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Review

An overview of quorum sensing in shaping activated sludge forms: Mechanisms, applications and challenges

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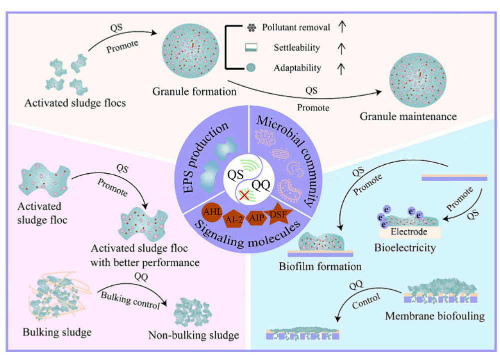
HIGHLIGHTS

- The form and performance of activated sludge are adjusted by QS.
- Signaling molecules, EPS and microorganisms are three key parts of QS regulation.
- Selective enhancement of QS/QQ improve the overall performance of activated sludge.
- QS/QQ strategy develops towards efficiency, economy and environmental friendliness.
- Many challenges in QS/QQ strategy for activated sludge process needs further research.

GRAPHICAL ABSTRACT



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ABSTRACT

Activated sludge method is an effective method for the wastewater treatment and has been widely applied. Activated sludge usually exists in various forms such as activated sludge floc, biofilm and granule. Due to the different character and function for each sludge type, the role and mechanism in the wastewater treatment process are also different, but all were crucial. The quorum sensing (QS) /quorum quenching (QQ) have been demonstrated and proved to regulate the group behavior by secreting signaling molecules among microorganisms and thus affect the manifestation of sludge. However, the complex mechanisms and regulatory strategies of QS/QQ in sludge forms have not been systematically summarized. This review provided an overview on the mechanism of QS/QQ shaping sludge forms from macro to micro (Explore it through signaling molecules, extracellular polymeric substances and microorganisms). In addition, the application and challenges of QS/QQ regulating sludge forms in various wastewater treatment processes including biofilm batch reactor, granule sludge and membrane bioreactor were discussed. Finally, some suggestions for further research and development of effective and economical QS/QQ strategies are put forward.

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1. Introduction

Biological wastewater treatment processes typically rely on microorganisms in activated sludge to remove pollutants, and these microorganisms often aggregate to form activated sludge floc, granule and biofilm (Mpongwana and Rathilal, 2022; Shi et al., 2017). Activated sludge flocs (ASFs) are formed by microorganisms, inorganic granules, extracellular polymeric substances (EPS) and polyvalent cations through various physicochemical interactions (Christwardana et al., 2019). ASF is a basic microbial unit, and its spatial structure, chemical composition and microbial community characteristics will affect the wastewater treatment efficiency (Yan et al., 2020). The formation of biofilm is a way for microorganisms to cope with external stimuli (He et al., 2023; Sun et al., 2021). Biofilm plays an important role in the removal of chemical and biological pollutants, and is widely used in many reactors, such as trickle filter, moving bed biofilm reactor, rotating reactor and so on (Huang et al., 2019b; Mpongwana and Rathilal, 2022). Microorganisms form granule by self-immobilization (Li et al., 2023b; Liu et al., 2023). Granule is a unique spherical biofilm with great impact resistance, superior settling performance, and high pollutant removal efficiency (Zhang et al., 2017). The problems preventing their widespread application are issues such as filamentous bulking of ASFs, long biofilm start-up time and poor granule stability (Lan et al., 2021; Lu et al., 2023b; Zhang et al., 2021a).

Microorganisms in activated sludge communicate by producing signaling molecules called quorum sensing (QS) (Yeon et al., 2009a). Quorum quenching (QQ) is a strategy of inhibiting QS among microorganisms (Yeon et al., 2009b). QS affects the formation and performance of various forms of sludge through the manipulation of microbial aggregation, EPS production, pollutant removal and so on (Waheed et al., 2020). Therefore, a series of strategies based on QS and QQ have been developed for application to activated sludge. In the past, there have been many reviews on QS in activated sludge. For example, the existence and function of QS in membrane filtration, granular sludge (Huang et al., 2019c) and biological power generation (Oh and Lee, 2018), and the origin and development of QQ control membrane biofouling (Anburajan et al., 2021), as well as the application and advantages of QQ inhibits the filamentous bulking of ASFs (Lu et al., 2023b). The above review is to summarize the role of QS according to different wastewater treatment systems or the prospect and development of QQ, an emerging strategy to solve problems. The form and performance of activated sludge are the key to wastewater treatment and cause of problems. But the mechanism, application and challenge of QS in three sludge forms have not been well summarized.

