REVIEW ARTICLE

Environmental factors shaping the ecological niches of ammonia-oxidizing archaea

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Abstract

For more than 100 years it was believed that bacteria were the only group responsible for the oxidation of ammonia. However, recently, a new strain of archaea bearing a putative ammonia monooxygenase subunit A (*amoA*) gene and able to oxidize ammonia was isolated from a marine aquarium tank. Ammonia-oxidizing archaea (AOA) were subsequently discovered in many ecosystems of varied characteristics and even found as the predominant causal organisms in some environments. Here, we summarize the current knowledge on the environmental conditions related to the presence of AOA and discuss the possible site-related properties. Considering these data, we deduct the possible niches of AOA based on pH, sulfide and phosphate levels. It is proposed that the AOA might be important actors within the nitrogen cycle in low-nutrient, low-pH, and sulfide-containing environments.

Introduction

Until recently, autotrophic ammonia/ammonium oxidation was assumed to be restricted to aerobic ammonia-oxidizing bacteria (AOB) and anaerobic ammonium-oxidizing (Anammox) bacteria. This has been changed with the detection of a unique ammonia monooxygenase (AMO) gene on an archaeal-associated scaffold from the samples of the Sargasso Sea, a nutrient-limited open-ocean environment (Venter *et al.*, 2004) and on genomic fragments of archaea from a large-insert environmental fosmid library of calcareous grassland soil (Treusch *et al.*, 2005). The first strain of ammonia-oxidizing archaea (AOA), *Nitrosopumilis maritimus*, was isolated from the rocky substratum of a tropical marine aquarium tank (Könneke *et al.*, 2005). The cultivated archaeon revealed the near-stoichiometric aerobic oxidation of ammonia to nitrite, the fixation of inorganic carbon and growth inhibition in the presence of organic carbon. It is the first chemolithoautotrophic nitrifier in the domain archaea and the first mesophilic species in the marine group 1 of the crenarchaeota (Könneke *et al.*, 2005). Putative archaeal *amoA* gene (α-subunit of AMO) clusters were also discovered from the sponge symbiont *Cenarchaeum symbiosum* (Hallam *et al.*, 2006b). Most recently, a thermophilic ammonia-oxidizing archaeon, *Candidatus* Nitrosocaldus yellowstonii, was cultivated from the sediments of a hot spring in Yellowstone National Park (de la Torre *et al.*, 2008) as well as the moderately thermophilic ammonia-oxidizing crenarchaeote, *Candidatus* Nitrososphaera gargensis, enriched from the biomass of a hot spring (Hatzenpichler *et al.*, 2008).

Studies indicate that the archaeal *amoA* gene is ubiquitous. The presence of the archaeal *amoA* gene was demonstrated in coastal and marine waters (Francis *et al.*, 2005; Wuchter *et al.*, 2006; Coolen *et al.*, 2007; Herfort *et al.*, 2007; Lam *et al.*, 2007; Mincer *et al.*, 2007; Nakagawa *et al.*, 2007; Agogue *et al.*, 2008; Beman *et al.*, 2008), in subterranean estuary (Santoro *et al.*, 2008), in coastal, estuarine and cold seep sediments (Francis *et al.*, 2005; Beman & Francis, 2006; Caffrey *et al.*, 2007; Nakagawa *et al.*, 2007; Mosier & Francis, 2008; Park *et al.*, 2008; Sahan & Muyzer, 2008), in freshwater sediments (Francis *et al.*, 2005; Herrmann *et al.*, 2008), in a subsurface of radioactive thermal spring and neighboring biofilms (Weidler *et al.*, 2007), in the sediments and microbial mats/mud of hot springs and geothermal biofabrics (Spear *et al.*, 2007; de la Torre *et al.*, 2008; Hatzenpichler

et al., 2008; Reigstad *et al.*, 2008), and in coral reefs (Beman *et al.*, 2007; Siboni *et al.*, 2008). Moreover, it was reported in terrestrial systems both in sandy, agricultural, semiarid and forest soils, and grasslands (Treusch *et al.*, 2005; Leininger *et al.*, 2006; He *et al.*, 2007; Adair & Schwartz, 2008; Boyle-Yarwood *et al.*, 2008; Hansel *et al.*, 2008; Le Roux *et al.*, 2008; Shen *et al.*, 2008; Tourna *et al.*, 2008) and in the rhizosphere of the freshwater macrophyte *Littorella uniflora* (Herrmann *et al.*, 2008) and in paddy soils (Chen *et al.*, 2008). Finally, it has also been detected in man-made systems such as aquarium biofilm systems (Urakawa *et al.*, 2008) and groundwater filter (de Vet *et al.*, 2009) as well as activated sludge bioreactors (Park *et al.*, 2006). Most remarkably, in the majority of the soil samples from terrestrial sites, the estuarine and hot spring sediment samples, and coastal and marine waters/ecosystems where the abundances of archaeal and bacterial *amoA* gene copies were investigated, the archaeal *amoA* ones were dominant over the bacterial ones (Leininger *et al.*, 2006; Wuchter *et al.*, 2006; Beman *et al.*, 2007; Caffrey *et al.*, 2007; He *et al.*, 2007; Nakagawa *et al.*, 2007; Adair & Schwartz, 2008; de la Torre *et al.*, 2008; Hatzenpichler *et al.*, 2008; Park *et al.*, 2008; Reigstad *et al.*, 2008; Shen *et al.*, 2008). In coastal and open ocean, the archaeal to bacterial *amoA* ratio and crenarchaeotal to bacterial *amoA* ratio were in the ranges of 10–100 and 10–1000, respectively (Wuchter *et al.*, 2006). Beman *et al.* (2008) also demonstrated that AOA outnumbered *Betaproteobacteria* AOB by a factor of 37–217 in the surface waters of the Gulf of California. The abundance ratio of archaeal to bacterial *amoA* genes ranged from 17 to $>$ 1600 in semiarid soil samples taken along an elevation gradient (1556–2620 m) (Adair & Schwartz, 2008) and was as much as 80 in estuarine sediments (Caffrey *et al.*, 2007). Moreover, in surface sediments (Francis *et al.*, 2005), in the samples taken from hot spring sediments (de la Torre *et al.*, 2008; Hatzenpichler *et al.*, 2008; Reigstad *et al.*, 2008), in one of the activated sludge samples (Park *et al.*, 2006), and in the samples taken from corals and reefs (Beman *et al.*, 2007) no bacterial *amoA* but only archaeal *amoA* were detected. Based on the majority of the quantitative and qualitative analyses, it can be deduced that AOA are potentially important actors of the nitrogen cycle in many ecosystems, even if some exceptions can be observed in terms of abundances of AOA being lower than AOB (Caffrey *et al.*, 2007; Lam *et al.*, 2007; Mosier & Francis, 2008; Santoro *et al.*, 2008). Nicol & Schleper (2006) have summarized the information on crenarchaeal marine and terrestrial ammonia oxidation and speculated on their possible contribution to global nitrogen cycling. Francis *et al.* (2007) reviewed archaeal ammonia oxidation considering the current knowledge and discussed the unknowns and its possible implications on global nitrogen and carbon cycles. Prosser & Nicol (2008) also reviewed the relative contribution of bacterial and archaeal ammonia oxidizers in many environments while highlighting the requirements and limitations in techniques used in retrieval of the genes and their assessment. Indeed, the contribution of AOA to the oceanic ammonia oxidation has been recently assessed by ^{15}N-labeled NH_4^+ in the Gulf of California upper water column (0.01–93.1 nmol N L^{-1} day^{-1}), where AOB are relatively low in numbers or undetectable (Beman *et al.*, 2008). Lam *et al.* (2007) also revealed the contribution of AOA to nitrification in the Black Sea. AOA were reported to support half of the nitrite required for the anammox reaction in the Black Sea. The recent recovery of the archaeal *amoA* genes from hot springs (de la Torre *et al.*, 2008; Reigstad *et al.*, 2008), and the enrichment and *in situ* activity studies (Reigstad *et al.*, 2008) indicate that archaeal ammonia oxidation is even possible at very high temperatures (74 and 85 °C).

