Pergamon

DEEP-SEA RESEARCH
PART II

Deep-Sea Research II 45 (1998) 881–892

Nitrate respiration associated with detrital aggregates in aerobic bottom waters of the abyssal NE Pacific

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Received 15 April 1997; received in revised form 21 October 1997; accepted 3 November 1997

Abstract

Rates of nitrate utilization in tube core respirometers (TCR) placed over aggregates on the seafloor at an abyssal site (Station M) in the eastern North Pacific Ocean increased at times of high particle flux. In the presence of aggregates, both oxygen and nitrate were used in respiration. The ratio of $O_2:NO_3$ concentrations in ambient waters was 3.9, while $O_2:NO_3$ utilization rates in TCR overlying and TCR aggregate pore waters were 2.6 and 0.6, respectively. We postulated that denitrification was occurring in microzones of the particle-rich oxygenated (135 μM) waters. To test this, nitrate respiration was measured aboard a ship in oxygen-minimum (~ 26 μM) water supplemented with particulate matter collected by a surface net tow. Dissolved oxygen consumption occurred immediately, followed by nitrate utilization while oxygen was still present. Calculations from cell densities indicated 0.6 μM of the original 42 μM of nitrate was assimilated into bacterial biomass during 36 h of incubation, suggesting the major portion of the utilized nitrate was used in respiration. Nitrate utilization rates in the *in situ* incubation study and those of the shipboard experiment were 3.1 and 2.7 $\mu M\,d^{-1}$, respectively. The results of the present studies suggest nitrate respiration occurs in microzones of aggregates in oxygenated bottom waters at times of high particle flux and causes some loss of fixed nitrogen.

1. Introduction

Present day models indicate the loss of fixed nitrogen is primarily due to denitrification in oxygen minimum waters and sediments and to organic nitrogen burial in

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0967-0645/98/$19.00
PII: S0967-0645(98)00006-X

sediments (Codispoti and Christensen, 1985; Christensen et al., 1987; Ganeshram et al., 1995). Dissimilative nitrate reduction occurs under anaerobic or microaerobic environments. Using GEOSECS data Broecker and Peng (1982) found NO_3^- levels lower in waters of the Bering Sea than in the open Pacific. They concluded that denitrification was occurring within the deep Bering Sea, speculating that, despite the fact that these waters are well oxygenated, sinking pellets could become anaerobic and allow NO_3^- reduction to occur. Recently, Brandes and Devol (1995) reported that nitrate and oxygen respiration occurred simultaneously in microzones in sediments of Washington continental margin and other areas. Loss of fixed nitrogen from low-oxygen environments has been estimated to be greater than 175–205 Tg per year (Codispoti and Christensen, 1985; Ganeshram et al., 1995). Other environments where denitrification may occur include microbial mats of coastal areas (e.g., Joye and Paerl, 1994; Fossing et al., 1995) and possibly particle-rich waters (e.g., Codispoti and Christensen, 1985; Alldredge and Cohen, 1987; Shanks and Reeder, 1993).

We have observed that at times of high particle flux in the water column of a time-series study site in the eastern North Pacific waters enclosed in bottom respirometers showed a marked depletion of nitrate compared to ambient levels. Nitrate loss was related to the presence and density of particles or aggregates as evidenced in transmissometer data (Beaulieu and Baldwin, 1998) and measurements of suspended particulate organic carbon (Druffel et al., 1998). Denitrification would seemingly be ruled out as a cause for the lower nitrate values since the concentration of dissolved oxygen in these waters is about 135 μM, with some variation over seasonal to interannual timescales. This communication describes field and laboratory studies where our primary objective was to investigate nitrate respiration in oxygenated deep waters containing particle aggregates.

2. Materials and methods

2.1. Study site

Three cruises, Pulse 21 (15–28 August, 1994), Pulse 22 (15–28 September, 1994) and Pulse 25 (21 April–4 May, 1995) were taken aboard the *R/V Atlantis II* and *DSRV ALVIN* to the study site, Station M (34°50′N, 123°00′W; depth of 4100 m). This abyssal site is 220 km west of the central California coast. Surface waters are influenced by the western portion of the California Current where pronounced chlorophyll plumes exist from spring through summer (Smith et al., 1988; Michaelsen et al., 1988; Hayward and Mantyla, 1990). This site has been studied by K.L. Smith and associates since 1989 (e.g., Smith et al., 1994). Previous findings indicate a maximal summer time flux of particulate organic matter (POM) to the benthic boundary layer, which is defined as the water column between the sediments to a height of 650 m above the bottom (mab). Abundant detrital aggregates were present on the seafloor during Pulse 21 and 22 while few were observed during Pulse 25. Aggregates are defined as POM that contain detrital and living materials and have a size range of macroscopic to microscopic dimensions.

