Estuarine, Coastal and Shelf Science 88 (2010) 1–11

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Invited Feature

Estuarine nitrifiers: New players, patterns and processes

Anne E. Bernhard[a,*], Annette Bollmann[b]

[a] Department of Biology, Connecticut College, New London, CT 06320, USA
[b] Department of Microbiology, Miami University, Oxford, OH 45056, USA

ARTICLE INFO

Article history:
Received 20 October 2009
Accepted 21 January 2010
Available online 1 February 2010

Keywords:
ammonia-oxidizing archaea
ammonia-oxidizing bacteria
salt marsh
Estuary
amoA
Nitrosopumilus maritimus

ABSTRACT

Ever since the first descriptions of ammonia-oxidizing *Bacteria* by Winogradsky in the late 1800s, the metabolic capability of aerobic ammonia oxidation has been restricted to a phylogenetically narrow group of bacteria. However, the recent discovery of ammonia-oxidizing *Archaea* has forced microbiologists and ecologists to re-evaluate long-held paradigms and the role of niche partitioning between bacterial and archaeal ammonia oxidizers. Much of the current research has been conducted in open ocean or terrestrial systems, where community patterns of archaeal and bacterial ammonia oxidizers are highly congruent. Studies of archaeal and bacterial ammonia oxidizers in estuarine systems, however, present a very different picture, with highly variable patterns of archaeal and bacterial ammonia oxidizer abundances. Although salinity is often identified as an important factor regulating abundance, distribution, and diversity of both archaeal and bacterial ammonia oxidizers, the data suggest that the variability in the observed patterns is likely not due to a simple salinity effect. Here we review current knowledge of ammonia oxidizers in estuaries and propose that because of their steep physico-chemical gradients, estuaries may serve as important natural laboratories in which to investigate the relationships between archaeal and bacterial ammonia oxidizers.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

Nitrification, the sequential oxidation of ammonia to nitrite and then nitrate, is a critical step in the nitrogen cycle, and is carried out by phylogenetically and physiologically distinct microorganisms. In coastal systems, nitrification is often coupled to denitrification (Jenkins and Kemp, 1984; Sebilo et al., 2006), resulting in the ultimate return of nitrogen to the atmosphere. Thus, the fate of ammonia plays a major role in the regulation of primary productivity, particularly in marine systems where nitrogen is often the limiting nutrient (Howarth, 1988). Despite the obvious ecological importance of nitrification, regulation of microbial populations that mediate it is poorly understood, particularly as new pathways of ammonia oxidation and new groups of ammonia-oxidizing organisms are discovered. Identifying environmental factors that regulate the diversity, distribution, and activity of nitrifiers is paramount to gain a more complete understanding of nitrogen-cycling, particularly in nitrogen-sensitive environments, such as estuaries and salt marshes.

The mixing of freshwater and saltwater in estuaries and salt marshes creates steep physico-chemical gradients that are accompanied by shifts in the resident microbial communities. Steep gradients of salinity, nitrogen, pH, oxygen, sulfide, and organic loading are common and some of these have been shown to correlate with shifts in microbial communities (del Giorgio and Bouvier, 2002; Crump et al., 2004; Hewson and Fuhrman, 2004; Bernhard et al., 2005a). Many of the parameters known to shift along the estuarine gradient are also known to be important factors impacting ammonia oxidizers (e.g. Bernhard et al., 2005b, 2007; Mosier and Francis, 2008; Santoro et al., 2008). Because of the steep gradients and the documented changes in activity and community composition of nitrifiers in estuaries and salt marshes, these habitats are ideal natural laboratories in which to study the dynamics of nitrifiers.

