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UNIVERSITY OF MARYLAND CENTER for ENVIRONMENTAL SCIENCE
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MEASUREMENTS OF DENITRIFICATION IN AQUATIC ECOSYSTEMS:

LITERATURE REVIEW AND DATA REPORT

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Measurements of Denitrification in Aquatic Ecosystems: Literature Review and Data Report

Prepared by:

S. E. Greene[1], Graduate Research Assistant

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University of Maryland System
Center for Environmental Science

[1]Chesapeake Biological Laboratory
P.O. Box 38, Solomons, MD 20688-0038

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Introduction

With some exceptions, nitrogen (N) is the principal nutrient limiting primary production in coastal marine environments (Ryther and Dunstan 1971). Since the industrial revolution, fixation of biologically inaccessible N in the atmospheric pool to bioavailable forms in the terrestrial pool has doubled due to human activity (Vitousek et al. 1997). As a result, N inputs to the coastal ocean have increased. Elevated N concentrations in coastal waters support increased primary productivity, and the direct and indirect effects of enhanced production bring about readily observable, ecosystem-scale changes in coastal environments (e.g. Nixon 1995, Kemp et al. 2005). Recognition of the large impact of enhanced N inputs on coastal systems has fostered interest in removal mechanisms for N. Denitrification, the microbially-mediated conversion of dissolved nitrate (NO_3) to dinitrogen (N_2) gas, is an important pathway in the global N budget (Seitzinger 1988) as well as in the N budgets of many coastal ecosystems (Boynton et al. 1995). This process is of special interest in eutrophic coastal ecosystems because it results in permanent removal of anthropogenic N from aquatic systems.

Microbial and ecological significance of denitrification

Nitrate can be used by heterotrophic bacteria as an alternative terminal electron acceptor (TEA) in the absence of oxygen (O_2). Whether NO_3 or a different TEA is used depends on the specific redox regime of the environment, as well as the relative abundance of the various TEA's (Santschi et al. 1990). Bacterial use of NO_3 as a TEA involves a stepwise reduction to N_2, with each step catalyzed by a different enzyme. Of particular interest, and perhaps of greatest ecological significance, is the step in which nitrite (NO_2) is reduced to nitric oxide (NO). At this point, N that is in a bioavailable, dissolved form becomes a biologically inert gas. Upon further reduction of NO to N_2, the N reaches a more chemically stable state and diffuses to the atmosphere. This closes a major loop in the anthropogenic N cycle, as large amounts of N_2 are removed from the atmosphere by humans to make fertilizer. Nitrogen fixed from the atmospheric N pool for fertilizer is moved around the terrestrial landscape and applied to agricultural fields. Residual, biologically active forms of N may then be nitrified to NO_3 and move from the terrestrial N pool into inland and coastal waters (aquatic/oceanic N pool). Denitrifiers in aquatic and marine sediments return this N to the atmospheric pool as N_2. In addition to returning N to the atmospheric pool, the ecological significance of denitrification is that it permanently removes from a system N that would otherwise be available for primary production. This sort of loss is of special interest in eutrophic, N-limited systems where substantial anthropogenic N inputs support high primary productivity, with a host of ecological and economic implications (Kemp et al. 2005). Denitrification is also of interest because it is the only mechanism (short of physical export) by which N is truly removed from the system; N taken up by biota or buried in sediments can be made available again via decomposition or erosion processes.

Measuring denitrification

A fundamental hurdle in measuring denitrification is that the increase of N_2 due to denitrification is small relative to atmospheric or dissolved aqueous background

concentrations of N_2. Any direct measurement of denitrification must allow resolution of this small difference, and several techniques have been developed for this purpose. An earlier, indirect approach (the acetylene blockage technique) involved measurement of the less-abundant intermediate gas, N_2O, for which small changes in concentration are easier to resolve than for N_2 (e.g. Jorgensen and Soerensen 1985, Kemp et al. 1990). More recent approaches (e.g. isotopic techniques or use of N_2:Ar ratios) involve direct measurement of N_2 (e.g. Nielsen and Glud 1996, Kana et al. 1998).

