

Review

Nitrogen Contribution Rate of Anammox in Different Systems and Its Relationship with Environmental Factors

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Abstract: Anammox bacteria can remove ammonium directly, which is different from what was previously believed. This is an important process for the global nitrogen cycle. Anammox bacteria were first identified in sewage treatment systems and were later proven to exist widely in natural ecosystems. To better understand the relationship between the anammox reaction and different systems, and to maintain the stability of the nitrogen cycle, anammox functional microorganisms found in different natural environments were summarized. In addition, anammox nitrogen production rate and the contribution of anammox to nitrogen were discussed under different ecological environments. A literature analysis showed that the contribution rate of nitrogen removal of anammox was the highest in the Terrestrial ecosystem, up to 87.5%. The Terrestrial ecosystem is more likely to form an anoxic or even anaerobic environment conducive to anaerobic ammonification. Therefore, the control of DO is an important factor in the activity of anaerobic ammonification. Other environmental factors affecting the contribution of anammox to nitrogen removal include temperature, pH, organic matter content, inorganic nitrogen concentration, and salinity. However, the dominant influencing factors of anammox reactions in different ecosystems are evidently different. Therefore, the mechanism of the impact of different environmental factors on the anaerobic ammonia oxidation process is necessary to discuss. This provides a scientific basis for the global nitrogen cycle and is of great significance to improve nitrogen's biogeochemical cycle in the ecosystem.



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Keywords: anaerobic ammonia oxidation; contribution rate; ecosystem; environmental factor; nitrogen cycle; wastewater treatment system

1. Introduction

For many years, nitrification and denitrification have been considered the main processes of the biogeochemical nitrogen cycle. With the discovery of anaerobic ammonia oxidation (anammox) bacteria [1], it was found that denitrification was not the only method that transforms inorganic nitrogen into N₂ in the natural environment; subsequently, the anammox process rapidly gained interest [2]. Nitrate is also transformed into ammonium via DNRA, which is called Dissimilatory Nitrate Reduction to Ammonium. The nitrogen cycling process is shown in Figure 1. Denitrification and anammox bacteria can produce N₂. In the anammox process, anammox bacteria take NH₄⁺ as the electron donor, NO₂⁻ as the electron acceptor under anaerobic conditions, and finally produce N₂ (NH₄⁺ + NO₂⁻ → N₂↑ + 2H₂O) [1]. In an oxygen-deprived environment, anammox is the main driver for the loss of fixed nitrogen, in addition to the reoxidation of nitrite to nitrate in freshwater and marine ecosystems [3]. Anammox can release approximately 3.8–50% of N₂ into the atmosphere in the natural environment [4,5]. In natural ecosystems, anammox bacteria are found in oceans [6,7], rivers [8,9], lakes [10,11], estuaries [12], paddy soil [13,14], and natural wetlands [15,16]. In artificial systems, anammox bacteria have been found in bioreactors [17,18]

and artificial wetlands [19,20]. Figure 2 shows the development of the anammox bacteria. In 1998, anammox bacteria were successfully enriched using a Sequencing Batch-Reactor-Activated Sludge Process (SBR). Studies on anammox have revealed that these bacteria have a wide distribution range, and may have evolved unique structural and metabolic characteristics [5].

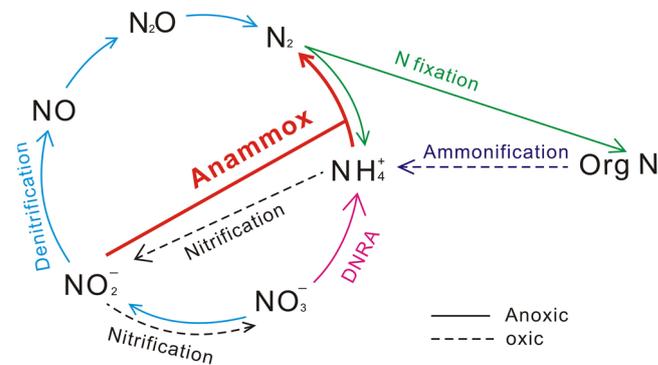


Figure 1. Schematic of the nitrogen cycle in the natural ecological environment.

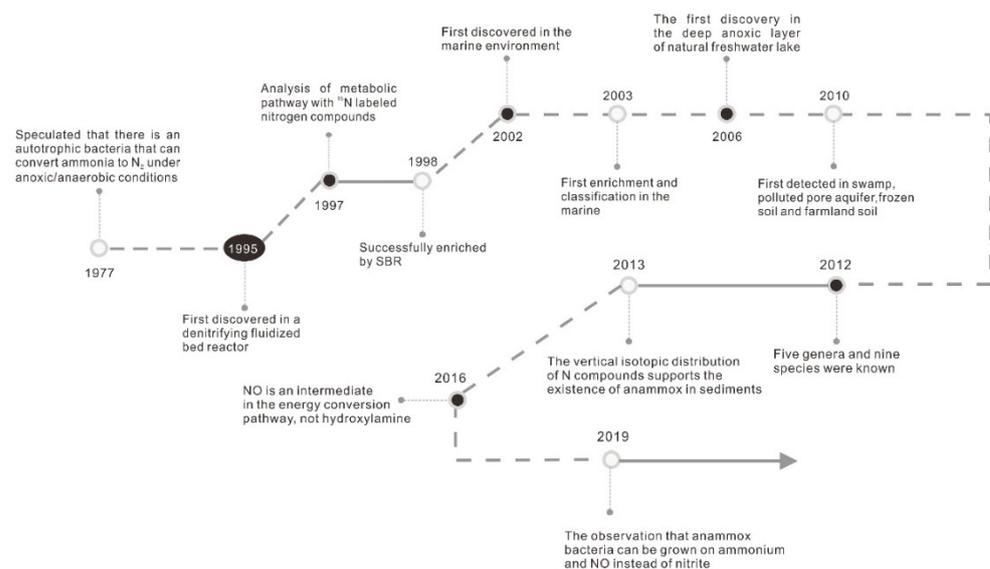


Figure 2. Schematic of the research and development on anammox.