To date, there are no known microbes that can oxidize ammonia all the way to nitrate. Instead, ammonia-oxidizers convert ammonia to nitrite, while another group of organisms, nitrite-oxidizing bacteria, convert nitrite to nitrate. Until recently, the only known aerobic ammonia oxidizers belonged to two separate lineages within the domain *Bacteria*, the *Beta* and *Gammaproteobacteria* (Woese et al., 1984, 1985). Ammonia-oxidizing *Bacteria* (AOB) use O_2 as their electron acceptor and NH_3 as their sole energy source, channeling some of the energy produced to fix CO_2. Although both ammonia- and nitrite-oxidizers are required for the complete oxidation of ammonia, most research has focused on ammonia oxidizers since they carry out the rate limiting step (Prosser, 1989).

---

* Corresponding author.
E-mail address: aeber@conncoll.edu (A.E. Bernhard).

0272-7714/$ – see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecss.2010.01.023

What was once a fairly simple phylogenetic and physiological picture, however, is now known to be far more complex. The recent discovery of aerobic ammonia oxidation within the domain *Archaea* (Könneke et al., 2005; Treusch et al., 2005) has led to a dramatic shift in the current model of nitrification, and to new questions of niche differentiation between ammonia-oxidizing *Archaea* (AOA) and the more well-studied AOB. Much of what we know about marine AOA has come from studies in open ocean environments, where patterns of AOA are generally similar, with AOA far outnumbering AOB (Wuchter et al., 2006; Mincer et al., 2007; Beman et al., 2008), suggesting that AOA are likely the predominant nitrifiers in the ocean. However, several recent studies of AOA and AOB in estuarine systems suggest a more complex picture of ammonia oxidizer ecology, so we focus here on the ammonia oxidizers in estuarine systems, where the patterns and processes appear to differ significantly from those in pelagic systems.

1.1. *Nitrification in estuaries and salt marshes*

Effects of changes in physico-chemical conditions along an estuarine gradient on nitrification rates have been well documented, and indicate decreased nitrification as the salinity increases (Seitzinger, 1988; Rysgaard et al., 1999). However, the precise cause of the decrease in nitrification is less clear. It is known that salinity plays a major role in controlling NH_4^+ adsorption capacity of the sediment (Boatman and Murray, 1982), with increased NH_4^+ efflux as salinity increases (Boynton and Kemp, 1985). But salinity has also been shown to affect species composition of nitrifying communities (de Bie et al., 2001; Bollmann and Laanbroek, 2002), and functionally distinct communities of AOB along a salinity gradient have recently been reported (Bernhard et al., 2007). Thus, decreases in nitrification may be due to substrate limitation or, alternatively, a shift in the nitrifying community.

Nitrification has received much attention in estuaries and other coastal systems, but relatively few studies have been conducted in salt marshes. Despite the paucity of measurements in salt marshes, reported values of nitrification vary widely, and may depend on the type of vegetation sampled or the methods used. Dollhopf et al. (2005) found an order of magnitude difference in nitrification rates in tall-form *Spartina alterniflora* compared to short-form *S. alterniflora* and unvegetated creek banks. However, Moin et al. (2009) reported no significant differences in potential rates among three different salt marsh grasses. Other studies have reported nitrification in only one type of vegetation (Anderson et al., 1997; Tobias et al., 2001) or have not provided detailed information on the vegetation types (Thompson et al., 1995). Because the roots help to oxygenate the sediments (Mendelssohn et al., 1981), it is thought that this may help to stimulate nitrification (An and Joye, 2001). Conversely, others have reported inhibition by the presence of microalgae, possibly due to competition for ammonium (Risgaard-Petersen et al., 2004). Therefore, our understanding of nitrification in salt marshes and the microorganisms responsible is severely lacking at present, despite the importance of nitrification in regulating nitrogen in these systems.

It is possible that much of the variability observed among nitrifying communities in estuaries and salt marshes is due at least in part to the difficulties of collecting comparable samples in these systems. Tidal cycles, type of vegetation or distance from vegetation are all critical factors that may significantly impact the communities that are present or active, but are often not adequately reported or accounted for in the studies. As tides ebb and flow, edaphic conditions may shift dramatically over only a few hours. The dynamic nature of estuaries and salt marshes may create a unique natural laboratory for studying nitrifying communities and the factors that regulate them, but it also creates inherent sampling difficulties and subsequent comparisons between studies, and may contribute to some of the variability in estuarine nitrifying communities.