Objectives

This document is a review of denitrification measurements made during the past four-and-a-half decades in global aquatic environments. The primary objectives of this review are to:

1. Collect information regarding denitrification rates in different aquatic environments;
2. Characterize the distribution of denitrification rates that have been measured (i.e. maximum, minimum and median rates);
3. Document the use of different techniques for measuring denitrification, and the degree to which these have changed during the review period.

Methods

Literature reviewed in this document was located primarily within the Cambridge Scientific Abstracts (CSA) Aquatic Sciences and Fisheries Abstracts online database (www.csa.com). A search was conducted for all publications within the database containing the word "denitrification" in the abstract. Where journal-specific abstract or title databases were available, journals identified within the CSA database as containing at least one article with "denitrification" in the abstract were searched individually as well. Finally, literature cited in articles identified within the database was reviewed so as to detect publications not contained in the database. In a few cases, it was evident that measurements from a single study were reported in multiple publications, or previously-published data were included by another author in a table in a later publication. Care was taken to ensure that no measurement was reported more than once in this document. Several non-peer reviewed reports were also identified. Though it was not efficient to obtain copies of all of these works, it should be noted that denitrification measurements reported in gray literature are often published in peer reviewed venues as well. Due to the large number of measurements made with the acetylene blockage technique and the poor capacity of this technique to reflect natural conditions, some acetylene studies were judiciously rejected from inclusion in this review. It should also be noted that a substantial number of measurements of denitrification in terrestrial soils have been made (primarily using the acetylene blockage technique). An exhaustive review of that body of literature was not conducted, as the focus of this report is aquatic ecosystems.

In total, 164 studies were reviewed and 1929 measurements of denitrification recorded. The following environments were represented: inland (fresh) wetlands, freshwater creeks, lakes, coastal wetlands, mudflats, seagrass beds, lagoons, estuaries, reefs, continental shelves and human engineered systems (constructed wetlands and systems influenced directly by agriculture). The majority of reviewed measurements (60%) were made in estuarine systems. All measurements were converted to units of

μmol N m^{-2} hr^{-1} to facilitate comparisons. Where rates were originally reported on an areal basis, quantities of N were converted to μmoles, area converted to square meters and time to hours. Where rates were reported per volume of sediment or water, rates were multiplied by the sample depth or increment, based on information given in the publication.

Some rates were reported in units of N per gram of sediment weight. For these, information given in the text or assumptions regarding sediment bulk density were used for conversion to areal rates. Bulk densities of 0.2 – 0.9 g cm^{-3} (derived after assumption of 60-80% water) were assumed for estuarine sediments, based on the equation:

$$\text{Bulk density (g cm}^{-3}) = \frac{(100 - \%H_2O)}{[(\%H_2O) + ((100 - \%H_2O)/2.5)]}$$

A bulk density of 1.4 was assumed for terrestrial soils.

In addition to denitrification rates, the following associated environmental parameters were recorded where data were available: geographic region, salinity class, temperature, month or season and year of collection, depth of measurement, station code or description, water column nitrate concentration, dissolved oxygen status of water adjacent to sediments, measurement technique, original units of measurement, and specific information regarding experimental manipulations (Table 1).

Table 1. Additional information reported with denitrification rates.

Column Title	Content Description
Location	Gives the name of the body of water or other environment in which denitrification measurements were made. In some cases, more information is given (e.g. specific region of a large body of water; country name; USA state name).
Environment Code	Classifies study areas by environment type (see Table 2).
Geographic Region	Gives the name of the general region in which studies were performed.
Station Code/Description	Gives the station name or code given by authors for specific sites in which measurements were made; or gives important information about site characteristics (e.g. high marsh, low marsh, algal mat, sediment characteristics).
Salinity Class	Gives the salinity class where measurements were made (Hypersaline, >40; Euhaline, 30-40; Polyhaline, 18-30; Mesohaline, 5-18; Oligohaline, 0.5-5; Tidal Fresh, <0.5 with tidal influence; Nontidal Fresh, <0.5 without tidal influence).
Station or Sample Depth	Gives the depth of stations where sediment denitrification measurements were made, or the depth at which water column denitrification measurements were made (numbers indicating depths of water column samples are followed by an asterisk "*").

