

Research Progress on Aerobic Starvation Treatment of Wastewater: Efficacy, Mechanisms, and Applications

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Abstract

Aerobic starvation, as a low-cost and easy-to-operate regulatory strategy in biological wastewater treatment, modulates microbial metabolism and community structure by constructing a substrate-depleted environment, thereby altering wastewater treatment performance. Studies have demonstrated that the efficacy of aerobic starvation exhibits significant pollutant specificity and complexity: there is no unified and precise temporal definition for short-term versus long-term aerobic starvation, with most literature defaulting to a treatment duration exceeding 30 days as long-term, while short-term refers to a relatively brief phase of substrate scarcity. Regarding pollutant removal effects, most studies indicate that both short-term and long-term aerobic starvation generally inhibit phosphorus (P) and chemical oxygen demand (COD) removal. However, only a single early study suggested the potential promotional effect of short-term starvation, and recent investigations have further confirmed its enhancement effect on biological phosphorus removal systems, providing additional evidence for the feasibility of short-term promotion. For nitrogen (N) removal, inhibitory effects dominate irrespective of duration. The differential responses of functional microorganisms are the core drivers of performance variations: ammonia-oxidizing bacteria (AOB) and polyphosphate-accumulating organisms (PAOs) exhibit relatively strong tolerance to short-term starvation, whereas nitrite-oxidizing bacteria (NOB) and conventional denitrifying bacteria are susceptible to inhibition. This review systematically summarizes relevant domestic and international studies, focusing on advances in multiple dimensions, including the classification characteristics of aerobic starvation, wastewater treatment performance responses, functional microbial mechanisms, applications of microbiome technologies, and practical engineering implications. Furthermore, existing studies still have gaps in the application of advanced omics technologies, verification of the promotional effects of long-term starvation, and standardization of engineering parameters. Multidisciplinary integration is required to drive the optimization, improvement, and large-scale application of the technical system.

Keywords

Aerobic Starvation; Biological Wastewater Treatment; Pollutant Removal; Functional Microorganisms; Efficacy Regulation.

1. Introduction

The core of biological wastewater treatment relies on microbial metabolism for pollutant removal. In practical operations, substrate fluctuations and equipment shutdowns frequently expose microorganisms to starvation stress [1]. Owing to its elimination of additional chemical agents and simple operation, aerobic starvation has emerged as a highly promising process regulation method [2]. In recent years, relevant studies have confirmed that aerobic starvation can affect the removal efficacy of pollutants such as N, P, and COD by reshaping microbial communities and regulating functional gene expression, but research findings remain significantly controversial-with inhibitory effects predominating overall and only a very limited number of studies showing promotional signs. For instance, a recent experiment verified that short-term aerobic starvation indeed exerts significant benefits in promoting P and COD removal [3], while most studies indicate that both short-term and long-term starvation tend to reduce the activity of functional microorganisms such as PAOs and nitrifying bacteria [1,4]. The complexity and controversy of these effects highlight the critical practical significance of in-depth exploration into the regulatory laws and mechanisms of aerobic starvation for optimizing biological wastewater treatment processes and improving treatment stability [5].

Existing studies exhibit multiple dimensional gaps in the field of aerobic starvation. In terms of classification, research has predominantly focused on short-term aerobic starvation. For example, 7-day starvation can rapidly initiate partial nitrification [2,5], while the effects of long-term treatment remain unclear, particularly the lack of systematic verification of its promotional effects. Only a limited number of studies have reported that synergistic processes (e.g., PD/anammox) can tolerate long-term starvation [6]. In terms of efficacy, the promotional mechanisms of short-term aerobic starvation on P and COD removal have not been fully elucidated, and the impact laws of long-term treatment on various pollutants are inconsistent. For example, long-term starvation may lead to "ineffective phosphorus release" by PAOs [7], but the specific regulatory conditions remain unclear. In terms of technology, microbial analysis still relies primarily on traditional metagenomics [1,6], and the application of advanced technologies such as metatranscriptomics and metabolomics is insufficient, making it difficult to reveal the dynamic metabolic response processes of functional microorganisms [8]. In terms of application, there is a lack of unified standards for regulatory parameters (e.g., duration, dissolved oxygen) of aerobic starvation in practical engineering, and technical feasibility and economy still require more empirical support [9].