Here, in view of recent knowledge, we summarize the environmental conditions related to the presence and/or dominance of AOA and discuss the possible site-related properties and the potential niche of AOA. Considering the limited number of cultivated strains or enrichments, the missing *in situ* archaeal ammonia oxidation activities in the majority of the hitherto research studies and the potential nitrification rates (PNRs) that have not been optimized for AOA, the difficulty of giving an overview on the topic should be noted. It should also be noted that the abundance of AOA over AOB in terms of *amoA* gene numbers might not necessarily be related to the dominant archaeal ammonia oxidation activity, considering the cell sizes of both oxidizers and the possible inadequacy in targeting both groups with the current primers and/or due to their presence in low levels. Yet, the physico-chemical properties of the sites where archaeal (or crenarchaeotal) *amoA* genes have been discovered, particularly, sulfide in this study, warrant examination as still being indicative of possible growth conditions and the potential niche of AOA.

Site-related growth conditions with respect to the occurrence of AOA

Ammonium levels

Typical ammonium concentrations in the open ocean are $<$ 0.03–1 μM (Könneke *et al.*, 2005; Wuchter *et al.*, 2006; Herfort *et al.*, 2007; Beman *et al.*, 2008). Ammonium concentrations in the estuaries are reported to be usually $<$ 22–45 μM, and up to 115 μM in estuaries receiving agricultural run-off (Beman & Francis, 2006; Santoro *et al.*, 2008). The archaeal or crenarchaeotal *amoA* genes were retrieved in low ammonium-containing environments such as open-ocean, marine water columns, sediments and hot springs (Wuchter *et al.*, 2006; Coolen *et al.*, 2007; Lam *et al.*, 2007; Hatzenpichler *et al.*, 2008; Herrmann *et al.*, 2008;

Reigstad *et al.*, 2008). It has been stated that low ammonium concentrations might result in the limited growth of AOA in marine or low N-containing ecosystems (Könneke *et al.*, 2005; Reigstad *et al.*, 2008). On the other hand, Könneke *et al.* (2005) speculated that marine crenarchaeota keep ammonium concentrations low. The isolated archaeon *N. maritimus* can grow to a maximum density with a growth rate of 0.78 day^{-1} in a defined medium with 0.5 mM NH_4^+ (Könneke *et al.*, 2005), which is similar to that of the autotrophic thermophilic ammonia-oxidizing archaeon (0.8 day^{-1}) cultivated from hot spring sediments in a medium with 1 mM NH_4Cl (de la Torre *et al.*, 2008). The moderately thermophilic ammonia-oxidizing archaeon, *C.* Nitrososphaera gargensis, enriched from the biomass of hot springs with 5.9 μM NH_4^+, was partially inhibited at an ammonium level of 3.1 mM, whereas it was highly active at ammonium levels of 0.14 and 0.8 mM (Hatzenpichler *et al.*, 2008). However, archaeal *amoA* genes were also detected at relatively higher total ammonium concentrations between 1.2 and 3.2 mM (Park *et al.*, 2006) and *amoA* expression was identified even at 10 mM NH_4Cl (Treusch *et al.*, 2005). The majority of the studies indicate the retrieval of archaeal *amoA* genes and *in situ* AOA activities (Beman *et al.*, 2008; Reigstad *et al.*, 2008) in low ammonium-containing environments, and it is likely that some AOA ecotypes have a versatile nature. It should also be noted that through the depth of North Atlantic (< 1000 m), where very low ammonium levels (< 5 nM) are observed, the archaeal *amoA* gene numbers decrease markedly from subsurface waters to 4000 m depth, and from subpolar to equatorial deep waters (Agogue *et al.*, 2008). Yet, they are still abundant over *Betaproteobacteria* counterparts.

Organic carbon

Nitrosopumilis maritimus was reported to be inhibited by organic substrates even at very low concentrations and to be capable of autotrophic oxidation of ammonia to nitrite, and inorganic carbon fixation (Könneke *et al.*, 2005). The incorporation of bicarbonate into single ammonia-oxidizing archaeal cells was observed in the presence of ammonium, but was absent in medium lacking ammonium, as monitored by microautoradiography and catalyzed reporter deposition-FISH (CARD-FISH) (Hatzenpichler *et al.*, 2008). The cultivated thermophilic *C.* Nitrosocaldus yellowstonii also displayed autotrophic ammonia oxidation using the bicarbonate (5 mM) as sole carbon source (de la Torre *et al.*, 2008). Diluted yeast extract (0.2 mg L^{-1}), acetate (2 mM) or H_2 (716 torr, *c.* 1 atm.) resulted in the inhibition of the nitrite production. Yet, Hallam *et al.* (2006b) retrieved genes in *C. symbiosum* predicted to encode components of a modified 3-hydroxypropionate cycle, known in carbon-fixing thermophilic crenarchaeota as well as a near-complete oxidative tricarboxylic acid cycle. This is consistent with both autotrophic and organotrophic lifestyles and *C. symbiosum* may function either as a strict autotroph or as a mixotroph utilizing both carbon dioxide and organic material as carbon sources (Hallam *et al.*, 2006a, b).

Temperature

The nonthermophilic (i.e. *N. maritimus* and *C. symbiosum*) and thermophilic (i.e. *C.* Nitrosocaldus yellowstonii and *C.* Nitrososphaera gargensis) members of the ammonia-oxidizing crenarchaeota, and the archaeal *amoA* genes so far were detected at sites with very low (down to 0.2 °C) to high (up to 97 °C) temperatures. The archaeal *amoA* genes were retrieved in aquarium biofilm systems with a water temperature of 5.5 °C (Urakawa *et al.*, 2008), in estuaries of 4 °C (Sahan & Muyzer, 2008) and in marine water columns of 2000 and 2956 m depth with temperatures as low as 0.2 °C (Nakagawa *et al.*, 2007). They have been detected in the moderately hot springs, and in the sediments, microbial mats and mud of hot springs with water temperatures of 42 and 46 °C (Weidler *et al.*, 2007; Hatzenpichler *et al.*, 2008) and 60–97 °C (de la Torre *et al.*, 2008; Reigstad et al., 2008), respectively.

The thermophilic ammonia-oxidizing archaeon *C.* Nitrosocaldus yellowstonii displayed appreciable nitrite production (26–45 μmol day^{-1}) at temperatures between 60 and 74 °C with an optimal growth in the range of 65–72 °C (de la Torre *et al.*, 2008). Above 74 °C nitrite production was not observed in the primary enrichments of sediment samples (de la Torre *et al.*, 2008). Yet, Reigstad *et al.* (2008) observed considerable *in situ* gross nitrification rates (13–21 μmol nitrate L^{-1} mud day^{-1}) using the ^{15}N-pool dilution technique at 84–85 °C doubling with the increase in the ammonium levels from 0.3–14 μM to 0.5 mM. The retrieval of archaeal *amoA* genes in such a wide temperature range and their hitherto expression under low to very high temperature environments indicate the broad distribution and diversity of AOA.