The efficiency of wastewater treatment by activated sludge process may be related to one or more characteristics of sludge, such as morphology, structure, microbial structure, sedimentation, hydrophobicity, and EPS content. Signal molecules, EPS and microbial community are the three key parts of QS to shape sludge form, and there are interactions and relations among these parts. Their presence, effects and influencing factors in activated sludge have been extensively and separately studied. The mechanism of QS in affecting sludge form and properties was summarized from the aspects of signal molecules, EPS and microorganisms. And the application and exploration of improving sludge performance based on QS and QQ are also introduced. The purpose of this review is to address those points not covered by published reviews and to update the latest developments based on QS and QQ strategies. To further improve the efficiency and energy savings of the sludge system, suggestions and research needs for future study are made based on the findings. It is expected to provide ideas for the development of more effective and sustainable QS and QQ strategies and make some contributions to accelerate the application in practical engineering.

2. Regulation mechanism of QS in activated sludge

QS shaping sludge forms can be summarized into the following process: First, the initial colonizing microorganisms come into contact, triggering QS when the signaling molecules secreted by these microorganisms reach a certain concentration, and then the microorganisms gather in the thin EPS secreted. Next, this cluster of cells attracts the adhesion of other microorganisms and secretes more EPS to fill the gaps between them. Finally, due to different reactor and hydraulic conditions, these microbial aggregates were shaped into different shapes of ASFs, biofilms and granules. In the whole process, signal molecules, EPS and microbial communities are the three key parts of QS in shaping sludge forms (Shi et al., 2017; Świątczak and Cydzik-Kwiatkowska, 2017). The interaction between them is shown in Fig. 1. Although QS in the three sludge forms have been extensively studied in isolation, these lack comparative studies. Determining the unified concept of QS in shaping sludge forms and some unique characteristics in the three sludge forms is conducive to fully understanding the regulation mechanism and thinking about how to regulate effectively.

2.1. Presence of signaling molecules in activated sludge

The main signaling molecules found so far are N-acylhomoserine lactones (AHLs) communicated by Gram-negative bacteria, autoinducing peptide (AIP) communicated by Gram-positive bacteria, autoinducer-2 (AI-2) communicated by Gram-negative bacteria and Gram-positive bacteria, and *Pseudomonas* quinolone signal (PQS) communicated by *Pseudomonas aeruginosa* (Oh and Lee, 2018). The diffusible signal factor (DSF) and cyclic dimeric guanosine monophosphate (*c*-di-GMP), the second messenger, have also been reported to be involved in controlling varies of biological processes (Oh and Lee, 2018). The mechanism of some signaling molecules mediating QS is shown in Fig. 2. Three sludge forms exhibit distinct characteristics and distributions of signal molecules. As the communication bridge of microorganisms, the determination of the main types, distribution and functions of signal molecules in sludge is the premise of exploring the mechanism of the formation of sludge by QS.

AHLs are the main signaling molecules in bacterial cell signaling and have been extensively studied. For AHLs without β-substituents, the longer the N-group side chain length, the stronger the ability to promote microbial adhesion growth. The opposite is true if the substituent of AHL is carbon (Li et al., 2015a). AHLs are mainly present in the matrix of ASFs, but not in the aqueous phase of sludge (Chong et al., 2012; Hu et al., 2016a). The main AHLs of ASFs are C4-HSL, C6-HSL and C8-HSL (Li et al., 2019a; Yan et al., 2020). C4-HSL is conducive to the conversion of ASF to biofilm and granule. C6-HSL and C8-HSL increase the irregularity, porosity, and particle size of ASF (Yan et al., 2020). During the formation of biofilm, AHLs are manifested as short chain to long chain (Huang et al., 2009). The main AHLs in biofilms are C8-HSL, C10-HSL, C12-HSL and 3-oxo-C10-HSL (Li et al., 2019a). C8-HSL is the main AHL causing membrane biofouling (Yeon et al., 2009a). C10-HSL and C12-HSL were significantly correlated with the adhesion activity of biofilms (Li et al., 2019a). The main AHLs in granules are C6-HSL, C8-HSL, 3OHC8-HSL, C10-HSL, C12-HSL and 3OHC12-HSL (Li et al., 2015a; Zhang et al., 2019). Small granules secrete more long acyl chain AHLs than large granules because of their increased specific surface area, better nutrient absorption and material metabolism capacity of attached growing microorganisms (Feng et al., 2014). And short chain AHLs tend to diffuse in water, while long chain AHLs tend to remain in the sludge phase, which may be due to the better water solubility of short chain AHLs (Feng et al., 2014). C6-HSL improves granule activity by increasing the abundance of functional microorganisms or stimulating the expression of related active genes (Li et al., 2019a; Zhang et al., 2019b). Li et al. (2019b) and Zhang et al. (2020) reported C8-HSL could also promote the adhesion and growth of microorganisms, thus promoting sedimentation and nitrogen removal capacity of granules (Li et al., 2019b; Zhang et al., 2020). The type, function and distribution of AHLs change dynamically with the development of sludge form, but there is no systematic conclusion on the distribution of AHLs in sludge.