2.2. Sample collection

Water samples were obtained during each cruise from several sources using various sampling devices: (1) 30 l Go-Flo® bottle samples were used in the shipboard experiments; (2) 1.7 l and 5 l Niskin bottles attached to DSRV ALVIN and tripped to collect water approximately 1 m above the sea floor; (3) 1.7 l Niskin bottles placed on the sea floor during DSRV ALVIN dives, and (4) tube cores (TC) or tube core respirometers (TCR) were placed into the sediments during the various ALVIN dives. Each TCR (7 cm i.d., 30 cm length) was beveled at one end that it was inserted into the sediments by the ALVIN manipulator arm such that approximately 500 ml of overlying water was enclosed. The TC had a plastic end cap and the TCR was stoppered by a specially constructed PVC/aluminium housing that contained a battery to operate a stirrer and the electronics package used in recording biological O_2 consumption. The TCR is more fully described in Smith et al. (1998).

Subsamples from 1–4 (above) were carefully transferred to wide-lip 125 ml iodine flasks for O_2 analysis and to receiving bottles. The overlying water in the TCR was subsampled for NO_3^- and NO_2^- by carefully inserting a sterile pipette to the mid-water level of the core-tube and drawing a sample which was then filtered free of particles. All necessary precautions were taken to avoid contamination. A portion of the subsample was passed through baked (500°C) 1 μm GF/F filters for NO_3^- analysis. Samples were either immediately analyzed aboard ship or frozen for shore-based analysis. Samples for bacterial enumeration were taken from receiving bottles or unfiltered TCR water and then fixed in 2% formalin. Macroscopic aggregates and surrounding waters just above the sediments in TC and TCR samples were sampled by wide-mouth pipettes and transferred to receiving bottles (Smith et al., 1998). The waters were separated from the aggregates by centrifugation and the supernatant (porewaters) were analyzed for nitrate.

2.3. Nitrate reduction experimental

A series of twenty 500 ml acid cleaned PVC bottles were filled with water collected at 666 m depth in the oxygen-minimum zone (26 μM O_2) to simulate the low oxygen/high nitrate environment under which denitrifying bacteria are expected to be present. A number of these bottles were supplemented with a 5 ml suspension of three times helium-degassed (shaken vigorously with intermittent helium sparging) "phytoplankton" particulate organic matter. This material was derived from a surface net tow of 30 min duration. Each bottle contained a final concentration of 5.34 mM dissolved organic carbon (DOC) as determined by high temperature combustion analysis. Four of these bottles were bubbled with oxygen for 15 s at time zero to give saturated conditions. Four bottles were sparged for 3 s at 108 h to attain approximate bottom oxygen concentrations. Five bottles remained unamended and served as controls. All bottles were incubated in a cold room at a temperature of 4 ± 1°C. Bottles were periodically sacrificed and the waters analyzed for NO_3^-, NO_2^-, bacterial numbers, and dissolved O_2.

2.4. Analyses

Nitrate and nitrite were determined within an accuracy of 1–3% by acidic vanadium reduction to nitric oxide according to the methods of Garside (1982) and Braman and Hendrix (1989). DOC was measured by the high temperature combustion technique described in Williams et al. (1993). Dissolved oxygen was measured by the micro-Winkler technique (Strickland and Parsons, 1972). For bacteria enumeration, slides for microscopy were prepared immediately aboard ship and frozen until enumeration. Abundances of bacteria were determined by a modification of the epifluoresence technique of Hobbie et al. (1977).