Salinity

Archaeal *amoA* genes were detected in marine water columns of the Sargasso Sea (at a depth of 0–300 m) with high practical salinity units (psu) such as 36.6 (Venter *et al.*, 2004). In estuarine sediments, PNRs were positively correlated with the archaeal *amoA* genes but not with the AOB *amoA* genes and increased with decreasing salinity (Caffrey *et al.*, 2007). In subterranean estuarine sediments sampled along a salinity gradient (0.5–33 psu), the archaeal *amoA* copy numbers were relatively more constant than the bacterial counterparts, decreasing with decreasing salinity both in winter and in summer (Santoro *et al.*, 2008). The retrieval of archaeal *amoA* genes in estuarine sediments with

psu ranging from 0 to 38 (Francis *et al.*, 2005; Beman & Francis, 2006; Caffrey *et al.*, 2007), even in oligohaline and euryhaline estuarine sites (Caffrey *et al.*, 2007), and the almost constant archaeal *amoA* copies with changing salinities from 0.5 to 33 (Santoro *et al.*, 2008) indicate the high tolerance of AOA ecotypes to salinity in specific environments and/or possible dominant ecotypes selected by specific salinity ranges. Depending on the site, salinity was shown to be a significant factor in determining the diversity of AOA community structure (Francis *et al.*, 2005; Mosier & Francis, 2008) and their spatial distribution (Sahan & Muyzer, 2008). Francis *et al.* (2005) have discovered archaeal *amoA* sequences from North San Francisco Bay (0.5 psu) completely falling into one distinct phylogenetic cluster, thus, indicating a possible unique low-salinity AOA type. It is likely that, in addition to the AOA species tolerant to the wide range of salinity conditions, some AOA ecotypes are specific for a narrow niche.

In coastal and open-ocean (salinity $>$ 27 psu), the archaeal to bacterial *amoA* ratios and crenarchaeotal to bacterial *amoA* ratios were found in the range of 10–100 and 10–1000, respectively (Wuchter *et al.*, 2006; Mincer *et al.*, 2007; Beman *et al.*, 2008). Yet, Santoro *et al.* (2008) reported that AOA were 30 times less abundant than the *Betaproteobacteria* AOB in the oxic saline portions of the aquifer, and 10 times more abundant in the low-oxygen fresh-water and brackish portions of the aquifer. The relation between the ratio of *Betaproteobacteria* AOB to AOA and salinity was found to be strong in subterranean estuarine sediments, but was no longer significant after dissolved oxygen (DO) was also considered (decrease from $r = 0.89$–0.58) (Santoro *et al.*, 2008). It should be noted that the archaeal *amoA* copy numbers were relatively more constant at salinity and oxygen gradients of 0.5–33 psu and 0.1–0.2 mM, respectively, while the bacterial counterparts decreased with decreasing salinity and/or DO (Santoro *et al.*, 2008). It is likely that, as well as salinity, DO is also an important parameter in determining the dominant ammonia oxidizer phylotype in estuarine sediments. Similarly, Mosier & Francis (2008) detected that the *Betaproteobacteria amoA* in the coastal aquifer sediments of San Francisco Bay estuary was up to 30-fold more abundant than the archaeal *amoA* at high salinities (22–31 psu) and low C/N (7–9) conditions. On the other hand, under low salinity (0.2–9) and high C/N (12–25) archaeal *amoA* genes were more abundant than *Betaproteobacteria amoA* genes (Mosier & Francis, 2008).

DO levels

The lower range of DO levels might be among the most determinative parameters of the sites where archaeal *amoA* have been detected. The existence of archaeal *amoA* was demonstrated in activated sludge bioreactors with low DO concentrations ($< 6.3\,\mu M$) operating under oxic–anoxic conditions, enabling simultaneous nitrification–denitrification (Park *et al.*, 2006). AOA have also been detected in the water columns of Eastern Tropical North Pacific, one of the largest pelagic oxygen minimum zones (OMZs) in the ocean, at a depth of 200 m with DO levels $< 3.1\,\mu M$ (Francis *et al.*, 2005) as well as in suboxic water columns of the Black Sea with a DO level of 1 μM (Coolen *et al.*, 2007). Yet, Santoro *et al.* (2008) retrieved almost constant archaeal *amoA* gene copies in aerobic subterranean aquifer sediments with pore water DO levels of 0.1–0.2 mM. Könneke *et al.* (2005) reported the fully aerobic growth of *N. maritimus* during cultivation and near-stoichiometric conversion of ammonium to nitrite. Similar aerobic ammonium-oxidation and stoichiometric nitrite production was also depicted for the thermophilic archaeon *C.* Nitrososphaera gargensis at a DO level of 0.2 mM (Hatzenpichler *et al.*, 2008). It is likely that AOA or some specific ecotypes tolerate a wide range of oxygen levels from $< 3.1\,\mu M$ to 0.2 mM. However, some ecotypes might be more suited to the low-oxygen and oxic–anoxic environments. How long AOA can withstand high levels of oxygen merits examination to understand the contribution of archaeal ammonia oxidation in fully aerobic natural and engineered systems.

pH

The pH values of the environments, where archaeal *amoA* genes were found, vary over a wide range, going from 3.7 (He *et al.*, 2007) to 8.65 (Wuchter *et al.*, 2006; Shen *et al.*, 2008; Urakawa *et al.*, 2008) (Table 1). Thermophilic archaeal *amoA* genes were detected in sediments, microbial mats and mud of hot springs with predominantly alkaline (pH = 8.0–9.0) or acidic (pH = 2.5) conditions (de la Torre *et al.*, 2008; Reigstad *et al.*, 2008). It appears that AOA have a wide ecological and phylogenetic diversity.

In the hot springs with pH values of 2.5–7, no bacterial but archaeal *amoA* genes were detected (Reigstad *et al.*, 2008). Hansel *et al.* (2008) could not retrieve any common AOB or *Betaproteobacteria amoA* genes along the soil profile with pH ranges of 4.5–6.9, but they detected archaeal *amoA* genes. Furthermore, Schmidt *et al.* (2007) reported the low abundance of AOB in acidic soils (pH = 2.9) subjected to nitrogen and sulfur deposition, and suggested the negligible contribution of autotrophic AOB to nitrification even after 6 years of continual application. Yet, the existence or selection of specific AOB in acidic and neutral soils and the autotrophic ammonia oxidation in these environments have been demonstrated (de Boer & Kowalchuk, 2001; Nugroho *et al.*, 2006). Interestingly, quantitative molecular analyses performed for soil samples indicate that AOA are more dominant than AOB in majority of the soils with pH values

Table 1. Schematic positioning of the literature references with respect to the occurrences of AOA in relation to the pH values

	pH range*						
Sample type	2.00–2.99	3.00–3.99	4.00–4.99	5.00–5.99	6.00–6.99	7.00–7.99	8.00–9.00
Sediments and microbial mats of hot springs	1	1, 2		1	1, 2	1, 2, 3	2, 4
Biofabrics in the geothermal mine					5		
Unfertilized and long-term fertilized soil samples, forest soil		6	6, 7, 8, 9	6, 7, 9, 10	7, 9, 10	10, 11	12
Aquarium biofiltration systems							13
Marine-related waters, cultivation studies						14	15

*1, Reigstad *et al*. (2008); 2, de la Torre *et al*. (2008); 3, Hatzenpichler *et al*. (2008); 4, Weidler *et al*. (2007); 5, Spear *et al*. (2007); 6, He *et al*. (2007); 7, Nicol *et al*. (2008); 8, Boyle-Yarwood *et al*. (2008); 9, Hansel *et al*. (2008); 10, Leininger *et al*. (2006); 11, Tourna *et al*. (2008); 12, Shen *et al*. (2008); 13, Urakawa *et al*. (2008); 14, Könneke *et al*. (2005); 15, Wuchter *et al*. (2006).

