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Review

A review of the phosphorus removal of polyphosphate-accumulating organisms in natural and engineered systems

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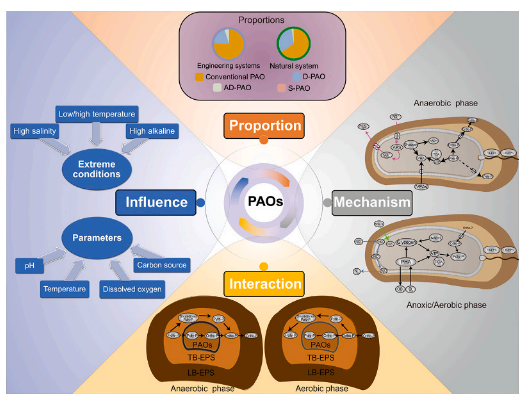
HIGHLIGHTS

- PAOs have a greater potential for phosphorus removal in extreme condition.
- Some of the efficient PAOs in natural systems can potentially be utilized by engineered systems.
- The characteristics and mechanisms of AD-PAOs and S-PAOs are described.

GRAPHICAL ABSTRACT



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ABSTRACT

Increasing eutrophication has led to a continuous deterioration of many aquatic ecosystems. Polyphosphate-accumulating organisms (PAOs) can provide insight into the human response to this challenge, as they initiate enhanced biological phosphorus removal (EBPR) through cyclical anaerobic phosphorus release and aerobic phosphorus uptake. Although the limiting environmental factors for PAO growth and phosphorus removal have been widely discussed, there remains a gap in the knowledge surrounding the differences in the type and phosphorus removal efficiencies of natural and engineered PAO systems. Furthermore, due to the limitations of PAOs in conventional wastewater treatment environments, there is an urgent need to find functional PAOs in extreme environments for better wastewater treatment. Therefore, it is necessary to explore the effects of extreme conditions on the phosphorus removal efficiency of PAOs as well as the types, sources, and characteristics of PAOs. In this paper, we summarize the response mechanisms of PAOs, denitrifying polyphosphate-accumulating organisms (D-PAOs), aerobic denitrifying polyphosphate-accumulating organisms (AD-PAOs),

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and sulfur-related PAOs (S-PAOs). The mechanism of nitrogen and phosphorus removal in PAOs is related to the coupling cycles of carbon, nitrogen, phosphorus, and sulfur. The genera of PAOs differ in natural and engineered systems, but PAOs have more diversity in aquatic environments and soils. Recent studies on the impact of several parameters (e.g., temperature, carbon source, pH, and dissolved oxygen) and extracellular polymer substances on the phosphorus removal efficiency of PAOs in natural and engineered systems are further discussed. Most of the PAOs screened under extreme conditions still had high phosphorus removal efficiencies (>80.0 %). These results provide a reference for searching for PAOs with different adaptations to achieve better wastewater treatment.

1. Introduction

Eutrophication in aquatic ecosystems is a global environmental problem, and phosphorus is considered the limiting factor that triggers eutrophication in these ecosystems (Zamparas and Zacharias, 2014). Therefore, phosphorus removal is of great importance to the management of aquatic ecosystems. The enhanced biological phosphorus removal (EBPR) process is a sustainable method for removing phosphorus from wastewater and protecting aquatic ecosystems from eutrophication (Liu et al., 2007). In this process, polyphosphate-accumulating organisms (PAOs) are widely used and are capable of accumulating polyphosphate (poly-P) into microorganisms (Oehmen et al., 2007). However, previous studies have shown that the phosphorus removal efficiency of PAOs is often limited by environmental factors such as the carbon source, pH, temperature, and dissolved oxygen (DO). In addition, as a major component of activated sludge, extracellular polymeric substances (EPSs) have recently been regarded as a limiting factor for anaerobic phosphorus release (Shi et al., 2017). These limitations resulted in the phosphorus removal of PAOs not fully meeting the growing demand for wastewater treatment in municipal WWTPs worldwide. In light of the above gaps in research, it is necessary to expand the current knowledge of PAOs in natural environments, engineered systems, and extreme conditions to identify functional PAOs that can be used to sustain biological phosphorus removal processes in a variety of environments and to apply reasonably effective PAOs to wastewater treatment situations.

1.1. PAOs

PAOs enrich poly-P through metabolism and become the dominant strain in EBPR systems (Saad et al., 2016). In 1975, *Acinetobacter* sp. was the first genus of PAO to be isolated from activated sludge in WWTPs (Fuhs and Chen, 1975). After decades of research, it is now recognized that *Candidatus* Accumulibacter (Types I and II), *Candidatus Accumulimonas*, and *Tetrasphaera* are the functional bacteria with high phosphorus aggregation capacities in EBPR systems (Wu et al., 2019a).

Later, denitrifying polyphosphate-accumulating organisms (D-PAOs) were discovered using nitrate in an aerobic/anoxic alternating sequencing batch reactor (SBR) (Kuba et al., 1993). Although conventional PAOs can coexist with denitrifying bacteria to treat nitrogen and phosphorus in wastewater simultaneously, they can result in competition over carbon sources and differences in sludge age (Kishida et al., 2006; Yu and Li, 2015). The discovery of D-PAOs provided a good solution to the problem in wastewater treatment to achieve the simultaneous removal of nitrogen and phosphorus. For example, *Azoarcus tolulyticus* and *Thauera mechernichensis* are both D-PAOs (Tsuneda et al., 2005). In 1988, the concept of aerobic denitrification was introduced (Robertson et al., 1988). Later, it was further shown that the presence of PAOs can achieve nitrogen and phosphorus removal during the process of aerobic denitrification (Oehmen et al., 2007). *Bacillus subtilis* is a recently discovered species that is capable of nitrogen and phosphorus removal under alternating anaerobic and aerobic conditions; this type of PAO is called an aerobic denitrifying polyphosphate-accumulating organism (AD-PAO) (Zhang et al., 2021). Using AD-PAOs in the EBPR process may intensify the process and lower the cost of phosphorus removal relative to D-PAO-dominant EBPR systems.

The sulfur cycle is also important in the natural environment. Wu et al. (2013) combined the sulfate reduction, autotrophic denitrification and nitrification integrated (SANI®), and EBPR processes to develop a novel denitrifying-sulfur cycle associated with the EBPR process (DS-EBPR). This process links intracellular phosphorus accumulation to sulfur, where sulfur carries electrons and energy in biological phosphorus removal (Wu et al., 2013; Wu et al., 2012; Zhang et al., 2017). The DS-EBPR process can function with operating temperatures and seawater salinity of up to 30 °C and 20.0 %, respectively, while producing less sludge (Wu et al., 2014). In addition, sulfur-related PAOs (S-PAOs) (Wang et al., 2019a; Zhang et al., 2019) are often present in the DS-EBPR process and are used synergistically with sulfate-reducing bacteria and sulfide-oxidizing bacteria for sulfur conversion and phosphorus removal (Guo et al., 2016a). Currently, an increasing number of functional microbial species associated with poly-P have been identified. Regardless of the type of PAO, their cellular growth and phosphorus removal efficiency is governed by environmental factors such as the carbon source, pH, temperature, and dissolved oxygen (DO) (De Farias Silva et al., 2017; Lopez-Vazquez et al., 2008a; Oehmen et al., 2007). Meanwhile, competition or cooperation between PAOs and glycogen-accumulating organisms (GAOs) has always existed under different conditions. Usually, GAOs compete with PAOs for carbon sources, reducing the efficiency of phosphorus removal (Cech and Hartman, 1993; Saunders et al., 2003). Therefore, suitable growth and dephosphorization conditions for PAOs are needed to improve the performance of the EBPR process and inhibit the proliferation of GAOs. However, several types of PAOs are affected by environmental factors differently, and knowledge of AD-PAOs and S-PAOs is still limited.

1.2. Interactions between EPSs and PAOs

Factors influencing the phosphorus removal efficiency of PAOs in engineered systems often involve comparing various influent conditions for achieving a higher phosphorus removal efficiency. However, this study considers one external condition that affects PAOs in activated sludge: the impact of EPSs on phosphorus removal in engineered systems. The aim of this is to summarize the phosphorus removal efficiency and gain a deeper understanding of the relationship between external conditions and the phosphorus removal efficiency.

EPSs are biopolymers with a gel-like structure produced by microorganisms, and are composed of various biological metabolites, including polysaccharides, proteins, nucleic acids, PHAs, glycogen, and poly-P. It is worth noting that not all species of PAOs can spontaneously secrete EPSs, and the various mechanisms that induce PAOs to secrete EPSs are currently under consideration (Ni et al., 2023). Additionally, the EPS matrix may contain components not secreted by the organisms themselves, such as humic substances, metal sediments, and nanoparticles. In addition, EPSs have a critical influence on both PAO metabolism as well as the EBPR process, as they have been found to contain approximately 30.0 % of the total phosphorus in the activated sludge and contribute simultaneously to the phosphorus removal rate during aerobic processes (Sheng et al., 2010; Wang et al., 2019b; Zeng et al., 2019). In fact, the PAOs in activated sludge are surrounded by EPSs, and the exchange of substances between PAOs and the external solution during the process of biological phosphorus removal needs to be transmitted through the EPS matrix (More et al., 2014). Therefore, the relationship between EPSs and PAOs should not be ignored, and this has been the direction of recent research.

1.3. Extreme conditions

Industrial processes produce wastewater with a complex composition, and research into categories of industrial water treatment commonly considers high-temperature (≥30 °C) (Wang et al., 2020b; Qiu et al., 2022), low-temperature (≤10 °C) (Luo et al., 2022), and high-salinity wastewater (≤5 %) (Li et al., 2021). The living conditions required by PAOs have been adversely affected in biological treatment systems used for these types of wastewaters, which has reduced the efficiency of phosphorus removal. For example, wastewater from mariculture in coastal areas is characterized by high salinity and high nitrogen and phosphorus contents, resulting in heavily increased wastewater treatment costs. Thus, a deeper understanding of the types and characteristics of phosphorus removal from PAOs in extreme conditions is required to meet the demand for phosphorus removal from wastewater under these extreme conditions.