In addition, when conducting quantitative analysis of AHLs, it is also necessary to consider its own characteristics, such as solubility, diffusion rate, and the influence of different environmental conditions, which may help to explain the differences in the study and better regulate AHLs.

AI-2 can enhance interspecific bacterial communication, regulate microbial physiological properties such as EPS secretion, flagellar activity, and promote bacterial growth from floating to attached growth (Zhang et al., 2017). These properties are closely related to biofilm formation and granule stability. The concentration of AI-2 was lowest in loosely bound biofilms and highest on the membrane surface. AI-2 can enhance interspecific bacterial communication, induce the expression of related genes, and promote bacterial growth from floating to attached growth (Wang et al., 2018). Without AI-2, biofilm growth is impeded or even stalled (Wang et al., 2017). AI-2 is not involved in the initial aggregation of particles but is essential for the further development of small granules into large, mature granules (Wang et al., 2017; Zhang et al., 2017). AI-2 regulated granule growth faster than AHLs. It may be that interspecific QS regulation allows more microbes to participate in aggregation, and the cooperation between multicellular cells makes the performance more prominent. AIP interferes with the initial attachment of *Staphylococcus aureus* and participates in the maturation of biofilm (Anburajan et al., 2021). High concentrations of *c*-di-GMP affect biofilm-related functions by promoting the formation of various adhesins and extracellular polysaccharides (Hengge, 2009). Contrary to other signaling molecules, DSF promotes biofilm diffusion (Li et al., 2019a). The existence of multiple signal molecules and the interaction between signal molecules make the QS mechanism in activated sludge more complicated. During the anaerobic granule formation, DSF content was positively correlated with short and medium acyl chain AHLs and negatively correlated with long acyl chain AHLs. At the same time, DSF, which has the opposite effect, also has a positive correlation with AI-2 (Feng et al., 2014). These phenomena have not been explained in detail. At present, the research mainly focuses on the main types of signal molecules and their roles. However, the distribution of signal molecules and the complex interactions between signal molecules still need to be further studied.

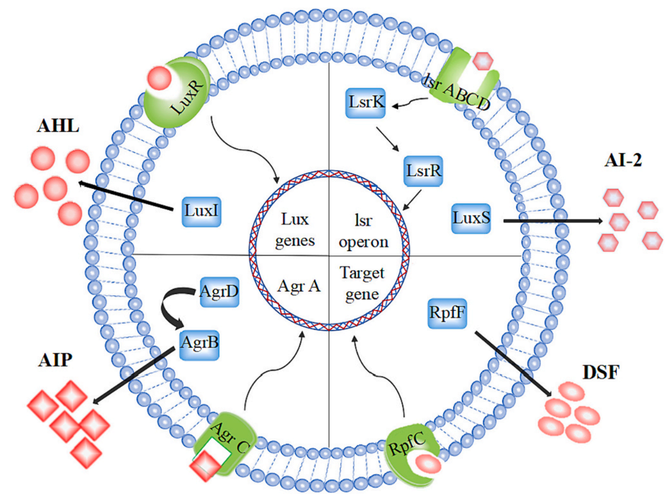

Fig. 2. Diagram of some signal molecules that mediate the QS mechanism.