as low as 3.7 (Leininger *et al*., 2006; He *et al*., 2007; Boyle-Yarwood *et al*., 2008; Nicol *et al*., 2008). Some of the data from the studies of Leininger *et al*. (2006) and He *et al*. (2007) are given in Table 2. Leininger *et al*. (2006) detected archaeal *amoA* genes in acidic to neutral pristine and fertilized soils with a pH range of 5.5–7.3, where the archaeal *amoA* gene copy numbers were 1.5–230 times more abundant than the bacterial *amoA* genes in topsoils (0–10 cm). He *et al*. (2007) also demonstrated higher ratios of archaeal to bacterial *amoA* gene copy numbers (1.02–12.36) in long-term fertilized and unfertilized soils (0–20 cm) with relatively lower pH values of 3.7–5.8 both in winter and summer. Similarly, Nicol *et al*. (2008) found that bacterial *amoA* genes made up 0.8–3.1% of archaeal *amoA* genes across all soils of varied pH ranging from 4.9 to 7.5. They have also demonstrated that different bacterial and archaeal ammonia-oxidizer phylotypes are selected in soils of different pH and each group has distinct physiological and ecological niches. They stated that the archaeal *amoA* gene abundance decreased with increasing pH, and bacterial *amoA* gene abundance was generally lower. Boyle-Yarwood *et al*. (2008) could only detect bacterial *amoA* genes in forest soils of pH 5. However, the archaeal to bacterial *amoA* gene ratios were found as 0.42–1.8 in the forest soils with pH 4 and vegetated with different types of trees, where higher nitrification rates (2.86 μg N g^{-1} dry soil day^{-1}) were observed compared with soils with higher pH (0.88 μg N g^{-1} dry soil day^{-1}) (Boyle-Yarwood *et al*., 2008). It appears in general that AOA ecotypes in the topsoils are more tolerant to low pH values than AOB ecotypes.

Nicol *et al*. (2008) investigated the effect of soil pH (4.9–7.5) on the transcriptional activity of ammonia-oxidizers, which indicated decreasing archaeal and increasing bacterial transcript abundances with increasing pH. The transcript abundance may not reflect protein production and activity (Nicol *et al*., 2008). Yet, the presence of distinct phylotypes and the highest ratio of archaeal vs. bacterial transcriptional activity occurring in the lowest pH soils indicate that autotrophic ammonia oxidation in acidic soils may be attributable largely to archaea (Nicol *et al*., 2008). It was also noted that the change in the measured nitrification rates were more closely correlated with the bacterial *amoA* gene and transcript abundances. On the other hand, nitrite production (26–45 μmol day^{-1}) was observed in primary enrichments of hot spring sediments with pH 8.3, where no bacterial but archaeal *amoA* genes were detected (de la Torre *et al*., 2008). Although nitrite production was not observed in the enriched samples taken from alkaline springs (pH 8.0–9.0) and acidic hot spring (pH 3.0) (de la Torre *et al*., 2008), Reigstad *et al*. (2008) detected *in situ* gross nitrification rates of 13–21 μmol nitrate L^{-1} mud day^{-1} from the samples of hot springs with pH 3. Leininger *et al*. (2006) demonstrated that the archaea in the soils with pH 5.5–7.1 were active *in situ* by reverse transcription quantitative PCR studies and DNA analyses. Furthermore, He *et al*. (2007) observed noticeable PNR values of 6.2–105.8 μg NO_2^--N g^{-1} dry soil day^{-1} in long-term fertilized and unfertilized acidic soils (0–20 cm, pH range 3.7–5.8) where the archaeal *amoA* gene copies were always higher than that of AOB (1.02–12.36) (Table 2). Although PNR measurements do not reflect the real *in situ* activity in the soils, the PNR values are comparable to the gross nitrification rates (6–170 μg N g^{-1} dry soil day^{-1}) detected in the soils (peat, mineral and agricultural soils) with a pH range of 4.1–7.0 (Mørkved *et al*., 2007). These results indeed may indicate the possible contribution of AOA in ammonia oxidation in soils with pH values as low as 3.7.

In addition to pH, other factors such as soil type, water content, temporal changes, fertilization type and nutrient bioavailability might affect the population sizes and community structure of ammonia oxidizers, and in turn the nitrification rates in soils (Nugroho *et al*., 2006; Schmidt *et al*., 2007; Hansel *et al*., 2008). He *et al*. (2007) reported the highest PNR values of 50.4 and 105.6 μg NO_2^--N g^{-1} dry soil day^{-1} for fallow soils and nitrogen/phosphorus/potassium+organic manure (NPK+OM)-treated soils, respectively, with almost the same pH values (5.8) (Table 2). The highest AOA and AOB population sizes (in summer) were

Table 2. Comparison of the archaeal and bacterial *amoA* gene copy numbers given in two studies performed in soils of acidic to neutral conditions (Leininger *et al.*, 2006; He *et al.*, 2007)

							amoA copies (g^{-1} dry soil)		Ratio of AOA *amoA* to AOB *amoA* gene copies	
Usage and soil type	Depth (cm)	pH range	WEON	WEOC	OM	PNR	AOA	AOB		References
Fertilized or unfertilized;	0–10	5.5–7.3	0.9–4.8	3–85.1	ND	ND	7×10^6–1×10^8	6.5×10^4–5.2×10^7	1.5–230	Leininger *et al*. (2006)
all types of soil	0–20	3.7–5.8	ND	ND	13.7–21.3	6.2–105.8	4.1×10^6–9.6×10^7	5.8×10^5–9.3×10^7	1.02–12.36	He *et al*. (2007)
Agr., N		3.7	ND	ND	15.2	11.3	$8.3 \times 10^{6*}$	$2.8 \times 10^{6*}$	3.0†	
Agr., NK	0–20	3.8			14.3	23.4	$2.6 \times 10^{7*}$	$3.8 \times 10^{6*}$	6.59	He *et al*. (2007)
Agr., CK		5.5			13.6	35.8	$2.8 \times 10^{7*}$	$5.6 \times 10^{6*}$	5.12	
Agr., fallow soil		5.8			13.7	49.7	$7.1 \times 10^{7*}$	$4.5 \times 10^{7*}$	1.58†	
Agr., NPK+OM		5.8			21.3	105.8	$9.6 \times 10^{7*}$	$9.3 \times 10^{7*}$	1.03†	
Agr., unfertilized		6.4	1.2	35.2			1.5×10^7	6.5×10^4	232	
Agr., mineral fertilized		6.3	2.3	57.1			5.6×10^7	7.2×10^5	78	
Agr., mineral+organic fertilized		6.7	4.8	85.1			7.0×10^7	4.7×10^5	149	
Pristine, sandy	0–10	7.1	0.9	7.6	ND	ND	5.5×10^7	1.0×10^6	53	
Pristine, limestone soil		6.9	1.1	10.2			3.5×10^7	2.5×10^6	14	Leininger *et al*. (2006)
Agr., pasture land		6.1	3.8	25.9			4.7×10^7	3.2×10^7	1.5	
Agr., grassland		5.5	1.2	5.5			1.3×10^8	5.2×10^7	2.5	
Agr., ploughed site		7.3	2.4	7.7			6.1×10^7	6.6×10^5	92	
Agr., barley field		6.0	0.6	3			7.3×10^6	2.6×10^6	2.8	

*Not given in detail, but derived from figures considering the summer data.

†Calculated from the data.