In several natural ecosystems, owing to the lack of oxygen or the limited supply of electron donors (sulfide or organic matter), a host of NO_2^- is generated. Low oxygen and sufficient nitrite levels provide favorable conditions for anammox bacteria. In the artificial reactor system, the anammox activity and its denitrification effect are mostly evaluated by measuring the decrease of $\text{NH}_4^+\text{-N}$ and $\text{NO}_2^-\text{-N}$ and the increase of $\text{NO}_3^-\text{-N}$ in the inlet and outlet of the reactor. Anammox occurring in environmental ecosystems is usually characterized by the ^{15}N isotope-tracing technology. Anammox activity in the natural environment was evaluated by generating $^{29}\text{N}_2$ from ^{15}N -labeled $^{15}\text{NO}_3^-\text{-N}$, which is the potential activity. The experiments were designed accordingly. After a period of culture, the resulting $^{28}\text{N}_2$, $^{29}\text{N}_2$, and $^{30}\text{N}_2$ concentrations were measured by a membrane-sampling mass spectrometer, isotope ratio mass spectrometer, or gas chromatography–mass spectrometry. Through calculation, we can judge whether there is an anammox reaction and its reaction rate [21]. In addition to utilizing the stable ^{15}N isotope-tracing technology to study the activity of anammox, there are also molecular biology, bioinformatics, and other technologies to conduct in-depth research on anammox bacteria. These include, for example, 16S rRNA-PCR, 16S rRNA-PCR-DGGE, 16S Real time-PCR, and fluorescence in

situ hybridization (FISH) techniques. These research methods provide a technical basis for understanding the diversity, abundance, and distribution of anammox bacteria.

Recently, many researchers have studied anammox in different types of natural ecosystems, but there is still a lack of review articles on this aspect, so this paper provides a summary. This paper introduced the reaction principle of anammox, combed the development history of anammox bacteria, analyzed the Web of Science data of more than 20 years since the discovery of anammox bacteria, and used SPSS software to classify and summarize the bacterial species and categories of anammox bacteria in various ecosystems. The analysis results showed that the activity of anammox varies greatly in the nitrogen cycle; the contribution rate is also significantly different in different environments, which plays an important role. Existing studies have revealed that environmental factors have a significant impact on the composition, abundance, and distribution of anammox bacteria in various natural habitats. In addition, anammox bacteria have different N_2 losses in different ecosystems. Therefore, based on the existing research, this study explains the physiological mechanisms of anammox. We studied the impact of marine, freshwater, terrestrial, and other ecosystem types on the anammox process to clarify the impact of different environmental factors on anammox, and to provide a scientific basis for further research of anammox's role in the nitrogen cycle in natural environments.

2. Anammox Microorganisms and Their Biochemical Reaction Mechanism

Anammox is a biological nitrogen removal process in which NH_4^+ is used as an electron donor and NO_2^- is used as an electron acceptor to directly oxidize ammonia nitrogen into N_2 under anaerobic conditions ($NH_4^+ + NO_2^- \rightarrow N_2 \uparrow + 2H_2O$). This process includes three main reactions [22,23] (Figure 3). First, NO_2^- is reduced to NO or hydroxylamine by nitrite reductase (Nir). Subsequently, NO is converted into NH_2OH by hydroxylamine oxidase (HAO). Following this, NH_2OH and NH_4^+ are condensed into N_2H_4 by hydrazine hydrolase (HH). Finally, hydrazine oxidase (HZO) catalyzes the oxidation of N_2H_4 to N_2 and H_2O , while nitrite oxidase (Nar) oxidizes NO_2^- to NO_3^- . Owing to its unique structure and reaction process, anammox can occur in a variety of low-substrate, -nitrogen, and -oxygen environments.

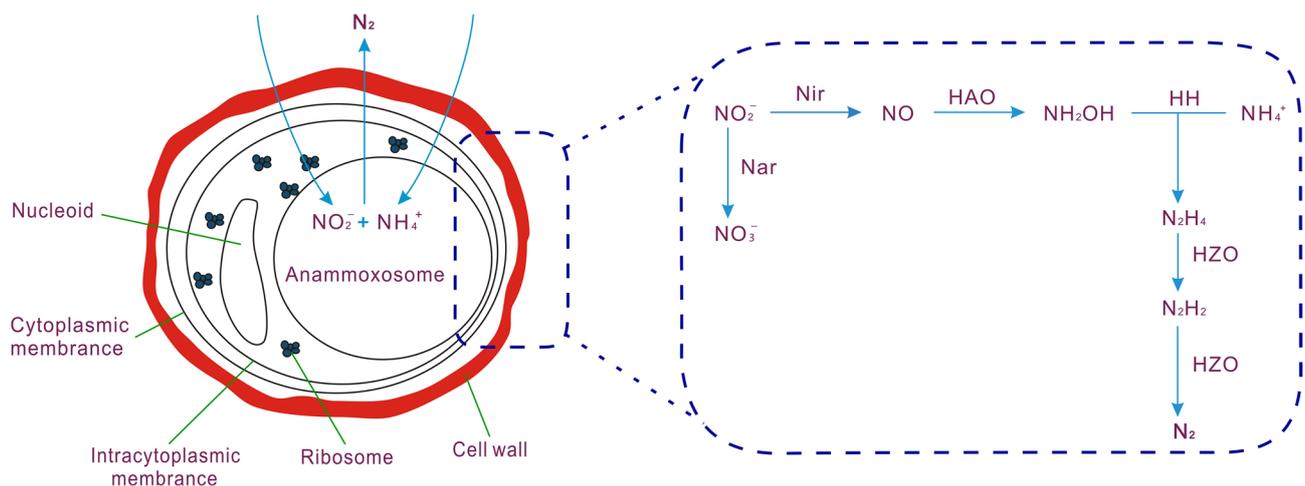


Figure 3. Structure of anammox bacteria and its mechanism.