2.2. EPS regulated by QS in activated sludge

EPS is a complex mixture of polysaccharides (PS), proteins (PN),

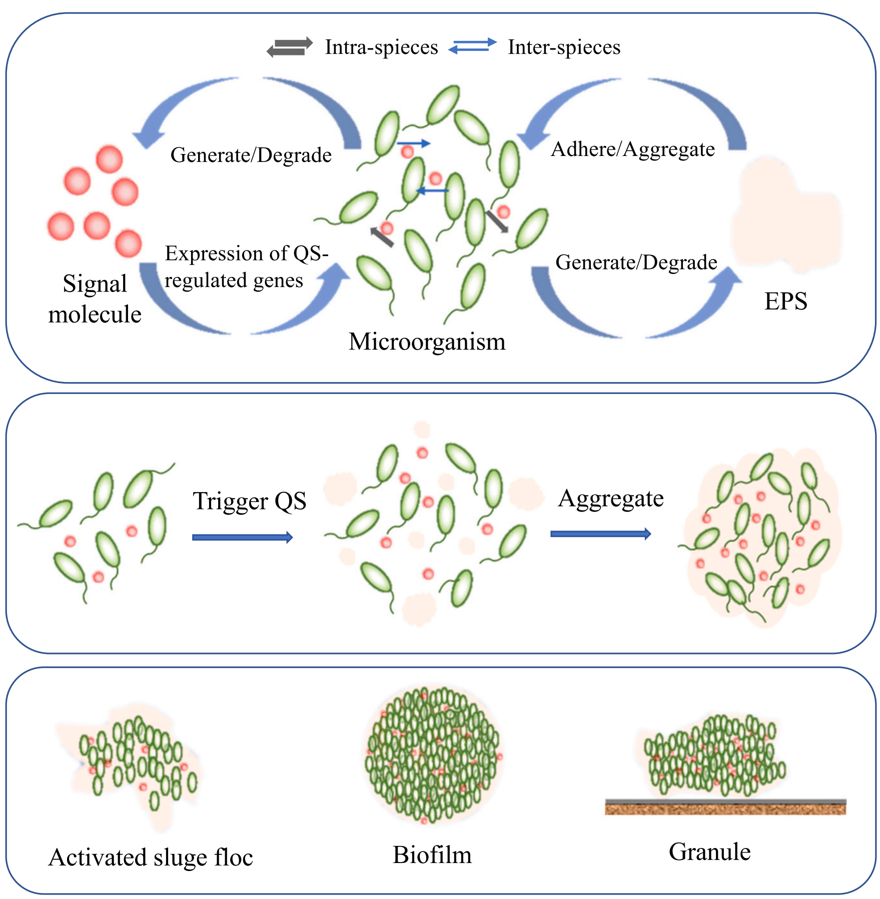

Fig. 1. QS regulation mechanism in three types of sludge.

humic acids, nucleic acids and other compounds (Shi et al., 2017). It can be categorized into loosely bound EPS (LB-EPS), which is distributed in the outer layer, and tightly bound EPS (TB-EPS), which is distributed in the inner layer. (Maqbool et al., 2015). EPS is the main component of the three sludge forms, and affects the form and performance of the sludge due to its properties of adhesion, hydrophobicity and surface charge (Shi et al., 2017; Xu et al., 2020). QS regulates EPS synthesis by regulating the expression of genes related to adenosine triphosphate (ATP) synthesis and carbon source metabolism (Lv et al., 2024). On the one hand, QS directly promotes ATP synthesis by increasing the expression of nuoB and atpE genes that are directly associated with oxidative phosphorylated and proton motive force-driven ATP biosynthesis(An et al., 2014). On the other hand, QS can regulate some carbon metabolic pathways involved in ATP synthesis, including trichloroacetic acid (TCA) cycle, glycolysis (EMP) pathway and hexose monophosphate (HMP) pathway, and indirectly promote ATP synthesis(Lv et al., 2024). The regulatory mechanisms of QS on EPS production are varied in different bacterial species. *Vibrio cholerae* and *Pseudomonas* produce AHLs, which bind and activate their receptor protein LuxR, and then the activation of the AHL-LuxR protein complex, which is usually homodimerizes and binds to the QS promoter, activating the EPS formation expression (Fig. 3) (Sakuragi and Kolter, 2007; Shi et al., 2017). High concentrations of *c*-di-GMP promote microbial the secretion of CdrA by *Pseudomonas aeruginosa*, which can bind to polysaccharide Psil, thus promoting the production of EPS (Shi et al., 2017). QS does not only have a positive promoting effect on EPS. Ding et al. (2015) found that the addition of exogenous DSF inhibited the production of EPS in anaerobic granular sludge. However, He and Zhang (2008) found that the addition of exogenous DSF restored EPS production in DSF-deficient mutant strains of *Xanthomonas*. This contradictory conclusion suggests that the relationship between signal molecules and EPS may vary depending on operating conditions, microbial communities, and water quality. The micro-mechanism of QS regulation of EPS is worth further exploration.

The concentration of EPS is crucial for the development and maintenance of the spatial structure of activated sludge (Sheng et al., 2010; Shi et al., 2017). QS maintains the structure and adhesion of ASFs by promoting the generation of EPS and promotes the growth of functional microorganisms. However, excessive EPS will lead to poor settling performance and intercellular adhesion (Sheng et al., 2010; Shi et al., 2017). A crucial stage in the formation of a biofilm, the initial microbial deposition on the membrane surface, is facilitated by EPS. It then consolidates this deposition by adhering to organic matter and other solutes, progressively forming the biofilm (Huang et al., 2019a; Mpongwana and Rathilal, 2022). QS affects the interaction between microorganisms and membrane surface by regulating EPS, thus affecting the formation and structure of biofilm. Granules have a stable structure with little change in EPS, and a higher tendency to form gel, ensuring high biological density (Li et al., 2014). Granule stability is facilitated by the distribution of biodegradable EPS in the inner layer and non-biodegradable EPS in the outer layer. (Iorhemen et al., 2019; Shi et al., 2017). AHLs, particularly C8-HSL and 3OHC8-HSL, are positively associated with tryptophan and protein-like substances, the main components of EPS in granules (Zhang et al., 2019e). And AI-2 stimulates high MW EPS and accumulation of hydrophobic EPS in the outer layer, promoting granule stability (Zhang et al., 2017).