1.2. *Taxonomy of AOB*

The majority of AOB form a monophyletic lineage within the *Betaproteobacteria* (Fig. 1), comprised of two major genera *Nitrosomonas* and *Nitrosospira* (Head et al., 1993). Two other species, *Nitrosococcus oceani* and *Nitrosococcus halophilus*, are affiliated with the *Gammaproteobacteria* (Holmes et al., 1995; Purkhold et al., 2000), and appear to be restricted to marine or saline environments.

All autotrophic aerobic ammonia-oxidizing *Bacteria* have ammonia monooxygenase (AMO), the enzyme responsible for the first step in ammonia oxidation. The gene encoding the alpha subunit of AMO (*amo*A) has been used extensively as a molecular marker for studies of ammonia oxidizer diversity and distribution (see review by Kowalchuk and Stephen, 2001). The forms of AMO differ significantly between the *Beta*- and *Gammaproteobacteria* AOB. In fact, analysis of *amo*A sequences (the gene encoding the subunit containing the active site) indicates that genes from *Gammaproteobacteria* AOB have higher similarities to sequences of *pmo*A, the gene coding for a subunit of the particulate methane monooxygenase, than to *amo*A genes from the *Betaproteobacteria* AOB (β-AOB) (Holmes et al., 1995). However, due to the apparent lack of gammaproteobacterial ammonia oxidizers in estuaries (Bernhard et al., 2005b; Ward et al., 2007) or salt marshes (Moin et al., 2009), they will not be considered further in this review.

Although all aerobic AOB carry out the same basic metabolic processes, there exists great ecophysiological diversity among the cultivated strains. The β-AOB are represented by 14 cultivated strains (Koops and Pommerening-Roser, 2001), divided into two main clusters, *Nitrosomonas* and *Nitrosospira*. The greatest physiological and phylogenetic diversity exists within the *Nitrosomonas* cluster, which contains the type species, *Nitrosomonas europaea*. Several species (*Nitrosomonas marina, Nitrosomonas aestuarii*, and *Nitrosomonas cryotolerans*) are obligately halophilic, while the remaining species in the *Nitrosomonas* and *Nitrosospira* genera either have no salt requirement, are halotolerant or moderately halophilic (Koops and Pommerening-Roser, 2001). Among the 14 species, there are also widely differing substrate affinities, with *Nitrosomonas oligotropha* and *Nitrosomonas ureae* displaying the lowest K_s values (1.9–4.2 μM NH_3), and *N. europaea* and related species having the highest K_s values (30–61 μM NH_3) (Koops and Pommerening-Roser, 2001). Based on the broad physiological differences among the AOB, one might expect that they will be differentially distributed in the environment.

Unfortunately, most cultured ammonia-oxidizing bacteria do not represent the majority of AOB found in natural environments based on sequence analysis of 16S rRNA genes and the functional gene, ammonia monooxygenase (see review by Kowalchuk and Stephen, 2001). The lack of environmentally-relevant AOB in culture collections represents a significant barrier to understanding their ecophysiology and is likely a reflection of substantial differences in their nutritional requirements and physiological limitations compared to cultivated AOB.

1.3. *Discovery of ammonia oxidizing archaea*

Until recently, our understanding of the diversity of aerobic ammonia oxidizers was restricted to members of the *Proteobacteria*. However, the new taxonomy for ammonia oxidizers must now include members from the Domain *Archaea*. When *Archaea* were first described in the late 1970s, they were considered

Download English Version:

https://daneshyari.com/en/article/4540870

Download Persian Version:

https://daneshyari.com/article/4540870

Daneshyari.com