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MINI-REVIEW

Review of ammonia-oxidizing bacteria and archaea in freshwater ponds

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Abstract Aquaculture ponds are simple and unique ecosystems, which are affected intensively by human activities. In this mini-review, we focus our attention on the distribution and community diversity of ammonia-oxidizing bacteria (AOB) and ammonia-oxidizing archaea (AOA) in pond water and sediments, as well as the possible ecological mechanisms involved. Moreover, we discuss the possibility of increasing the activity of ammonia-oxidizing organisms in order to improve the water quality in aquaculture ponds. Compared with eutrophic lakes, the significantly higher ammonia concentration in pond water does not lead to significantly higher AOB levels, and the abundance of AOA is too low to quantify accurately. Similar to eutrophic lakes, high abundances of AOA and AOB are present in the surface sediments at the same time, where the oxidation of ammonia is performed mainly by AOB. AOB and AOA exhibit significant seasonal variations in aquaculture ponds, which are affected by the temperature, pH, and dissolved oxygen. The dominant AOB species are *Nitrosomonas* and the *Nitrosospira* lineage in pond environments. *Nitrososphaera* or members of the *Nitrososphaera*-like cluster dominate the AOA species in surface sediments, whereas the *Nitrosopumilus* cluster dominates the deeper sediments. AOB and AOA can be enriched on artificial substrates suspended in the pond water, thereby potentially improving the water quality.

Keywords Ammonia-oxidizing archaea · Ammonia-oxidizing bacteria · Aquaculture water · Artificial substrate · Distribution · Freshwater aquaculture pond · Sediment

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1 Introduction

Freshwater pond aquaculture plays an important role in the supply of aquatic products throughout the world. China has 2,762,604 ha of freshwater ponds and their annual production is 22.86 million metric tonnes, which accounts for about 45% of China's total aquaculture production (Fishery National Bureau of Statistics of China 2017, http://www.stats.gov.cn/english/statisticaldata/AnnualData/2017). An aquaculture pond is a relatively closed water environment, with only the occasional replenishment or replacement of a small amount of water. In the breeding season, large amounts of feed are placed in the pond every day, but less than 30% of the nitrogen can be absorbed and utilized by aquatic animals. The remaining nitrogen is released directly into the pond aquaculture environment (Ackefors and Enell 1994). Ammonia is one of the most toxic substances produced by intensive fish farming (Handy and Poxton 1993). Ammonia is toxic to all vertebrates and it can cause convulsions, coma, and death (Randall and Tsui 2002).

In the pond aquaculture environment, some of the ammonia can be absorbed by phytoplankton and assimilated again by filter-feeding animals, and another proportion of the ammonia is oxidized by ammonia-oxidizing microorganisms (Ebeling et al. 2006). The oxidation of ammonia to nitrite is the first step during nitrification and it is also the speed-limiting step (Adair and Schwartz 2011). Traditionally, ammonia-oxidizing bacteria (AOB) were considered the main drivers of ammonia oxidation (Fig. 1), but this was recently challenged by the discovery of ammonia-oxidizing archaea (AOA) (Könneke et al. 2005), which were subsequently found in various aquatic environments such as oceans, lakes, and rivers, where they play important roles. The importance of AOA in freshwater aquaculture ponds also has attracted the attention of researchers in recent years (Fig. 1). Aquaculture ponds are very different from oceans, lakes, and rivers because they have small areas and shallow depths, and they are greatly influenced by people. Ammonia-oxidizing microorganisms are affected by the pH, temperature (Lee et al. 2011), light (French et al. 2012; Merbt et al. 2012), and oxygen (Luo et al. 2014; Qin et al. 2017). AOA and AOB may also differ greatly in various habitats. The relative importance of AOB and AOA in freshwater ponds is still not fully understood. In this review, we consider the spatial and temporal distribution characteristics, seasonal variations, and possible ecological mechanisms related to AOA and AOB in freshwater ponds in order to enhance our theoretical understanding of the nitrogen cycle in freshwater ponds, thereby facilitating improvements to the pond culture environment in the future.