The regulation of EPS by QS should pay more attention to the change of composition. Excessive LB-EPS is not conducive to microbial attachment and aggregation due to electrostatic repulsion (An et al., 2023; Chen et al., 2019). TB-EPS promotes aggregation due to ion bridging (An et al., 2023). The correlation between AHLs and LB-EPS and TB-EPS was different in different cases. In ASFs, AHLs have a great effect on the concentration and characteristic functional groups of LB-EPS, but a weak effect on TB-EPS (Yan et al., 2020). During the formation of aerobic granules, both TB-EPS and LB-EPS are regulated by AHLs (Yue et al., 2020). A strong positive correlation between AHLs and TB-EPS was observed during anaerobic granule formation, but no such correlation was found during granule maturation (Ma et al., 2018). The change of PN/PS in EPS is more important than the concentration. PN and PS are the main components of EPS, and QS affects the production of them by regulating their metabolites and metabolic pathways (Yan et al., 2020). QS promotes the synthesis of certain amino acids by regulating pentose phosphate pathway and the abundance of genes

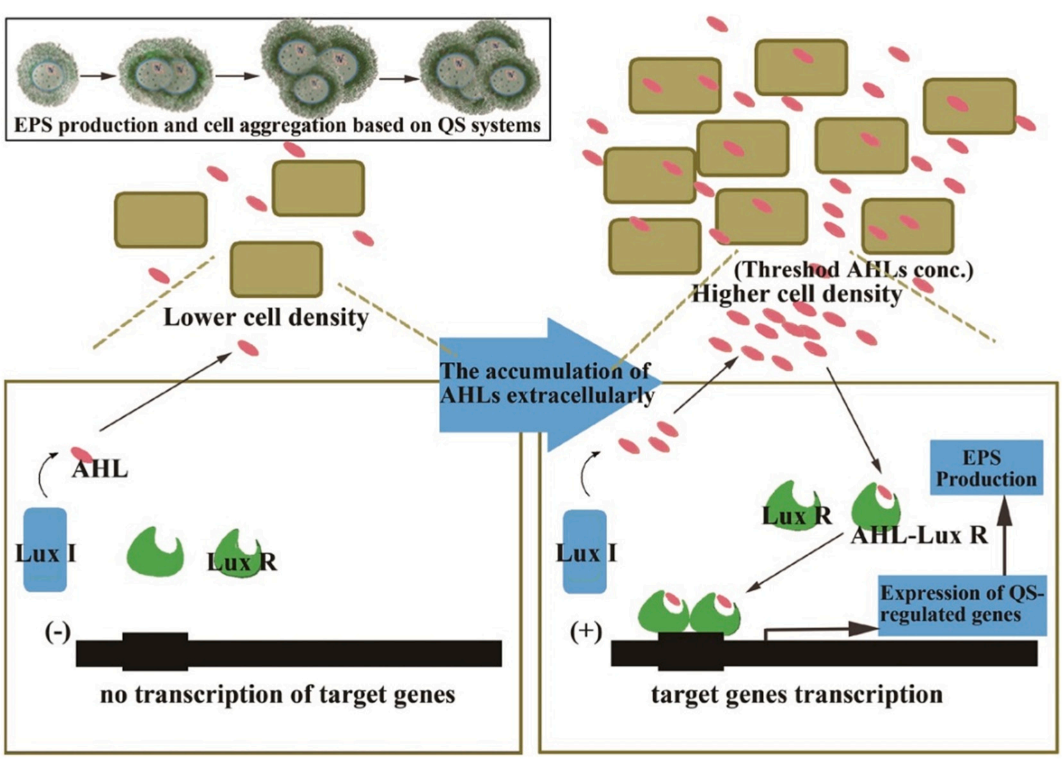

Fig. 3. Diagram of EPS regulation based on AHL (Shi et al., 2017). Copyright,2017, Elsevier.

Table 1
QS and QQ microorganisms common in three sludge forms.