According to 16S rRNA homology, anammox can be classified as a single-line branch of *Brocadia* in *Planctomycetia* [24]. Anammox bacteria are globular, ovoid, and rod-shaped. The cell body is red, and it is a gram-negative bacterium. To date, no pure culture strains for anammox exist. However, 16S rRNA, *hzo*, *hzsB* (key genes of hydrazine synthetase), and other genes can be detected using common polymerase chain reaction (PCR) and fluorescence quantitative PCR using modern molecular biology techniques, which can quantify bacterial abundance [5,25]. Among them, the *hzsB* functional gene has been used

several times in quantitative research on anammox bacteria. It can be used as an anammox biomarker and can display the diversity of anammox bacteria more comprehensively than other genes [16]. Currently, seven genera and 26 species of *Candidatus* (*Brocadia*, *Kuenenia*, *Jettenia*, *Scalindua*, *Anammoxoglobus*, *Anammoximicrobium*, and *Brasilis*) have been identified [26]. Details on the diversity of anammox microorganisms are presented in Table 1 [27–29]. *Ca. Scalindua* was found to dominate all surveyed oceans [30]. The biological diversity of anammox bacteria detected in freshwater ecosystems was low, and most of them belong to *Ca. Brocadia* [31] and *Ca. Kuenenia* [32]. Most anammox bacteria found in terrestrial ecosystems belong to *Ca. Jettenia*, *Ca. Brocadia* [33], and *Ca. Kuenenia* [34].

Table 1. Microbial diversity of anammox bacteria.

Phylum	Family	Genus	Species	Origin	Ref.
			<i>Candidatus Scalindua manna</i>	-	-
			<i>Candidatus Scalindua zhenghei</i>	the South China Sea	[35]
			<i>Candidatus Scalindua brodae</i>	five Rotating Biological Contactors (RBCs)	[36]
			<i>Candidatus Scalindua wagneri</i>		
		<i>Candidatus Scalindua</i>	<i>Candidatus Scalindua sorokinii</i>	the Black Sea	[37]
			<i>Candidatus Scalindua arabica</i>	the Arabian Sea and the Peruvian OMZ	[38]
			<i>Candidatus Scalindua profunda</i>	the Gullmar Fjord	[39]
			<i>Candidatus Scalindua japonica</i>	a Hiroshima bay sediment	[40]
			<i>Candidatus Scalindua sinooilfield</i>	High-Temperature Petroleum Reservoirs	[41]
<i>Planctomycetia</i>	<i>Anammoxaceae</i>	<i>candidatus Kuenenia</i>	<i>candidatus Kuenenia stuttgartiensis</i>	A two-stage semi-technical trickling filter reactor system	[42]
			<i>Candidatus Brocadia anammoxidans</i>	-	[43]
			<i>Candidatus Brocadia fulgida</i>	SBR	[44]
		<i>candidatus Brocadia</i>	<i>Candidatus Brocadia sinica</i>	Upflow Anaerobic Sludge Bed (UASB)	[45]
			<i>Candidatus Brocadia caroliniensis</i>	a glycerol-fed digester liquid effluent treatment process	[46]
		<i>candidatus Jettenia</i>	<i>Candidatus Jettenia asiatica</i>	Anammox	[47]
			<i>Candidatus Jettenia caeni</i>	-	-
		<i>Candidatus anammoximicrobium</i>	<i>Anammoximicrobium moscomii</i>	-	-
			<i>Candidatus Anammoxoglobus propionicus</i>	fed-batch enrichments	[27]
		<i>Candidatus anammoxoglobus</i>	<i>Candidatus Anammoxoglobus sulfate</i>	Non-woven rotating biological contactor (NRBC)	[48]

Anammox bacteria contain an organelle structure that is dense and has low permeability, known as anammoxosome [22,49]. Anammoxosome occupies most of the space within anammox bacterial cells and is the core component of anammox metabolic reactions. In addition, anammoxosomes can maintain an appropriate matrix concentration gradient within and outside the intracytoplasmic membrane when the anammox bacteria are in a low metabolism reaction [49]. A unique ladderane structure was found in anammox bacteria in previous studies. It requires 3–5 cyclobutanes in a series as the core structure

and is only synthesized by anammox bacteria. It can be used as a biomarker for the detection of anammox bacteria [50]. The deposited ladderane lipids have been proven to be biomarkers of fossil molecules, which can reflect the existence and past changes in anammox bacteria [6].

3. Distribution and Ecological Diversity of Anammox in Different Systems

Anammox is an anaerobic process. The process is mediated by a group of chemolithoautotrophic bacteria. Therefore, compared with traditional nitrification and denitrification processes, the anammox process has a higher denitrification capacity and does not consume oxygen and organic substrate without N_2O as the intermediate product [51]. Therefore, anammox bacteria have the ability to survive in many natural environments. Anaerobic ammonoxidation is a more effective and environmentally friendly way to reduce the production of greenhouse gases such as NO and N_2O in the process of nitrogen removal. Global nitrogen loss caused by anammox cannot be ignored; in addition, it is of great significance for the slowing of the global greenhouse effect. In an anoxic region and ecotone environment, a supersaturated water condition and an anoxic environment result in the mineralization of organic matter to form many NH_4^+ cations. The NH_4^+ cation is also produced by DNRA. These two pathways can provide a large number of reaction substrates for anammox. In some ecosystems, a large quantity of artificial nitrogen is inputted, which makes NH_4^+ , NO_3^- , NO_2^- , and other nitrogen-containing nutrients accumulate, subsequently providing a material basis for the survival and reproduction of anammox. However, the diversity and community structure of anammox bacteria differs in different ecosystems owing to the environmental background, demonstrating a specific distribution according to the ecological niche [52]. Scholars worldwide have used molecular biology, ^{15}N isotope tracing, and other technologies to conduct extensive research on this topic. Research areas are widely distributed, and the main ecosystem types that have been researched are marine, lake, river sediment, farmland soil, forest soil, and low-oxygen water areas. Table 2 presents the main research results.

Table 2. Anammox in different ecosystems.

