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Driving factors and microbiology for the enrichment of denitrifying anaerobic methane oxidation (DAMO) microorganisms

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ABSTRACT

The application of the denitrifying anaerobic methane oxidation (DAMO) in a biological nitrogen removal system has received much attention since methane is used as the sole carbon source and produced in the anaerobic digestion process of wastewater treatment plant. DAMO reaction is performed by DAMO archaea (*Methanoperedens nitroreducens*) and DAMO bacteria (*Methylomirabilis oxyfera*, *M. sinica*, *M. limnetica*, and *M. lanthanidiphyla* belonging to NC10 phylum). In the presence of methane, nitrate, or nitrite are used as the substrate, then the reaction takes place under the anoxic condition. Due to extremely slow growth and stringent metabolic requirements, these microbes are difficult to be cultured and applied in the wastewater treatment. In this paper, driving factors and microbiology for the enrichment of DAMO process in previous studies are reviewed, especially the effects of inoculum, reactor types, and environmental factors (substrate concentration, pH, dissolved oxygen, and temperature) on the DAMO process. Besides, key factors that can effectively control microbial community structures and enhance the optimization strategies for DAMO enrichment are identified in this review. In the future study, there are still some challenges to be addressed, such as growth factors affecting DAMO process performance and the stable operation of ecosystem in the cultivation process.

Keywords: Denitrifying anaerobic methane oxidation (DAMO); Enrichment; Driving factors; Biological nitrogen removal

1. Introduction

As an important greenhouse gas in the atmosphere, methane (CH_4) is rated to be 28 for its global warming potential for a time horizon of 100 y [1–5]. If methane was not properly treated and directly discharged into the atmosphere, secondary pollution can be caused by the methane from industrial anaerobic digestion. Since the 1970s, the potential and advantages of denitrifying anaerobic methane oxidation (DAMO) have been recognized to reduce the methane emission [Eqs. (1) and (2)] [6,7]. The DAMO is a novel process in which methane is utilized as the sole electron donor to reduce nitrate or nitrite to nitrogen gas under the anoxic condition [8]. As an important link between the nitrogen and carbon cycles, DAMO process has been highlighted for its advantages. In the aspects of industrial application, methane utilization and biological denitrification can be realized by DAMO process simultaneously, resulting in the removal of CH_4 originated from anaerobic digestion and nitrogen in sewage. This process is a promising method with minimal input and comprehensive utilization of resources for future sewage treatment [9].

$$8NO_3^- + CH_4 + 8H^+ \rightarrow 4N_2 + 5CO_2 + 14H_2O \quad (1)$$

$$\Delta G^\circ = -765 \text{ kJ/mol}$$

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$$8NO_2^- + 3CH_4 + 8H^+ \rightarrow 4\,N_2 + 3CO_2 + 10H_2O \quad (2)$$

$\Delta G° = -928$ kJ/mol

In 2004, Strous and Jetten [3] suggested that some heterotrophic microorganisms, which can use nitrite/nitrate as electron acceptor for anaerobic oxidation of methane (AOM), might exist in nature. In the same year, Islas-Lima et al. [9] revealed the possibility of DAMO process by sequencing batch experiments, while the microorganisms performing the oxidation of methane and denitrification have not been investigated in their paper [10]. Until 2006, Raghoebarsing et al. [11] successfully enriched DAMO microorganisms with the sediment of a laboratory-scale sludge digester in the Netherlands. Since then, microorganisms used in DAMO process have been successfully enriched by several research groups. Moreover, research progress has been achieved in physiology, mechanisms, and kinetics of responsible microorganisms (Table 1). However, DAMO has not been industrialized in the wastewater treatment system, due to the long doubling time of DAMO microorganisms, high requirement for anaerobic environment, biomass flush-out problems, and unstable microbial community structure.

Therefore, it is significant to understand operational parameters in microorganisms activities for the improvement of DAMO process, such as inoculums, reactor configurations, operational parameters, and synergistic relationships with other microorganisms. In this review, previous studies on DAMO enrichment are summarized, bacteria, and archaea that have high nitrogen removal efficiency and collaborative microbes with the DAMO process are mainly explored. In addition, appropriate selection of inoculums during cultivation, configuration of bioreactors, and factors affecting the nitrogen removal efficiency are also concluded in this review.

2. DAMO process

2.1. Responsible microorganisms

To date, there are four different DAMO bacteria of the genus *Candidatus Methylomirabilis* that can denitrify nitrite with methane, namely "*Candidatus Methylomirabilis oxyfera*" (extensively studied) [8], "*Candidatus Methylomirabilis sinica*" [12], "*Candidatus Methylomirabilis limnetica*" [13], and "*Candidatus Methylomirabilis lanthanidiphyla*" [14].