2 Pond water

2.1 Characteristic distributions in pond water

Aquatic animals excrete large amounts of ammonium and urea into pond water every day. In theory, the continuous supply of nitrogen can promote the growth of ammonia-oxidizing microorganisms. However, the

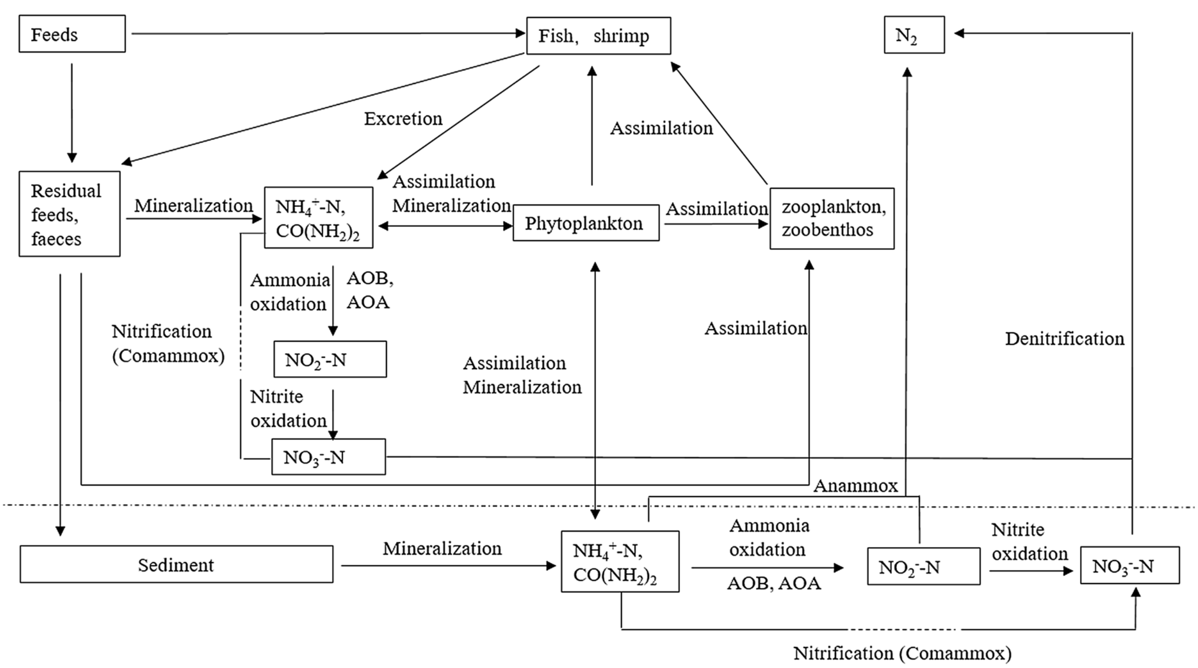

Fig. 1 Schematic illustration of the key processes in the nitrogen cycle in freshwater aquaculture ponds. AOB and AOA are two key types of microorganisms responsible for the oxidation of ammonia. The stippled line for comammox indicates that nitrite is an intermediate but it is oxidized to nitrate by the same organism (Daims et al. 2015; van Kessel et al. 2015)

abundances of ammonia-oxidizing microorganisms are not greater compared with those in eutrophic freshwater lakes. Quantitative analyses using real-time PCR showed that the abundance of the AOB gene *amoA* ranged from 1.55 (± 8.41) × 10^2 copies/mL to 8.56 (± 11.3) × 10^4 copies/mL in the surface water of a grass carp pond in Central China (Lu et al. 2015b). Each AOB contains two or three *amoA* gene copies (Norton et al. 2002), so the abundance of AOB in the pond water was estimated at 10^2–10^4 cell/mL. Using the most probable number method, an Indian study showed that the abundances of cultivable AOB ranged from 720.5 (± 8.1) to 1673.23 (± 0.36)/mL in pond water (Kumari et al. 2011). Using the same method, the abundance of AOB was determined to be 2.0 × 10^3 cfu/mL in the water in *Penaeus vannamei* ponds (Ma et al. 2008). Clearly, although different research methods were employed, these studies concluded that the abundances of AOB in pond water were roughly the same, i.e., 10^2–10^4 cell/mL, which are more or less than those found in eutrophic freshwater lakes. The abundances of AOB were reported to range from 10^4 to 10^5 cells/mL in eutrophic lake water (Yang et al. 2016; Hampel et al. 2018). Under laboratory conditions, increasing the NH_4^+-N concentration from 0.21 to 14 mg/L could significantly enhance the growth rates and reduce the lag phases for AOB isolated from a freshwater lake (French et al. 2012). The average concentration of ammonia in pond water ranged from 1.02 to 2.80 mg/L throughout the year according to Lu et al. (2015b), whereas the mean ammonia concentration was determined to be less than 0.52 mg/L throughout the year in a eutrophic lake (Hampel et al. 2018). Compared with eutrophic lakes, the significantly higher ammonia concentration does not lead to significantly higher AOB abundances in aquaculture ponds. It has been suggested that compared with lakes, the ammonia concentration is not a major ecological factor that determines the growth of AOB in pond water.