3. Results

The nitrate values in bottom water enclosed for 48 h in TCRs (overlying water) of Pulse 22 and Pulse 25 were compared with those in "freshly collected" or "ambient" Niskin-bottle waters (Tables 1 and 2). The findings of six ALVIN dives, two on Pulse 22 and four on Pulse 25, show NO_3^- values in TCR overlying waters were always lower by about 5 μM than in ambient waters. This is likely due to the numerous aggregates

Table 1
Nitrate concentrations in deep water (ambient), and in overlying water and aggregate porewaters from Tube Cores (TC) and/or Tube Core Respirometers (TCR) collected on ALVIN dives during Pulse 22 (September 1994). TCRs were left on the seafloor at Sta M for 48 h. Ambient waters were collected at 0.5 mab with a 1.71 Niskin bottle and served as control values for nitrate

Dive	Ambient NO_3^- μM	TC/TCR number	NO_3^- μM Overlying water
2827	38.0 ± 0.2	R2	35.6 ± 0.5[a]
		R22	33.2 ± 0.9
		R28	30.9 ± 0.2[a]
2830	36.3 ± 0.3	R4	31.0 ± 0.1[a]
		R5	33.4 ± 0.0[a]
		R30	31.2 ± 0.1[a]
			Aggregate Porewaters
2822		6	3.4 ± 0.0[a]
2826		2	30.9 ± 0.3[a]
		3	35.0 ± 0.1[a]
2827		R2	23.7 ± 0.0[a]
		7	35.3 ± 0.3[a]
2828	39.5 ± 0.0	4	36.9 ± 0.4[a]
		8	34.7 ± 0.3[a]
2830		5	16.9 ± 0.3[a]
		9	18.5 ± 0.4[a]

[a] Macroscopic detrital aggregates visible in tube core.

Table 2
Nitrate concentrations in deep water (ambient) and in overlying water of tube-core respirometer (TCR) collected on ALVIN dives 2913, 2915, and 2916 during (Pulse 25, April–May, 1995). Tube-Core Respirometers were left on the seafloor at Sta M for 48 h. Ambient waters were collected at 0.5 mab with a 1.7 l Niskin bottle and served as control values for nitrate.

Dive	Ambient NO_3^- μM	TCR number	NO_3^- μM overlying water
2913	37.7 ± 0.3	R3	34.3 ± 0.2
		R4	31.7 ± 0.1
		R5	31.5 ± 0.8
		R6	34.7 ± 0.4
		R9	35.9 ± 0.2
		R13	35.4 ± 0.3
		R25	35.4 ± 0.3
		R29	35.5 ± 1.0
2915	38.9 ± 0.3	R17	32.6 ± 0.1
		R18	32.7 ± 0.1
2916	37.1 ± 0.5	R8	34.5 ± 0.9
		R11	30.6 ± 0.2
		R16	29.1 ± 0.5
2917	37.6 ± 0.5	R2	33.5 ± 0.2
		R3	33.5 ± 0.1

present in the TCRs, which provided the suboxic microzones needed for nitrate respiration to occur. On Pulse 22 (Table 1), where visible aggregates were present in TCRs, NO_3^- values were lower than in comparable Pulse 25 samples (Table 2), where there were no macroscopic aggregates.

In TC and TCR aggregate porewaters, nitrate levels were also lower than those in ambient waters (Table 1). Nitrate concentrations were, in most cases, lower in aggregate porewaters than in the TCR overlying water. These data suggest that nitrate respiration occurred in aggregates even in the presence of dissolved oxygen. In measuring oxygen consumption in TCRs, Smith et al. (1998) did not find anaerobic conditions in any of the incubated TCRs. Nitrite levels for Sta M deep water determined for a few samples did not exceed 0.1 μM, and in those TCRs where nitrate had been reduced the level of nitrite ranged between 0.4 and 0.9 μM.

Fig. 1a and b and Table 3 summarize the results of the shipboard nitrate reduction experiment. Both oxygen and nitrate utilization occurred in the presence of low levels of O_2. The added POM (from net tows) provided particulate matter where anaerobic conditions could develop in microzones. Growth of the natural microbial population showed a brief "lag period" during which time the populations apparently adapted to the added POM. Nitrate reduction and oxygen utilzation rates were low during the first 36 h, followed by rapid decreases between 36 h and 60 h. Nitrate was exhausted by 60 h, and oxygen decreased to an undetectable level in 84 h. Nitrite, the first product of nitrate reduction, increased rapidly between 35 and 60 h, followed by a rate similar to the previous nitrate decrease until 84 h and then slowed for 60 h before becoming exhausted.