Some PAOs have been found in extreme conditions are highly adaptable, developing unique functions, structures, and genetics adapted to particular environments, and therefore are able to survive in those environments (Shu and Huang, 2022), such as environments with high salinity (Rothschild and Mancinelli, 2001; Zhang et al., 2022), low temperatures (Luo et al., 2022), high temperatures (Huang et al., 2010), and strong alkaline conditions (Li et al., 2019). The PAOs found in extreme conditions can be converted into a very valuable resource for humans if they can be modified for use in WWTPs. However, we do not yet know much about the specific genotypes, specific physiological mechanisms, specific metabolic processes, and other characteristics of PAOs that occur naturally in extreme conditions. Research on the biodiversity and microbial function of PAOs in extreme conditions is still lacking.

As shown in the graphical abstract, this review aims to discuss the relationships and effects between different environments and PAOs. The primary focus of the review is to explore the effects of PAOs from extreme conditions on phosphorus removal. Mechanisms related to PAOs, the interactions between the EPSs and parameters and PAOs, as well as an exploration of the effects of PAOs from extreme conditions on phosphorus removal are the focus of the following discussion. In addition, existing studies regarding conventional PAOs include a relatively high percentage of the total global distribution of PAOs, followed by D-PAOs, in both natural and engineered systems. The influence sampling methodologies during different growth stages, the specific abundances of their electron acceptors, and the anoxic living conditions required for D-PAOs need to be considered. In addition, considerable portions of conventional PAOs only increase in population during specific oxygen-related stages (Li et al., 2020).

The primary focus of this review is to explore the effects of PAOs from normal to extreme conditions on phosphorus removal. Through this discussion, we hope to identify the optimal conditions for the use of PAOs in the biological phosphorus removal process and learn how to apply them in engineered systems to improve the effectiveness of wastewater treatment.

2. Review methodology

A systematic literature review was conducted on Google Scholar and the Web of Science based on a topic search of titles, abstracts, and keywords. The literature search involved the use of various keywords from related fields. Some of these keywords included, but were not limited to: "polyphosphate accumulating organism," "denitrifying polyphosphate accumulating organism," "EBPR," "DS-EBPR", "active sludge", "anaerobic condition", "phosphorus removal efficiency", "extracellular polymer substances", "carbon source", and "eutrophication". The search was conducted on published papers with those keywords and based on the direct and indirect relationships between various environmental factors and PAOs. More than 4000 articles were initially found, with 204 articles included in the study, while >490 records were obtained. To ensure the feasibility of the study evaluation method, we considered the following research aspects for the review, and we established the following criteria.

1) The period of the literature search for the PAO information was 1995–2023, and especially after 2010.
2) We searched for information on various types of PAOs primarily from natural aquatic ecosystems, soils, reactors, and wastewater treatment plants. We defined natural aquatic ecosystems as water bodies or substrates in natural environments, such as lakes, oceans, and rivers. We also included wastewater generated anthropogenically that was discharged into natural environments, such as wastewater from phosphate mining areas, slaughterhouses, and restaurants.
3) We collected information regarding polyphosphate accumulating organisms found in China and worldwide. The metadata recorded in the dataset included the PAO strain name and strain type, geographical location, environment, carbon source, pH, temperature, and phosphorus removal efficiency. Information on the phylum, class, order, family, genus, and species of the PAOs can be found at the following website: https://www.ncbi.nlm.nih.gov/.

3. Metabolism and ecology of phosphorus removal for PAOs

PAOs can be classified as conventional, nitrogen metabolism, or sulfur-related PAOs according to the elements involved in their phosphate accumulation. The following details the mechanism and types of polyphosphates for different types of PAOs.

3.1. Phosphorus metabolism of PAOs

PAOs are typically cultured under alternating anaerobic and aerobic conditions. PAOs release phosphorus under anaerobic conditions; they obtain energy by decomposing intracellular poly-P and glycogen while absorbing extracellular volatile fatty acids (VFAs). PAOs subsequently convert VFAs into energy-containing poly-β-hydroxyalkanoates (PHAs) for storage in PAO cells. PAOs absorb phosphorus under aerobic conditions, using oxygen (O_2) as the electron acceptor while oxidizing and decomposing the stored PHAs to obtain energy. The energy obtained for its growth and the uptake of external phosphorus, which accumulates in the form of poly-P in the cells, completes the process of phosphorus aggregation. Finally, high-phosphorus sludge is discharged from the system to achieve the purpose of phosphorus removal. The core of this process is the storage and conversion of carbon sources. The reaction equations for PAOs are provided in what follows.

For anaerobic conditions:

$$2\ C_2H_4O_2 + HPO_3 + H_2O \rightarrow C_2H_4O_2 + PO_4^{3-} + 3H^+$$

For aerobic conditions:

$$C_2H_4O_2 + 0.16\ NH_4^+ + 1.2\ O_2 + 0.2\ PO_4^{3-} \rightarrow 0.16\ C_5H_7NO_2 + 1.2\ CO_2 + 0.2\ HPO_3\ (PAO) + 0.44\ OH^- + 1.44\ H_2O$$

Many microorganisms are involved in the EBPR process; some of them are also GAOs (Saunders et al., 2003), such as *Amaricoccus kaplicensis* and *Tetracoccus cechii*. These bacteria only take up VFAs, have no phosphorus aggregation capacity, and compete with PAOs for carbon sources (Lopez-Vazquez et al., 2008b; Oehmen et al., 2005). It has been reported that common PAOs, including *Acinetobacter* sp. (Li et al., 2009), *Bacillus* sp. (Wu et al., 2016), *Pseudomonas* sp. (Wu et al., 2016), *Candidatus Accumulibacter* sp. (Peterson et al., 2008), *Tetrasphaera* sp. (Wang et al., 2009), *Halomonas* sp. (Ren et al., 2008), and *Microlunatus* sp. (She et al., 2018), are distributed in the phyla *Proteobacteria*, *Actinobacteria,* and *Firmicutes*.

Accumulibacter uses VFA as carbon source for aerobic phosphorus absorption, referring to the differences in the poly-phosphate kinase gene (*ppk1*) that can be divided into two types (Types I and II) (He et al., 2007). Type I can be further divided into five evolutionary clades (Types IA-E), and Type II can be further divided into seven evolutionary clades (Types IIA-G). The PAOs of the different evolutionary clades show various physiological properties, with clade IA being able to combine nitrate reduction with phosphorus uptake, while clade IIA cannot (Flowers et al., 2009). In addition, during the sludge bulking stage when *Accumulibacter* is excluded from the systems, *Candidatus Microthrix parvicella* plays the primary role in phosphorus removal (Wang et al., 2014). Additionally, it was also found that *Comamonadaceae* is a key novel PAO in biological phosphorus removal (Ge et al., 2015).

Compared with *Accumulibacter*, *Tetrasphaera* not only relies on VFAs uptake, but also can rely on the fermentation of glucose, glutamic acid, aspartic acid, and other macromolecular organic matter to obtain energy for cell maintenance or proliferation (Close et al., 2021), which is beneficial for biological phosphorus removal in low VFAs wastewater. Therefore, *Tetrasphaera* has a more stable and efficient phosphorus removal performance. However, existing studies remain inconclusive on the ability of *Tetrasphaera* species for biological phosphorus removal (Nguyen Hien Thi et al., 2015). It has been reported that the removal efficiency of phosphorus by *Tetrasphaera* is closely related to the composition of its branches in this microbiota. Previous studies have characterized several species of *Tetrasphaera*, and these clades show differences in various aspects such as the electron acceptors used, the ability to perform PHA storage, and the utilization of multiple carbon sources (Liu et al., 2019). Interestingly, *Tetrasphaera* and *Accumulibacter* also appear to have interactions in the biological removal of phosphorus. The fermentation capacity of *Tetrasphaera* allows it to use readily fermentable substances for its own growth in the absence of a carbon source and with few macromolecular organic carbon compounds to gain a competitive advantage over *Accumulibacter*. However, *Tetrasphaera* fermentation products can also provide VFA to *Accumulibacter* for its growth (Marques et al., 2017; Nielsen et al., 2019).

Accumulibacter is generally accepted as the primary phosphorus-polymerizing bacterium of the EBPR process, but the abundance of *Tetrasphaera* (1.0 % to 30.5 %) in some WWTPs was higher when compared with that of *Accumulibacter* (1.0 % to 18.0 %) (Hao et al., 2020), although the level of abundance does not represent the phosphorus removal effect. *Accumulibacter* was detected in both freshwater and estuarine sediments; however, they rarely appeared in soil samples (Kunin et al., 2008).

3.2. Nitrogen metabolism of PAOs

PAOs related to the nitrogen metabolism include D-PAOs and AD-PAOs which are described in detail below; these two types of PAOs have different phosphorus removal mechanisms and characteristics.