Table 1
Percentages of relative studies on DAMO process with each property

Relative studies	Percentage
Influencing factors	24%
Enrichment	21%
Ecology	17%
Molecular detection	12%
Synergy with other microbes	9%
Mechanism	8%
Nitrogen removal	6%
Biomass characteristics	3%

On the contrary, only one DAMO archaea, "*Candidatus Methanoperedens nitroreducens*" can perform denitrifying nitrate to nitrite in the presence of methane [15].

"*Candidatus Methylomirabilis oxyfera*," which belongs to the NC10 phylum without pure culture [11], is a gram-negative bacterium with the reduction ability of nitrite to nitrogen gas [8,16]. FISH (fluorescence *in situ* hybridization) analysis showed that *M. oxyfera* has thin rod shapes, and it is 0.8–1.1 μm long and 0.25–0.5 μm wide, with DNA concentrated in the center of the cell [8]. In the freshwater sediments, the methane affinity constant of *M. oxyfera* is about 0.092 mmol/L [17], the nitrite affinity constant of *M. oxyfera* is about 0.91 mmol/L [17]. *M. oxyfera* bacteria in the enrichment culture are mainly divided into two groups, namely "Group A" and "Group B" [18]. It was studied that, the members of "Group B" dominated in the early enrichment stage, while the members of "Group A" gradually occupied more niche after the prolonged incubation [19]. A novel branch of NC10 clade, "*Candidatus Methylomirabilis sinica*" (*M. sinica*), was enriched from paddy soil [12], fresh water [20], and halophilic marine environments [21]. The cell of *M. sinica* is roughly coccus-shaped with the radius of 0.7–1.2 μm, which is larger than *M. oxyfera* [12]. In both halophilic marine sediments and fresh water, the methane affinity constant and nitrite affinity constant are 7.8 ± 1.2 and 8.9 ± 2.9 μmol/L, respectively [12,21]. The growth rate of *M. sinica* is probably 0.028/d [12], and the doubling time is nearly 25 d, which is longer than that of *M. oxyfera* [8,17]. Another new species of NC10 member, namely "*Candidatus Methylomirabilis limnetica*" (*M. limnetica*), grows in deep anoxic layer in Lake Zug [13]. The 16S rRNA gene sequence revealed that the homology of *M. limnetica* with *M. oxyfera* is 96.3%, and the identity to *M. sinica* is 95.1% [13]. "*Candidatus Methylomirabilis lanthanidiphyla*" (*M. lanthanidiphyla*) is the fourth species in NC10 phylum, and presents in a small amount in the initial inoculum of a ditch sediment [14]. *M. lanthanidiphyla* shows 97.5% identity to both *M. oxyfera* and *M. sinica*, and 96.3% identity to *M. limnetica* [13]. *M. lanthanidiphyla* has all the genes for denitrifying nitrite detected in *M. oxyfera* to nitrogen gas, including several heme-copper oxidases that make NO disambiguation to N_2 and O_2 [14].

As the anaerobic methanotrophic archaea (ANME) [15], "*Candidatus Methanoperedens nitroreducens*" grows as irregular cocci with 1–3 μm in diameter and is typically found as sarcina-like clusters and assembled into 3–6 μm round [11,15]. The reduction of nitrate to nitrite coupling anaerobic methane oxidation is performed by *M. nitroreducens* [15] at mesophilic temperatures within the pH of 7–8 [22]. In the freshwater sediments, the nitrate affinity constant of *M. nitroreducens* is about 7.85 mmol/L, while these affinity constants are obtained by a mathematical model on the denitrification couple anaerobic methane oxidation [23]. Recently, Lu et al. [24] claimed that the anaerobic methane oxidation rate constant of *M. nitroreducens* is 0.019 ± 0.006 /h, while the affinity constant for nitrate of *M. nitroreducens* is 2.1 ± 0.4 mgN/L according to Monod type kinetic model.

2.2. Physiology of DAMO

Two different hypotheses are proposed for the physiology of DAMO process: (1) a new pathway, namely "inter-aerobic

nitrite-driven anaerobic methane oxidation denitrification" by DAMO bacteria [8]; and (2) a general pathway, namely "reverse methanogenesis" executed by DAMO archaea [15].