No significant differences were found in the abundances of AOB in the water at the surface and on the bottom of freshwater ponds (Qin et al. 2016), probably because the ponds are very shallow, where the depth is generally about 2 m. Moreover, wind and aerators often stir the water, but this phenomenon differs from that in deep lakes and oceans. In general, the abundance and diversity of AOB exhibit significant vertical distribution patterns in deep lakes and ocean water columns (De Corte et al. 2009; Vissers et al. 2013).

AOB exhibit significant seasonal variations in pond water (Fig. 2). Lu et al. found that the abundances of AOB were significantly higher during the summer than the other three seasons, and there were no significant differences in the other three seasons in grass carp ponds in Central China (Lu et al. 2015b) (Fig. 2c). Similarly, Qin et al. showed that the AOB *amoA* gene copy numbers exhibited seasonal variations in pond water, with significantly higher levels in the summer compared with the spring and autumn ($P < 0.05$), and no significant differences between the

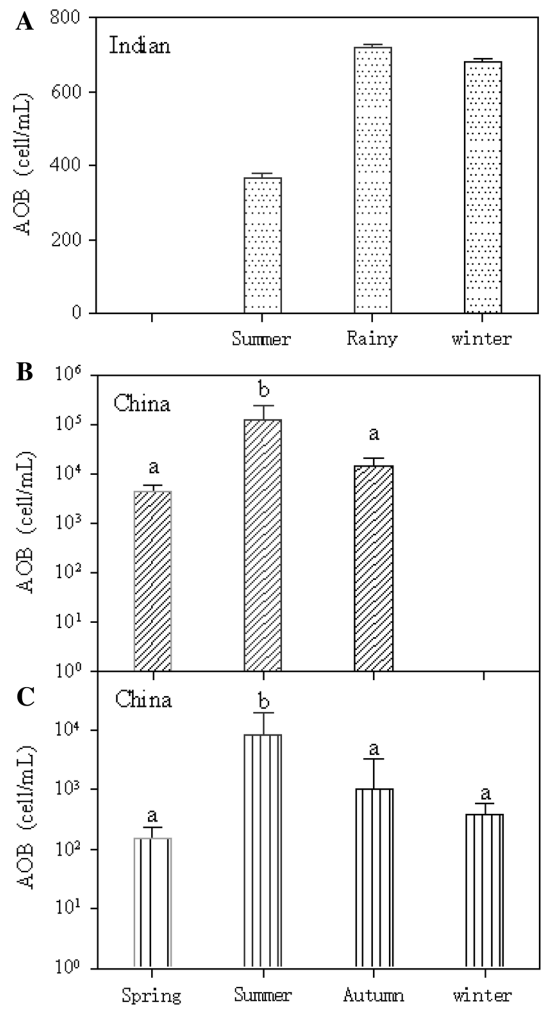

Fig. 2 Seasonal variations in AOB in freshwater aquaculture pond water in China and India. **a** is from the study by Kumari et al. (2011), **b** is from the study by Qin et al. (2016), and **c** is from the study by Lu et al. (2015b)

spring and autumn seasons ($P > 0.05$) (Qin et al. 2016) (Fig. 2b). These seasonal variations may be attributed to the temperature. A statistical analysis by Lu et al. (2015b) showed that there was a significant positive correlation between the AOB *amoA* gene abundance and temperature ($r = 0.597$, $P < 0.01$; nonparametric correlations) during the aquaculture cycle. However, the abundance and activity of AOB were found to be significantly higher in pond water during the rainy season than the winter and summer seasons in India (Kumari et al. 2011) (Fig. 2a). There are obvious differences in the variations in AOB in pond water between these two regions, possibly because the climate in China differs from that in India. The average water temperature of in every season is below 20 °C throughout the year in Central China, except in the summer (Lu et al. 2015b). However, the temperature of pond water varies from 24.6 to 32.1 °C throughout the year in India, and nitrifying bacteria require optimum temperatures between 20 °C to 28 °C for their survival and growth (Verstraete and Focht 1977). Therefore, the growth of AOB is not restricted by the temperature in ponds in India. In the optimum temperature range, the pH might be a key factor that restricts growth in ponds (Kumari et al. 2011). Photosynthesis is relatively weak in the rainy season and the pH is close to neutral, and the optimum pH for growth by nitrifying bacteria is between pH 7 and 8 (Alleman 1985; He et al. 2012).