3.2.1. Phosphorus removal by D-PAOs

Unlike conventional PAOs, D-PAOs use nitrate (NO_3^-) and nitrite anions (NO_2^-) as electron acceptors for phosphate uptake and the synthesis of glycogen under alternating anaerobic/anoxic conditions. The D-PAOs convert NO_3^- or NO_2^- into nitrogen (Fig. 1a). In this process, PHAs not only provide energy for phosphate uptake and poly-P synthesis, but also provide carbon sources for the denitrification reaction (Martín et al., 2006), resulting in competition for carbon sources. It was found that certain PAOs can use O_2, NO_3^-, and NO_2^- as electron acceptors (Hu et al., 2003). Complete denitrification from NO_3^- to N_2 consists of four reduction steps with NO_2^-, NO, and N_2O as intermediates. Among them, N_2O is continuously produced during the denitrification process, but it is typically reduced to nitrogen. Hence, four nitrogen oxides can be electron acceptors. However, free nitrous acid is an inhibitor of N_2O reduction, which is determined by nitrite and pH. With 3.0–4.0 mg of NO_2^--N/L and at pH 7, the reduction rate of N_2O occurs at a low level

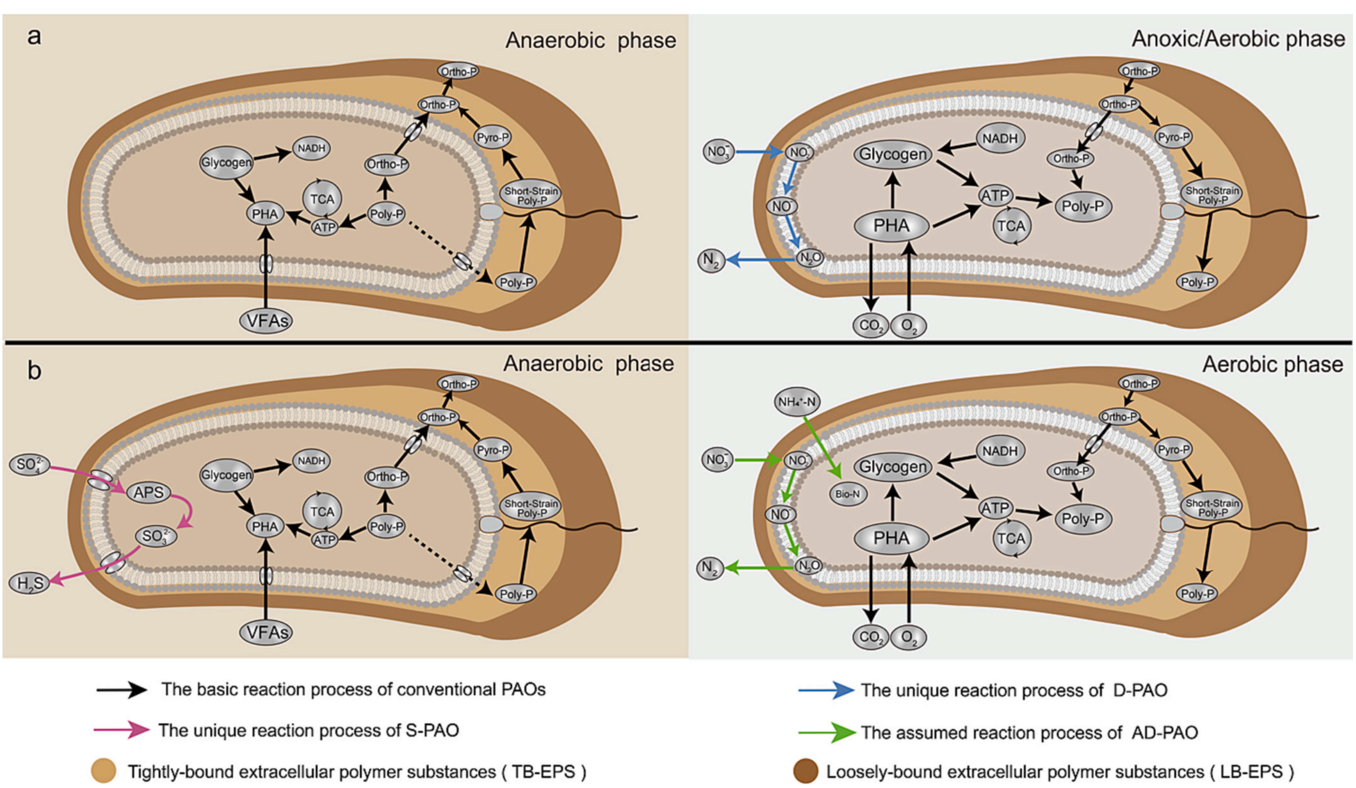

Fig. 1. Diagram of the metabolic mechanism of polyphosphate accumulating organisms: (a) denitrifying (D)-Polyphosphate-accumulating organisms (PAOs); (b) sulfur-related (*S*)-PAOs.

(Zhou et al., 2008). In addition, short-cut D-PAOs can absorb more phosphate under anoxic conditions, using nitrite as an acceptor. Some spherical *Accumulibacter* facultatively use nitrite or oxygen as electron acceptors (Carvalho et al., 2007). Nitrite can replace O_2 and NO_3^- as electron acceptors as long as the nitrite concentration is below 115.0 mg/L (Hu et al., 2003).

Dechloromonas is able to use VFA as carbon source and nitrate as electron acceptor to absorb phosphorus through hypoxia. In a 12-year study of 20 Danish WWTPs, researchers concluded that *Candidatus Dechloromonas phosphorivorans* and *Candidatus Dechloromonas phosphoritropha* belonged to the genus *Dechloromonas*, the second most abundant genus of PAOs (Petriglieri et al., 2021).

3.2.2. D-PAOs and AD-PAOs are definitely different types of bacteria

In previous studies, AD-PAOs were found to use NO_3^- and O_2 as electron acceptors to synchronize denitrification and the uptake of excessive phosphorus (Su et al., 2001). The energy sources for aerobic phosphorus removal by AD-PAOs are glycogen and poly-β-hydroxybutyrate (Zhang et al., 2021) that can accumulate poly-P under aerobic conditions. This group of microorganisms does not release phosphorus under anaerobic conditions, but does under aerobic conditions (Zhang et al., 2020). Therefore, the concentration of oxygen may affect phosphorus removal by AD-PAOs. Because denitrification and intracellular phosphorus accumulation occur under aerobic conditions, these simultaneous processes simplify the construction of reaction tanks and greatly reduce the production of sludge (Seifi and Fazaelipoor, 2012). Interestingly, this property contrasts with conventional processes in which denitrifying microorganisms can only denitrify under anoxic conditions (Luo et al., 2016), and where AD-PAO can utilize ammonium by assimilation and can accomplish both nitrification and denitrification under aerobic conditions (Hou et al., 2021). This result is similar to previously reported results for heterotrophic nitrifying and aerobic denitrifying microorganisms (HNADMs), Microorganisms capable of simultaneous nitrogen and phosphorus removal have also been reported to be included in the classification of HNADMs that have been defined as simultaneous heterotrophic nitrification-aerobic denitrification phosphorus removal (SNDPR) organisms (Chen et al., 2021; Song et al., 2021). The alkalinity produced during aerobic denitrification can compensate for the alkalinity consumption during nitrification. Hence, the method has a high nitrogen and phosphorus removal efficiency (Rout et al., 2017; Wu, 2019).

At the genus level, the reported AD-PAOs are *Achromobacter* sp. (Nie et al., 2017), *Bacillus subtilis* (Zhang et al., 2021), *Pseudomonas* sp. (Cui and Huang, 2022; Li et al., 2021), *Acinetobacter* sp. (Zhao, 2020), *Escherichia coli* (Ru, 2018), *Arthrobacter* sp. (Zhang et al., 2020), and *Brevundimonas* sp. (Nie et al., 2017). In contrast, the D-PAOs belong to a class of facultative anaerobic bacteria that can operate under alternating anaerobic-anoxic conditions and perform denitrification processes while accomplishing phosphorus uptake. In addition, among the strains that have been reported as heterotrophic nitrifying and aerobic denitrifying (HN-AD), *Thauera* sp. SND5 reported by Wang and He removes N via the pathway under aerobic conditions and functions as a D-PAO to remove P under alternating anaerobic and anoxic conditions (Wang and He, 2020), while *Bacillus* sp. *subtilis* GHSP10 reported by Zhang et al. found that subtilis GHSP10 and *Arthrobacter* sp. HHEP5 demonstrated phosphorus release under aerobic conditions, contrary to what is known for conventional D-PAOs (Zhang et al., 2020; Song et al., 2021). Therefore, the definitions for AD-PAOs and D-PAOs are quite different, with AD-PAOs having more emphasis on the two characteristics of nitrification-aerobic denitrification and simultaneous nitrogen and phosphorus removal. More importantly, the current study of AD-PAOs has not yet confirmed the process of heterotrophic nitrification, but rather the direct conversion to Bio-N via ammonium assimilation for cellular uptake (Hou et al., 2021). Based on the assumptions above, the metabolism of AD-PAOs is described in Fig. 1. For the SNDPR process, the lower level of carbon source in the wastewater challenged the chemical oxidation requirements for PAOs and limited the application of PAOs in SNDPR, and the identification of defined AD-PAOs in the SNDPR process is a solution to successfully overcome the biosustainability strategy of SNDPR and to adapt to the changing requirements of microbial communities induced by different processes (Shukla et al., 2020).

3.3. Sulfur metabolism of S-PAOs

The mechanism of S-PAOs may be as follows (Fig. 1b). In the anaerobic phase, phosphorus is released, and energy materials (PHAs) are stored in the cell. The sulfate is reduced to sulfide and polysulfides (poly-S), then accumulated in the cell. In the anoxic or microaerobic phase, phosphorus is absorbed, PHAs in the cell provide energy for the cell, and sulfide and poly-S are oxidized to sulfate, thus completing a sulfur cycle (Wu et al., 2013; Wu et al., 2014; Zhang et al., 2019). However, the conversion of poly-S in a SBR is not determined by the reaction stage, but by the state of energy, poly-S may be a potential electron and energy storage material (Yu et al., 2016).

The DS-EBPR ecological model established by macrogenomics and reported that PAOs related to *Desulfobacteraceae* may be associated with sulfur metabolism, while PAOs related to *Thauera* sp. may be associated with nitrogen metabolism. Both *Desulfobacteraceae* and *Thauera* sp. are able to adapt to the pH range of 6.9–7.1 and an operating temperature of 22 ± 2 °C. In addition, high-throughput sequencing revealed that a member of the *Rhodobacteraceae* may be an S-PAO in an SBR operated at 30 °C (Wang et al., 2019a). Two families of S-PAOs, *Desulfobacteraceae* and *Rhodobacteraceae*, have phosphorus removal efficiencies of about 50.0 % under suitable growth conditions (Table S1). In the DS-EBPR system, conventional PAOs were not detected due to the growth inhibition effect of sulfate (Baetens et al., 2001). However, sulfate reducing bacteria during the anaerobic phase competes with PAOs for a substrate, resulting in the incomplete removal of phosphorus. In addition, sulfate reducing bacteria that produce H_2S have a further inhibitory effect on PAOs (Valverde-Perez et al., 2016). At 25–30 °C and a pH of 7.0–7.5, sulfate-reducing bacteria and sulfide-oxidizing bacteria synergistic communities had the advantage of competing with GAOs and controlling the mixture of acetate and propionate (75.0–25.0 % and 50.0–50.0 %) that contributed to the removal of phosphorus in the DS-EBPR (Guo et al., 2018; Guo et al., 2017; Guo et al., 2016b). The maximum phosphorus absorption rate occurs when the carbon-to-sulfur mass ratio is 150:200 (Zhao et al., 2016). Nonetheless, the sludge concentration was low and may be enriched with GAOs (Guo et al., 2016a). The mutual cooperation among microorganisms may result in a more efficient phosphorus removal process (Jayadi and Baharuddin, 2013). This synergy can enable microorganisms to more effectively remove phosphorus in wastewater treatment or wastewater treatment systems (Wang et al., 2022), thereby helping mitigate the issue of phosphorus pollution in the environment. This is of significant importance for environmental conservation and sustainable wastewater treatment.