Ecosystem	Research Object	Research Area	Nitrogen Removal Contribution Rate	Reaction Rate	Main Microorganisms	Reference		
Marine ecosystem	Marine sediment	Skagerrak	24–67%	1.25 $\mu\text{molN}\cdot\text{h}^{-1}$	—	[21]		
		Black sea	10–15%	$2.92 \times 10^{-4} \mu\text{molN}\cdot\text{L}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Scalindua</i>	[37]		
		Arabian Sea (NE)	30–50%	$1.76 \times 10^{-4} \pm 0.146 \times 10^{-4} \mu\text{mol}^{-1}\cdot\text{h}^{-1}$	—	[53]		
		Gullmarsfjorden, Sweden	48%	$6.64 \mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[54]		
		East Sea, Ulleung Basin	17–56%	$1.3\text{--}4.1 \mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[55]		
		East Sea, China	13–50%	$2 \mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[56]		
		Northern Gulf of Finland, Baltic Sea	10–15%	$0.42 \mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}\text{--}1.25 \mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[57]		
		Golfo Dulce, Costa Rica	19–35%	$1570\text{--}2542 \mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[58]		
		Southern New England estuarine	4–42%	$0\text{--}8.7 \mu\text{molN}\cdot\text{L}^{-1}\cdot\text{h}^{-1}$	—	[59]		
		North sea, UK	10–20%	$0.2\text{--}5.7 \mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[60]		
		Coasts of Greenland (EW)	1–35%	$0.04\text{--}3.83 \mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[61]		
		South pacific coastal, Peru	48%	$1.8\text{--}44.2 \mu\text{molN}\cdot\text{L}\cdot\text{h}^{-1}$	<i>Ca. Scalindua</i>	[62]		
		Aarhus Bay	2%	$0.625\text{--}1.333 \mu\text{molN}\cdot\text{h}^{-1}$	—	[21]		
		Beibu Gulf	13–34%	$0.13\text{--}1.22 \mu\text{molN}\cdot\text{L}^{-1}\cdot\text{h}^{-1}$	—	[63]		
		Northeast of Daya Bay, China	0.84%	$1.26 \mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	—	[64]		
		Bay sediment	Jiaozhou Bay (JZB)	Chesapeake Bay	0.07–18.55%	$0.01 \pm 0.00\text{--}0.24 \pm 0.03 \mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Scalindua</i> , <i>Ca. Brocadia</i>	[65]
				Shaws Bay, New South Wales, Australia	0–22%	—	<i>Ca. Kuenenia</i> <i>Ca. Scalindua</i>	[66]
				Arcachon Bay, Atlantic Ocean, France	74%	$0.18 \mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[67]
	14–45%			$0.617 \pm 0.15\text{--}9.921 \pm 6.533 \mu\text{molN}\cdot\text{L}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Scalindua</i>	[68]		

Table 2. Cont.

Ecosystem	Research Object	Research Area	Nitrogen Removal Contribution Rate	Reaction Rate	Main Microorganisms	Reference	
Freshwater ecosystem	Estuary sediment	Yangtze Estuary, China	6.6–12.9%	0.94–6.61 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Scalindua</i> <i>Ca. Brocadia</i> <i>Ca. Kuenenia</i>	[69]	
		Estuaries of Southeast England	0.57–10.93%	—	—	[70]	
		Colne Estuary, UK	30%	157 ± 15 $\mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	<i>Ca. Scalindua</i>	[71]	
		St. Lawrence Estuary, Canada	33%	5.5 ± 1.7 $\mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[72]	
		Cavado River estuary, NW Portugal	17–72%	0–3.3 $\mu\text{mol}\cdot\text{L}\cdot\text{h}^{-1}$	—	[73]	
		Yincungang River, Jiangsu, China	0.8 ± 0.00–10.7 ± 0.03%	0.11 ± 0.07 $\mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ –3.08 ± 0.95 $\mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	<i>Ca. Kuenenia</i> <i>Ca. Scalindua</i> <i>Ca. Jettenia</i>	[32]	
		Geng River, Henan, China	4.2 ± 0.02–10.2 ± 0.01%	1.27 ± 0.68 $\mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ –6.79 ± 1.28 $\mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	<i>Ca. Kuenenia</i> <i>Ca. Scalindua</i> <i>Ca. Jettenia</i> <i>Ca. Brocadia</i> <i>Ca. Kuenenia</i>	[8]	
		Yangtze River, China	3.5–82.8%	6.76 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Jettenia</i> <i>Ca. Scalindua</i> <i>Ca. anammoxoglobus</i>	[8]	
		River and Lake sediment					
		Shanghai River Network, China	0.34–81.6%	0.0404–23.7 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	—	[74]	
		Portugal, Ave River	5.5–35.1%	0.8–8.4 $\mu\text{molN}\cdot\text{L}\cdot\text{h}^{-1}$	—	[75]	
		Portugal, Douro River	0–54.0%	0–2.9 $\mu\text{molN}\cdot\text{L}\cdot\text{h}^{-1}$	—		
		Lake tanganyika, East Africa	13%	0.01 $\mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	<i>Ca. Scalindua</i>	[10]	
		Donghu Lake, Nanhu Lake, Wuhan, China	10.4%	87 ± 26 $\mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ –237 ± 83 $\mu\text{molN}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[76]	
		Subtropical region, Taiwan	0–0.76%	4.17 × 10 ^{−4} –66.67 × 10 ^{−4} $\text{mg}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[77]	
		Constructed wetland	Beijing, china	33%	18 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Jettenia</i> <i>Ca. Brocadia</i> <i>Ca. anammoxoglobus</i>	[78]
		Underground water	Mito, Japan	3.1%	50.3 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Brocadia</i> <i>Ca. Jettenia</i>	[79]
			Thuringia, Germany	83%	1.46 × 10 ^{−4} –1.96 × 10 ^{−4} $\mu\text{mol}\cdot\text{L}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Brocadia</i>	[80]
			Elmira, Canada	18–36%	13.3 × 10 ^{−3} –31.3 × 10 ^{−3} $\mu\text{mol}\cdot\text{L}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Brocadia</i>	[81]
		Wetland sediment	Logan/Albert River, Australia	0–9%	0.5–8 $\mu\text{molN}\cdot\text{L}\cdot\text{h}^{-1}$	—	[82]
		Goa, India	15–25%	101.15 ± 87.73 $\mu\text{molN}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	—	[83]	
		Baiyangdian Wetland	2.4–35%	0.8–240 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Brocadia</i> <i>Ca. Kuenenia</i>	[84]	
	Upland soil	Zhangjiang Estuary, China	1.61–16.70%	0.20–11.56 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	—	[16]	
		Tianjin, China	41–67%	0.23–0.74 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Brocadia</i>	[33]	
	Coastal saline-alkali soil	Basel, Switzerland	37.5–58.3%	0.005–0.68 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Brocadia</i> <i>Ca. Scalindua</i> <i>Ca. Kuenenia</i>	[85]	
		Cixi, Ningbo, China	40–87.5%	0.09–1.32 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Kuenenia</i> <i>Ca. Brocadia</i> <i>Ca. Jettenia</i> <i>Ca. Kuenenia</i>	[86]	
	Vegetable field soil	Nanjing, Jiangsu, China	1.4–18.4%	0.046–0.729 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Brocadia</i> <i>Ca. Jettenia</i> <i>Ca. Kuenenia</i> <i>Ca. anammoxoglobus</i>	[34]	
Terrestrial ecosystem		Zhejiang, China	4–37%	0.5–2.9 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Jettenia</i> <i>Ca. Brocadia</i>		
		Zhejiang, Hunan, Jiangxi, China	1.5–35.1%	0.11–3.64 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	—	[12]	
		Jiaxing, China	3.1–8.1%	0.78–1.60 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. brocadia</i> <i>Ca. kuenenia</i>	[87]	
	Paddy soil	Binhai, Leizhou, Taoyuan, China	0.4–12.2%	0.02–0.77 $\mu\text{molN}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Brocadia</i> <i>Ca. Kuenenia</i> <i>Ca. Jettenia</i>	[88]	
		Changshu, Jiangsu, China	3.58–8.17%	0.56–1.47 $\mu\text{mol N}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Brocadia</i> <i>Ca. Jettenia</i>	[89]	
		Riverina, New South Wales (NSW), Australia	17%	4.58 × 10 ^{−3} $\text{g}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	—	[90]	