This review is organized around the logic of "classification-efficacy-mechanisms-technology-application", with the core objective of integrating the differential effects of short-term and long-term aerobic starvation and systematically analyzing their regulatory laws on different pollutants and functional microorganisms. By comparing the application progress of microbiome technologies, summarizing the practical engineering significance of aerobic starvation technology, and finally clarifying current research gaps and future directions, this review provides a clear framework for in-depth research and practical application in this field.

2. Classification Characteristics and Wastewater Treatment Efficacy of Aerobic Starvation

2.1. Classification Characteristics and Wastewater Treatment Efficacy of Aerobic Starvation

There is no unified and precise temporal definition for short-term versus long-term aerobic starvation. Most literature defaults to a treatment duration exceeding 30 days as long-term, while short-term refers to a relatively brief phase of substrate scarcity. Differences in their efficacy are mainly regulated by key operating parameters. From existing studies, both short-

term and long-term aerobic starvation generally inhibit pollutant removal, with only a very limited number of experiments showing that short-term starvation can promote P and COD removal [3]. This specific effect is closely associated with the activation of microbial emergency metabolism and the enrichment of functional microbial communities. Core operating parameters include dissolved oxygen (DO), temperature, and sludge characteristics: most studies control DO at 3~8 mg/L, and a high-DO environment accelerates microbial endogenous metabolism [4]; room temperature (20~25°C) and neutral pH (7.0~7.5) are optimal conditions, while low temperatures or extreme pH values amplify the inhibitory effect of starvation [1]; the higher the abundance of functional microbial communities (e.g., PAOs, AOB) in the inoculated sludge, the stronger the tolerance to starvation [5].

Consistent with the consensus of most literature, long-term aerobic starvation exerts a more significant inhibitory effect on N/P removal due to the continuous attenuation of microbial activity and community structure imbalance [1,7]. However, synergistic processes such as PD/anammox can still recover rapidly after long-term starvation [6], and their applicable conditions and regulatory mechanisms require further verification. Notably, the core difference between short-term and long-term starvation lies in whether microorganisms transition from the "stress adaptation phase" to the "activity attenuation phase," rather than the absolute division of specific days. The occasional promotional effects of P and COD removal in short-term starvation have only been reported in a single literature and recent partial experiments, and no unified conclusion has been formed-this also lays the foundation for subsequent exploration of whether long-term starvation exhibits promotional effects.

2.2. Efficacy Differences in the Removal of Different Pollutants

2.2.1. COD Removal

From existing research data, most studies indicate that both short-term and long-term aerobic starvation generally inhibit COD removal, with only a few studies suggesting the potential promotional effect of short-term starvation. In recent years, some experiments have also discovered and confirmed this possibility. Such promotional effects account for a very low proportion, and the core mechanism is that microorganisms activate the metabolism of intracellular storage polymers (e.g., poly- β -hydroxyalkanoate, PHA) and enhance the degradation capacity of refractory organic compounds under substrate depletion [8]. For example, relevant experiments have shown that short-term starvation can enrich microbial communities such as *Sphingomonas* and *Achromobacter*, promoting the removal of refractory pollutants such as bisphenol A (BPA) with an efficiency increase of 20%~30% [8], or enrich *Tetrasphaera*, which provides carbon sources for COD-degrading bacteria (e.g., *Chryseolinea*, *Bacillus*) through fermentation, thereby facilitating COD degradation [3]. However, such cases have not formed a universal law.

