suppressed under conditions of severe hypoxia (DO < 1.0 mg l^{-1}). Suppression of sediment denitrification will effectively act to increase the benthic flux of bioavailable nitrogen to the water column. Benthic flux of nutrients to the water column is frequently associated with increased primary productivity (Twilley et al. 1999) — a primary factor in the formation of the hypoxic zone — thus exacerbating hypoxic conditions.

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