Table 2. Cont.

Ecosystem	Research Object	Research Area	Nitrogen Removal Contribution Rate	Reaction Rate	Main Microorganisms	Reference
Other ecosystems		Ibaraki Prefecture, Japan	1–5%	2.2–2.7 $\mu\text{mol}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	<i>Ca. Brocadia</i> <i>Ca. Kuenenia</i>	[91]
	Heaven pond	Tianshan, China	82%	1.162 $\mu\text{mol}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$	Between <i>Ca. Brocadia</i> and <i>Ca. Jettenia</i>	[92]
	Hydrothermal samples	Mid-Atlantic Ridge	—	$1.25 \times 10^{-3} \mu\text{mol}\cdot\text{h}^{-1}$	<i>Ca. Scalindua</i> <i>Ca. Kuenenia</i>	[93]
	Hot springs	California and Nevada	—	—	<i>Ca. Brocadia</i> <i>Ca. Kuenenia</i>	[94]
	Marine sponges	Conch Reef, Key Largo, Florida	—	—	<i>Ca. Brocadia</i>	[95]

3.1. Anammox in Marine Ecosystems

Marine sediments are often in an anoxic state. Under these conditions, the decomposition of organic matter yields $\text{NH}_4^+\text{-N}$. Denitrification and short-cut nitrification produce $\text{NO}_2^-\text{-N}$, an intermediate product, which can provide favorable living conditions for anammox bacteria. Thamdrup and Dalsgaard [21] first detected anammox activity in Danish coastal sediments using the ^{15}N stable isotope tracer method, which confirmed the existence of anammox in natural ecosystems. Subsequently, anammox was detected in marine sediments in several regions. Anammox is of great significance to the biogeochemical cycles of marine nitrogen and marine ecology [30]. Based on 16S rRNA and *hzs* gene research, Dang et al. [96] found that anammox bacteria accounted for 0.094×10^{-4} – 0.21×10^{-4} copies·g⁻¹ of the total microbial biomass in Jiaozhou Bay. Fu et al. [97] found that the ratio of anammox bacteria to total microbial biomass was only 0.020×10^{-4} – 0.051×10^{-4} copies·g⁻¹. Hou et al. [69] identified that the ratio of anammox bacteria in the Yangtze River estuary and adjacent waters was between 9.86×10^6 and 1.02×10^8 copies·g⁻¹. *Ca. scalindua*, which has a high salt tolerance and plays a critical role in nitrogen production in marine environments. The anammox bacteria contribute 1–67%, or even higher to N_2 production in the marine nitrogen cycle (Table 2). In particular, the anoxic oceanic area is an important location for anammox, and the contribution rate of anammox in different oceanic areas is considerably different. In the East Sea Ulleung Basin, the anammox contribution rate to the nitrogen cycle was 56%, which exceeded that of denitrification [55]. Bulow et al. [53] also detected high anammox reaction activity from the Oman coast to the central–northeast Arabian Sea. It was found to contribute 30–50% of the nitrogen cycle in the region, which was equivalent to the denitrification intensity. However, the contribution of anammox to the nitrogen cycle in some marine sediments is relatively low [60]. For example, the contribution rate of anammox measured by Hietanen and Kuparinen [57] in the northern Gulf of Finland was only 10–15%, and denitrification was found to play a leading role. In conclusion, anammox activity is different in different sea areas, which may be related to the different environmental factors (ecological niches) in different sea areas. Therefore, the contribution rate of anammox to the sediment nitrogen cycle is different in different sea areas.

The contribution rate of anammox to nitrogen in the bay is 0.07–74%, and the N_2 production contribution of anammox bacteria in estuarine is up to 30% [71].

It has been observed that there are anammox bacteria of the genera *Ca. Brocadia*, *Ca. Kuenenia*, and *Ca. Scalindua* in the Zhangjiang estuary wetland [16]. Estuaries are among the areas with the most intense land–ocean interactions and the most complex ecological structure, which can create a microenvironment suitable for the survival of different types of anammox bacteria. In addition, *Ca. Brocadia* and *Ca. Kuenenia* were found in the sediments of estuaries and bays, indicating that the anammox bacteria of these two genera have a salt tolerance capacity in the alternating freshwater and ocean zones. The ecological and physiological differences in these anammox bacteria are also the drivers of the anammox community's geographical distribution pattern in estuaries and bays.