Bacterial genus	Distribution	Type	Role	Ref
Acinetobacter	ASF Biofilm	QS QQ	Degrade long AHLs	(Huang et al., 2019a, Li et al., 2023a)
Aeromonas	ASF Granule	QS	Biofilm formation	(Huang et al., 2019b, Li et al., 2020)
Azotobacter	Biofilm	QS	Synthesize alginate	(Jo et al., 2016)
Bosea	ASF Biofilm Granule	QQ	Degrade AHLs	(Li et al., 2020, Li et al., 2023a)
Dechloromonas	Biofilm Granule	QS	Metabolize organic matter and nitrogen	(Jo et al., 2016)
Ferruginibacter	ASF Biofilm	QS	EPS production	(Burton et al., 2005)
Flavobacterium	ASF Biofilm Granule	QQ	Denitrification	(Jo et al., 2016, Li et al., 2020, Li et al., 2023a)
Methanobateria	Biofilm Granule	QS	EPS production	(Ma et al., 2019)
Nitrosomonas	ASF Granule	QS	Nitrification	(Li et al., 2020, Li et al., 2023a)
Nitrosospira	ASF Granule	QS	Nitrozation	(Li et al., 2020, Li et al., 2023a)
Nitrospira	ASF Biofilm Granule	QS	Oxidize nitrite to nitrate, Biofilm fomation	(Jo et al., 2016, Li et al., 2023a)
Nocardia	ASF	QS	Filamentous bulking	(Ouyang et al., 2020)
Pedobacter	ASF Biofilm Granule	QQ	Degrade AHLs	(Li et al., 2023a)
Penicillium	ASF	QS	Filamentous bulking	(Li et al., 2023a)
Pseudomonas	ASF Granule	QS QQ	Biofilm formation, EPS production, Denitrification	(Huang et al., 2019c, Li et al., 2023a)
Rhodococcus	Biofilm	QQ	Inhibit biofilm formation	(Li et al., 2020)
Rhodoferax	ASF Biofilm	QS	Metabolize organic matter and nitrogen	(Ouyang et al., 2020)
Rubrivivax	ASF Biofilm	QS	Removal of organic matter and nitrogen	(Jo et al., 2016)
Sphingomonas	Biofilm	QS	EPS production, Denitrification	(Ouyang et al., 2020)
Sphingopyxis	ASF	QQ	Degrade AHLs	(Li et al., 2023a)
Thauera	Biofilm Granule	QS	EPS production	(Hamza et al., 2018)
Thiothrix	ASF	QS	Filamentous bulking	(Lu et al., 2023b)
Variovorax	Biofilm	QQ	Degrade AHLs	(Li et al., 2019a)
Vibrio	Biofilm Granule	QS	Biofilm formation	(Burton et al., 2005)
Saprospiraceae	Biofilm Granule	QS	Hydrolyzed proteins and polysaccharides	(Li et al., 2019a)
Xanthomonadaceae	ASF Biofilm	QS	Hidden EPS	(Mhedbi-Hajri et al., 2011)

associated with amino acid synthesis, such as Met, Thr, Gly, and Trp, and thus promotes PN production (Lv et al., 2024; Ma et al., 2022). At the same time, QS can promote PS production by regulating gluconeogenic pathway (Lv et al., 2024). PN affects microbial adhesion and aggregation by altering surface charge and hydrophobicity (Chen et al., 2019; Li et al., 2022). PS forms a network layer that aids in microbial flocculation and granule formation (Chen et al., 2019; Zhao et al., 2016). The change of PN/PS affects the zeta potential and surface hydrophobicity, thus affecting the form and performance of sludge(Shi et al., 2022; Waheed et al., 2020). The structure of activated sludge with lower PS/PN is more stable, compact and has good settling ability (Zhao et al., 2016). To sum up, the mechanism of QS affecting sludge form and sludge properties is to regulate the concentration, composition and distribution of EPS. The regulation effect of QS on EPS and the function of different EPS components vary with different sludge forms. Further identification and elucidation of these differences are of great significance for better regulation of QS.

2.3. QS and QQ microorganisms in activated sludge

The production of signal molecules is the result of microbial community selection (Jo et al., 2016; Liu et al., 2022). QS and QQ microorganisms and their functions in three sludge forms are shown in Table 1. In ASFs, flocculating microorganisms and filamentous bacteria are interdependent (Burger et al., 2017). Filamentous bacteria constituted the rigid skeleton of ASFs, while flocculating bacteria attached to the skeleton by secreting EPS. Excessive proliferation of filamentous bacteria will reduce the diversity of microbial population structure and lead to filamentous bulking (Lu et al., 2023a; Shi et al., 2021). Excessive proliferation of filamentous bacteria will wrap the flocs, and the filamentous bacteria will be connected to each other, which will increase the volume of the flocs and loose the structure, resulting in filamentous bulking and poor sludge settling performance (Sam et al., 2022). Filamentous bacteria gradually evolve genes related to AHLs during proliferation, and QS promoted the evolution of the microbial community to the dominant filamentous bacteria in bulked sludge (Lu et al., 2023b; Shi et al., 2022). C7-HSL can induce filamentous bulking of *Penicillium* or *Galactomyces* (Feng et al., 2022; Lu et al., 2023b). 3-OH-C10-HSL promotes the secretion of galactose by *S.natans cells* through driving TCA cycle reversal and gluconeogenesis, and further promotes the formation of filamentous sheath (Lu et al., 2023a; Lu et al., 2023b). AHL also promotes the proliferation of filamentous bacteria by regulating energy metabolism and activating the expression of related genes associated with hyphal formation. (Lu et al., 2023b). Revealing the complex mechanism of filamentation mediated by QS will be of great significance for controlling filamentous bulking based on QQ. Some QQ microorganisms, like *Bosea*, *Microbacterium* and *Pedobacter*, have a relatively high abundance in flocs, which may lead to higher QQ activity in ASFs than other forms (Li et al., 2023b). Therefore, when multiple sludge forms coexist, attention should be paid to the effect of high QQ activity of ASFs on other sludge forms.