Long-term aerobic starvation is dominated by inhibitory effects, with approximately 80% of studies showing a 10%~50% decrease in COD removal efficiency [1]. Only acclimated denitrifying sludge can maintain stable removal performance [7]. This difference stems from the exhaustion of intracellular storage substances in microorganisms under long-term starvation, the massive loss of functional microbial communities, and only heterotrophic bacteria (OHOs) can maintain partial activity by degrading intracellular substances of dead bacteria [8].

2.2.2. Nitrogen Removal

The response of nitrogen removal to aerobic starvation is time-dependent. Under short-term aerobic starvation, approximately 70% of studies show inhibitory effects, with a decrease in total nitrogen (TN) removal efficiency-mainly due to the sensitivity of nitrifying bacteria (AOB/NOB) to starvation and the temporary inhibition of their activity [1]. However, some studies have found that short-term starvation can selectively inhibit NOB, promote nitrite

accumulation, and provide support for the partial nitrification-anaerobic ammonium oxidation (PNA) process [2,5]. A 7-day aerobic starvation can achieve a nitrite accumulation rate (NAR) exceeding 95% [2].

Under long-term aerobic starvation, nitrogen removal exhibits significant inhibitory effects. The activity attenuation rate of AOB/NOB reaches more than 50%, and the recovery rate of NOB is slower than that of AOB [1,6]. For example, as reported previously [6], after long-term starvation of the PD/anammox system, the TN removal efficiency is still higher than that of the single Anammox system, with microbial synergy being the key. In traditional activated sludge systems, long-term starvation can lead to the collapse of nitrification function, and the recovery cycle takes 1~2 weeks [9].

2.2.3. Phosphorus Removal

The efficacy law of phosphorus removal is similar to that of COD. Most studies confirm that both short-term and long-term aerobic starvation generally inhibit phosphorus removal, with only a few studies suggesting the potential promotional effect of short-term starvation. In recent years, some experiments have also discovered that short-term aerobic starvation can promote phosphorus removal. The latter clearly confirms that aerobic starvation exerts an enhancement effect on biological phosphorus removal systems. In such cases, PAOs can effectively preserve intracellular PHA under short-term starvation, and rapidly initiate excessive phosphorus uptake after substrate restoration, increasing the phosphorus removal efficiency by 15%~30% [4]. Studies by Wang et al. also verified that PAOs can still maintain 79% of phosphorus uptake activity after short-term aerobic starvation [4], but such conclusions have not been widely validated. Precisely because the promotional effect of short-term starvation is only observed in a limited number of cases, and the effect of long-term starvation is generally inhibitory, whether long-term aerobic starvation exhibits promotional effects has become one of the current core research gaps.

Long-term aerobic starvation is dominated by inhibitory effects. Studies [7] have confirmed that PAOs exhaust storage polymers due to endogenous metabolism, with an activity attenuation rate of more than 60%, and will experience "ineffective phosphorus release"-phosphorus produced by polyphosphate hydrolysis cannot be effectively utilized, but instead leads to an increase in effluent phosphorus concentration. Denitrifying polyphosphate-accumulating organisms (DPAOs) have stronger tolerance to starvation than conventional PAOs, but their coupled nitrogen and phosphorus removal capacity will still be significantly attenuated under long-term starvation [7].

2.3. Core Driving Factors of Efficacy Differences

The differences in wastewater treatment efficacy caused by aerobic starvation are mainly driven by three types of factors. Starvation duration is a key variable: in the short term, microorganisms are in the "stress adaptation phase," functional microbial communities are not lost in large quantities, and emergency metabolism may be activated to produce promotional effects [5,8]; in the long term, microorganisms enter the "activity attenuation phase," with cell death and community imbalance becoming dominant, and inhibitory effects becoming prominent [1,7].

Pollutant types also significantly affect response outcomes: the removal of COD (especially easily degradable COD) and P is more sensitive to short-term starvation [4,8], while nitrogen removal (relying on the synergy of nitrifying/denitrifying microbial communities) is more susceptible to inhibition by long-term starvation [6]. In addition, process background is also important: processes such as enhanced biological phosphorus removal (EBPR) and PD/anammox have a high enrichment of functional microbial communities and stronger tolerance to short-term starvation [4,6], while traditional activated sludge processes are more sensitive to starvation [1].