3.2. Anammox in River Ecosystems

Anammox bacteria in freshwater ecosystems differ from those in oceanic ecosystems. The river basin nitrogen contribution rate in most freshwater areas remains lower than that of the marine environment. The contribution rate of anammox in the Ave River of Portugal is 5.5–35.1%, and the reaction rate is 0.8–8.4 nmol N·cm⁻³·h⁻¹ [75]. Meyer et al. [82] found that the N₂ contribution rate of anammox in the Logan/Albert River system in the subtropical area of southeast Queensland, Australia is 0–9%, and the reaction rate is similar to that of the Ave River, which is 0.5–8 nmol N·cm⁻³·h⁻¹. These studies show that the contribution rate of anammox to nitrogen in freshwater is low, and denitrification plays an important role in the nitrogen cycle. The reason for this may be because the organic carbon content in freshwater sediments is rich, and most denitrifying bacteria are heterotrophic bacteria, so anammox bacteria cannot gain an advantage when they coexist and compete with denitrifying bacteria. Most anammox bacteria in freshwater ecosystems belong to *Ca. Brocadia* [31] and *Ca. Kuenenia* [32]. Chen et al. [8] found abundant anammox bacteria in the Yangtze River Basin of China, including four types of *Ca. Brocadia*: *Ca. Kuenenia*, *Ca. Jettenia*, *Ca. Scalindua*, and *Ca. Anammoxoglobus*. The anammox contribution rate was 3.5–82.8%, and the reaction rate was 6.76 nmol Ng⁻¹h⁻¹. This is because the sediments along the Yangtze River contain a certain amount of anammox bacteria with high spatial heterogeneity, so the nitrogen loss shows heterogeneity.

Owing to its fluidity and external pollution, the activity and contribution of anammox are significantly different in different locations [65]. Bohlke et al. [98] first detected anammox in groundwater using the isotope tracer method and identified a rate of 0.027 μmol·L⁻¹·d⁻¹, indicating that anammox plays a secondary role in the groundwater nitrogen cycle. Moore et al. [81] reported the activity of anammox bacteria in groundwater polluted with ammonium in Elmira, Canada. They detected four types of anammox microbial species and found that the reaction with ammonium caused 18–36% nitrogen loss. Smits et al. [99] also found that anaerobic anammox bacteria were present in ammonia-contaminated groundwater, in addition to anammoxidation, and found that this reaction contributed 39–90% of the potential N₂ production. These results indicate that anammox plays a key role in denitrification in nitrogen-polluted groundwater. Therefore, it is speculated that there may be a specific heterogeneity in the distribution of anammox bacteria in groundwater systems.

3.3. Anammox in Lake Ecosystem

Schubert et al. [10] first reported the distribution of anammox bacteria in a natural freshwater ecosystem in Lake Tanganyika, mainly in the *Ca. Scalindua*. The maximum activity of the anammox bacteria was 10 nmol·N₂·h⁻¹. The anammox bacteria's contribution rate to the nitrogen cycle in this area is 13%, in addition, their activity and contribution rates are not inferior to those of anammox bacteria in some marine habitats [56,61]. The contribution of N₂ to anammox in a constructed wetland in the subtropical region of Taiwan was only 0–0.76% [77]. However, in the eutrophic freshwater Puhu Lake, Hubei Province, the relative contribution of the anammox process to nitrogen production is high. From this, up to 40% of N₂ production is related to anammox activity. The study found a positive correlation between NO₃⁻ concentration and nitrogen production contribution rate of the anammox process, indicating that NO₃⁻ concentration is the key factor for the development and activity of anammox bacteria in this freshwater habitat [100].

3.4. Anammox in Terrestrial Ecosystems

Some areas in the terrestrial ecosystem can provide suitable living conditions for anammox bacteria. In recent years, human activities have resulted in an influx of large amounts of nitrogen into marshlands, farmlands, and other terrestrial ecosystems. Anammox is likely to occur in selected areas lacking oxygen. However, currently, research on anammox in terrestrial ecosystems is mainly focused on farmland soils. Humbert et al. [13] first detected *Ca. Scalindua*, *Ca. Kuenenia*, *Ca. Brocadia*, and *Ca. Jettenia* in different terrestrial

environments such as swamps, polluted interstitial aquifers, permafrost, and farmland soil. Anammox bacteria are only found in soil to a certain depth. The highest rate of anammox was identified in the 20–30 cm layer, which indicated that the spatial heterogeneity and distribution of anammox bacteria in terrestrial ecosystems only exist in specific ecological environments. In China, the contribution rate of anammox to N_2 is 4–37% in Zhejiang paddy soil [34], 1.5–35.1% in Hunan and Jiangxi paddy soil [12], and 3.1–8.1% in Jiaying paddy soil [87]. Among them, *Ca. Brocadia* and *Ca. Kuenenia* were the most dominant bacterium. Most of these soils are dominated by *Ca. Brocadia*. However, in the saline–alkali soil of a Hai-han horticultural farm in Ci-xi, Ningbo, the highest rate of anammox is 40–87.5%, and the reaction rate is 0.09–1.32 $\text{nmol N}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$. This is because the terrestrial ecosystem is more likely to form an anoxic or even anaerobic environment conducive to anaerobic ammoxidation. Therefore, the control of DO is an important factor in the activity of anaerobic ammoxidation. The dominant bacteria is similar to that of marine ecosystems, mainly the salt-tolerant *Ca. Scalindua* with a small proportion of *Ca. Brocadia* and *Ca. Kuenenia* also being detected. Clearly, many microbial niches in the soil were found to support the ecological and physiological functions of different anammox bacteria [101].

3.5. Anammox in Other Ecosystems

In addition to these ecosystems, anammox bacteria are distributed in other ecosystems. Jaeschke et al. [94] observed the presence of anammox bacteria in hot springs at 65 °C. According to 16S rRNA phylogenetic analysis, *Ca. Brocadia fulgida*, *Ca. Brocadia anammoxidans* and *Ca. Kuenenia stuttgartiensis* are present in hot springs. Byrne et al. [93] also detected *Ca. Scalindua* in the deep sea hydrothermal vents of the Mid-Atlantic Ridge with temperatures up to 60–85 °C and confirmed its anammox activity. Anammox bacteria found in hydrothermal ecosystems can be used to improve the understanding of the nitrogen cycle in the deep sea. Mohamed et al. [95] observed the distribution of anammox bacteria in marine sponges. The anammox bacteria detected in this study had a relatively distant relationship with *Ca. Brocadia fulgida*. Anammox bacteria were also detected and found to dominate in the sediment samples of the lakeside water–land boundary zone of Tianshan Tian-chi, a low-temperature and high-altitude area in China, with a contribution rate of 82%, which is higher than that previously reported in other environments [92]. The distribution of anammox in these ecosystems shows that anammox plays an important role in the nitrogen cycle of certain specific ecosystems and that the extremity of the environment is not a controlling factor of anammox activity.