Excluding AOB, AOA were recently identified as the dominant ammonia oxidizers in most freshwater aquaria (Bagchi et al. 2014). AOA were also detected in aquaculture water using PCR, but accurate quantification was not possible because of their low abundance (Lu 2014), which may be attributed to the high ammonia concentration in freshwater ponds, i.e., more than 1 mg/L throughout the year. AOA are at a disadvantage when competing with AOB for ammonia in a hypereutrophic system, which has been confirmed in lake and river environments. For example, in a eutrophic lake, it was shown that AOB could thrive close to the nearshore where the mean ammonia concentration was 0.52 mg/L, whereas AOA were more abundant in the center of the lake where the mean ammonia concentration was 0.05 mg/L (Yang et al. 2016; Hampel et al. 2018). In an oligotrophic lake, the ammonia concentration in the water column ranged from 0.001 to 0.06 mg/L and only the archaeal *amoA* gene was found, which had a strong correlation with the nitrite concentration, and the bacterial *amoA* gene was not detected (Auguet et al. 2012). In Dongjiang river, the water is used as a drinking water source and the highest ratio of archaeal and bacterial *amoA* gene copies was found in sampling sites with the lowest concentration of ammonia (Liu et al. 2011). However, when *Ipomoea aquatica* Forsk. was planted in pond water, the abundance of the *amoA* gene in AOA that adhered to the roots reached 10^4–10^5 copies/g, which was about one order of magnitude less than the abundance of AOB (Lu 2014). The roots may create a microenvironment that is suitable for AOA growth, where the ammonia concentration is much lower than that in the pond water, but further research is needed to elucidate the specific mechanism involved.

2.2 Diversity

According to previous studies, AOB include the genera *Nitrosomonas*, *Nitrosospira*, *Nitrosolobus*, *Nitrosovibrio*, and *Nitrosococcus* (Watson and Mandel 1971). Lu found that the AOB in the water in a grass carp pond comprised *Nitrosomonas* and *Nitrosospira* with proportions of 89.19% and 10.81%, respectively (Lu 2014). The AOB that attached to *Ipomoea aquatica* Forsk. roots in a pond all belonged to the genus *Nitrosomonas* (Lu 2014), which may be attributed to the eutrophic environment in the pond because the genus *Nitrosomonas* is often found in wastewater treatment plants with a high concentration of ammonia and rich nutrient levels (Merbt et al. 2015).

AOA can be grouped into five major clusters: *Nitrosopumilus* cluster (also called group I.1a AOA), *Nitrosotalea* cluster (also called group I.1a-associated AOA), *Nitrososphaera* cluster (also called group I.1b AOA), *Nitrososphaera* sister cluster, and *Nitrosocaldus* cluster (also called thermophilic AOA) (Pester et al. 2012). The abundances of AOA are very low in pond water, and thus few studies have considered the diversity of AOA in freshwater pond water. Indeed, only one study was identified, which showed that 97% of the AOA in a crab aquaculture pond water belonged to the *Nitrosopumilus* cluster and the other 3% to the *Nitrososphaera* cluster (Zhang et al. 2016). The *Nitrosopumilus* cluster is considered to be ubiquitous in various freshwater ecosystems including river and lake environments (Wu et al. 2010; Liu et al. 2011; Huang et al. 2016; Li et al. 2018).