4. Phosphorus removal of PAOs in natural and engineered systems

4.1. Natural ecosystems

4.1.1. Water environments

Recent studies on PAOs have focused on natural aquatic ecosystems in low phosphorus environments (Hupfer et al., 2007) and on EBPR with high phosphorus concentrations (Xu et al., 2011; Zhang et al., 2013). Studies of PAOs in natural aquatic ecosystems have mainly focused on surface water, lake, and river substrates. There seem to be no studies that have reported on the nature of PAOs in groundwater systems, although research has shown that polluted water from eutrophic lakes may infiltrate into groundwater (Ye et al., 2021). Natural environments are complex and highly variable; therefore, PAO activity in natural aquatic ecosystems is unstable. Existing studies have mainly analyzed the seasonal differences in PAO communities in natural aquatic environments. For example, PAO diversity in summer sediments was significantly higher than in autumn and winter (Balaji Prasath et al., 2021; She et al., 2018; She et al., 2019). In addition, PAOs show different growth characteristics in grass- and algal-type sediments, having spatial heterogeneity (Hu et al., 2012). Forty genera of traditional PAOs and six genera of D-PAOs are known to exist in natural aquatic environments where *Arthrobacter* sp. and *Pseudomonas putida* are the only AD-PAOs known to occur in these environments (Table S1). The existence of S-PAOs has not been confirmed in natural aquatic ecosystems (including lakes, oceans, and rivers), while AD-PAOs have not been found in the ocean.

In surface water, the most frequent carbon sources used to enrich PAOs include acetate (Li et al., 2020), glucose (Nguyen et al., 2011), and sodium citrate (Xie et al., 2015). The phosphorus removal efficiency of *Rhodococcus* sp. Was approximately 90.0 % when ethanol was used as the carbon source, but <40.0 % with lactose, xylose, sucrose, glucose, maltose, or soluble starch was used as the sole carbon source (Wang et al., 2020a). A few PAOs in natural water substrates were found to use glucose as a carbon source since other microorganisms in activated sludge can break it down into smaller molecules that PAOs can uptake (Nan et al., 2013). Some studies have reported that *Staphylococcus aureus* can make good use of macromolecular organic matter, such as glucose and peptone (Nan et al., 2013). *Stenotrophomonas acidaminiphila*, which can use sucrose as its carbon source while boosting its phosphorus removal rate to 50.1 %, has been found in Taihu Lake sediments (Qu et al., 2014). Being the only two genera of AD-PAOs associated with nitrogen metabolism, *Achromobacter* sp. And *Brevundimonas* sp. Can use glucose as their carbon source (Table S2). Therefore, it has been inferred that in surface water habitats, carbon sources can be a relatively important environmental factor influencing the growth of PAOs in terms of phosphorus removal.

However, few studies have addressed the growth conditions and phosphorus removal efficiency of PAOs in natural aquatic ecosystems. Potential obstacles may be identified in the following areas. First, natural aquatic ecosystems are complex environments with varying constraints in lakes, rivers, and marine ecosystems, and modeling the role of phosphorus cycling in them often leads to a reduction in theoretical credibility in terms of increased complexity as well as the neglect of a number of biochemical processes (Robson, 2014; Ruttenberg, 2014). Second, phosphorus does not participate in the global atmospheric cycle, and although many global phosphorus budgets have been proposed, the rapid exchange of phosphorus between different reservoirs, coupled with large anthropogenic impacts on the budgets and the difficulty of quantifying widely dispersed phosphorus exports from marine sediments, make it challenging to accurately quantify and balance this budget (Paytan and McLaughlin, 2007). This is also the reason why there has been less discussion of phosphorus cycling in aquatic ecosystems. Complex microbial communities exist in aquatic ecosystems, sediments, and substrates that are largely unmodified by humans. Further discussion and research are needed to elucidate how the interactions between PAOs and other complex microbial communities can affect the growth and phosphorus removal mechanism of PAOs.

4.1.2. Soil

The phosphorus cycle in natural ecosystems is the circulation of phosphorus between soil, plants, animals, and microorganisms. However, the phosphorus cycle in aquatic conditions has rarely been reported. Due to the use of P-containing fertilizers, the phosphorus in soil solutions has increased (Oldroyd and Leyser, 2020). PAOs are potential participants in the phosphorus cycle in soil (Akbari et al., 2021), and soils support different types of PAOs. A comparison of PAOs in soils and WWTPs revealed that more genera of PAOs were found in soil than in activated sludge of WWTPs (Run et al., 2012). The PAOs found in the soil were only those associated with phosphorus metabolism, and no PAOs associated with either nitrogen or sulfur metabolism were found up to the time of data collection. Three phyla of PAOs have been detected from the soil, namely *Actinobacteria*, *Proteobacteria* and *Firmicutes*. Three strains of PAOs (*Actinobacillus* sp., *Corynebacterium* sp., and *Serratia* sp.) were specific to the soil habitat. *Arthrobacter* sp. is an efficient PAO strain screened from maize inter-rhizosphere soils (Li et al., 2013). Changes in soil pH cause changes in the genera and the number of microorganisms, with PAOs being abundant in neutral and alkaline soils. The PAOs screened from the soil of vegetable greenhouses (pH = 7.0–8.5), such as *Arthrobacter* sp., *Bacillus* sp., *Microbacterium* sp., and *Rhodococcus* sp., have biological characteristics of salt tolerance, heat resistance, and pathogen resistance, and can adapt to complex environments (Wu et al., 2019b). These PAOs use glucose as a carbon source in the soil and have a phosphorus removal rate of over 50.0 % in both weakly acidic and 26–36 °C conditions (Wu et al., 2019b). Thus, the soil is an essential resource for the isolation of PAOs.

4.2. Engineered systems

4.2.1. Effect of carbon sources on phosphorus removal

In an engineered system, different carbon sources have different effects and limits on different types of PAOs. Acetate and propionate (Mao et al., 2013) have been widely used in experiments to enrich PAOs (Table S2), and acetate is considered to be the optimal carbon source for most PAOs. Fluorescence in situ hybridization (FISH) analysis revealed that *Accumulibacter* would be very abundant in an EBPR system using acetate as the sole carbon source, with little or no added GAOs (McMahon et al., 2002). However, it could be more beneficial to access the dominant status of PAOs in an EBPR system by only using propionate as their substrate (Oehmen et al., 2010). It is worth mentioning that ten species of PAOs, including *Brachymonas* sp., *Candidatus Accumulibacter* sp., and *Dechloromonas* sp., may use propionate as a carbon source (Table S2). Some amino acids are potential carbon sources for the EBPR; FISH combined with 40,6-dia-midino-2-phenylindole (DAPI) staining confirmed that *Candidatus Accumulibacter* sp., *Tetrasphaera* sp., and *Rhodocyclus* sp. could accumulate poly-P when aspartic acid or glutamic acid was used as the carbon source (Zengin et al., 2011). Additionally, some studies have reported that *Tetrasphaera* can use acetate as a carbon source to release and absorb phosphorus more efficiently than glycerol and glucose. Glycerol and glucose provide more energy when fermented but may hinder phosphorus release (Yu et al., 2023). Moreover, two recently discovered families of bacteria that have been found in reactors, *Desulfobacteraceae* and *Rhodobacteraceae*, related to the sulfur metabolism of PAOs, use acetate as their carbon source (Wang et al., 2019a; Zhang et al., 2019). In addition, in the EBPR system, the use of compound carbon sources of acetate and propionate at 30 °C can reduce the proliferation of GAO, which is conducive to the growth and phosphorus removal of PAOs (Wang et al., 2020a; Wang et al., 2020b). Using multiple carbon sources (e.g., glucose, sodium acetate, and casein hydrolysate) and a low concentration of thiourea (1.0 mg/L) can efficiently enrich *Tetrasphaera*. This enriched microbial community achieved enhanced phosphorus removal efficiency (85.0 %) and nitrogen removal efficiency (80.0 %) (Wang et al., 2023). The above studies indicate that a composite carbon source as the substrate seems to be more beneficial for the phosphorus removal efficiency of PAOs (Wang et al., 2019a; Zhang et al., 2019).

Unlike *Accumulibacter*, *Tetrasphaera* can rely not only on VFAs as a carbon source, but also on the fermentation of macromolecules, such as glucose and carbohydrates, for energy for their carbon sources (Close et al., 2021). Previous studies on the discrepancy between these two bacteria for utilizing glucose, as *Accumulibacter* cannot utilize glucose directly, considered another significant feature that distinguishes *Tetrasphaera* from *Accumulibacter* (Liu et al., 2019). This was further supported at the genetic level by the fact that *Tetrasphaera* has a gene encoding a glucose assimilatory enzyme and showed successful biological phosphorus removal using glucose in pure cultures of *Tetrasphaera* (Kristiansen et al., 2013; Nguyen et al., 2011). However, Ziliani et al.

reported for the first time on a reactor enriched with *Accumulibacter* that only utilized glucose as the sole carbon source for the biological phosphorus removal process, and this presented a new perspective on the assimilation process of glucose with *Accumulibacter* in conventional biological phosphorus removal systems (Ziliani et al., 2022). Therefore, although further evaluation of interference information is required. Several microscopy-based assays exist that require microscopy, such as FISH-DAPI (4,6-diamino-2-phenylindole) and FISH-MAR (micro-autoradiography), as well as FISH-Raman techniques based on vibrational spectroscopic techniques; these are the current and future methods for the differentiation of *Tetrasphaera* from *Accumulibacter* (Fernando et al., 2019; Kristiansen et al., 2013; Liu et al., 2019; Nguyen Hien Thi et al., 2015; Singleton et al., 2022; Yu et al., 2023).