Table 1 cntnd.

Column Title	Content Description
Year	Gives the year in which measurements were made.
Month/Season	Gives the month or season in which measurements were made.
Temperature	Gives the water temperature at which measurements were made.
Nitrate	Gives the nitrate (NO_3) concentration from the water column. In some cases, ambient NO_3 concentration was not specified, but the amount added for experimental purposes was (identified by an asterisk "*").
Oxygen	Gives the oxygen (O_2) concentration from the water column. In several publications, only general information describing aerobic, anaerobic, hypoxic or anoxic conditions was given. Such conditions were included in this report in lieu of actual concentrations.
Denitrification	Gives the denitrification rate measured, with all rates converted to μmol N m^{-2} hr^{-1}. When direct and coupled denitrification were measured separately, both rates are given. When a range of rates was measured, gives the full range.
Simplified Denitrification	Gives the total denitrification rate measured, in μmol N m^{-2} hr^{-1}, with direct and coupled denitrification rates summed and expressed as a single rate and ranges of rates expressed as a mean rate.
Method Description	Describes (briefly) the technique used to measure denitrification.
Technique code	Classifies techniques into general categories. (See Table 3)
Reference	Citations for publications in which measurements were reported.
Unit Conversions	Gives information as to whether or not a unit conversion was necessary to express published denitrification rates as μmol N m^{-2} hr^{-1}, as well as the original, published units. In several cases, it was unclear whether published rates were in units of "N", "N_2," or "N_2O". If the authors could not be contacted for clarification, assumptions are stated.
Comments	Gives additional information on specific experimental conditions/ manipulations, whether or not rates had to be estimated from a graph, and in some cases important conclusions made by the authors.
Original Values	When a unit conversion was made for which the conversion process was not immediately obvious, original published rates and any assumptions necessary to make the conversion are listed.
Assumptions	See "Original Values" above.

Table 2. Description of environmental groupings for denitrification measurement sites.

Environment	Code	Description
Human engineered	H	Systems constructed or heavily impacted by humans (e.g. aquaculture, constructed wetlands, immediate agricultural runoff)
Wetland (fresh)	W	Landlocked wetland receiving only freshwater inputs
Creek (fresh)	Ck	Natural stream of water smaller than a river; labeled as such by the author(s)
Lake	Lk	Landlocked bodies of standing, fresh water
Coastal wetland	CW	Wetlands receiving tidal inputs (i.e. tidal marshes and mangroves)
Mudflat	MF	Unvegetated bar of sediment submerged regularly by tides
Seagrass Bed	SB	Area densely populated by submerged aquatic vegetation; labeled as such by the authors
Lagoon	Lg	Shallow body of water, cut off from open coastal waters by sand bars; labeled as such by the authors
Estuary	E	Semi-enclosed bodies of water receiving inputs from both terrestrial (freshwater) sources and the ocean
Reef	R	Sites in close proximity to coral reefs
Continental Shelf	CS	Open coastal waters near a major landmass

Table 3. Codes for various techniques used to measure denitrification.

Code	Technique
A	Acetylene
ISA	*In situ* acetylene
DN2	Direct measurement of N2 flux
ISDN2	*In situ* direct measurement of N2 flux
GP	Gas Partitioning
HA	"Heavy" ammonium ($^{15}NH_4$) addition
HN	"Heavy" nitrate ($^{15}NO_3$) addition
HNA	"Heavy" nitrate & ammonium addition
IP	Isotope Pairing
M	MIMS
MB	Mass balance
MO	Miscellaneous other