2.2.1. Inter-aerobic nitrite-driven anaerobic methane oxidation denitrification

In 2010, Ettwig et al. [8] confirmed that the DAMO can be carried out independently by DAMO bacteria. The culture was inhabited by a diverse population of NC10 bacteria via assembling the complete genome with metagenomics technology. Genes for the reduction of nitrate to nitrite (*narFHJI*, *napAB*), nitrite to nitric oxide (*nirSJFD/GH/L*), nitric oxide to nitrous oxide (*norZ* = *qnor*) were obtained, as well as genes encoding the complete pathway for aerobic methane. However, the gene for reducing nitrous oxide to dinitrogen gas was missing. Therefore, coupling anaerobic methane oxidation to denitrification, a new pathway mediated by "*Candidatus Methylomirabilis oxyfera*" was proposed. As shown in Fig. 1, NO_2^- is firstly reduced by nitrite enzyme to NO, then NO is subsequently split into N_2 and O_2 with an unknown NO dismutase [8]. The produced O_2 is partly (75%) used for aerobic oxidation of methane [25], and the surplus is used for normal respiration [26]. Finally, the fourth biological pathway for oxygen production has been discovered in nature besides photosynthesis, chlorate respiration, and the detoxification of reactive oxygen species.

2.2.2. Reverse methanogenesis

It has been found that "*Candidatus Methanoperedens nitroreducens*" could couple anaerobic methane oxidation to nitrate reduction [15]. Methane is anaerobically oxidized to CO_2 via the "reverse methanogenesis" pathway, supplying electrons for the nitrate reduction (Fig. 2). However, *M. nitroreducens* lacks the genes encoded enzymes for the denitrification from nitrite to nitrogen gas, indicating that the full denitrification process cannot be completed by *M. nitroreducens*. Hence, collaborating with *M. nitroreducens*, the reduction of nitrite to N_2 is accomplished by other microorganisms [27]. Interestingly, apart from the genes for the complete "reverse methanogenesis" pathway, the genes responsible for the reductive acetyl-CoA pathway and acetyl-CoA synthetase also exist in *M. nitroreducens*. It indicates that *M. nitroreducens* have the potential to oxidize methane into acetate. The results are consistent with the previous prediction that some of the ANME archaea can produce acetate from methane [28–31].

3. Factors affecting DAMO enrichment

In this paper, a variety of influencing factors during DAMO enrichment process are summarized, including inoculums, reactor configurations, and operating conditions (nutrient substrates, methane partial pressure, pH, temperature, and dissolved oxygen). Table 2 shows the relevant data from references.

3.1. Inoculum sources

The proper selection of seeding sludge is a crucial step for a successful enrichment with a rapid start-up of DAMO process. DAMO microorganisms can exist in methane-rich habitats with anoxic conditions for providing NO_3^-/NO_2^- [32], such as the anaerobic/anoxic interface of water and sediments [33]. Methane-rich sediments are usually contained in the marine, however, the storage of nitrate and nitrite as electron receptors is insufficient [34]. But microorganisms that can oxidize methane and reduce nitrate or nitrite are identified by the activity test and quantitative PCR [21]. Groundwater is often contaminated by nitrate and nitrite, while methane is insufficient acting as an electron donor [35]. Hence, the most possible niche for

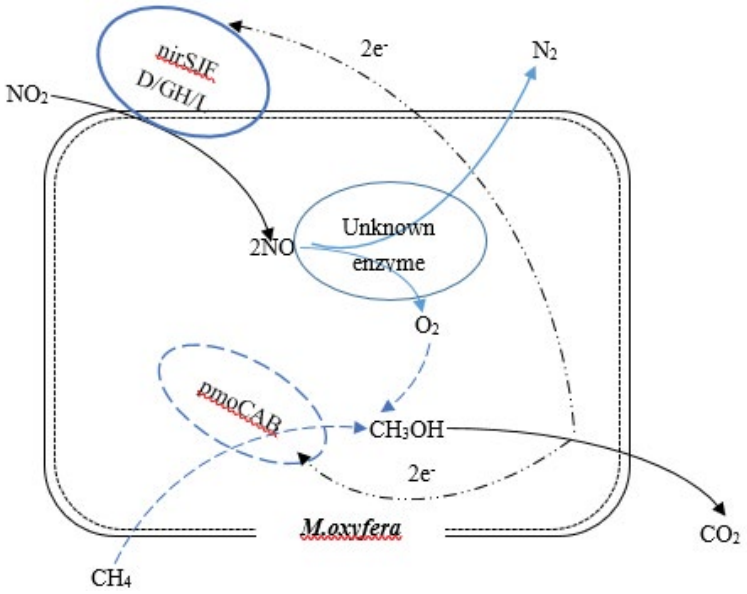

Fig. 1. Proposed pathways of *M. oxyfera* [8].