In addition, acetate as a carbon source is often discussed in the current bioenergetics of carbon sequestration. Acetate uptake by *Accumulibacter* is driven by the proton acetate symporter (ActP) driven by the proton motive force (PMF). The proton motive force is primarily generated by the sympathetic efflux of protons (H^+) with phosphate produced during the hydrolysis of polyphosphates via the inorganic phosphate transporter (Pit) (Chen et al., 2022). In the previous classification, although all four *Tetrasphaera* genomes contain an acetate transporter protein gene (actP) and genes involved in acetate activation (acs, ackA, and pta), controversy exists regarding their ability to utilize acetate (Kong et al., 2004; Kristiansen et al., 2013; Nguyen et al., 2011). In a study, it was found that both *T. elongata* (a species that has been recently been reclassified as *Phycicoccus elongatus*) and *T. japonica* can utilize acetate, but the poor growth rates of both species when acetate was used as the sole carbon source were explained by the absence of the acetate shunt gene (Kristiansen et al., 2013; Zhang and Kinyua, 2020). In the present categorization, a recent genome-based phylogeny has shown that isolated members of the genus *Tetrasphaera* should belong to *Phycicoccus* (*T. elongata*), *Knoellia* (*T. remsis*), and *Tetrasphaera* (*T. australiensis*), with *T. japonica* as the outgroup. In addition, with a complete analysis of the bacterial genome tree that further refined these clusters, reclassifying their parent family as *Dermatophilaceae* would support the separation of *T. japonica* from *T. australiensis* and *T. jenkinsii*. In this category, only the Ca. *P. hodrii* and Pbr3 metagenome-assembled genome (MAGs) (which belonged to *Tetrasphaera* clade 3 in the previous category based on the 16S rRNA gene) encoded the full fermentation to the acetate pathway, while the other, Ca. *Phosphoribacter* MAGs, lacked the pta and ackA genes (Singleton et al., 2022). Recently, a new fermentative *Tetrasphaera* clade has also been reported at the laboratory scale as one of the few strains that can utilize PHA (*Torilis japonica* synthesized PHA after uptake glucose) that also has the ability to utilize acetate to synthesize PHA, and it showed better phosphorus removal efficiencies when acetate was used as a carbon source. These results further deepen our understanding of the carbon source on the impact of *Tetrasphaera* during the biological phosphorus removal process (Yu et al., 2023). Moreover, it is worth noting that advances in taxonomy related to *Tetrasphaera* and the mechanism of its utilization of acetate are continuously being discussed, and a clearer and more rational classification would facilitate a summary of related studies.

Research on the type of carbon source considered as a factor that affects the efficiency of biological phosphorus removal has been widely discussed; however, the concentration of the carbon source has also been considered as a limiting factor in some studies. Previous studies have shown that PAOs produce sufficient adenosine triphosphate (ATP) for the active translocation of acetate into the cell during the anaerobic phase of EBPR, whereas GAOs have little or no ATP available for acetate translocation, thus giving PAOs an advantage over GAOs at low concentrations of acetate (Schuler and Jenkins, 2003). Tu and Schuler (2013) conducted a study on the effects of controlling the feed of acetate to the SBR and the pH changes, and the effect of competition between PAOs and GAOs in EBPR was investigated through the failure and recurrence process of EBPR. The results suggested that PAOs may be inhibited when higher concentrations of acetic acid at lower pHs are combined with the relatively high concentrations that occur during rapid addition in the SBR. However, competition for GAOs may not be the primary cause of EBPR failure (Tu and Schuler, 2013). In a full-scale EBPR system, control of the feed concentration of the carbon source (acetate) will often be lower than at the laboratory scale; hence, the effect of changes in the carbon source concentration on the EBPR in a full-scale system requires further research, especially with the recent revisiting of the interactions between PAOs and GAOs in EBPR due to the complementary knowledge of genomics and microbiology. Hence, the effect of the ethyl carbon source on their impact also requires further research (Nielsen et al., 2019).

Generally speaking, the differences in the use of carbon sources by different species of PAOs in engineered systems may be limited by the study conditions or related to the properties of PAOs. However, the specific uptake of carbon sources by most species of PAOs is not known. The effect of combinatorial feeding between different carbon sources on biological phosphorus removal requires more in-depth investigations.

4.2.2. Effect of pH on phosphorus removal

The role of pH in the growth and phosphorus removal process of PAOs is mainly reflected in several aspects. First, pH can change the charge of the cell membrane. The resulting difference in membrane charge means that different microorganisms have different abilities to absorb nutrients, which affects their vital activities (De Farias Silva et al., 2017). Second, changes in pH can also affect the biochemical reactions in the phosphorus removal process of the cells of PAOs by affecting the activity of enzymes in their metabolic processes (Liu et al., 1996). Furthermore, a pH that is too high or too low can reduce the ability of microbes to tolerate high temperatures. Fig. 3a shows that the optimum pH of PAOs ranges from 6.0 to 8.0, because controlling the pH in this range helps to inhibit the growth of GAOs in a phosphorus removal system and provides a competitive benefit to PAOs. pH affects the formation of weak acids/bases that are the true substrates. When the pH is 7 to 7.5, VFA uptake is more difficult because a larger proportion of acetate is not protonated, requiring more energy to metabolize a certain number of organic substrates, such as acetate. In contrast, the acetate uptake rate of GAOs decreased with increasing pH, and this was accompanied by increased anaerobic glycogen consumption and poly-β-hydroxyvalerate accumulation (Oehmen et al., 2007). These results showed that this pH condition had a negative effect on the GAOs. In the anaerobic stage, the removal rate of soluble ortho-P (SOP) would be higher by controlling the pH to 6.4–7.2 (Liu et al., 2007). In addition, the activation of biological enzymes related to phosphorus removal, including polyphosphate kinase and adenylate kinase, also increased with increasing pH, contributing to poly-P degradation and synthesis (Liu et al., 2006). In contrast, the abundance of PAOs decreased significantly in the pH <6.0 and >8.0 ranges. Only *Acinetobacter* sp. and *Pseudomonas* sp. were found in engineered systems when the pH range was between 9.0 and 10.0, and only the conventional PAO of *Alcaligenes* sp. Was found in the pH range of 5.0–6.0 (Table S3). Under acidic conditions, the PAO uptake of nutrients was greatly hindered; this also allowed GAOs to proliferate (Li et al., 2013), which is not beneficial for biological phosphorus removal. The factors described above may lead to the precipitation of phosphorus, thus decreasing the ability of PAOs to use carbon sources and release phosphorus (Liu et al., 2021). In general, the pH of the EBPR system was suitable when controlled in neutral or weak alkaline conditions.

4.2.3. Effect of temperature on phosphorus removal

Temperature primarily affects the growth and phosphorus removal efficiency of PAOs by influencing the catalytic reaction rate of enzymes and the competition between PAOs and GAOs. It can also affect the phosphorus removal efficiency by affecting the biomass of strains of PAOs and GAOs. Fig. 3b shows that most of the PAO strains reach their maximum productivity in the temperature range of 20–30 °C, with the highest growth and phosphorus removal efficiency being found in this range. The appropriate temperature for the growth of only two strains of S-PAOs, *Desulfobacteraceae*, and *Rhodobacteraceae*, was between 20 °C and 30 °C. The common AD-PAOs (*Acinetobacter* sp., *Pseudomonas* sp.) were mostly activated between 20 °C and 40 °C (Table S4). This may be due to the presence of some essential enzymes related to phosphorus removal in the EBPR system, such as exopolyphosphatase and polyphosphate kinase (Jung et al., 2012). An increasing temperature within a certain range (20 °C to 30 °C) could enhance the activity of essential enzymes associated with phosphorus removal, which benefits the growth of PAOs and improves their activity, thus increasing the efficiency of phosphorus removal. Conversely, high or low temperatures may result in less effective system operation. At low temperatures, the uptake of phosphorus and the oxidation of PHAs is not beneficial to PAOs (Brdjanovic et al., 1998). It is generally believed that the percentage of PAOs is more than that of GAOs under low-temperature conditions (5–20 °C). In this way, the growth rate of PAOs becomes more rapid, while GAOs are affected by temperature and limited by the presence of PAOs. Thus, these conditions lead to a higher phosphorus removal efficiency in the EBPR system under these low-temperature conditions (Lopez-Vazquez et al., 2008a; López-Vázquez et al., 2007; Lopez-Vazquez et al., 2008b; Oehmen et al., 2007). With the discovery of cryophilic bacteria (*Acinetobacter Johnson* ii), the efficiency of phosphorus removal can be >80 %, which provides a powerful theoretical basis for this conclusion (Liu et al., 2012). It is worth mentioning that experimental studies on PAOs at low temperatures have also often recorded some failure situations (Helmer and Kunst, 1998).