N, nitrogen; NK, nitrogen/potassium; CK, control without fertilizer; NPK+OM, nitrogen/phosphorus/potassium+organic manure; Agr., agricultural; WEON, water extractable organic nitrogen (mg kg^{-1} dry soil); WEOC, water-extractable organic carbon (mg kg^{-1} dry soil); OM, organic matter (g kg^{-1}); PNR, potential nitrification rate (μg NO_2^--N g^{-1} dry soil day^{-1}); ND., no data.

Table 3. Comparison of the archaeal and bacterial *amoA* gene copy numbers through the depth of varied soil types (Leininger *et al.*, 2006)

Usage and soil type	Depth (cm)	WEON	WEOC	pH	*amoA* copies (g^{-1} dry soil) AOA	*amoA* copies (g^{-1} dry soil) AOB	Ratio of AOA *amoA* to AOB *amoA* gene copies *
Agricultural, unfertilized	0–15	1.22	35.2	6.4	1.5×10^7	6.5×10^4	231
	15–30	1.09	28.4	ND	1.8×10^7	2.7×10^4	667
	30–40	0.99	27.3		1.4×10^7	4.6×10^3	3043
Agricultural, mineral fertilized	0–15	2.34	57.1	6.3	5.6×10^7	7.2×10^5	78
	15–30	1.44	53.3	ND	4.2×10^7	9.7×10^4	433
	30–40	3.37	57.5		1.5×10^7	2.2×10^4	682
Agricultural, mineral+organic fertilized	0–15	4.76	85.1	6.7	7.0×10^7	4.7×10^5	149
	15–30	5.24	85.6	ND	9.3×10^7	7.3×10^5	127
	30–40	7.87	78.2		5.2×10^7	2.1×10^5	248
Pristine, sandy	0–10	0.9	7.6	7.1	5.5×10^7	1.0×10^6	55
	10–20	0.9	7.6		7.2×10^7	4.3×10^5	167
	20–30	0.7	6.3		3.6×10^7	2.1×10^5	171
	30–40	0.6	5.9	ND	1.4×10^7	5.9×10^4	237
	40–50	0.4	5.3		1.8×10^7	1.6×10^4	1125
	60–70	0.4	4.5		3.2×10^6	3.8×10^3	842

*Calculated from the data.

WEON, water-extractable organic nitrogen (mg kg^{-1} dry soil); WEOC, water-extractable organic carbon (mg kg^{-1} dry soil); ND, no data.

also detected in NPK+OM-treated soils followed by fallow soils. The mineral+organic manure application resulted in a clearer increase in the AOB *amoA* gene copy numbers than did AOA (Table 2). In other words, AOA may tend to be prevalent under conditions of chronic energy shortage, as stated for other archaea (Valentine, 2007). A similar result was also observed by Leininger *et al.* (2006) for unfertilized, mineral-fertilized and mineral+organic-fertilized soils through the soil depth (Table 3). With increasing depth, a decrease in the bacterial *amoA* gene copy numbers was observed, whereas the archaeal *amoA* copy numbers remained constant. As a result, ratios of AOA to AOB *amoA* gene copies reached a maximum value of 3000 in unfertilized soil, $>$ 500 in mineral-fertilized soil and around 250 in mineral+organic-fertilized soils (Fig. 1). The decrease in the ratios of AOA to AOB *amoA* copy numbers in order from unfertilized to mineral+organic-fertilized soils was attributed to the increased amount of nitrogen and carbon in the fertilized soils as well as their bioavailability through the depth (Table 3). The significant increase in the total *amoA* gene copy numbers (Leininger *et al.*, 2006; He *et al.*, 2007) as well as in the PNR values (He *et al.*, 2007) observed with the increasing nitrogen or carbon sources was mainly due to the increase in the AOB copy numbers and their possible contribution. The archaeal *amoA* gene copies did not change significantly as their counterpart through the depth in the agricultural soils whether fertilization was applied or not. The decrease in the archaeal *amoA* gene copies with the increasing depth through the sandy pristine soil might be attributed to the lower nitrogen and carbon availability compared with the agricultural soils with higher water-extractable nitrogen and carbon (Leininger *et al.*, 2006) (Table 3, Fig. 1). Yet, the decrease in the AOB *amoA* gene copies is still much more drastic than that of AOA. Adair & Schwartz (2008) detected no correlation between the AOA population sizes and soil C/N, but the population sizes of the bacterial ammonia oxidizers were reported to correlate to soil C/N as well as to temperature, percent sand and precipitation. The effect of the available nutrient and carbon content on the selection of the dominant ammonia-oxidizer phylotypes and their activities requires further research.

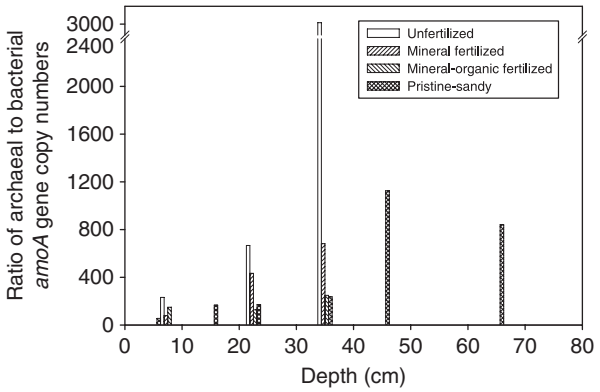

Fig. 1. Ratio of archaeal to bacterial *amoA* gene copy numbers through the depth of varied soil types (Leininger *et al.*, 2006). Figure indicates the higher archaeal *amoA* gene abundance in the low nutrient-containing soils compared with the treated soils. The AOA abundance displays an increasing trend with increasing depth (depth data correspond to the mid-depth values of the original data given in Table 3).

Sulfide levels

Recently, archaeal *amoA* genes were detected in the biofabrics of speleothems obtained from a hot geothermal mine (50 °C) with a soluble H_2S concentration of 50 μM and pH 6.4 (Spear *et al.*, 2007). They were retrieved from moderately hot to hot springs (Weidler *et al.*, 2007; de la Torre *et al.*, 2008; Hatzenpichler *et al.*, 2008; Reigstad *et al.*, 2008) usually known to have sulfidic properties (Langner *et al.*, 2001; Elshahed *et al.*, 2003, 2007) and from possible sulfide-containing cold seep sediments (Nakagawa *et al.*, 2007). Archaeal *amoA* genes were also detected in estuarine sediments (0–0.5 cm) with pore water sulfide concentrations of 0.1–0.5 mM (Caffrey *et al.*, 2007). Besides, at the upper 15–30 m of the anoxic water columns of the Black Sea with prevailing sulfide concentrations up to 30 μM, both archaeal *amoA* and marine crenarchaeotal phylotypes were detected (Coolen *et al.*, 2007). In another study, it was reported that the ratio of crenarchaeotal to total AOB *amoA* gene copies decreased from 4.6–44.1 to 0.4–0.6 through the oxic and suboxic zones of the Black Sea to the suboxic–anoxic and anoxic zones, respectively (where the maximum sulfide concentration of 5 μM was detected below the suboxic zone, i.e. anoxic zone) (Lam *et al.*, 2007). Yet, AOA were found to be among the important nitrifiers in the Black Sea, being mainly responsible for the NO_x production in the lower oxic zone, whereas the γ-AOB were active in the suboxic zone. Caffrey *et al.* (2007) reported a negative correlation ($r = -0.46$) between AOA *amoA* and sulfide concentrations. However, they also reported a positive correlation between AOA and potential nitrification ($r = 0.80$ and 0.66 for two different sites). The increasing nitrification rate with the abundance of archaeal *amoA* genes in estuarine sediments with sulfide concentrations of 0.1–0.5 mM might indicate the tolerance of AOA to sulfide (Caffrey *et al.*, 2007). The *in situ* archaeal ammonia oxidation was already reported in the possible sulfidic and acidic hot springs (Reigstad *et al.*, 2008). Thus, AOA, or at least some ecotypes, are likely to be tolerant to sulfide and able to oxidize ammonia in its presence.