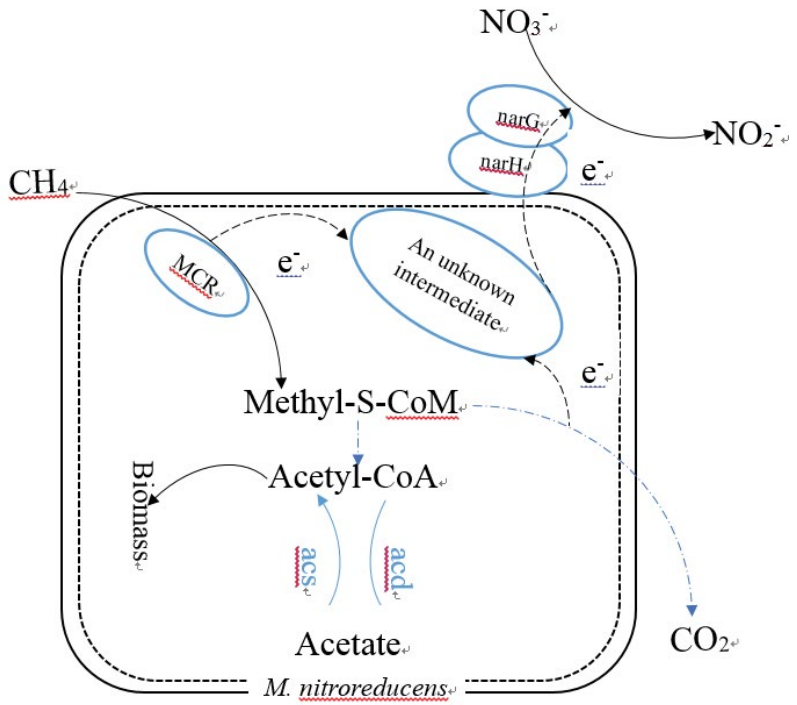

Fig. 2. Proposed pathways of *M. nitroreducens* [15].

DAMO microorganisms is predicted to be a millimeters oxic–anoxic interface in freshwater, which can be easily missed from detection [35].

Qian et al. [36] founded that DAMO process was successfully detected after only two months of operation in freshwater inoculum (Table 2). In addition, Hu et al. [22] successfully enriched DAMO microorganisms by a mixed inoculum including a freshwater lake sediment, an anaerobic digester sludge, and a return activated sludge from a sewage treatment plant. With further study, researchers have discovered the existence of DAMO microorganisms in different habitats, such as wetland and ocean, even in Gobi [22,37], and successfully enriched the DAMO microorganisms with the corresponding inoculum. Hatamoto et al. [38] seeded with the sediment of wetland soils as a DAMO culture in which DAMO bacteria and archaea were successfully enriched. He et al. [21] sourced *M. oxyfera* from marine sediments and established a new enrichment. After 20 months of incubation, more than 70% of *M. oxyfera* bacteria were detected in the culture and the nitrite consumption rate reached 0.457 mg N/L/d. Then, He et al. [12] sourced the paddy soil for further enrichment on the new species of the NC10 phylum naming *M. Sinica*. Versantvoort et al. [14] set up an enrichment bioreactor originally seeded from Ooijpolder. Two years later, in the presence of cerium but without nitrate, a high quality species of *M. lanthanidiphyla* have been enriched. Additionally, different inocula, such as anaerobic digestion sludge, denitrification activated sludge, were used to enrich DAMO microorganisms [20,39,40].

He et al. [41] investigated the effect of inoculum sources on the enrichment of DAMO bacteria. In this study, three different inocula including methanogenic sludge, paddy soil, and freshwater sediment were used to enrich DAMO bacteria. Considering the results of the DAMO activity test and qPCR analysis, paddy soil was the optimal inoculum. Firstly, methanogenic sludge contained an amount of organic matters, then denitrifying bacteria was more competitive than the slow-growth DAMO bacteria under such conditions. Secondly, the doubling time of DAMO bacteria in paddy soil was estimated to be 2.1 months, which was shorter than that in methanogenic sludge and freshwater sediment [20].

3.2. Reactor configurations

The reactor configuration during the enrichment is a key factor affecting the microbial community structure [49]. Due to the slow growth rate of DAMO microorganisms, a bioreactor with an effective biomass retaining ability is superior for long-term operations [50]. Typical examples of bioreactor configurations used in the culture process are discussed below.