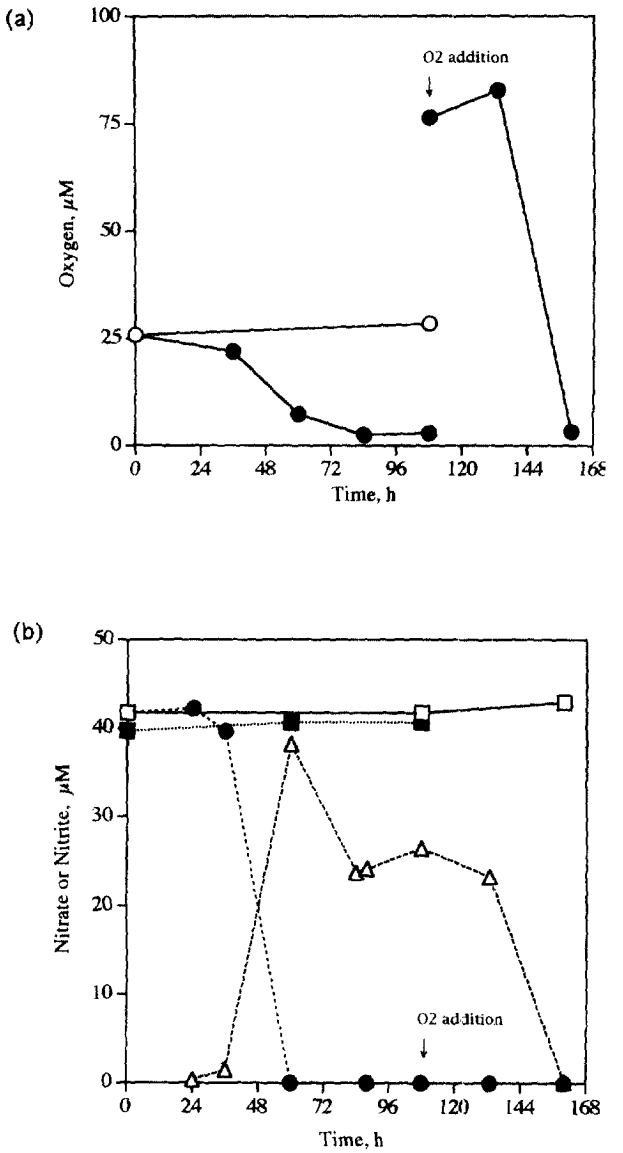

Fig. 1. Dissolved oxygen(a), and nitrate and/or nitrite (b) utilization in oxygen-minimum waters supplemented with POM and incubated at 4 ± 1°C aboard ship (a) –○– control; –●– POM supplemented water; (b) –□– unsupplemented water, –●– POM supplemented water, –■– POM supplemented water + oxygen at $T = 0$, –△– nitrite in POM supplemented water).

Table 3
Bacterial numbers, carbon, and nitrogen in POM-supplemented oxygen-minimum waters incubated at 4 ± 1°C aboard ship. Dissolved oxygen and nitrate utilized, and carbon respired via nitrate and via oxygen over 36 h.

Time (h)	Bacterial numbers ($\times 10^8$/l)	Bacterial C (μM)[a]	Bacterial N (μM)[a]	O_2 utilized (μM)[b]	NO_3^- utilized (μM)[b]	C respired by	
						O_2 (μM)[c]	NO_3 (μM)[c]
0	3.81	0.63	0.13	0	0	0.00	0
12	3.07	0.51	0.10	0.91	0	0.01	0
24	7.78	1.29	0.26	2.29	0	0.06	0
36	19.21	3.20	0.64	8.22	4	0.57	6

[a]Bacterial carbon assumes each cell has a mass 2×10^{-14} g C (Lee and Fuhrman, 1987), bacterial nitrogen calculated from C/N = 5.
[b]Dissolved oxygen and nitrate utilized from Fig. 1.
[c]Carbon respired calculated from 1 μM O_2 = 1 μM C oxidized; and carbon respired from 1 μM NO_3 = 1.5 μM C oxidized.

Assuming that denitrification occurs in environments where 10 μM or less of oxygen is present, it took about 52 h for oxygen to reach this level (Fig. 1a). Likewise, after 52 h, nitrate and nitrite levels were 16 μM and 21 μM, respectively. The sum of nitrate and nitrite concentrations is 37 μM, which is also observed after 60 h when all the nitrate is reduced and nitrite is present at the 37 μM level. Therefore, of the 42 μM of nitrate originally present, 5 μM was reduced beyond nitrite and most likely used in denitrification. The low O_2 content (26 μM) of the original 666-m water did not change in control bottles. Hence, there was no apparent O_2 contamination in the experimental bottles. Table 3 also shows that in particle-rich, low O_2 waters, the calculated amount of carbon respired is greater with NO_3^- than with oxygen. Although we did not measure the gaseous end products (N_2O, N_2) of denitrification in our shipboard experiment, we assumed the amount of nitrate utilized in excess of that which would be needed for assimilation was used for respiration.