3 Pond sediments

3.1 Characteristic distributions in pond sediments

It was reported that about 60–70% of the N could remain in the sediments during the aquaculture process (Kaggwa et al. 2010). Thus, it is very important to understand the distributions of AOA and AOB in sediments. Lu et al. found that the abundance of the AOA *amoA* gene ranged from 4.05 (± 3.83) × 10^4 to 3.11 (± 1.65) × 10^5 copies/g in the surface sediment (0–5 cm) from a grass carp pond in Central China, which was about one order of magnitude higher than that of AOB (Lu et al. 2015b). Lu et al. obtained similar results for surface sediments from a Wuchang bream (*Megalobrama amblycephala*) fish pond in East China (Lu et al. 2016). However, this contradicts the prevalent viewpoint that AOA prefer to live in low ammonia and oligotrophic environments (Shilta et al. 2016), where the concentration of interstitial water ammonia is often higher than 30 mg/L, which may be explained by the potential for AOA mixotrophic metabolism.

Bioinformatics analysis of AOA genomes indicates the potential for mixotrophic metabolism (Walker et al. 2010) but the AOA isolates also exhibit obligate mixotrophy, where they can assimilate organic carbon compounds, such as α-ketoglutaric acid (Qin et al. 2014), cyanate (Palatinszky et al. 2015), urea (Tolar et al. 2016), and pyruvate (Tourna et al. 2011). Thus, AOA may play a greater role in freshwater pond sediments in addition to NH_4^+-N oxidation. Another explanation is that sessile type AOA and planktonic type AOA exist in nature, which have quite different requirements in terms of the ammonia concentration and nutritional conditions.

AOA and AOB are present in surface sediments in fishponds at the same time, but the oxidation of ammonia is performed mainly by AOB in the surface sediments. Lu et al. found that the depth limits for detecting the AOA and AOB *amoA* genes in a freshwater pond sediment were at 25 cm and 6 cm, respectively, while the expression of the AOA and AOB *amoA* genes could be detected at 25 cm and 15 cm (Lu et al. 2016). According to *amoA* mRNA expression analysis, the abundance of AOB *amoA* mRNA was 2.5–39.9 times higher than that of AOA *amoA* mRNA in the top 0–10 cm surface sediment layer (Lu et al. 2016), thereby indicating that AOB were more active than AOA in the surface sediments. The average abundance of the AOB *amoA* gene was 9.8 × 10^6 copies/g in the surface sediments from mandarin fish ponds in the suburbs of Wuhan City (Zhou et al. 2017), which was more than two times higher than that of AOA, and the AOB abundance was significantly positively correlated with the concentration of active phosphorus in the interstitial water in the sediment. However, the AOA diversity was negatively correlated with the concentration of ammonia in the interstitial water. To some extent, these results suggest that AOB were the main ammonia-oxidizing microorganism in the sediments from mandarin fishponds. Based on the findings described above, AOA and AOB are present at the same time in surface sediments in fishponds, and the abundance of AOB may be higher or lower than that of AOA. However, all previous studies agree that the oxidation of ammonia is performed mainly by AOB rather than AOA, which was confirmed by studies of the sediments in Taihu Lake (Wu et al. 2010; Hampel et al. 2018).

AOA and AOB exhibit significant seasonal variations in pond sediments, which are very different from those in pond water. According to Lu et al. (2015b), the maximum abundances of AOA and AOB occurred during the winter and autumn in the top 0–5 cm layer of surface sediments in a grass carp pond, with the lowest abundance in the summer. These differences may be attributed to the dissolved oxygen levels. Lu et al. (2016) found that the dissolved oxygen was often in a super-saturated state in the surface water of a pond, but the dissolved oxygen was at the detection limit at a depth of only 500 μm, and the dissolved oxygen concentration ranged from 0 to 48.01 μmol/L. Heterotrophic bacteria are active in the summer due to high temperatures and they consume large amounts of dissolved oxygen, which may inhibit autotrophic bacteria such as AOA and AOB.