3.6. Anammox in Wastewater Treatment System

Anammox has been detected in several natural ecosystems globally. As the largest biotechnology application, wastewater treatment plants (WWTPs) play an important role in the global nitrogen cycle [102]. The anammox rate of municipal sewage treatment plants in winter is 0.08–0.36 $\mu\text{mol N}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ and 0.12–1.20 $\mu\text{mol N}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ in summer. The contribution to N_2 production is 2.05–6.86% and 1.71–7.26% respectively, which verifies the substantive contribution of the anammox process in municipal sewage treatment for the first time [103]. Research by Meng et al. displayed that the abundance of planctomycetes in WWTPs of mainstream cities and towns was 41.873–96.565%, mainly including four anaerobes: *Ca. brocadia*, *Ca. kuenenia*, unclassified *Ca. brocadiaceae*, and *Ca. anammoxoglobus*. The dominant anaerobe was unclassified *Ca. brocadiaceae*, with an abundance of 33.363–95.346%. Simultaneously, anaerobe diversity analysis showed that the diversity was low in WWTPs in mainstream cities and towns. Different biological units in the same WWTPs could be distributed in the same quadrant. The biological units of different WWTPs are both similar and different [104]. According to Lu et al. [105], when the salinity increases to 160 $\text{mmol}\cdot\text{L}^{-1}$ during wastewater treatment, and the main functional bacteria change from *Ca. kuenenia* to unclassified *Ca. brocadiaceae*. There are great differences in the optimal temperature, pH, and salinity of different anaerobes in the wastewater treatment system [16].

4. Influential Factors on Anammox Distribution

Differences in the anammox bacteria distribution in the natural environment may be due to environmental factor restrictions. Different ecological substrates affect the community structure and activity of the anammox bacteria. In recent years, many studies have discussed anammox community diversity, abundance, and activity in different environments. Correlations between these aspects and environmental factors provide a theoretical basis for revealing the cause of the spatial heterogeneity and environmental functions of anammox [106]. The environmental factors affecting anammox include temperature, pH, substrate concentration, organic matter content, dissolved oxygen (DO), and water salinity.

4.1. Temperature

Temperature dependence is an important limiting factor affecting the operation of biological nitrogen removal systems [107]. In different ecosystems, anammox exhibits a strong temperature adaptation range of -2 – 80 °C. Anammox bacteria can survive in a wide temperature range and can exist in extreme environments, such as hot springs and hydrothermal vents with temperatures up to 60 – 80 °C, or river and marine sediments at temperatures of -5 – 4 °C [108]. However, low temperatures affect the growth rate of the anammox bacteria. Laurenzi et al. [109] showed that reducing the temperature from 29 °C to 12.5 °C increased the doubling time from 18 to 79 d. Lotti et al. [110] achieved a specific anammox growth rate of 0.02 d⁻¹ at 20 °C, and the doubling time was 35 d. Lowering the temperature to 15 °C resulted in a decrease in the growth rate to 0.009 d⁻¹ and a doubling of time to 77 d. The optimal temperature of anammox in WWTPs is 33 ± 1 °C [111], which is lower than that of most natural ecosystems. The optimal temperature range for anammox activity in estuarine sediments is 14 – 16 °C, which is very similar to the previously reported optimal temperature of 12 – 15 °C in marine sediments [61]. In a natural environment, denitrification and anammox can produce a large amount of N₂, and denitrification can promote the anammox. In the summer, more nitrites are produced as intermediate products by enhancing denitrification. This could stimulate the growth of anammox bacteria during the warm season, and increase the incidence of anammox reactions. However, in a study by Cheng et al. [74], the denitrification rate in summer was higher than that in winter, whereas the anammox rate in winter was higher than that in summer. Rysgaard et al. [61] determined that the optimal temperature for anammox activity in the Arctic Ocean was 12 °C. Anammox bacteria exhibit a strong temperature adaptability in the natural environment. Therefore, seasonal and spatial changes in anammox activity may be regulated by water temperature and substrate content in the sediment.

4.2. pH

The most suitable pH condition for the anammox bacteria as identified in a reactor is a neutral or weak alkaline range between 6.7 and 8.3 [18,112]. The pH of unpolluted water and sediment in natural habitats is within this range and is suitable for the growth of microorganisms. Nevertheless, active anammox bacteria were also detected in extreme freshwater environments with pH values of 3.88 and 8.91 [108]. Temperature and pH have significant effects on the anammox process, and anammox bacteria are particularly sensitive to changes in pH. On the one hand, pH strongly inhibits the anammox process by affecting the substrate concentration (ammonium and nitrite) [113]. However, pH directly affects the anammox bacteria community structure and diversity, thus affecting the anammox process. Wang and Gu et al. [114] showed that high pH (9.0) had a great impact on the community structure of anammox bacteria, whereas low pH (5.0) had little impact. However, compared to the control group at pH 7.0, the biodiversity of both cases increased. This may be because of the promotion of NH₄⁺ and NO₂⁻ generation after acid or alkali treatment, thus forming an environment conducive to the growth and development of anammox bacteria. In addition, high pH also causes the unavailability of trace elements [115]. It is clear that anammox bacteria exhibit better activity in acidic environments.

4.3. DO and Salinity

Anammox bacteria is an anaerobic microorganism that is sensitive to changes in oxygen concentration. They can survive in an environment with less than 5% oxygen saturation where oxygen partial pressure activity of more than 18% oxygen saturation may be inhibited (reversible inhibition). However, the oxygen content in the natural environment varies in the sediment or water layer. Therefore, anammox bacteria in the natural environment may have a higher oxygen tolerance. However, areas with low oxygen content had a high incidence of anammox bacteria. Therefore, the factors affecting anammox activity change with sampling depth [116].