In the suboxic and sulfidic zones of the Black Sea (central station) nine unique phylotypes of archaeal *amoA* were revealed, with a shift in the relative distribution of the different *amoA* phylotypes, which is explained as the adaptation of AOA to different oxygen levels and sulfide (Coolen *et al.*, 2007). A unique archaeal *amoA* band from the samples of sulfidic water (eastern and western stations) was also detected at 130 m below the sulfidic chemocline, which was not retrieved in the suboxic zone (Coolen *et al.*, 2007). The relative abundance of crenarchaeotal *amoA* was up to 50% of the total archaeal copies at this sulfidic zone. Crenarchaeol (distinct membrane lipid biomarker for planktonic archaea/crenarchaeota) concentrations were predominant in the suboxic layer and reached maximum concentrations (40–45 ng L^{-1}) below the suboxic zone with sulfide concentrations up to several tens of micromoles (Coolen *et al.*, 2007). The authors depicted that these biomarkers were due to the living cells rather than the accumulated dead cells, where the abundance of the latter was found in the upper suboxic zone but not within the sulfidic zone. The observed increase in the crenarchaeol below the suboxic zone may reveal the species-specific variability in the level of cellular crenarchaeol biosynthesis (Coolen *et al.*, 2007) as well as the changing AOA metabolism with sulfide exposure.

The survival of AOA or certain ecotypes under sulfide exposure, instead of inhibition as observed for AOB carrying the copper-containing AMO (Hooper & Terry, 1973; Sears *et al.*, 2004), merits further investigation. Possible tolerance strategies can be proposed. The application of 100 μM allylthiourea, a dose known to completely inhibit AOB by interfering with catalyses by AMO (Hooper & Terry, 1973), did not result in a complete inhibition of AOA enriched from moderately thermophilic springs (46 °C) and a residual bicarbonate incorporation activity was detected using CARD-FISH and microautoradiography (Hatzenpichler *et al.*, 2008). This was attributed to either the build-up of energy storage compounds in the absence of allylthiourea during the preincubation period or the higher affinities of archaeal *amoA* genes and/or not being as dependent on copper as bacterial *amoA* (Hatzenpichler *et al.*, 2008). Genes predicting a modified 3-hydroxypropionate cycle, known in thermophilic archaea, *Sulfolobales*, metabolizing sulfur, pyrite or hydrogen, were also retrieved from the *C. symbiosum* genome (Hallam *et al.*, 2006b). AOA may have unique enzymes/genes similar to their relatives *Sulfolobales*, which make them thrive and oxidize ammonia under sulfide conditions. The reason of the AOA tolerance to sulfide is unclear. Nevertheless, it is worthwhile investigating the tolerance levels, because AOA might oxidize ammonia in sulfide-containing environments.

Phosphate

Herfort *et al.* (2007) demonstrated the positive correlation between crenarchaeotal 16S rRNA gene copies and phosphate concentrations ($r = 0.71$–0.76 for bottom waters and 0.78 for surface waters) as well as with ammonia, nitrate and nitrite concentrations in the southern North Sea through the three seasons. They have detected crenarchaeotal *amoA* genes (0.04–55×10^3 copies mL^{-1}) in surface waters of the southern North Sea, where dissolved organic phosphorus (DOP) ranges from 0.01 to 2.43 μM and phosphate from 0.02 to 0.85 μM. Crenarchaeotal *amoA* genes (0.1–50×10^3 copies mL^{-1}) were also detected in the bottom waters where DOP and phosphate were in the ranges of 0.01–0.37 and 0.02–0.63 μM, respectively. The high correlation

between crenarchaeotal 16S rRNA and *amoA* gene copies ($r = 0.95$–0.97) through the year both in surface and bottom waters also suggests a positive correlation between crenarchaeotal *amoA* genes and low phosphate concentrations. In surface waters of the Gulf of California, where the dissolved phosphorus concentrations are $> 0.3\,\mu M$ and AOB were undetectable or very low in numbers, ammonia oxidation was correlated to the archaeal *amoA* genes (up to 1.3×10^4 copies mL^{-1}) (Beman *et al.*, 2008). Herfort *et al.* (2007) reported an inverse relation between chlorophyll *a* and crenarchaeota ($r = -0.61$). They stated that crenarchaeota were not abundant when larger phytoplankton ($> 3\,\mu m$) dominated the algal production. A positive correlation was found between crenarchaeota and picoplankton ($< 3\,\mu m$), where the latter is more efficient in uptake of nutrients than larger phytoplankton (Herfort *et al.*, 2007). These results suggest that AOA or some ecotypes might prevail in environments with low bioavailability of phosphate. Yet, the archaeal *amoA* genes were detected in estuarine sediments where the phosphate concentrations in the estuary were relatively higher (7–115 μM) (Sahan & Muyzer, 2008). Cultivated *N. maritimus* produced nitrite at higher phosphate levels of 0.29 mM (Könneke *et al.*, 2005). So far, the contribution of AOA to ammonia oxidation or their dominance in the high phosphate-containing niche has not been established. The relation between the phosphate levels and the existence and activity of AOA should be investigated further.

Sulfide effect on autotrophic ammonia oxidation

Of special interest is that AOA appear to be more widespread and they could be more abundant than AOB in estuarine sediments (Francis *et al.*, 2005; Beman & Francis, 2006). Estuarine or coastal sediments are usually linked to sulfide formation due to the existence of sulfate-reducing bacteria (SRB). Many stratified lakes or marine basins and fjords have stagnant, H_2S-rich bottom water (Jørgensen *et al.*, 1979). The common range for HS^- concentrations lies within 0–30 μM in freshwater sediment pore waters, 7–200 μM in estuarine sediments and is > 1 mM in organic-rich sediments (Goldhaber & Kaplan, 1975; Chanton *et al.*, 1987; Jørgensen, 1990; Joye & Hollibaugh, 1995). On the other hand, the main sites of denitrification usually are the sediments (Seitzinger, 1988). The recent discovery of AOA in sulfide-containing estuarine sediments and water columns (Caffrey *et al.*, 2007; Coolen *et al.*, 2007) and in the biofabrics of a sulfidic geothermal mine and sulfate-rich sulfide-related hot springs (Spear *et al.*, 2007; Weidler *et al.*, 2007; Reigstad *et al.*, 2008) may help to understand the nitrogen cycle and the possible AOA properties in these habitats.

There is as yet no available information to establish the inhibitory effect of sulfide on AOA. However, studies on bacterial nitrification inhibitors indicate a broad range of S-containing compounds, which are well reviewed by McCarty (1999). In a nitrifying culture exposed to sulfide for 2 h under aerated conditions, the complete inhibition of AOB was observed at a total soluble sulfide concentration as low as 7.8 μM (Sears *et al.*, 2004). A sodium sulfide dose of 0.1 mM resulted in the inhibition of both ammonia and hydroxylamine oxidation (Hooper & Terry, 1973), while a concentration of 0.9 μM was reported to severely inhibit AOB activity in a subgravel filter (Srna & Baggaley, 1975). Joye & Hollibaugh (1995) observed 50% and 100% decreased nitrification activity in estuarine sediments with HS^- doses of 60 and 100 μM, respectively. They speculated that the sulfide inhibition of nitrification might explain the spatial and temporal differences in nitrification (Kemp *et al.*, 1990; Gardner *et al.*, 1991). The increase in N regeneration observed in estuarine/marine sediments but not in freshwater sediments in summer (Kemp *et al.*, 1990; Gardner *et al.*, 1991; Caffrey *et al.*, 1993) was attributed to the inhibitory sulfide effect on nitrification (Joye & Hollibaugh, 1995) rather than the oxygen limitation and in turn minimum coupled sediment nitrification–denitrification. Joye & Hollibaugh (1995) explained this by the fluctuating oxygen concentrations also observed in the freshwater sediments but without concomitant HS^- production.