3.2.1. Suspension bioreactor

The suspension bioreactors for the cultivation of DAMO include the sequencing batch reactor (SBR), continuous stirred tank reactor (CSTR), magnetically stirred gas lift reactor (MSGLR), up-flow anaerobic sludge blanket (UASB), and membrane bioreactor (MBR).

SBR is usually used for the biomass enrichment due to its high biomass retaining ability, the effective promotion for a homogenous mix of the biomass and substrate, long-term stable operation, and the improvement of sludge settling property [51]. In 2006, the first DAMO enrichment reactor was established using SBR with the sediment of a laboratory-scale sludge digester in the Netherlands. After 16 months

Table 2
Enrichment cultures of DAMO process and operational conditions in previous studies

Inoculum	Reactor type	Temperature (°C)	pH	Nitrogen feeding		Composition (%)		Maximum conversion rate (mg N/L/d)	References
				NO_3^-	NO_2^-	NC10	Archaea		
Canal sediments	SBR	25	7.0–7.5	√√	√√	80	10	15.3	[11]
Canal sediments	CSTR	30	7.3–7.6	√√	√√	70	0	9.6	[16]
Canal sediments	SBR	30	6.9–7.5	√		70	0	36.1	[35]
Mixed inoculum[a]	SBR	22	7.0–7.5	√		15	0	0.91	[22]
	SBR	35	7.0–7.5	√		30	40	28	
Wastewater sludge	SBR	20–23	6.8–7.3	√	√	60–70	–	5.1	[40]
Ditch sediments	SBR	20–30	7.0–8.0	√	√	70–80	–	37.8	[42]
Minerotrophic peatland	SBR	25	6.0–6.2	√	√	80	–	–	[43]
Mixed inoculum	MBfR	25	7.0–7.5	√		20–30	20–30	250	[44]
Wastewater sludge	MBR	20	6.5–8.0		√	60–70	–	36	[45]
	MBR	20	6.5–8.0		√	70–80	–	16	
Paddy soil	UFCR	30	7.4	√		58	7	70.4	[38]
	UFCR	30	7.4		√	68	0	51.0	
–	SBR	30	7.0–7.2		√	>50	–	11.4	[46]
–	CSTR	30	7.0–7.2		√	>50	–	26.4	[46]
–	MSGLR	30	7.0–7.2		√	>50	–	76.9	[46]
Freshwater sediments	MBfR	35	7.0–8.0	√	√	–	–	50	[36]
Taihu sediments	MBR	10–25	7.0	√	√	73	–	14	[47]
–	MBR	28	6.3–8.5		√	50.2	–	116	[48]
Coastal sediment	SBR	25	7.0		√	70–80	–	5.49	[21]
Methanogenic sludge	SBR	30	7.0–8.0		√	>50	–	4.62	[20]
Freshwater sediment	SBR	30	7.0–8.0		√	>50	–	4.76	[20]
Paddy soil	SBR	30	7.0–8.0		√	>50	–	4.48	[20]
Paddy soil	SBR	35	7.2–7.4		√	–	–	0.0739	[12]
Paddy soil	DHS	30	7.0–8.0	√	√	50–70	–	84.4	[19]
Ditch sediment	SBR	30	7.2–7.4	√	√	68	–	–	[14]
Digester sludge	UASB	33	7.3	√		–	–	63.3	[39]

[a]Mixed inoculum: including sediments from a lake, activated sludge and digester sludge from a wastewater treatment

of operation, a culture of DAMO microorganisms containing 10% archaea and 80% NC10 bacteria was obtained and nitrite conversion rate reached 15.3 mg N/L/d [11]. Ettwig et al. [35] started a DAMO reactor in another SBR in which NC10 bacteria accounted for about 70% of the total microorganisms after 7 months operation in 2009, and the maximum nitrite conversion rate was 29.3 mg N/L/d. Those experimental results proved that SBR is suitable for long-term DAMO bacterial cultivation in which more than 1 y is required for the enrichment. However, Luesken et al. [40] showed that the use of SBR can also achieve DAMO activity within 112 d, and the nitrite conversion rate is 5.1 mg N/L/d (Table 2).