Summary of Preliminary Findings

Techniques used to measure denitrification

Scientists have been aware of denitrification for over a century (Zumft 1997). Though investigations of denitrification were published in the 1950's (e.g. Wijler and Delwiche 1954, Hauck et al. 1958), attempts to actually *measure* the process were not made until the 1960's (Goering and Dugdale 1966). The earliest estimates of denitrification were made via N mass balances and isotopic studies in which $^{15}N\text{-}NO_3$ was added to an environment and dissolved N_2 was analyzed for ^{15}N after an incubation period (Goering and Dugdale 1966). Important new measurement techniques have appeared since the 1960's, most notably the acetylene blockage technique in the 1970's (e.g. Balderston et al. 1976), direct measurement of N_2 production from sediment cores in the 1980's (e.g. Seitzinger et al. 1980, Seitzinger 1988), and the MIMS (membrane inlet mass spectrometry, Kana et al. 1994) and isotope pairing (Nielsen 1992) techniques in the 1990's.

More denitrification measurements appear to have been made with the acetylene blockage technique than with any other technique (Fig. 1). This technique owes its popularity to the fact that it circumvents the central quandary in measuring denitrification - the need to distinguish relatively small changes in N_2 against a large atmospheric (and by equilibration, dissolved aqueous) background. By blocking the final step in denitrification (reduction of N_2O to N_2), acetylene permits accumulation and detection of the more easily measurable gas, N_2O, as a proxy for N_2 (Balderston et al. 1976). However, acetylene also inhibits nitrification (Hynes and Knowles 1978), which can be an important source of NO_3 for denitrification, so this technique can lead to underestimates of *in situ* rates (Kemp et al. 1990). Acetylene studies do not appear as popular in the current decade as in previous decades, likely due to the development of other direct techniques that do not involve inhibitors and associated problems (Fig. 1).

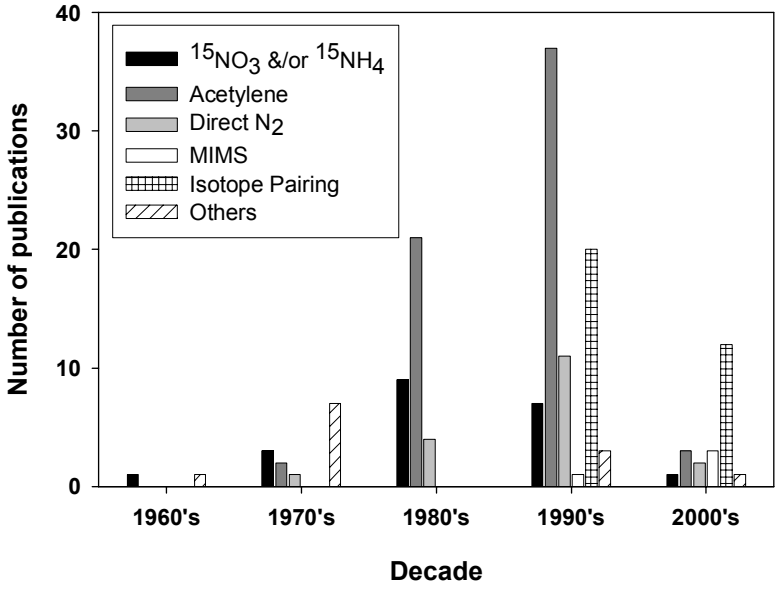

Figure 1. Number of publications reporting denitrification rate measurements made with various techniques.

Seitzinger made direct measurements of N_2 fluxes by lowering the background N_2 concentration via sparging core headspaces with an atmosphere-like mixture of gases in which N_2 is replaced by helium (Seitzinger et al. 1980). This technique has the disadvantage of requiring long pre-incubation periods, and despite attempts at correction, there is also the issue of distinguishing the N_2 flux due to denitrification from the flux due to chemical gradients (Seitzinger 1988, Cornwell et al. 1999). Nowicki (1994) has used anoxic control cores to overcome the problem of sediment-porewater degassing, such that the anoxic core flux of N_2 can be assumed to be due solely to chemical gradients. The reducing conditions brought on by anoxia cause quick depletion of NO_3 stocks and also inhibit nitrification, both of which prevent denitrification from occurring in anoxic control cores.