Ca. *Accumulibacter* operates well at 35 °C in EBPR for a long and stable period under slow feed conditions (Qiu et al., 2022). When collecting materials for this study, we failed to find any records of PAOs in an environment of above 40 °C. We must consider that GAOs tend to proliferate at high temperatures and thus gain a competitive advantage in EPBR systems (Oehmen et al., 2007). Most likely, during EBPR, when temperatures are too high (>30 °C) or too low (<20 °C), functional enzyme activity is reduced, which may adversely impact metabolism, resulting in a failure of the biological phosphorus removal system to operate effectively. However, EBPRs have been widely applied in northern Europe and North America, with winter temperatures well below 20 °C (Onnis-Hayden et al., 2020). This may indicate that in some EBPRs, other environmental conditions, such as DO, carbon sources, and a solid retention time, compensate for the adverse effects of low temperatures, and this would lead to a low temperature that may have a limited influence on the phosphorus removal effect of PAOs. It is worth noting that the fermentation of GAOs in engineered systems has been recognized as a limiting factor for PAOs in previous studies, and the failure of the EBPR process at high temperatures has often been defined as a predominance of GAOs in competition with PAOs for carbon sources. These studies identified temperature as a limiting condition in limiting biological phosphorus removal (Lopez-Vazquez et al., 2009; Qiu et al., 2022; Zeng et al., 2019). However, with advances in genomic analysis and recent developments in biological phosphorus removal processes involving fermentative organisms such as *Tetrasphaera* PAOs and *Micropruina* GAOs, there have been significant changes in biological phosphorus removal processes that differ from the initial characterization of PAOs and GAOs. Some strains of *Tetrasphaera* PAOs and *Micropruina* GAOs have the ability to ferment amino acids and sugars under anaerobic conditions and therefore can grow in both anaerobic and aerobic environments. In low-carbon environments where VFAs are scarce, this property makes them dominant species, displacing Ca. *accumulibacter*. In other words, it can be hypothesized that GAOs can only grow in the presence of an excess of volatile fatty acids or other fermentable substrates (Nielsen et al., 2019). This hypothesis provides a theoretical basis for the successful implementation of EBPR at high temperatures.

4.2.4. Effect of DO on phosphorus removal

DO is also an important factor that influences PAOs. The anaerobic phase should maintain a low DO in order to be more conducive to the fermentation of anaerobic bacteria to produce acid and allows PAOs to better release phosphorus. In addition, less DO is more conducive to reducing the consumption of easily degradable organic matter that would allow the PAOs to synthesize more PHB. In contrast, DO is needed in the aerobic phase that is more conducive to the decomposition of stored PHB substances by PAOs to obtain energy to absorb dissolved phosphate synthesizing cells in the sewage preferentially and rapidly (Zeng et al., 2023). The DO control during the anaerobic phase is below 0.3 mg/L, while that in the aerobic phase is above 2.0 mg/L, to ensure the smooth progress of anaerobic phosphorus release and aerobic phosphorus absorption.

A lack of DO causes filamentous bulking in activated sludge that is not conducive to wastewater treatment. However, wastewater treatment plants often have the problem of over-aeration, resulting in energy waste. Therefore, controlling reasonable DO conditions can reduce energy consumption that can reduce the operation cost of wastewater treatment plants. Compared with conventional nitrification/denitrification systems and conventional biological nutrient removal plants, a low DO partial nitrification-denitrifying phosphorus removal process (0.25 mg/L–0.35 mg/L) achieved reduced carbon and aeration energy requirements by approximately 49.0 % and 47.0 %, respectively (Zaman et al., 2021).

4.2.5. Effect of EPSs on phosphorus removal

Previous studies have examined the factors that influence the accumulation characteristics, transformation, and phosphorus accumulation performance of EPSs in EBPR systems. These studies have demonstrated that both the physical structure and biochemistry of EPSs can either promote or inhibit the phosphorus removal process (Huang et al., 2022; Li et al., 2015; More et al., 2014). Currently, researchers are actively investigating the transport mechanism of phosphorus by EPSs during the biological phosphorus removal process, as well as the impact of EPSs in protecting PAOs against toxicants, including organic and inorganic pollutants. Moreover, they are further exploring the factors that affect the efficiency of phosphorus removal in EBPR (Long et al., 2021; Meng et al., 2023; Yang et al., 2022). By studying the effects of EPSs on the phosphorus removal efficiency in engineered systems, we can expand our understanding of the factors that influence PAOs in EBPR and enhance our knowledge of phosphorus removal in biological systems.

The EPSs present in engineered systems can generally be classified into two types: bound EPSs and soluble EPSs, based on their degree of binding to the cell. Nielsen and Jahn (1999) proposed a structural model for intercellular bound EPSs that identified two distinct types: loosely bound EPSs (LB-EPSs) and tightly bound extracellular polymeric substances (TB-EPSs) that are unevenly distributed outside the cell. Moreover, the phosphorus in EPSs exists in different forms, including Ortho-P, Pyro-P, and Poly-P, and these can undergo transformations between anaerobic hydrolysis and aerobic processes. The distribution of these forms within EPSs is heterogeneous, with ortho-phosphorus primarily found in TB-EPSs. The anaerobic hydrolysis process facilitates the uptake of VFAs by PAOs, and anion exchange may establish a gradient for VFAs to enter bacteria through LB-EPSs and TB-EPSs. However, extracellular PHA undergoes continuous hydrolysis during aerobic processes, obtaining energy from hydrolysis within PAOs (Fig. 1) (Long et al., 2021). Previous studies investigating the factors and influences of EPSs on the phosphorus removal efficiency have encompassed carbon sources, pH, temperature, and the dissolved oxygen concentration as control parameters for bacterial metabolism, as well as the inherent nature of the EPS itself (e.g., hydrophilicity/hydrophobicity and metal adsorption) (Wang et al., 2019a). These influencing factors will be discussed according to their respective categories.

However, current research lacks a detailed discussion on how to quantitatively assess the impact of the EPS content and structure on the phosphorus removal efficiency of PAOs. This gap in research can be attributed to previous studies treating phosphorus polymerization of

EPSs and phosphorus removal through EBPR as separate directions of investigation. However, the number of new influences on the relationship between EPSs and PAOs and the phosphorus removal efficiency that have not been identified in previous studies is very high, and the relevance of the various factors affecting the biological phosphorus removal process has not yet been confirmed. Consequently, there has been little adequate discussion of the interactions between EPSs and various substances inside and outside the PAO that can affect the phosphorus removal efficiency. Furthermore, the effects of different factors on EPSs and PAOs do not always exhibit synchronized trends. For instance, low C/N ratios are tolerated in EPSs, but the absence of carbon sources can impact denitrification in PAOs (Wei et al., 2017). Regarding the effect of temperature on both, it has also been reported that at moderate temperatures, more EPSs are generated, but the phosphorus removal efficiency declines (Ni et al., 2023).

Regarding the relationship between EPSs and PAOs, there remain many different mechanisms under discussion in the current research, and their effects on the process of heavy biological phosphorus removal in engineered systems vary (Ni et al., 2023). Therefore, it is essential to consider the combined optimization of these factors on the phosphorus removal process in addition to using the phosphorus removal efficiency as an indicator to evaluate the contributions of EPSs and PAOs during the biological phosphorus removal process. Exploring this direction of research would be valuable for future studies.

4.2.5.1. Effect of the carbon source on EPSs. Previous studies have demonstrated that carbon sources have an influence on the production and structure of EPSs, consequently impacting the biological phosphorus removal process (Li and Yang, 2007). Additionally, EPSs, being extracellularly produced, can be degraded into smaller molecules in the absence of carbon sources, which can then serve as a carbon and energy sources for the growth of PAOs (Park and Novak, 2007; Acevedo et al., 2012). Research indicates that changes in the EPS structure due to different carbon sources (e.g., glucose and acetate) are reflected in an increased LB-EPS content in sludge. EPS production was also observed to be higher in glucose cultures compared to acetate cultures (Li and Yang, 2007). Moreover, Liu et al. recently demonstrated that carrier-attached biofilms fed with sodium propionate exhibited higher protein concentrations compared to sodium acetate and starch, thereby promoting phosphorus accumulation in TB-EPSs (Liu et al., 2022). It has also been reported by Yan et al. (2021) that the mixing of acetic acid and propionic acid leads to higher concentrations of EPS and PHA production, thus promoting N_2O production through the aerobic denitrification pathway. Furthermore, Liu et al. (2022) found that sodium propionate promoted the growth of PAOs while sodium acetate favored the growth of D-PAO, providing new insights into the utilization of carbon sources during the EBPR process.

Several scholars have discussed the impact of the effect of the carbon-to-nitrogen (C/N) ratio in EPSs on the biological phosphorus removal system. The C/N ratio not only affects the nitrogen removal efficiency and cell growth but also influences the structure and flocculation characteristics of EPS. However, the optimum C/N ratio for EPSs remains inconsistent across different studies, possibly due to variations in the activated sludge composition and microbial populations. In a study conducted by Wei et al. (2017), the EPS content increased within the range of the C/N ratios from 3 to 15. Notably, in the low C/N ratio interval (3 to 6) and the high C/N ratio interval (15), the protein content in the latter interval was twice as high as in the former. Additionally, Ye et al. (2011) found that a C/N ratio of approximately 20 favored EPS production. As the C/N ratio continued to increase, the protein content of LB-EPSs decreased, while the protein content of TB-EPSs remained unchanged.

4.2.5.2. Effect of pH on EPSs. The effect of pH on both EPSs and the phosphorus removal efficiency primarily manifests as the alteration of the EPS' surface structure and properties. pH variations can induce changes in the adsorption and oxidation-dissolution processes of functional groups on the EPS surface with metals, leading to the release of certain metal anions when the pH decreases (Wang et al., 2019b). Furthermore, pH fluctuations also influence the physicochemical properties of substances within EPS. For instance, under pH changes, long-chain Poly-P can undergo hydrolysis, resulting in the formation of shorter-chain Poly-P, or even further hydrolysis into Ortho-P (Cade-Menun et al., 2006).

Previous studies have examined the migration and transformation of EPSs and metal ions in activated sludge, focusing on how changes in pH affect these processes. These studies have proposed hypotheses regarding the interactions between metal ions, phosphate complexes, PAOs, EPS, and the surrounding solution. The hypothesis elucidates the mechanisms of EPS accumulation under anaerobic conditions and the elevation of pH and phosphate accumulation in EPSs under aerobic conditions. Additionally, it highlights the unique kinetic changes observed in metal ions, such as calcium and magnesium ions. These findings contribute to a deeper understanding of the effect of pH on the interactions between metal ions within EPS, PAOs, and the external solution, as well as the resulting changes in the phosphorus removal efficiency (Li et al., 2015).