QS microorganisms have different biofilm forming abilities, which is more important than microbial abundance (Jeong et al., 2016; Jo et al., 2016). The abundance of some QS microorganisms such as *Nitrospira* in biofilm was higher than in ASF, which may be related to their biofilm-forming ability. EPS accumulation on biofilm is also the result of enrichment of related microorganisms. *Xanthomonas* can hide EPS and increase EPS content on biofilm (Jeong et al., 2016; Mhedbi-Hajri et al., 2011). And *Sphingomonas* produces a large amount of EPS to modify the membrane surface, which promotes the attachment and proliferation of other microorganisms, thus promoting the maturation of the biofilm (Burton et al., 2005). Certain microbial populations, such as *Dyella* and *Enterobacter*, have been found to appear mainly in the early and late stages of membrane biofouling (Jo et al., 2016). This means that some microorganisms may play a key role in membrane biofouling, and special attention should be paid to these key microorganisms when using the QQ strategy to control membrane biofouling.

The ratio of QS to QQ microorganisms is an important factor affecting granulation (Li et al., 2016). In the granule formation, the dominant microorganisms are *Thauera*, *Clostridium*, *Pseudomonas*, and *Arthrobacter* (Lv et al., 2014).In the granule disintegration, many functional bacteria (such as *Thauera* and *Acinetobacter*) will gradually disappear (Zhang et al., 2017). QS controls *Methanosaeta's* filamentous growth, cell assembly, and EPS production, which are key to the formation of granule precursors (Ma et al., 2019). And QS regulates *Thauera*, *Flavobacterium*, *Flavihumibacter* and other microorganisms to produce EPS, so that the granular sludge has a strong adhesion potential, which is conducive to the further development of the granule structure and the maintenance of high biological activity (Hamza et al., 2018). The core becomes anaerobic when signal molecules are added to increase granule size. This allows anaerobic bacteria like *Dechloromonas*, *Thauera* and *Flavobacterium* to survive (Hamza et al., 2018; Świątczak and Cydzik-Kwiatkowska, 2017). These anaerobic bacteria enhance the ability of nitrogen and phosphorus removal (Świątczak and Cydzik-Kwiatkowska, 2017). Therefore, regulating QS to promote the enrichment of microorganisms related to EPS generation and pollutant removal is an effective strategy to accelerate granulation and improve performance.

3. Exploration and application of QS to shape sludge forms

3.1. Signaling in activated sludge flocs

3.1.1. Improving the performance of ASFs based on QS

The ASFs morphology range from tip flocs to diffuse flocs, and their size are generally in the range of 10–70 μm (Li and Pagilla, 2017). The size and structure of the flocs affect the sedimentation performance, dehydration performance and specific oxygen uptake rate (SOUR) (Burger et al., 2017; Waheed et al., 2020). In the activated sludge process, the removal of pollutants is closely related to the physicochemical properties of ASFs (Yan et al., 2020). The smaller floc size and lower EPS result in high oxygen diffusivity, which facilitates the nitrification process (Fan et al., 2017). However, if the size is too small, the sludge volume index (SVI) and even the turbidity of the wastewater will increase (Waheed et al., 2020). The enhancement of QS promoted the secretion of EPS, thus promoting the formation of dense and round flocs (Li and Pagilla, 2017; Zhang et al., 2019e). The addition of signal molecules enhanced the ASF's size, irregularity, and internal mass transfer resistance as well as the variety and richness of functional microorganisms, all of which aided in the removal of contaminants (Yan et al., 2020). Most of the microorganisms involved in nitrogen metabolism carry AHL-related genes, so the nitrogen removal capacity of ASFs can be improved by adding AHLs (Li et al., 2022). The addition of C6-HSL and C8-HSL increased the abundance of ammonia-oxidizing bacteria (AOB), denitrifying bacteria (DNB), nitrite-oxidizing bacteria (NOB) and EPS secreting microorganisms, which was beneficial to improve the nitrogen removal efficiency of ASFs (Yan et al., 2020). At the same time, the concentration of signaling molecules in ASF is critical. If the signal molecules concentration is too low, ASF will dissolve and release EPS, while more easily adhering to the membrane surface, reducing the treatment efficiency (Xu et al., 2020). This indicates that the quenching intensity should be considered more carefully when applying QQ to inhibit membrane biological contamination. And when the concentration is too high, it will reduce the zeta potential and hydrophobicity of ASF, which is not good for microbial aggregation and adhesion, resulting in loose structure of flocs and poor mud-water separation effect (Shi et al., 2022).