3.2 Diversity

The AOB found in pond sediments mainly belong to the genera *Nitrosomonas* or *Nitrosospira*, which may be determined by the ammonia concentration in the interstitial water in surface sediments. For example, an analysis of the phylogenetic diversity of the AOB functional gene *amoA* in the top 0–5 cm layer of the sediments in a grass carp pond by Lu (2014) showed that 76.92% and 23.08% of the AOB belonged to the genera *Nitrosomonas* and *Nitrosospira*, respectively. Similar results were was also obtained in a Wuchang bream fish pond, where the AOB in the top 0–6 cm layer of the sediment contained two genera and they mainly belonged to the *Nitrosomonas* cluster (Lu et al. 2016). In a *Penaeus vannamei* freshwater aquaculture pond, all of the AOB belonged to *Nitrosomonas* and the *Nitrosomonas*-like cluster (Gao and Lin 2011). In another *Penaeus vannamei* pond, *Nitrosomonas* was the dominant species in the surface sediment, but the dominant AOB community was *Nitrosospira* in the soil surrounding the pond (Ma et al. 2008). However, in mandarin fish ponds located in the Hannan District of Wuhan City, China, all AOB were related to the *Nitrosospira* lineage (Zhou et al. 2017). Similar results were obtained using biofilters from a recirculating aquaculture system where all of the AOB *amoA* sequences were related to the *Nitrosospira* lineage (Sakami et al. 2012). In these studies, all of the AOB in the pond sediments belonged to the genus *Nitrosomonas* or the *Nitrosospira* lineage. *Nitrosomonas* prefers to live in high-ammonia environments, such as wastewater treatment plants (Geets et al. 2006; Merbt et al. 2015), and high ammonia levels can enhance the growth of *Nitrosomonas* spp. compared with *Nitrosospira* spp. (Bollmann et al. 2002, 2005). In the sediment from a grass carp pond, the ammonia concentration in the pore water was over 20 mg/L for most of the year (Lu et al. 2015b), and the ammonia concentration was 40 mg/L in a Wuchang bream fish pond (Lu et al. 2016). However, in mandarin fish ponds, the ammonia concentration in the interstitial water was only 2–4 mg/L from June to September (Zhou et al. 2017). Clearly, the ammonia concentration can affect the AOB diversity in pond sediments, and AOB such as *Nitrosomonas* may adapt to high-nutrient environments.

Studies have shown that *Nitrososphaera* or *Nitrososphaera*-like cluster comprise the dominant AOA species in surface sediments from freshwater ponds. In the top 0–5 cm layer from the surface sediment in grass carp fish ponds, all of the AOA were grouped into group I.1b (*Nitrososphaera*) and group I.1a (*Nitrosopumilus*) clusters, with 80% and 20%, respectively (Lu 2014). In the surface sediments from mandarin fish ponds, all of the AOA were affiliated with *Nitrosophaera* or the *Nitrososphaera*-like cluster (Zhou et al. 2017). In biofilters from a recirculating aquaculture system, all of the AOA *amoA* sequences belonged to a cluster that included Candidatus *Nitrosopumilus maritimus* (Sakami et al. 2012). The characteristics of the AOA community could be affected by ammonium. Studies suggest that *Nitrososphaera* AOA prefer living in environments with higher total organic carbon and NH_4^+-N levels than *Nitrosopumilus* AOA (Chen et al. 2008; Tourna et al. 2011; Liu et al. 2013). Indeed, the ammonia concentrations in recirculating aquaculture systems are much lower than those in pond sediment (Sakami et al. 2012). Similar results were obtained in the vertical distribution of pond sediments. Thus, in a Wuchang bream fish pond, the AOA in the top 0–2 cm layer of

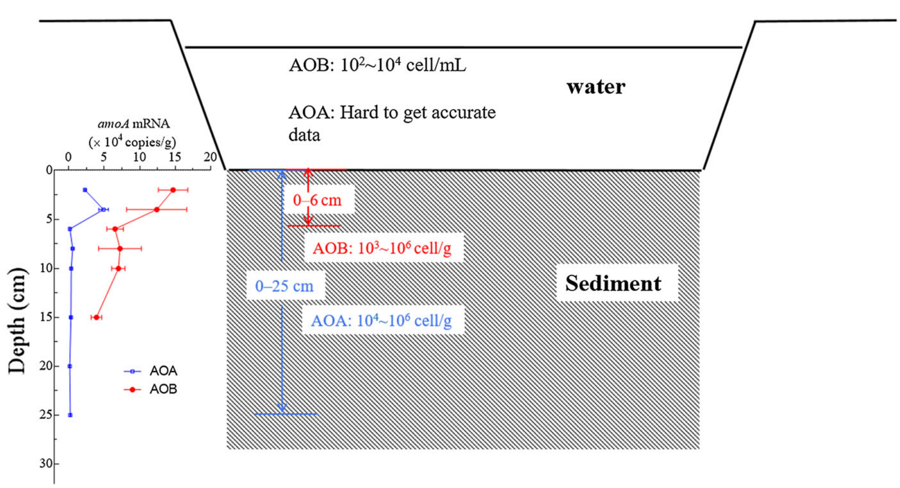

Fig. 3 Distribution and *amoA* mRNA expression levels for AOA and AOB in freshwater aquaculture pond environments. The mRNA expression levels are from the study by Lu et al. (2016)