With the change in salinity, the species of anammox bacteria and the rate of the anammox reaction also change [5]. Most bacteria in the ocean are *Ca. Scalindua*, which have strong salt tolerance, unlike the main bacteria found in freshwater systems and reactors. Sonthiphand et al. [117] used sequencing and nonparametric analyses using distance matrices to test several marine samples from around the world. They confirmed that salinity is the main factor affecting the global distribution of anammox bacteria. In addition, there is a significant correlation between anammox bacteria species richness and salinity. Dale et al. [106] noticed that the change in anammox bacterial abundance was closely related to the change in salinity in the Cape Verde estuary, which ranged between 0 and 9.9. Zheng et al. [118] found that the abundance of anammox bacteria was significantly correlated with the salinity of the Yangtze River Estuary ($p < 0.05$). Salinity has a great influence on the abundance of anammox in the Cape Verde and the Yangtze River estuaries. In areas with low or high salinity (15.65–34.46 or 34.47–34.48), the abundance of anammox bacteria was relatively low.

4.4. Substrate Concentration

Substrate concentration, such as NO_3^- and NO_2^- , and organic matter content both significantly affect the abundance and distribution of the anammox bacterial community. As a substrate, nitrite provides nutrients and energy to the anaerobic anammox bacteria. However, when the concentrations of ammonia nitrogen and nitrite exceed a threshold, the activity of anammox bacteria is inhibited. Studies have shown that the anammox rate is linearly correlated with the concentration of NO_3^- in Greenland [61]. Moreover, anammox bacteria are advantageous in sediments with high and stable NO_3^- conditions. Moreover, Wu et al. [65] found that high NO_3^- in Jiaozhou Bay is beneficial for the growth of different anammox bacteria in the surface sediment. The observed anammox activity in the Yangtze River estuary is more sensitive to nitrite [69], which may be because the nitrite content in the sediment is a controlling factor of anammox in the sediment. Nitrite is an intermediate product formed by denitrification by denitrifying bacteria, and its content in the natural environment is lower than that of other inorganic nitrogen salts; therefore, the content of nitrate or nitrite has become an important limiting factor for anammox.

4.5. Organic Matter Content

Anammox bacteria are chemoautotrophic bacteria that do not require organic carbon sources [119]. Furthermore, when the availability of electron donors in sediments becomes high, anammox may not exceed that of denitrification [120]. Nicholls and Trimmer [70] displayed that the abundance of anammox bacteria increases significantly with an increase in TOC. This is because more organic matter in the sediment can produce more NH_4^+ through ammonification and more NO_2^- through denitrification. This leads to a positive correlation between the anammox abundance and TOC. Trimmer et al. [121] studied the anammox process in the sediments of the Thames Estuary, UK. They also found that there is a significant positive correlation between the anammox process and organic matter content, which contributes 1–8% to the production of N_2 . Lu et al. [122] noted that in the low-organic-matter-content environments of Sandusky Lake, the amount of N_2 produced by anammox was higher than that produced by denitrification. This was owing to the high organic load in the study area which promoted the reduction of NO_3^- by denitrification

and made denitrification more advantageous than anammox. However, with a decrease in organic loading, denitrification activity decreased. Simultaneously, a large quantity of NO_2^- (which can be used by organisms) can provide favorable conditions for the anammox reaction and increase anammox activity. These results show that the diversity and activity of anammox increased with a decrease in organic carbon content. Therefore, an environment with a low organic carbon content is more favorable for the survival of anammox bacteria.

5. Expectation

Existing studies have only analyzed the anammox contribution rate to the nitrogen cycle in local ecosystems. The nitrogen cycle of global ecosystems, as well as the participation and contribution rate of anammox, remain unknown. Research on anammox processes in different natural and artificial ecosystems should be expanded to determine their actual contributions. By detecting sediment samples, isolating and identifying strains, establishing microbial metabolic models, etc., a deeper understanding of the anammox process can be gained, and the contribution of anammox to global nitrogen cycling can be quantified based on data. Further research can be carried out to explore its contribution to global nitrogen cycling by studying anammox processes in different ecosystems, exploring its advantages in nitrogen removal, considering its environmental impacts and safety issues, and quantifying its contribution through data analysis and modeling. Models can be established through numerical simulation to draw the activity distribution map of anammox reactions in global aquatic and terrestrial ecosystems, predict and evaluate the role of anammox in the spatial large-scale nitrogen cycle, accurately evaluate the important role of anammox reactions in the nitrogen cycle, comprehensively investigate all environmental factors in the ecosystem, and analyze the comprehensive effects of influencing factors on different systems. This is undertaken to provide a scientific basis for the global nitrogen cycle, which is of great significance for improving the biogeochemical cycle of nitrogen in ecosystems.

6. Conclusions

The anammox process is catalyzed by Nir, HAO, HH, HZO, and Nar. Anammox bacteria, which have unique anammox structures. At present, 26 species of anammox bacteria belonging to 7 genera have been identified in natural ecosystems. They exist widely in different ecosystems. In natural ecosystems, anammox maintains nitrogen balance by converting excess ammonia nitrogen into nitrogen. Anammox occurs under anoxic or anaerobic conditions, so it usually occurs at the top of the sediment or at the bottom of the water column. It makes an important contribution to the nitrogen cycle, especially when the nitrification/denitrification process is inhibited. The contribution of anammox to the marine ecosystem is the highest, the N_2 production rate can reach 67%, and the dominant bacteria in the ocean is *Ca. scalindua*. The nitrogen contribution rate of anammox to most freshwater areas was lower than that of the marine environment. Anammox bacteria play a key role in the nitrogen pollution of groundwater. The concentration of NO_3^- is a key factor for the development and activity of anaerobic anammox bacteria in lake ecosystems. The main functional bacteria in sewage treatment systems is *Ca. kuenenia*. The distribution of anammox bacteria in natural environment is affected by environmental factors such as temperature, pH, substrate concentration, organic content, dissolved oxygen, and salinity. Sometimes anammox bacteria exhibit thermophilic, acidophilic, and salt-tolerant characteristics. The study of environmental factors on the distribution of anammox bacteria is helpful to further analyze the global contribution of anammox to nitrogen.

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