4. Discussion

Nitrate respiration in the sea is observed primarily in environments with low dissolved oxygen content e.g., in the oxygen-minimum zone (e.g., Cline and Kaplan, 1975; Codispoti and Christensen, 1985), in sediments (e.g., Christensen et al., 1987; Codispoti et al., 1990; Codispoti and Christensen, 1985; Lipschultz et al., 1990; Altabet et al., 1995), and in microbial mat communities (e.g., Joye and Pearl, 1994). Nitrate respiration in these environments is responsible for a significant amount of fixed nitrogen removal from the oceans (Altabet et al., 1995; Ganeshram et al., 1995). This loss of fixed N from the ocean via denitrification may exceed the input of nitrogen

from sources such as nitrogen fixation, runoff, and precipitation (Christensen et al., 1987; Altabet et al., 1995). Climate induced changes in upwelling of nutrients often observed in these waters also may affect denitrification rates. If, for example, primary production rates are increased by climatic effects, denitrification may be affected since fast-sinking particulate organic matter is needed to provide energy for reduction (Altabet et al., 1995, Anderson and Sarmiento, 1994).

In association with K.L. Smith, we have been studying in detail the physical, chemical, and biological events in the deep water and benthos at Sta M in the eastern North Pacific Ocean since 1989 (Smith et al., 1994; 1998). The primary goal has been to evaluate the effect of POM on the benthos and sediment communities. At Sta M, between February 1990 and October 1991, particulate fluxes to the deep ocean showed strong seasonal variations in sediment trap content both at 600 and at 50 mab, with peaks from spring through fall and minima in winter (Smith et al., 1994, 1998). These investigators also observed a marked degree of variation between years, with a substantial increase in particle fluxes in spring and summer in 1991 compared to the same seasons of 1990. Aggregates were monitored on the sea floor with a time-lapse camera beween July 1990 and July 1991 (Smith et al., 1998). Aggregates appeared on the sea floor in early July 1990, and by early October five episodic pulses had been observed. With few exceptions, maximum inputs to the benthos appear to occur in late summer-early fall.

Similar observations were made in the 1994–1995 inputs (Table 4, Pulse 22), although average aggregate size was larger (Smith et al., 1998). During PULSE 22 and 25 cruises levels of oxygen and nitrate in TCR waters were less when compared to ambient waters. Nitrate concentrations in the TCRs appeared to be related to size and numbers of particles. Larger size and higher numbers of aggregates usually reflected lower nitrate levels. We postulated that particles provide centers, which first undergo aerobic decomposition. When these centers become oxygen-deficient, facultatitve micro-organisms continue decomposition via nitrate respiration (e.g., Broecker and

Table 4
Downward mass and POC fluxes. Data from 50 mab (Pulse 18,22,25) and 600 mab (Pulse 17)[a]. Mass flux and POC flux values calculated from sediment trap data, see Baldwin et al. (1998)

CRUISE/Date	Mass flux mg/m/d	POC flux mg/m/d
PULSE 17 14–22 Jul. 1993	333	20.8
PULSE 18 2–12 Nov. 1993	61.3	4.42
PULSE 22 15–28 Sept. 1994	301	16.9
PULSE 25 21 Apr.–4 May 1995	97.8	5.47

[a]Over a number of deployments values for Mass and POC fluxes showed little difference between 600 and 50 mab.

Table 5
Ratio of dissolved oxygen to nitrate in deep ambient water and in utilization rates in overlying and aggregate pore waters of the TCRs placed in the sediments at Sta M during PULSE 22 (Ratios calculated from NO_3^- data in Table 1 and O_2 data provided by K.L. Smith, see Smith et al. (1998)

DIVE	$O_2:NO_3^-$ (Molar) Ambient	$O_2:NO_3^-$ (Utilization rate, μM/d)	
		TCR overlying water	TCR aggregate porewaters
2827	3.8	2.5	1.4
2830	3.9	2.7	0.6

Peng, 1982; Alldredge and Cohen, 1987; Shanks and Reeder, 1993). In the presence of abundant aggregates, many microenvironments exist and the effect of nitrate respiration in all these "microzones" may be a reduction of a measurable amount of nitrate. An example of this removal can be seen in Table 3 where after 36 h of incubation bacteria assimilated 0.64 μM NO_3^- and dissimilatively respired 6 μM NO_3^-, indicating that > 5 μM was used for respiration. These values also assume that NO_3^- served as the sole nitrogen source for assimilation, an unlikely scenario because of the availibility of amino acids and ammonium resulting from organic matter decomposition. Furthermore, in comparing nitrate utilization rates between the shipboard experiment with those of the TCR study, we find they are similar, i.e. 2.7 and 3.1 μM d^{-1}, respectively.