4.2.5.3. Effect of temperature on EPSs. Regarding the relationship between temperature, PAOs, and EPSs, previous research has investigated the impact of temperature on the phosphorus removal efficiency of EPSs. Studies have shown that EPS production varies at different temperatures, with observations ranging from −2 to 45 degrees (More et al., 2014). However, high and low temperatures can inhibit microbial growth, subsequently affecting EPS production (Li et al., 2010; Sutherland, 2001).

Recent studies have further explored the relationship between temperature and EPSs, as well as PAOs. Zeng et al. demonstrated that temperature significantly influences EPS components. Specifically, lower temperatures lead to an increase in the polysaccharide content, enhancing the adsorption capacity of EPSs and their binding capacity to phosphorus. Conversely, as temperature increases, PAOs shift their metabolic pathway from phosphorus accumulation to the proliferation of GAOs within the free activated sludge. PAOs in anaerobic sludge preferentially utilize the energy generated by intracellular polyphosphate degradation, particularly long-chain polyphosphate, for metabolic activities to release phosphorus. The autolysis of microbial cells serves as the driving force for intracellular polyphosphate release, while polyphosphate hydrolysis ultimately leads to the release of orthophosphate (Zeng et al., 2019).

The experimental phenomena of Shao et al. (2021) also proved that low temperature conditions (12 and 18 °C) favored the storage of PHA by PAOs, whereas high temperature conditions (above 24 °C) resulted in a decrease in the EPS concentration and an increase in the bio metabolic activity. However, competition between GAOs and PAOs resulted in a decrease in biophosphorus capture and an enhancement of the effect of biosorbent phosphorus capture.

4.3. Comparison of phosphorus removal of PAOs in natural and engineered systems

In the natural ecosystem, the phosphorus removal efficiency of PAOs ranges from 53.90 % (*Stenotrophomonas* sp.) to 98.9 % (*Klebsiella* sp.), while in engineered systems, the range is from 40.0 % to 99.8 % (*Acinetobacter* sp.) (Table S5). Overall, there is little difference in the range of phosphorus removal efficiencies in natural environments compared with that in WWTPs. In natural and engineered systems, conventional PAOs remain the majority type, followed by D-PAOs. In natural environments, most PAOs are found in surface water, with only a small proportion of conventional PAOs were found in soil. In engineered systems, conventional PAOs, D-PAOs and AD-PAOs are present in both WWTPs and reactors (Fig. 2).

In engineered systems, environmental factors such as carbon source, pH, DO, and temperature are closely related to the stability of system operation and the effectiveness of phosphorus removal. Controlling the optimal growth and phosphorus removal conditions for PAOs can provide the maximum advantage of their actions and contribute to the development and progress in phosphorus aggregation technology. In particular, some experiments have shown that a mixture of four strains, including *Paracoccus versutus*, *Paracoccus* sp., *Pseudomonas* sp., and *Bacillus* sp., resulted in improved removal of both nitrogen and phosphorus (>84.0 %) compared to the use of a single strain of bacteria, thus providing an effective method for the removal of nitrogen and phosphorus from wastewater. In addition, the use of the microbial compounds formed by these four strains mixed with other microbial nutrients was feasible for removing pollutants in aquatic environments (Qiao et al., 2021). It may be that microorganisms synergize with each other and work together to improve phosphorus removal efficiency. By comparing the types and phosphorus removal efficiency of PAOs in natural and engineered systems, the PAOs with stronger phosphorus removal functions can be identified for practical wastewater treatment in the future.

5. Effects of extreme conditions on PAO phosphorus removal

Environmental factors have profound effects on the phosphorus removal efficiency of PAOs, so it is particularly important to screen for PAOs with powerful phosphorus removal capabilities in different environments. The PAOs under extreme conditions that this article discusses come from both extreme engineered systems and extreme natural environments. Under extreme conditions, most of the PAOs tend to have greater adaptability. We have analyzed and summarized information about some PAOs that occur in extreme conditions and the effects of these conditions on the effectiveness of phosphorus removal by PAOs (Seib et al., 2016; Zhang et al., 2022).

5.1. High salinity

PAOs are sensitive to changes in salinity; the anaerobic release and aerobic uptake of phosphorus are significantly inhibited under high salinity (salinity >1 %) conditions (Li et al., 2018). Therefore, the study of the effects of salinity on the growth of PAOs should not be ignored. The negative effects of salinity on microbial growth and reproduction occur because high salinity changes the osmotic pressure of bacterial strains, which affects the activity of intracellular enzymes and reduces the rate of metabolism (Deng et al., 2013). However, a salt-tolerant strain of *Halomonas YSR.3* was isolated by screening organisms in the Yellow Sea; this species can adapt to pH = 8 and a high salinity (3 %)

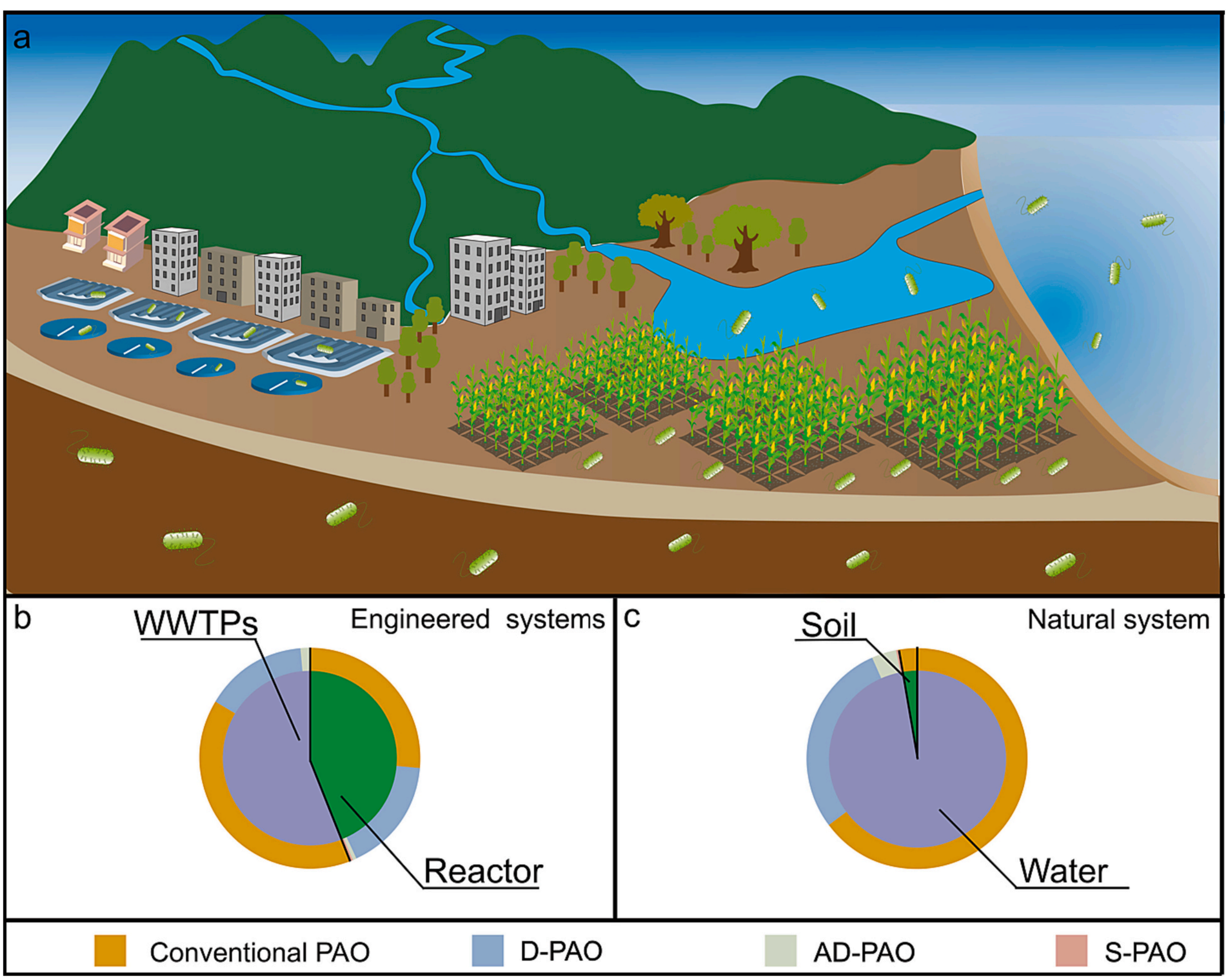

Fig. 2. Proportion of polyphosphate accumulating organisms (PAOs), denitrifying (D)-PAOs, aerobic denitrifying (AD)-PAOs, and sulfur-related (*S*)-PAOs in engineered systems and natural environments. (a) Geographic distribution of PAOs in natural and engineered systems. (b-c) Proportion of PAOs, D-PAOs, AD-PAOs, and S-PAOs in engineered and natural systems, including wastewater treatment plants (WWTPs), reactor, soil, and water.