3. Mechanisms of Action and Technical Support of Aerobic Starvation

3.1. Differential Responses of Functional Microorganisms

The differential responses of functional microorganisms are the core of changes in wastewater treatment efficacy under aerobic starvation. Different functional microbial communities exhibit significant differences in starvation tolerance and metabolic strategies. Fig. 1 intuitively illustrates the differences in metabolic pathways of core functional bacteria (e.g., PAOs, AOB, NOB, and OHOs) under varying conditions of starvation duration.

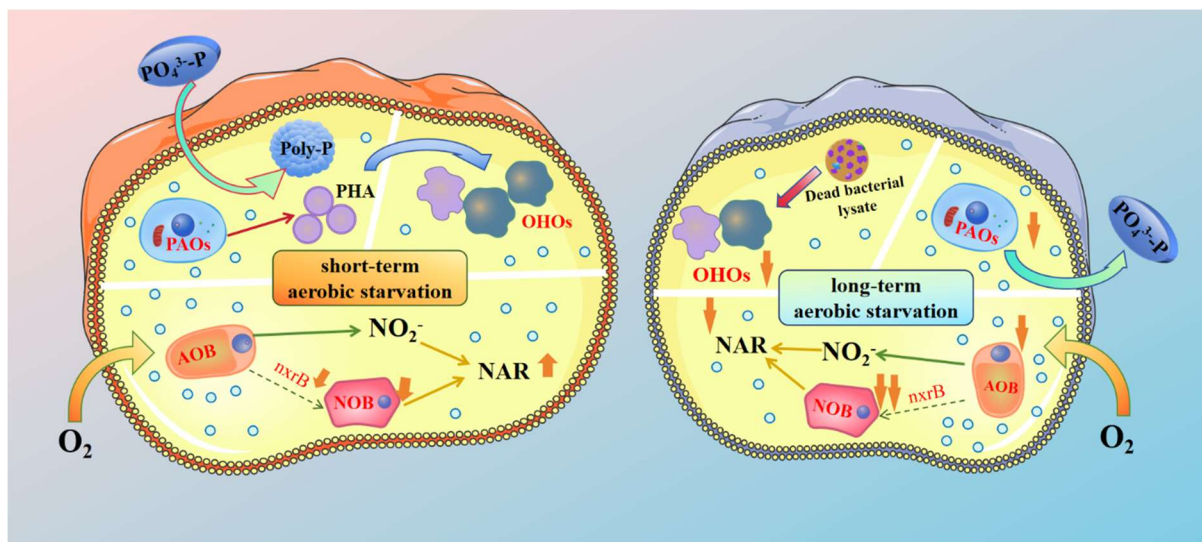


Fig. 1 Metabolic pathways of core functional bacteria under divergent starvation regimes

3.1.1. Nitrogen Cycle Functional Microorganisms

AOB exhibit strong adaptability under aerobic starvation. In the short term, AOB maintain survival by reducing maintenance energy requirements and stabilizing the activity of functional enzymes (e.g., ammonia monooxygenase), and their activity recovery rate ($0.180.29\ d^{-1}$) after substrate restoration is higher than that of NOB [2,5]; however, under long-term starvation, the abundance of AOB will decrease by 30%60%, and the expression of *amoA* genes is significantly downregulated [1].

NOB are the most sensitive to aerobic starvation. Under short-term starvation, their decay rate ($0.34\ d^{-1}$) is higher than that of AOB ($0.08\ d^{-1}$) [5]; under long-term starvation, their abundance can drop to less than 10% of the initial value, and the transcription of *nrxB* genes is blocked [2]. Even after substrate restoration, their activity recovery requires a longer time [1].

The response of denitrifying bacteria (DNB) differs: under short-term starvation, dominant microbial communities such as *Thauera* can maintain activity by metabolizing intracellular storage substances, and even promote denitrification efficiency [6]; however, under long-term starvation, the abundance of DNB decreases, and the expression of functional genes such as *narG* and *nirS* is weakened, leading to the inhibition of TN removal [7].