During PULSE 22 the molar ratio of $O_2:NO_3^-$ in deep ambient water at Sta M was 3.9 (Table 5, Dive 2830). The ratio of utilization rates for the two reductants after incubation for 48 h was lower in the overlying water of the TCRs having a value of 2.7, while the same ratio in the aggregate pore water was lower still at 0.6. In both the overlying and aggregate porewaters oxygen and nitrate concentrations decreased over 48 h; their rates of utilization, however, were different (Table 5). Based on these ratios, aggregate porewaters showed relatively greater utilization of nitrate than oxygen for respiration. Smith et al. (1998) have shown a strong correlation between aggregate weight, volume or milligrams carbon and oxygen demand. We envision a scenario within aggregates where microenvironments approach suboxic conditions and nitrate respiration predominates even though there may be high O_2 consumption by the aggregates, resulting in little change of the ambient $O_2:NO_3^-$ ratio in surrounding water. With increasing distance from these anaerobic microenvironments oxygen utilization increases. Oxygen microdiffusivity gradients have been reported at sediment/water interfaces (Gundersen and Jorgensen, 1990), which also may occur at our aggregate/water interfaces. Brandes and Devol (1995) report nitrate respiration may occur in coastal sediments in the presence of 100 μM O_2. If respiration occurs in aggregates under similar conditions, our observations can be more readily explained.

Christensen et al. (1987) and Ganeshram et al. (1995), among others, state that denitrification is a significant nitrogen sink. Denitrification in the oxygen-minimum zone of the water column and in anaerobic sediments results in significant nitrogen

removal. It is unlikely that denitrification in sediments at Sta M significantly depleted nitrate levels in deep water (Jahnke et al., 1990). These authors showed that in their benthic chamber experiments in the oxygenated upper sediments of Sta M, nitrate uptake rates were immeasurable. At a different station, at the base of the shelf slope, rates of nitrate decrease were at least two times less than our average 48 h values (4.4 μM, calculated from data in Table 1). Jahnke et al. (1990) stated that nitrification may have produced some nitrate. Since there is little loss to the sediments, this suggests that nitrate depletion in the TCs and TCRs was due primarily to nitrate respiration in aggregates.

Nitrate respiration in aggregate microzones occurs at Sta M only at times of high particle flux, when ambient NO_3^- levels in bottom waters may decrease by several μmoles. We do not expect this reduction to be widespread, but instead localized where there has been high particle input. In models of sediment porewater nitrate concentrations, denitrification primarily occurs at depths below the aerobic zone (Goloway et al., 1982; Jahnke et al., 1982; Jahnke, 1985). However, Jahnke et al. (1982) showed denitrification occurred in microzones around particles, an observation consistent with that made in this study with respect to bottom waters.

Some of our unpublished observations suggest that nitrate respiration may occur higher in the oxygenated water column of the deep sea at times of extremely high particle flux. It is tempting to speculate to what extent nitrate reduction in microzones of particles in oxygenated bottom water contributes to the loss of total fixed nitrogen. We suggest suboxic microenvironments form in bottom waters following periods of elevated primary production and increased particle flux, and nitrate respiration in microzones contributes, to some degree, to fixed nitrogen loss.

Acknowledgements

This work was supportedby NSF grants OCE-9101540 and OCE-9501531 to J.E. Bauer and OCE-8840531 to P.M. Williams, and OCE-8922620 to K.L. Smith, and by the Marine Life Research Group (AFC). We would like to thank Ken Smith and Ellen Druffel for providing us the opportunity to participate on this interdiciplanary project and for logistical support. Special thanks to R.J. Baldwin, Rob Glatts, Ron Kaufman, Lynn Lauerman and Stace Beaulieau for help with the field work and for providing results of chemical analyses (RJB). We thank Mr. Arnold Mantyla and Dr. Joris Gieskes for advice and information on nutrient distribution and ocean circulation. Finally, the officers and crew of the R/V Atlantis II and Deep Submersible R/V ALVIN provided us with excellent onboard and over the side ship support.

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