Although SBR is a good system for DAMO enrichment, the low load of conventional SBR reactors and high control requirements of automated procedures restrict its application. Other suspension reactors were also used to enrich DAMO microorganisms. Hu et al. [46] compared the effects of the reactor configuration (a magnetically stirred gas lift reactor (MSGLR), an SBR, and a CSTR on DAMO bacterial enrichment. The results showed that MSGLR had the optimal performance, and the maximum volumetric nitrogen removal rate was up to 76.9 mg N/L/d, which was much higher than that in previous studies. Compared with the other two reactors, MSGLR strengthened the mixing of gas–liquid–solid phases, improved the gas–liquid mass transfer, and reduced the inhibition of substrate [46]. As a novel anaerobic technology, UASB is used to treat wastewater and improve the function of strengthening three-phase mixing and gas–liquid mass transfer [52]. The UASB reactor is composed of the separator of gas, liquid, and solids for retaining granular sludge, thus a good sludge settling capability is provided. Ma et al. [39] reported that enrichment of NC10 bacteria was successfully obtained by using UASB reactor, and the abundance of which were two orders magnitude higher than that in previous studies by other types of suspension bioreactors [20].

The proposed bioreactors above indeed achieve the high nitrogen removal efficiency and obtain DAMO microorganisms, while a certain amount of biomass flushing out are founded in those configurations. To avoid the washout of biomass, Kampman et al. [45] proposed the use of three

membrane bioreactors (MBR), and achieved the maximum nitrogen conversion rate of 36 mg N/L/d. Similarly, Allegue et al. [48] utilized a fully-monitored MBR for the cultivation of DAMO bacteria, and obtained a high nitrite removal rate of 116 mg N/L/d.

3.2.2. Attached growth-type bioreactors

Attached growth-type bioreactors are suitable for the cultivation of the slow growing microorganisms because the effective solid–liquid separation and supporting material are used to retain the microbial population. The use of attached carrier material can increase the total surface area maintained by microorganisms, thereby the concentrations of microorganisms and volumetric loading rates of the DAMO activity are increased. Generally, there are two kinds of attached growth-type bioreactors, namely downflow hanging sponge reactor (DHS) [19] and membrane biofilm hollow fiber reactor (MBfR) [44].

Methane is a potential electron donor for denitrification. However, methane is a flammable and low aqueous solubility gas. This characteristic needs to be addressed before application of methane in wastewater treatment. In the DHS reactor, sponge is used as the carrier to improve the gas–liquid mass transfer efficiency of methane and enhance the impact load resistance of the system, thus the biological colony is more stable, and the activated sludge is rarely lost [19].

The mentioned problems can also be solved by MBfR [53]. On one hand, hollow fiber membranes are utilized for dispersing gas to the liquid. The hollow fiber configuration allows rapid transfer rates and provides a high interfacial gas transfer area. On the other hand, due to the large concentration gradient across the membrane, gases diffuse rapidly and dissolve directly into the water outside the membrane, finally, the high efficiency is achieved [54]. In addition, management costs of greenhouse gas can be decreased by MBfR due to the effective minimization of gas stripping losses to the atmosphere. The application of MBfR in delivering oxygen and hydrogen has been confirmed, with 100% hydrogen transfer efficiency and 99.5% hydrogen utilization efficiency [55–57]. In 2013, MBfR was first applied for synergizing anammox and DAMO, and methane was delivered from the interior of hollow fibers to the outer membrane that biomass grew on [44]. The results indicated that the activity of DAMO archaea in the outer biofilm was three times higher than that in the parent culture. Recently, the enrichment of DAMO microorganisms and anammox bacteria was synchronously obtained in MBfR. Due to the high efficiency of methane mass transfer, the activity of DAMO archaea continuously increases with the prolonging enrichment period, indicating that MBfR is a promising installation for the enrichment of DAMO archaea [58].

3.3. Environmental factors

3.3.1. Substrate concentration differences between nitrite and nitrate feeding

In recent years, DAMO microorganisms have been mainly inoculated from river sediments polluted by inorganic nitrogen or wastewater sludges with the rich nitrogen, and then cultured for long-term cultivation. It is concluded that different combinations of inorganic nitrogen (NO_2^-/NO_3^-) feeding can affect the activity of DAMO microorganisms and the selection of dominant strain [35,45,59]. Hu et al. [60] indicated that DAMO archaea were eliminated by nitrite feeding alone, while both archaea and bacteria existed with nitrate feeding. The results suggested that, compared with *M. nitroreducens* which were more effective in the nitrate reduction, *M. oxyfera* were more competitive in reducing nitrite [16]. The reason was obtained through research on the internal mechanism of archaea and bacteria: *M. nitroreducens* could reduce nitrate in the substrate to nitrite, which was required for *M. oxyfera* growth [8,15]. Therefore, these two kinds of microorganisms could co-exist in the enrichment with nitrate as the substrate. If there were no nitrate used in substrate, nutritional medium would be unavailable for *M. nitroreducens*, and the growth would be limited, besides, *M. oxyfera* would compete to be the dominant strain in this environment. However, Wang et al. [47] showed that the culture was dominated by DAMO bacteria when the only nitrate was fed. It indicated that DAMO bacteria were competing against DAMO archaea in the cultivation process. Further experiments have shown that complex nitrogen substrate is more beneficial to the growth of microbial diversity of DAMO than single nitrogen substrate [61,62].