Table 1 Diversity and proportions of AOA and AOB in different pond environments

Environment	Microorganism	Genus	Proportion (%)	References
Grass carp pond water	AOB	*Nitrosomonas* cluster	89.19	Lu (2014)
		Nitrosospira cluster	10.81	Lu (2014)
Crab pond water	AOA	*Nitrosopumilus* cluster	97	Zhang et al. (2016)
		Nitrososphaera cluster	3	Zhang et al. (2016)
Ipomoea aquatica Forsk roots in grass carp pond	AOB	*Nitrosomonas* cluster	100	Lu (2014)
0–5 cm deep sediment in a grass carp fish pond	AOB	*Nitrosomonas* cluster	76.92	Lu (2014)
		Nitrosospira cluster	23.08	Lu (2014)
Surface sediment from *Penaeus vannamei* pond	AOB	*Nitrosomonas* cluster	61.54	Gao and Lin (2011)
		Nitrosomonas-like cluster	38.46	Gao and Lin (2011)
0–6 cm deep in Wuchang bream pond sediment	AOB	*Nitrosomonas* cluster	68.42	Lu et al. (2016)
		Nitrosospira cluster	31.58	Lu et al. (2016)
Surface sediment from *Penaeus vannamei* pond	AOB	*Nitrosomonas* cluster	Most	Ma et al. (2008)
0–5 cm deep in grass carp fish pond sediment	AOA	*Nitrososphaera* cluster	80	Lu (2014)
		Nitrosopumilus cluster	20	Lu (2014)
0–2 cm deep in Wuchang bream fish pond sediment	AOA	*Nitrososphaera* cluster	100	Lu et al. (2016)
10–15 cm and 20–25 cm deep in Wuchang bream fish pond sediment	AOA	*Nitrosopumilus* cluster	100	Lu et al. (2016)
Surface sediment from Mandarin fish pond	AOA	*Nitrosophaera* cluster	19.4	Zhou et al. (2017)
		Nitrosophaera-like cluster	80.6	Zhou et al. (2017)

the sediment belonged to the *Nitrososphaera* cluster, whereas those in the 10–15 cm and 20–25 cm layers belonged to the *Nitrosopumilus* cluster, where the concentration of ammonia declined from 64.09 (± 11.01) mg/kg to 3.88 (± 0.45) mg/kg with the sediment depth (Lu et al. 2016).

4 Artificial substrates

Specialized nitrification systems are used in recirculating aquaculture system in order to remove the ammonia produced by aquaculture animals, thereby supporting intensive aquaculture (Rurangwa and Verdegem 2015). At present, the structure of freshwater pond ecosystems is relatively simple and a specific nitrification system is generally not present in ponds. However, some studies have shown that freshwater pond ecosystems have the ideal nutrient conditions for the growth of large amounts of ammonia-oxidizing microorganisms. For example, Lu found that a large number of AOA and AOB could become attached to the roots of *Ipomoea aquatica* Forsk. when planted in pond water (Lu 2014). A polyethylene and cotton filter was also suspended in the pond water and the AOB contents reached $\sim 10^7$ cell/cm^3 after incubation for about half a month, whereas the contents were only $\sim 10^2$ cell/cm^3 in the surrounding water during the same period (Lu et al. 2015a). The ammonia conversion rate reached 0.035 (± 0.002) mg N/cm^3 filter/h and within a specific range, the rate increased as the temperature, pH, and initial ammonia nitrogen concentration increased (Lu et al. 2015a). It has also been shown that the use of artificial substrates in freshwater pond water can significantly increase the production of animals and effectively improve the water quality (Shilta et al. 2016; Li et al. 2017; Qu et al. 2017). These findings suggest the possibility of building an efficient nitrification system for freshwater aquaculture ponds.

5 Conclusions

Figure 3 and Table 1 provide a more comprehensive understanding of the distributions of AOB and AOA in freshwater pond environments. Overall, most studies of AOA and AOB in pond environments have been limited to the molecular ecology level, and our understanding of the ecological mechanisms involved is still in the speculative stage.

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