The effect of sulfide on ammonia oxidation must also be considered in relation to the special niche occupied by the anammox bacteria (Van de Graaf *et al.*, 1996; Kalyuzhnyi *et al.*, 2006). The inhibitory effect of sulfide on anammox bacteria is less severe than its effect on AOB. The specific anammox activity was inhibited by 50% at a sulfide dose of 0.3 mM (Dapena-Mora *et al.*, 2007). However, this conflicts with reports in the literature. Van de Graaf *et al.* (1996) observed stimulation of anammox activity in both batch and continuous reactors at 1- or 5-mM sulfide doses, which was explained by the sulfide oxidation by nitrate and formation of nitrite for anammox bacteria. The anammox bacteria were initially reported in a denitrifying fluidized bed reactor with sulfate and S^{2-} concentrations of 0.3–1.6 and 2.8–4.1 mM, respectively (Mulder *et al.*, 1995). The protection of anammox bacteria might be related to the removal of inhibitory sulfide by associated sulfide-oxidizing bacteria (SOB).

Despite the inhibitory effect of sulfide on nitrification, no inhibition was reported in some studies (Bowker, 2000; Chung *et al.*, 2005; Kalyuzhnyi *et al.*, 2006) and in treatment plants where SRB were detected (Lens *et al.*, 1995). Kalyuzhnyi *et al.* (2006) reported complete ammonia oxidation in a nitrifying biofilter and activated sludge reactor of the denitrifying ammonium oxidation (deamox) process receiving sulfide concentrations as high as 4.5 mM. The protection

of the AOB and the nitrification process is attributed to the removal of sulfide either chemically with metals, oxygen or nitrite, or biologically by sulfide-oxidizing or iron-oxidizing bacteria (Buisman *et al.*, 1990; Janssen *et al.*, 1995; de Smul & Verstraete, 1999; Nielsen *et al.*, 2004; Okabe *et al.*, 2005; Gadekar *et al.*, 2006; Madigon & Martinko, 2006; Rempel *et al.*, 2006). The formation of anoxic and aerobic layers of varied thickness, which spatially and temporarily change due to many factors such as inputs of organic matter, benthic production, bioturbation and burrow irrigation (Joye & Hollibaugh, 1995), is the other possible explanation for the occurrence of nitrification in the sediments where sulfide is produced by sulfate reduction.

Potential niche of AOA in natural and engineered systems

It is proposed herein that a possible reason for the observation of rate-limiting ammonia oxidation and in turn nitrification in sulfide-containing places might be the existence of AOA. Low sulfide-containing places, such as freshwater sediments, where ammonia accumulation is not observed and where nitrification is detected (Gardner *et al.*, 1991), may be the potential niche of AOA. It is speculated that they can be among the responsible factors for the N_2 loss in freshwater sediments where sulfide concentration is low and ammonium regeneration is negligible. Besides, their niche might be specific for sulfide-containing marine or estuarine sediments with relatively higher sulfide concentrations where nitrous oxide (N_2O) and/or nitric oxide (NO) accumulation are detected (Sørensen, 1978). Hydrogen sulfide formation has been associated with the inhibition of denitrification and release of NO and N_2O in coastal marine sediments and in possible natural environments (Sørensen, 1978; Sørensen *et al.*, 1980). The partial inhibition of denitrification with formation of N_2O or NO might be linked to ongoing nitrification by AOA tolerant to the sulfide doses in the sediments, which merits investigation. Sinninghe Damste *et al.* (2002) proposed that archaea, which were detected by crenarchaeol in the OMZ of the Northwestern Arabian Sea, are facultative anaerobes capable of denitrification. Francis *et al.* (2005) speculated that these crenarchaeota are AOA and able to perform 'nitrifier denitrification' due to the observation of archaeal *nirK* gene (Treusch *et al.*, 2005). Beman *et al.* (2008) also pointed out the potential for coupled nitrification–denitrification in the OMZs of the Gulf of California where AOA were most abundant. There might exist specific AOA phylotypes that are capable to do so, because the enriched ammonia-oxidizing archaeon *C.* Nitrososphaera gargensis and *N. maritimus* produced only nitrite (Könneke *et al.*, 2005; Hatzenpichler *et al.*, 2008). Based on the genome sequencing results of *N. maritimus*, two putative nitrite reductases could be identified, possibly involved in denitrification (Könneke *et al.*, 2005).

The retrieval of archaeal *amoA* genes in the Black Sea was reported in places (Francis *et al.*, 2005) close to the anammox bacteria (Kuypers *et al.*, 2003), which has been reviewed by Francis *et al.* (2007). The highest relative abundance of archaeal *amoA* genes occurs at a depth of 95 m (Coolen *et al.*, 2007), within 5 m of the nitrite maximum where Kuypers *et al.* (2003) defined the second highest specific lipid biomarkers of anammox bacteria (ladderanes) in the Black Sea. On the other hand, Lam *et al.* (2007) stated the presence of AOA in the lower oxic zone of the Black Sea, with *Gammaproteobacteria* AOB alongside the anammox bacteria. Yet, the expression of the putative archaeal *amoA* and its effect on anammox were detected in the Black Sea and the use of nitrite, produced in the AOA layer as the electron acceptor by anammox bacteria, was confirmed (Lam *et al.*, 2007). Both ammonia-oxidizing crenarchaeota and *Gammaproteobacteria* AOB were found to be equally significant in supplying nitrite to anammox bacteria (based on ^{15}N-incubation experiments and modeled calculations) (Lam *et al.*, 2007). These recent results indicate two sources of the nitrite ions in the anammox reaction, which is attributed to the 30–50% portion of all the nitrogen losses occurring in pelagic OMZs in the open ocean (Kuypers *et al.*, 2005). Thus, it is worthwhile to investigate the exact role of the AOA as providers of nitrite to anammox bacteria and to examine the sites where the anammox reaction occurs as being the possible niche of AOA.

Two new processes, both including the anammox reaction, have been proposed for sulfate and nitrogen removal under anaerobic conditions (Fdz-Polanco *et al.*, 2001; Mulder, 2006). The deamox (denitrifying ammonium oxidation) process was proposed by Mulder (2006). It is aimed in the deamox reactor to achieve simultaneous anammox (Eqn 1) and autotrophic denitrification (Eqn 2) using sulfide as electron donor and producing nitrite for the anammox.

$$NH_4^+ + NO_2^- \rightarrow N_2 + 2H_2O \quad (1)$$

$$4NO_3^- + HS^- \rightarrow 4NO_2^- + SO_4^{2-} + H^+ \quad (2)$$

The same concept was studied by Kalyuzhnyi *et al.* (2006), this time with real wastewater, i.e. baker's yeast effluent in a deamox reactor (Fig. 2). Considering the complete nitrite removal and increased anammox activity under sulfide conditions (> 4.5 mM), they pointed out the proximity of anammox bacteria and sulfide-oxidizing denitrifiers in the deamox sludge, supplying a new type of syntrophy with interspecies transfer of nitrite. In the deamox reactor, a syntrophy between anammox bacteria and SOB might be possible (Kalyuzhnyi *et al.*, 2006) as also shown by Prokopenko *et al.* (2006) in the sediments of the Eastern

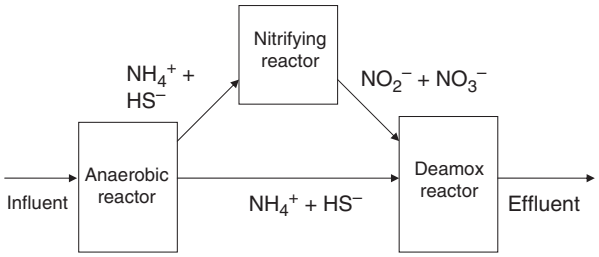

Fig. 2. Schematic representation of the process of Kalyuzhnyi *et al.* (2006).