Additionally, nitrite accumulation can damage the microorganisms structures, leading to the decrease of DAMO catabolic activity [60,63]. The activity of DAMO bacteria started to show toxic effects once exposed to nitrite at concentrations level of 1 mmol/L [60]. Research confirmed that the optimal concentration of nitrite was 1.92 mmol/L in the mixed medium of nitrate and nitrite by modeling actual performance [17]. Whether the toxic effect of nitrite on DAMO activity can be reduced by the reactor structure, physical control conditions, and nitrate exposure time need to be further verified.

3.3.2. Methane concentration

Methane is the sole electron donor and crucial substrate for DAMO process [64]. Thus, the partial pressure of methane and the difference in affinity constant between bacteria and archaea to methane have great influences on denitrification rates of DAMO microorganisms. Zhao et al. [65] explored the effect of partial pressure of methane on the DAMO process. The results indicated that the denitrification rate of DAMO firstly increased and then gradually kept stable, and the partial pressure of methane ranged from 0 to 49 kPa; while the denitrification rate slightly increased, and the partial pressure of methane ranged from 49 to 98 kPa [65]. Thereby, methane was not a limiting factor of DAMO process at a certain threshold, which was consistent with previous research [17,66].

Due to the low solubility of methane gas, the methane concentration in the liquid is one of the critical factors influencing the activity of DAMO process. Some measures have been proposed to boost the solubility of methane in the liquid solution. Besides the use of high-pressure of methane bioreactors [67,68], there are other effective measures, such as the addition of a second liquid phase [69], the proper

increase of stirring speed, and the moderate decrease of temperature, Fu et al. [70] found that adding 5% paraffin oil while culturing DAMO microorganisms and anammox bacteria can effectively increase methane solubility by 25%, thus DAMO microbes activity will be raised. Furthermore, Shi et al. [44] utilized MBfR for denitrification. Owing to methane was directly supplied through a bubble-free aeration hollow fiber film, its mass transfer efficiency could be enhanced [71,72]. Meanwhile, the denitrification rate of DAMO microorganisms would be controlled by adjusting the pressure [73].

3.3.3. pH

The stable denitrification performance of DAMO microorganisms can be achieved by adjusting environmental condition of an optimal pH. In this way, the activity of enzymes can be changed, thus the activity of microorganisms is affected. The inhibition of DAMO activity was reported to occur at pH values lower than 7, while high DAMO activity was observed between pH values of 7 and 8 [11]. However, Zhu et al. [43] successfully enriched DAMO microorganisms at pH value of 6.2 in 2012. This is the sole research on DAMO activity under acidic conditions. Furthermore, another study demonstrated that the culture has the lowest denitrification rate when the pH was 8.5 or 9.5, while DAMO had the strongest activity at the optimal pH of 7.5 [66].

3.3.4. Temperature

Temperature is considered as a significant factor affecting the structure of microorganisms. Based on previous studies, good DAMO activity levels were detected at temperatures ranging from 25°C to 35°C [74]. As the temperature gradually raised from 20°C to 35°C, DAMO activity showed a steady growth [22]. Not only the activity, but also the abundance of microbial populations and species are affected by temperature. According to culture comparison of DAMO microorganisms at different temperatures (22°C and 35°C), the influence of temperature on DAMO bacteria and DAMO archaea could be manifested [22]. Two microbes were contained in the enrichment at 35°C, including DAMO bacteria and archaea, while DAMO bacteria could be found without DAMO archaea at 22°C, suggesting that DAMO archaea might be more readily activated at the higher temperatures [22]. However, no denitrification activity was detected in the culture operating at 45°C after several days of cultivation [22]. Moreover, the researcher started DAMO process successfully within a low temperature of 10°C–25°C, and found that the relative abundance of NC10 bacteria reached 73% after the cultivation of 13 months [47].