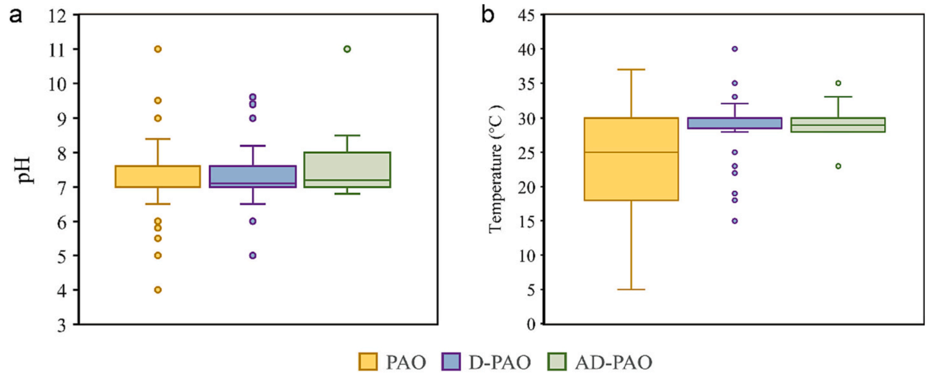

Fig. 3. (a) Proportion of polyphosphate accumulating organisms (PAOs), denitrifying (D)-PAOs, aerobic denitrifying (AD)-PAOs, and sulfur-related (*S*)-PAOs under different pH conditions; (b) proportions of PAOs, D-PAOs, AD-PAOs, and S-PAOs at different temperatures.

environment (Ren et al., 2006; Ren et al., 2008), although the osmotic pressure of this strain tends to increase with increasing salinity, which slows the rate of phosphorus removal. An AD-PAO strain, *Pseudomonas stutzeri*, showed high rates of nitrogen (95.8 %) and phosphorus (73.6 %) removal at 0–5 % salinity. The advantages of this AD-PAO are primarily for denitrification (Li et al., 2021). *Bacillus subtilis* and *Arthrobacter* sp. in mariculture pond wastewater were two AD-PAOs that were capable of thriving in a salinity range of 0–3 % (Zhang et al., 2020; Zhang et al., 2021). In addition, in South China Sea seawater the surface strains *Marinobacter* sp. and *Erythrobacter* sp., as well as the sediment strains *Alteromonas* sp. and *Pseudoalteromonas* sp., showed a wide range of adaptability under weak acidic or weak alkaline (pH = 7–9) conditions (Wang, 2017). Most of the PAOs found growing under high-salinity conditions were in natural environments; in particular, the eutrophication of coastal waters has accelerated in recent years as a result of imported nutrient salts from mariculture, while the increase in nitrogen and phosphorus provides nutrient elements for PAOs growth (Xu et al., 2022). In general, long-term exposure to high-salinity environments enabled the strains to develop their unique physiological characteristics and functions during the evolutionary process. The saline environment enables the PAOs to adapt to the impact of changes in external environmental salinity by adjusting their internal osmotic pressure, resulting in a relatively stable and high phosphorus removal efficiency (Li et al., 2018; Li et al., 2021; Xu et al., 2022). Marine waters and mariculture wastewater have high salinity, so most marine PAOs are salt-tolerant or halophilic. The discovery of salt-tolerant PAOs is valuable for phosphorus removal from both marine organisms and mariculture wastewater.

5.2. Low/high temperature

Temperatures below 10 °C (Luo et al., 2022) and above 30 °C (Wang et al., 2020b; Qiu et al., 2022) are usually extreme environments for PAOs. As shown in Table 1, different types of PAOs were present at low temperatures in the WWTPs, reactors, and natural environments. However, nitrogen and phosphorus removal rates of PAOs, such as *Candidatus Accumulibacter* sp. and *Pseudomonas* sp., are generally higher at low temperatures (≤10 °C). Particularly, *Candidatus Accumulibacter*

Table 1
Different extreme conditions of different types of polyphosphate-accumulating organisms (PAOs).

Extreme condition		Genus (species)	PAO type	Source	Phosphorus removal (%)	Reference
High salinity	2 %	*Pseudomonas* sp.	D-PAO	WWTP effluent from the coast, China	>80.0	(Chen, 2012)
	3 %	*Arthrobacter* sp.	AD-PAO	Wastewater from saline mariculture ponds, China	99.6	(Zhang and Kinyua, 2020)
	3 %	*Bacillus subtilis*	AD-PAO	Wastewater from saline mariculture ponds, China	86.6	(Zhang et al., 2021)
	3 %	*Pseudoalteromonas* sp.	PAO	Sediment in Jiaozhou Bay, China	98.0	(Gao, 2012)
	3 %	*Halomonas* sp.	PAO	The Yellow Sea	NA	(Ren et al., 2006)
	5 %	*Pseudomonas stutzeri*	AD-PAO	River sediment contaminated by restaurant wastewater, China	73.3	(Li et al., 2021)
Low temperature	4 °C	*Candidatus Accumulibacter* sp.	PAO	Reactor, Netherlands	NA	(Paez-Watson et al., 2023)
	7 °C	*Candidatus Accumulibacter* sp.	PAO	WWTP, China	93.0	(Chen, 2015)
	7 °C	*Pseudomonas* sp.	PAO	WWTP, China	93.0	(Chen, 2015)
	8 °C	*Pseudomonas* sp.	PAO	Chaohu Lake sediment, China	93.0	(Shao et al., 2015)
	8 °C	*Pseudomonas* sp.	D-PAO	Reactor, China	58.0	(Wang et al., 2007)
	8 °C	*Acinetobacter Johnsonii*	PAO	Reactor, China	NA	(Liu et al., 2012)
	10 °C	*Candidatus Accumulibacter* sp.	PAO	Reactor, Netherlands	NA	(Tian et al., 2017)
	10 °C	*Pseudomonas psychrophila*	AD-PAO	Reactor, China	24.6	(Luo et al., 2022)
High temperature	30 °C	*Dechloromonas*	D-PAO	Sequencing Biofilm Batch Reactor, China	92.9	(Xu et al., 2019)
	30 °C	*Pseudomonas*	D-PAO	Sequencing Biofilm Batch Reactor, China	92.9	(Xu et al., 2019)
	30 °C	*Candidatus Accumulibacter* sp.	PAO	Reactor, Singapore	NA	(Wang et al., 2020b)
	35 °C	*Candidatus Accumulibacter* sp.	PAO	Reactor, China	NA	(Qiu et al., 2022)
	40 °C	*Enterococcus* sp.	PAO	Aquaculture pond sludge, China	40.0	(Huang et al., 2010)
High alkalinity	pH = 11	Acinetobacter sp.	AD-PAO	Reactor, China	96.3	(Li et al., 2019)

sp. can still play the role of phosphorus removal at 4 °C (Paez-Watson et al., 2023). Some microorganisms are able to produce spores and thus survive in extreme environments (Fimlaid and Shen, 2015). One study screened the AD-PAO of *Pseudomonas psychrophila*, and found that a temperature decrease from 20 °C to 10 °C resulted in a 14.1 % increase in phosphorus removal efficiency (Luo et al., 2022). This effectively solved the problem of biotrophic nutrient removal in the winter. This is due to the fact that at 10 °C the strain ensures energy supply by up-regulating energy metabolism and ribosomes in order to adapt to the low-temperature environment (Luo et al., 2022). Furthermore, above 30 °C is the high temperature condition for PAOs (Wang et al., 2020b; Qiu et al., 2022). *Enterococcus* sp. is a high-temperature PAO (40 °C) originating from aquaculture pond effluent, with a phosphorus removal efficiency of only 40.0 %, and this is the group of PAOs that are currently thriving at the highest temperature (Huang et al., 2010). One of the reasons that PAOs species were found to be more abundant at low temperatures than at high temperatures and the phosphorus removal efficiency remained high is that most microorganisms do not deactivate at low temperatures, whereas at high temperatures this leads to the denaturation and deactivation of microbial proteins making PAOs more sensitive to high temperature conditions. Overall, *Pseudomonas* sp. and *Candidatus Accumulibacter* sp. were present under both high and low temperature conditions, indicating that these two bacteria can adapt to a wider range of temperatures.

5.3. High alkaline

Focusing on alkaline-resistant strains with resistance properties can help in finding PAOs adapted to different wastewater treatment conditions; an experimentally screen-isolated AD-PAO *Acinetobacter* sp. continued to show high rates of nitrogen removal (92.4 %) and phosphorus removal (94.2 %) under highly alkaline conditions (pH = 11) and 28 °C (Li et al., 2019).

In conclusion, most PAOs still maintain high phosphorus removal efficiency in extreme conditions, indicating that PAOs in extreme conditions have a strong utilization value. Meanwhile, microorganisms can gradually adapt to extreme conditions through domestication (Wang et al., 2016); this approach provides ideas for enriching and utilizing functional PAOs in extreme conditions. If more extreme environments (e.g., volcanoes, hot springs, submarine volcanoes, deep sea trenches, polar regions) can be screened for PAOs, perhaps those organisms can adapt to complex water environments and may benefit wastewater treatment systems in different environments.

6. Conclusions

The conclusions of this review are as follows:

- Under high salinity and low temperature conditions, the phosphorus removal efficiency of some PAOs still remained stable, while high temperature conditions had a great impact on the phosphorus removal of PAOs.
- As an important microorganism for biological phosphorus removal, PAOs are widely present in aquatic environments, soils, reactors, and WWTPs, but PAOs have more diversity in natural environments.
- The phosphorus removal capacity of PAOs associated with carbon, nitrogen, phosphorus, and sulfur metabolism were demonstrated. Recent studies have often focused on the development of S-PAOs phosphorus removal.

7. Outlook

Recent research advances have contributed to the discovery of AD-PAOs and S-PAOs. However, research on non-traditional PAOs in biological phosphorus removal and wastewater treatment is still in its nascent stage. One of the reasons for this is a lack of methods to extract high-purity cultures. In addition, there is a lack of knowledge regarding studies evaluating the use of AD-PAOs in biological phosphorus removal processes and the development of related models, which may become a researchable area for newly discovered PAOs. Furthermore, the functional genes of PAOs adapted to extreme environments have yet to be studied. In addition, there is a need to expand the knowledge of coupled carbon, nitrogen, phosphorus, and sulfur cycles in biogeochemical cycles. Future studies need to discover elements other than carbon, nitrogen, phosphorus, and sulfur that may be involved in the process of phosphorus aggregation by PAOs.

CRediT authorship contribution statement

Yan Zhang: Conceptualization, Writing - Original draft preparation. Xiaoqing Qiu: Writing- Original draft preparation. Jiahao Luo: Writing - Original draft preparation. Huishi Li: Writing - Original draft preparation. Seow-Wah How: Writing - Review & Editing. Di Wu: Writing - Original draft preparation. Juhua He: Writing - Original draft preparation. Zihang Cheng: Writing - Original draft preparation. Yunan Gao: Writing - Original draft preparation. Hui Lu: Conceptualization, Interpretation of the discussion of various sections and provided critical revision and editing of the article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.169103.

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