A large number of denitrification measurements have been made with the isotope pairing technique since the 1990's (e.g. Risgaard-Petersen et al. 1994, Rysgaard et al. 1995, Trimmer et al. 1999, Dong et al. 2000). In this method, ^{15}N-NO_3 is added to overlying water and N_2 evolved during incubation is analyzed for partitioning into $^{15}N^{15}N$, $^{15}N^{14}N$ and $^{14}N^{14}N$ (Nielsen 1992). The advantage of this technique is that the different pathways for denitrification can be distinguished (direct denitrification of water column NO_3 versus coupled nitrification-denitrification). By 2004 more denitrification measurements had been made with isotope pairing than with any other technique in the current decade (Fig. 1). However, several (perhaps questionable) underlying assumptions are required, namely that added $^{15}NO_3$ mixes homogeneously with the $^{14}NO_3$ pool, that added NO_3 does not change the rate of coupled nitrification-denitrification, that isotope fractionation can be neglected, and that diffusion of heavy and light NO_3 is similar (Middleburg et al. 1996).

In the mid-1990's, the MIMS technique was first applied to the study of denitrification in estuarine sediments (Kana et al. 1994, Kana et al. 1998). A membrane inlet mass spectrometer optimized for high-precision measurement of dissolved gasses is employed in this technique. A measurement coefficient of variation of <0.05% is achieved by measuring N_2 to argon (Ar) ratios in water samples, compared to precision levels of 0.5% when measuring N_2 alone (Kana et al. 1994). This technique has gained popularity since it's inception, though it has incited criticism from proponents of the isotope pairing technique (Eyre et al. 2002, Eyre et al. 2004). Even so, MIMS remains one of the preferred techniques for measuring denitrification in aquatic ecosystems. In general, the study of denitrification has gained momentum, and nearly as many studies using isotope pairing and MIMS have already been published in the first few years of the present decade as were published in the entire previous decade (Fig. 1).

Denitrification in aquatic environments

Since the 1960's, denitrification has been measured in a large variety of environments, both natural and engineered. Denitrification rates between 10 and 100 μmoles N m^{-2} h^{-1} are most frequently reported, though rates well over 1000 μmoles N m^{-2} h^{-1} have been observed in certain systems (Fig. 2; Table 4). Rates near 20,000 μmoles N m^{-2} h^{-1} have been measured in human engineered systems and estuaries, though median rates for these environments are not so high as to be outside the range of commonly measured rates (Table 4; Fig. 2). Median rates appear highest in lakes (37 μmol N m^{-2} h^{-1}), estuaries (40 μmol N m^{-2} h^{-1}) and coastal wetlands (54 μmol N m^{-2} h^{-1}; Table 4). In

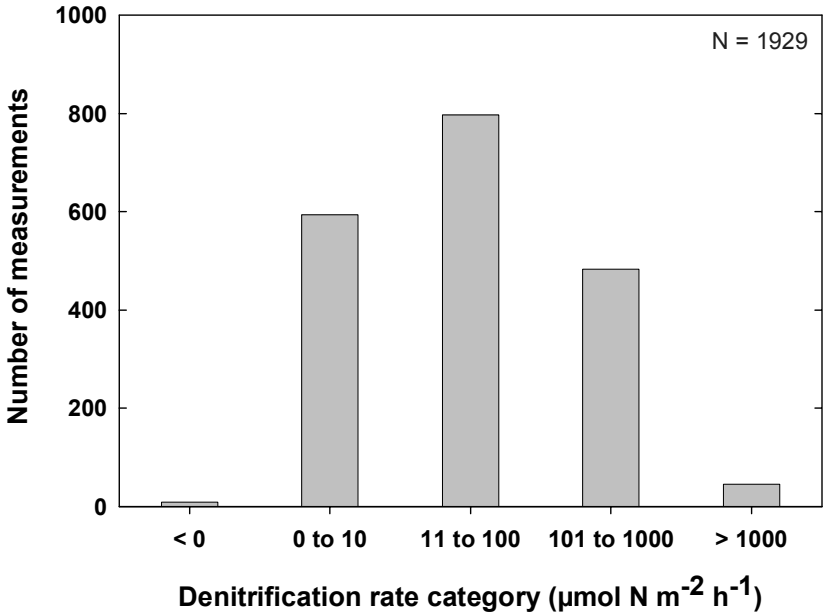

Figure 2. Frequency distribution of denitrification rates measured in aquatic environments.

estuaries, where more measurements of denitrification appear to have been made than in any other environment (Table 4), the most commonly reported rates are between 1 and 100 µmol N m^{-2} h^{-1} (Fig. 3), and more specifically between 1 and 50 µmol N m^{-2} h^{-1}. The range of rates measured in estuaries is higher than that of any other natural system by an order of magnitude (Table 4).