3.1.2. Phosphorus Cycle Functional Microorganisms

PAOs are the core functional microorganisms for phosphorus metabolism under aerobic starvation. In the short term, PAOs preferentially consume PHA and glycogen, retaining polyphosphate (Poly-P) hydrolysis capacity, laying the foundation for rapid phosphorus uptake after substrate restoration [4]; under long-term starvation, PHA and glycogen are exhausted, Poly-P is passively hydrolyzed, resulting in "ineffective phosphorus release," and the abundance of PAOs significantly decreases—for example, the abundance of *Candidatus Accumulibacter* can drop to 20% of the initial value [7].

DPAOs have stronger tolerance to starvation than conventional PAOs. Under short-term starvation, they can maintain activity through denitrifying metabolism, providing support for synchronous nitrogen and phosphorus removal [6]. However, their coupled nitrogen and phosphorus removal capacity will still be significantly attenuated under long-term starvation, which is closely related to the continuous consumption of intracellular storage substances and the downregulation of functional gene expression [7]. Other studies [10-12] have analyzed the decay process and endogenous metabolic characteristics of denitrifying phosphorus removal during anaerobic starvation, and found that the decay rate of DPAOs is closely related to sludge type (anaerobic end sludge/aerobic end sludge). This conclusion also provides a reference for analyzing the response mechanism of DPAOs under aerobic starvation.

3.1.3. Other Functional Microorganisms

Heterotrophic bacteria (OHOs) exhibit complex response characteristics under aerobic starvation. In the short term, the ability of OHOs to compete for substrates with autotrophic bacteria is enhanced, indirectly inhibiting nitrification [1]; under long-term starvation, OHOs can survive by degrading intracellular substances of dead bacteria, maintaining partial COD removal capacity [8].

The response of refractory organic compound-degrading bacteria is of positive significance: under short-term starvation, the abundance of microbial communities such as *Sphingomonas* and *Achromobacter* increases, and the expression of functional genes (e.g., dioxygenase genes) is enhanced, significantly promoting the removal of refractory pollutants such as BPA [8], providing new ideas for strengthening industrial wastewater treatment.

3.2. Application Progress of Microbiome Technologies

Microbiome technologies are key tools for analyzing the mechanisms of action of aerobic starvation, and their application has evolved from traditional structural description to advanced functional analysis.

3.2.1. Application and Limitations of Traditional Microbial Technologies

Traditional microbial technologies are widely used in aerobic starvation research, among which metagenomics accounts for approximately 70%. This technology can effectively analyze changes in microbial community structure-such as the increase in the abundance of *Proteobacteria* and the decrease in the abundance of *Bacteroidetes* in the PD/anammox system [6], and the significant increase in the abundance of *Firmicutes* in activated sludge under long-term starvation [1]. However, it cannot reflect the dynamic expression of functional genes, making it difficult to reveal the real-time metabolic state of microorganisms [8].

Quantitative PCR (qPCR) is often used to detect changes in the abundance of AOB/NOB/PAOs, such as verifying that the abundance of AOB is higher than that of NOB after short-term starvation [2]. However, it can only target a few known functional genes, making it difficult to cover the overall response of complex communities and easily underestimating microbial diversity and functional potential [1]. In general, traditional technologies focus more on community structure description and have obvious limitations in functional mechanism analysis.

3.2.2. Advantages and Application Potential of Advanced Omics Technologies

Advanced omics technologies provide stronger support for mechanism analysis. Metatranscriptomics can directly reveal the real-time expression dynamics of functional genes. For example, the expression of PHA synthesis genes (*phaC*) and phosphorus transport genes (*pit*) in PAOs is upregulated under short-term starvation, while the expression of these genes is significantly inhibited under long-term starvation [4,8], clearly demonstrating the metabolic regulatory strategies of PAOs in different starvation phases.