Subtropical North Pacific area between *Thioplaca* and anammox-like bacteria. Yet, the proximity of known anammox bacteria and SOB also means sulfide exposure of the former, which might result in inhibition at doses as high as 4.5 mM unless the sulfide oxidation rate is higher than the diffusion rate in biofilm. Different anammox species capable of surviving under sulfide conditions might explain the deamox process. Recently, novel *Planctomycetes* were discovered from anaerobic sulfide- and sulfur-rich Zodletone Spring, OK (Elshahed *et al.*, 2007). Their characterization revealed the ability to reduce elemental sulfur to sulfide under anaerobic conditions and produce acids from sugars and survive in these sulfide-rich environments. However, another possible explanation is the existence of ammonia-oxidizing archaeal types capable of surviving under sulfide-conditions with anammox bacteria and SOB. Koch *et al.* (2006) indicated the synchronized microbial community of crenarchaeota and *Thiothrix* in sulfide-containing cold-marsh waters. Whether these crenarchaeota belong to AOA or not has not been studied. However, it is likely that certain AOA types, capable of cooperating with SOB, might exist. SOB produce sulfur under limiting oxygen ($< 3.1\ \mu M$) conditions or at high sulfide-loading rates (Buisman *et al.*, 1990; Janssen *et al.*, 1995). AOA might provide a niche for anammox bacteria by decreasing the diffusion of sulfide and at the same time supplying nitrite, which might also explain the increase in the specific anammox activity when there is a supply of sulfide (Van de Graaf *et al.*, 1996; Kalyuzhnyi *et al.*, 2006).

Considering the relation among the AOA, the *Gammaproteobacteria* AOB and the anammox bacteria (Lam *et al.*, 2007), and the symbiotic relation between *C. symbiosum* and its sponge *Axinella mexicana* (Hallam *et al.*, 2006a), it is likely that AOA types might have a syntrophic relationship to different communities. A relationship was also speculated for the AOA and AOB, an anammox-like species, nitrite-oxidizing *Nitrospirae* and *Nitrospina* in thermal springs (Weidler *et al.*, 2007). Similarly, the combinations of AOA-*Nitrospina* in coastal and open-oceans (Mincer *et al.*, 2007), and AOA-coral hosts have been proposed (Beman *et al.*, 2007). Fdz-Polanco *et al.* (2001) accidentally observed simultaneous removal of nitrogen and sulfate in a granular activated carbon anaerobic fluidized-bed reactor. They proposed simultaneous anammox and sulfate reduction to account for this uncommon observation. Yet, in the view of the syntrophic relationship between different communities including AOA, the reaction occurring in the process studied by Fdz-Polanco *et al.* (2001) might be the syntrophic interaction of AOA, anammox bacteria, SOB and an unknown sulfate reducer, which merits further examination.

Concluding remarks

The wide distribution of AOA in the environment is currently well established. Their abundance over AOB is striking in many ecosystems. The recent information definitely indicates the contribution of AOA to ammonia oxidation in the upper water columns of the Gulf of California, in the Black Sea and in thermophilic springs (Lam *et al.*, 2007; Beman *et al.*, 2008; Reigstad *et al.*, 2008). However, information on the link between the occurrence of AOA and the environmental parameters is limited. Being retrieved by cultivation-independent phylogenetic surveys, the majority of the AOA studies reflect the site properties, which are clearly affected by hydrological and biogeochemical factors. Thus, it is hard to pinpoint one parameter as responsible for the AOA occurrence in these highly complex environments. However, the properties of the sites, where the AOA abundance was reported, were taken into consideration. AOA, being ubiquitous, seem to have a wide range of growth conditions, and some ecotypes might be unique to the specific environments as well. The questions of why AOA are dominant compared with AOB in the majority of the studied environments and what parameters are effective in their occurrence and abundance remain unclear. Many research questions need to be resolved: (1) the presence and activity of AOA in sulfide-containing environments; (2) the relationship between low ammonium-containing environments and the substrate affinity of the AOA; (3) their responses to the changes in the organic carbon or nutrient content in soils; (4) their affinity for phosphate compared with their bacterial counterparts; (5) their existence and, in some cases, abundance over AOB in low-pH, sulfidic, low-ammonium- and/or low-phosphate-containing environments. This speculation integrates the higher abundance of AOA in the low-pH environments and in the majority of the sulfide-containing sites, where the soluble phosphate will be more available despite the very phosphate-poor conditions. The schematic representation of the proposed speculation in terms of dominant/active ammonia-oxidizing community type with respect to phosphate, DO, ammonia and pH levels and the resultant possible sulfide exposures are shown in Fig. 3. The question of whether there are environmental factors shaping the specific niches of AOA or some ecotypes

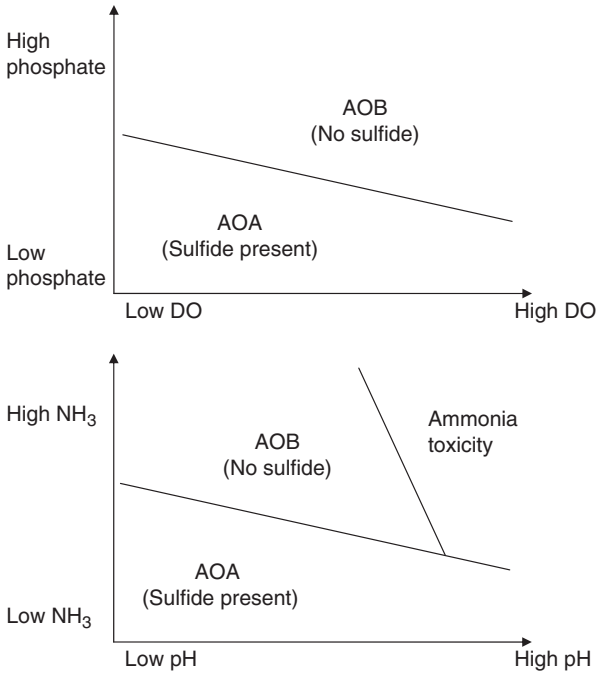

Fig. 3. The proposed dominant/active ammonia-oxidizing community type in response to the varying phosphate, pH, ammonia and DO values under the resultant possible sulfide exposures.

and their contribution to the nitrogen cycle will be the areas of active research.

It is, therefore, worthwhile to further investigate the low-nutrient environments and the niche of low pH as well as sulfide-containing natural and engineered systems for AOA. The examination of environments such as freshwater sediments, cold seeps sediments, acidic or alkaline lakes and soils, eutrophic to oligotrophic waters, biological nutrient removal systems, and also the sites involving anammox reaction will be essential for our understanding of these archaeal ammonia oxidizers and their role in the N and C cycles. Investigating the effect of environmental parameters (such as phosphate, pH, DO, ammonium and sulfide) and their concentration levels on the expression of archaeal *amoA* genes will help to identify their tolerance levels and further use, and even their management in natural and engineered systems.

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