Table 4. Minimum, maximum, mean, median and range of denitrification rates measured in a variety of aquatic environments. "n" = number of measurements. Rates are given in µmol N m^{-2} h^{-1}.

	Min	Max	Mean	Median	Range	n
Human engineered	0	24143	695	1	24143	68
Wetlands (fresh)	0	330	39	4	330	52
Creeks (fresh)	0	1200	195	32	1200	20
Lake	0	490	89	37	490	90
Coastal wetland	-200	1865	94	54	2065	167
Mudflat	2	213	71	31	211	61
Seagrass Bed	2	167	29	8	165	13
Lagoon	-20	290	21	9	310	116
Estuary	-93	19616	197	40	19709	1188
Reef	0	533	58	4	533	40
Continental Shelf	0	1658	104	15	1658	113

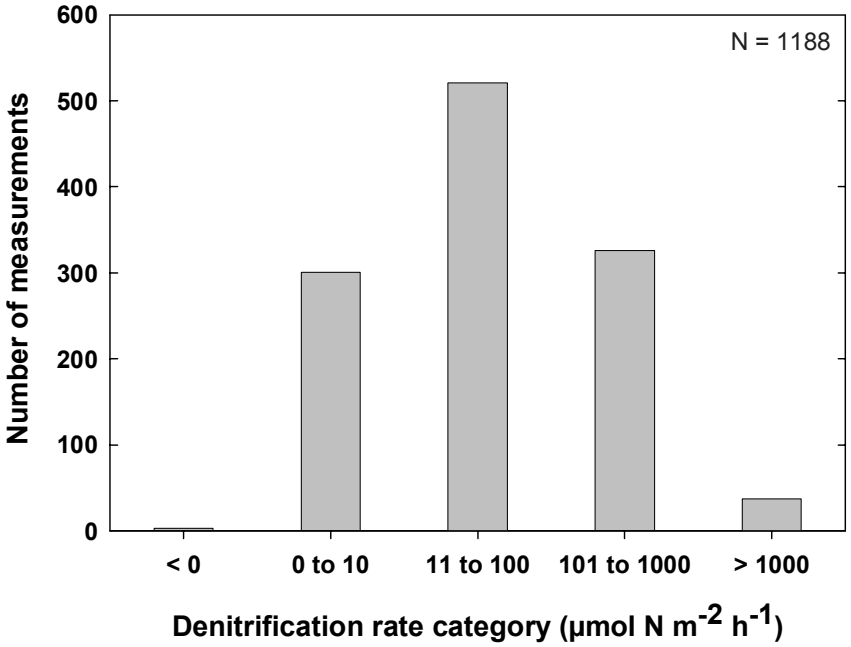

Figure 3. Frequency distribution of denitrification rates measured in estuaries.

Future Directions

Synthetic analyses of existing data promote scientific efficiency by highlighting needs for additional measurements and, perhaps more importantly, revealing areas for which additional measurement efforts would be redundant. To that end, data from this review should facilitate analyses of relationships between denitrification rate and environmental parameters such as salinity, temperature, oxygen concentration and depth. Such analyses will further a mechanistic understanding of denitrification and may aid in modeling efforts. These data may also be used to examine distributions of denitrification rates within specific environments (e.g. Fig. 3). Due to the large amount of information, all data are located in an electronic appendix (Microsoft Excel file "Appendix A.xls") on the accompanying CD.

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Appendix A

Measurements of Denitrification in Aquatic Environments – Data Set

Appendix B

References for Data in Appendix A

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