Metabolomics can capture changes in microbial metabolites-such as the increase in extracellular polymeric substances (EPS) synthesis under short-term starvation and the exhaustion of metabolites such as amino acids and nucleotides under long-term starvation [9]-providing direct evidence for understanding the starvation adaptation mechanisms of microorganisms. The combined application of multi-omics is more advantageous: the integration of metatranscriptomics and metabolomics can clarify the intrinsic correlation of "gene expression-metabolites-performance changes," such as the coupling relationship between the upregulation of *nirK* gene expression in DPAOs and the increase in NO_2^- consumption under short-term starvation [6], greatly deepening the understanding of action mechanisms.

3.2.3. Current Status and Gaps of Technology Application

In current aerobic starvation research, the application proportion of advanced omics technologies is less than 20%, and most studies still rely on traditional community structure analysis [1,6], making it difficult to deeply clarify microbial metabolic regulatory mechanisms. In existing studies, there are very few cases of combined application of multi-omics, and the analysis of the chain response of "gene-transcription-metabolism-function" is insufficient, leading to the mechanism of action of aerobic starvation remaining at the surface description [8]. For example, in studies on short-term starvation promoting the degradation of refractory organic compounds, only metagenomics is used to confirm the increase in the abundance of degrading bacteria, but transcriptomics is not combined to reveal the expression dynamics of functional genes [8]. In the future, it is necessary to strengthen the combined application of metatranscriptomics, metabolomics, and proteomics, focusing on the correlation analysis of functional genes-metabolic pathways-pollutant removal to fill the gap in technology application [2].

4. Engineering Application Value, Challenges, and Research Prospects

4.1. Engineering Application Value

Aerobic starvation has significant application value in wastewater treatment engineering, mainly reflected in two dimensions: process optimization and cost control.

In terms of process optimization, short-term aerobic starvation can selectively inhibit NOB, rapidly achieve nitrite accumulation (accumulation rate > 90%), and shorten the start-up time of the PNA process from more than 40 days to 7~14 days [2,5], greatly improving process start-up efficiency. For the removal of refractory pollutants, short-term aerobic starvation can enrich degrading bacteria, strengthen the removal of refractory organic compounds such as BPA and bisphenol AF (BPAF), with an efficiency increase of 20%~30% [8], providing a low-cost solution for industrial wastewater treatment. In addition, short-term aerobic starvation can improve sludge settling performance, reduce the risk of filamentous bulking, and decrease the membrane fouling rate of membrane bioreactors (MBR) [9], enhancing process operation stability. More notably, its optimization of sludge characteristics is also reflected in the sludge reduction effect. Recent experimental studies have confirmed that short-term aerobic starvation (e.g., 10 days) can achieve a sludge reduction rate of 72.8%, significantly reducing sludge disposal costs and further expanding its engineering application value [3].

In terms of cost control, aerobic starvation technology has prominent advantages. Under short-term aerobic starvation, PAOs can efficiently utilize intracellular stored carbon sources, reducing the dosage of external carbon sources (e.g., acetate). Verified by practical engineering, it can reduce operating costs by 15%~25% [4]. This technology does not require additional chemical agents (e.g., inhibitors, flocculants) and can achieve starvation treatment only by adjusting aeration time [2], with simple operation. It is particularly suitable for small and medium-sized wastewater treatment plants, which can significantly reduce the procurement

and management costs of chemical agents, while reducing labor intensity, further improving the economy of engineering application [9].

4.2. Practical Application Challenges

Despite its significant advantages, aerobic starvation still faces multiple challenges in practical application. In terms of parameter regulation, there is currently no unified standard for parameters such as starvation time and DO. The parameter requirements vary greatly for different wastewater qualities (e.g., C/N/P ratio), and personalized adjustments need to be made according to specific water quality [7], increasing the complexity of engineering application.