3.3.5. Dissolved oxygen concentration

DAMO microorganisms are obligate anaerobes, which are extremely sensitive to the presence of oxygen. DAMO bacteria could generate their own oxygen with oxidizing methane by a newly discovered intra-aerobic pathway [8]. Although O_2 is an intermediate in the metabolism of DAMO bacteria, the addition of 2%–8% oxygen from outside affected the gene expression of encoding methane oxidation and denitrification pathway [8,75].

3.3.6. Other factors

Besides the above-mentioned factors, some other factors can also affect DAMO process, such as salinity and the trace metal concentrations like iron and copper. Microorganisms tended to stagnate dormant or disappear in high salinity environment [76]. He et al. [41] found that the salinity was an important factor shaping the activity of DAMO bacteria cultured in freshwater. DAMO bacteria-specific activity decreased with the increasing NaCl salinity and almost disappeared at 20 g NaCl/L within a short time in batch cultivation. Interestingly, salinity adaption of DAMO bacteria was observed with the salinity stress level of 20 g NaCl/L after long-term cultivation [77]. Another study indicated that the activity of DAMO bacteria was detected in the marine sediment with the salinity of 25%, yet the growth of DAMO bacteria in freshwater experienced a lag phase the salinity of 1%. These results suggested that DAMO bacteria cultured in the marine have distinct physiological properties from those cultured in freshwater [78].

Studies have shown that metal elements have potential impacts on the metabolic pathway of DAMO microorganisms [79,80]. He et al. [41] concluded that DAMO activity increased with the increase in iron (II) and copper (II) at low concentrations (<20 μmol/L), but decreased slightly at high concentrations (>20 μmol/L). It suggested that 20 μmol/L of iron (II) and 10 μmol/L of copper (II) are suitable for the growth and metabolism of DAMO bacteria.

Several growth factors have been proposed to enhance nitrogen removal during the DAMO enrichment. As an auxiliary group of oxidoreductase, pyrroloquinoline quinone (PQQ) could participate in catalytic redox reactions in organisms, and it was reported to be a catalyst of the DAMO reaction [81]. Wang et al. [82] investigated the effects of growth factors like vitamin, heme, nucleobase, and betaine on DAMO microorganisms. The results indicated that 5 μg/L of nucleobase and 200 μg/L of betaine significantly stimulated the DAMO activity.

4. Interactions with other microbes

4.1. Anaerobic oxidation of methane

Under anaerobic conditions, the microbial-catalyzed methane oxidation process, called as AOM, can effectively reduce the methane. It has been evaluated that nearly 10^{12} kg methane can be oxidized anaerobically from the deposit sediments, contributing to a consortium of methanotrophic archaea (ANME) [2]. According to the different electron receptors in the culture environment, AOM can be divided into three types, including sulfate anaerobic methane oxidation (SAMO) [83], DAMO [9], and iron manganese-dependent anaerobic methane oxidation [84,85]. If nitrate or nitrite are final electron receptors in the AOM process, this process is called as DAMO [11]. Such microorganisms, which can couple the AOM and denitrification, are called as DAMO microorganisms, including DAMO archaea and DAMO bacteria [22].

4.2. Anammox

Anaerobic ammonium oxidation (anammox) is a reaction in which nitrite is used as electron acceptor and ammonia is oxidized to nitrogen gas under anaerobic conditions [51]. In the ocean, it was said that the 30%–50% of removal of ammonia nitrogen was caused by the anammox [3]. To date, the co-culture of anammox functional microorganisms and DAMO functional microorganisms has been studied widely [86]. In the process of co-culture of DAMO and anammox microorganisms, anammox consumed 77% of the ammonium as electron donor and nitrite to produce nitrate and nitrogen gas, while DAMO bacteria consumed the rest of nitrite with methane as reducing agent. At the same time, the nitrate produced in the process of anammox could be consumed by DAMO archaea [40].

5. Conclusion

In this review, microbial communities and key controlling factors for the enrichment of DAMO were summarized, including inoculums, reactor configurations, and environmental conditions (substrate concentration, pH, dissolved oxygen, and temperature). Overall, MBfR might be a suitable enrichment bioreactor because of the low biomass flush-out and high mass transfer efficiency. The optimal pH of the environment was around 7.5, and the synthetic nitrogen substrate was recommended for the microbial diversity of DAMO. Furthermore, more studies are required to explore some growth factors which affect the DAMO process performance (nucleobase, betaine, and vitamin) and ecological associations within wastewater ecosystems, so as to improve the performance of this nitrogen removal process. This review is essential for the implementation of nitrogen removal process in the wastewater treatment plant.

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