In terms of stability control, long-term starvation is prone to process efficacy collapse, with a long recovery cycle (1~2 weeks) [9], making it unsuitable for scenarios with high continuous operation requirements. In terms of application scope, the treatment effect of this technology on low C/N wastewater and industrial wastewater has not been fully verified [6,8]. Some high-concentration pollutants may amplify the inhibitory effect of starvation on microorganisms, limiting the widespread promotion of the technology. In addition, although the MBR system can recover after long-term starvation, membrane fouling is prone to occur initially due to the accumulation of soluble microbial products (SMP) [9], requiring supporting targeted control measures.

4.3. Research Gaps and Future Directions

4.3.1. Core Research Gaps

Current aerobic starvation research has multiple key gaps to be filled. The promotional effect of long-term aerobic starvation has not been clarified, and it is necessary to verify the possibility of promoting pollutant removal under specific conditions (e.g., acclimated sludge, combined regulation) and clarify the applicable scenarios and regulatory strategies [6]. The in-depth application of advanced omics technologies is insufficient, and there is a lack of combined research on metatranscriptomics-metabolomics-proteomics, making it difficult to reveal the complete correlation of microbial "gene expression-metabolic response-performance changes" [8]. The molecular mechanisms of short-term aerobic starvation promoting P and COD removal (e.g., functional gene regulation, signal transduction pathways) have not been elucidated, and in-depth exploration of the microbial stress metabolic network is required [4,8]. The optimization of engineering parameters is lagging behind, and there is a lack of aerobic starvation parameter (time, DO, sludge retention time) regulatory models based on water quality characteristics, making it difficult to guide practical engineering application [7,9].

4.3.2. Future Research Directions

Future research should focus on the above gaps. First, it is necessary to carry out verification of the promotional effect of long-term aerobic starvation, focusing on the survival mechanisms and efficacy maintenance laws of acclimated functional microbial communities (e.g., DPAOs, refractory organic compound-degrading bacteria) under long-term starvation [6,7], and clarify their applicable conditions. Second, it is necessary to strengthen multi-omics combined mechanism analysis, using integrated technologies of metatranscriptomics, metabolomics, and proteomics to construct a dynamic metabolic network of functional microorganisms under aerobic starvation [2,8], and reveal the molecular driving mechanism of performance changes. In terms of process application, it is necessary to deeply couple aerobic starvation with processes such as PNA and EBPR, optimize key parameters such as starvation time and DO, and establish standardized regulatory schemes [2,5]. Finally, more pilot-scale tests should be conducted to evaluate the feasibility and economy of aerobic starvation in the treatment of municipal wastewater and industrial wastewater [8,9], accumulate engineering application data, and promote the technology from laboratory to practical engineering.

5. Conclusion

Aerobic starvation, as a low-cost regulatory strategy for biological wastewater treatment, exhibits significant pollutant specificity and complexity in its efficacy: there is no unified and precise definition for short-term versus long-term, with most literature defaulting to a duration exceeding 30 days as long-term. In terms of effects, most studies indicate that both short-term and long-term aerobic starvation generally inhibit phosphorus and COD removal, while recent experiments have confirmed that short-term aerobic starvation exerts significant promotional effects on phosphorus and COD removal. For nitrogen removal, inhibitory effects dominate irrespective of duration. The response of functional microorganisms is the core driving factor of efficacy changes: AOB, PAOs, and refractory organic compound-degrading bacteria have relatively strong tolerance to short-term starvation, while NOB and conventional denitrifying bacteria are susceptible to starvation inhibition.

Existing studies still rely on traditional metagenomics in technical methods, with insufficient application of advanced omics technologies, and there are still research gaps in key issues such as the promotional effect of long-term aerobic starvation and engineering parameters. In the future, it is necessary to deepen mechanism analysis through multi-omics combined technologies, focus on verifying the promotional effect of long-term starvation, optimize engineering regulatory parameters, and promote the large-scale and stable application of aerobic starvation technology in wastewater treatment-providing technical support for energy conservation, consumption reduction, quality improvement, and efficiency enhancement of wastewater treatment.

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