3.1.2. QQ inhibits the filamentous bulking of ASFs

Filamentous bulking of ASFs is a common problem in wastewater treatment plants, which can lead to the deterioration of sludge settling performance, poor mud-water separation effect, and even the collapse of the whole system in serious cases (Shi et al., 2021). Conventional approaches to controlling filamentous bulking, including adding general disinfectants and boosting aeration intensity, inevitably lead to the destruction of flocs structure, sludge scour and energy consumption (Lu et al., 2023b). The filamentous bulking mechanism based on QS is shown in Fig. 4. The addition of AHL promotes the increase of filamentous bacteria abundance or induce the growth of mycelium (Shi et al., 2021; Shi et al., 2022). Therefore, QQ is a promising strategy for preventing and controlling filamentous bulking (Lu et al., 2023b; Shi et al., 2022).

Generally speaking, there are three QQ strategies: 1) block the synthesis of signal molecules; 2) Change the structure of the signal molecule to inactivate it; 3) Add signal molecule analogues to interfere with signal molecule receptors (Oh and Lee, 2018). Vanillin is a substance that inhibits the gene expression of synthetic signaling molecules and has a good inhibitory effect on short chain AHLs (Lu et al., 2023b). Vanillin at 50 mg/L has been used to inhibit the filamentous bulking without significant negative effects on microbial activity (Shi et al., 2021; Shi et al., 2022). And there has been proved that 3-OH-C10-HSL could promote the formation of *Sphaerotilus* silky sheath and its dominant position in ASFs, resulting in filamentous bulking (Lu et al., 2023b). By addition of 3-OH-C10-HSL analogue 3-OXO-C10-HSL interfering signal transmission, *Sphaerotilus* abundance, protruding silk and SVI decreased, and SOUR increased 26–35 % compared with non-expanded sludge and so that the structure stability and good biological activity of flocs were maintained (Lu et al., 2023a). Long chain AHL has a structure similar to that of fungal signal farnesol. Feng et al. (2022) added 5 μM C12-HSL and C14-HSL to the fungal bulked sludge every 24 h, and SVI in the two reactors decreased by 6.1 % and 39.7 % within 72 h respectively. In summary, these QQ methods are an innovative bio-friendly strategy for precise control of filamentous bulking.

3.2. Signaling in biofilms

Microorganisms attach to the carrier surface to form biofilm, which plays a dual role in membrane process (Mpongwana and Rathilal, 2022; Shi et al., 2019a). Microorganisms can resist interference from adverse external environment to better remove toxic and harmful pollutants in wastewater by forming biofilms (Mpongwana and Rathilal, 2022; Shi et al., 2019b). The formation of biofilms also leads to membrane biofouling, reduce membrane permeability, and increase operating costs (Liu et al., 2024a; Oh et al., 2017). Therefore, it is necessary to adjust the biofilm according to the needs of different reactors. The role and regulation of QS in biofilm and the application of biofilm are summarized in Fig. 5.

3.2.1. QS enhancement promotes biofilm formation

QS enhancement can be achieved by directly adding signal molecules or stimulating the secretion of endogenous signal molecules. The initial attachment of microorganisms is a necessary process for biofilm formation, which is unstable and time-consuming (Hu et al., 2016a; Wang et al., 2020). QS enhancement accelerates the initial adhesion of urban and industrial wastewater, rapidly initiate biofilm formation, and increase the thickness and density of biofilm (Wang et al., 2020). Adjusting pH can accelerate the release of endogenous signaling molecules and promote the formation of biofilms (Mpongwana and Rathilal, 2022; Zhang et al., 2019c). Moreover, the direct addition of C6-HSL and C8-HSL can accelerate the start-up of anammox biofilm at low temperatures, thus widening the treatment range of anammox biofilm reactor (Zhang et al., 2022a). At the same time, adding AHLs to damaged nitrifying biofilms can stimulate rapid microbial growth and accelerate biofilm recovery (Hu et al., 2016a). And biofilms formed by functional microorganisms are more effective in bio-enhancement. The addition of C6-HSL and 3OC6-HSL promoted the formation of thick and structured biofilm by pyridine degrading strain *Paracoccus*, rapidly started the bio-enhanced reactor and promoted the nitrogen removal (Xiong et al., 2020). The QS enhancement can accelerate the biofilm formation and start-up of wastewater treatment, but there are still relatively few studies on the migration and action process of AHLs on the material surface, which can provide a theoretical basis for guiding the strengthening of AHLs. Moreover, in the actual wastewater treatment process, the price of exogenous AHLs should be considered, which indicates that more effective and economical QS enhancement methods should be explored in the future.

QS enhancement affects the thickness, pollutant removal efficiency and performance of biofilm. The thickness of biofilm changes the efficiency of biofilm by affecting the transfer of oxygen and nutrients and affecting the growth of microorganisms (Mpongwana and Rathilal,

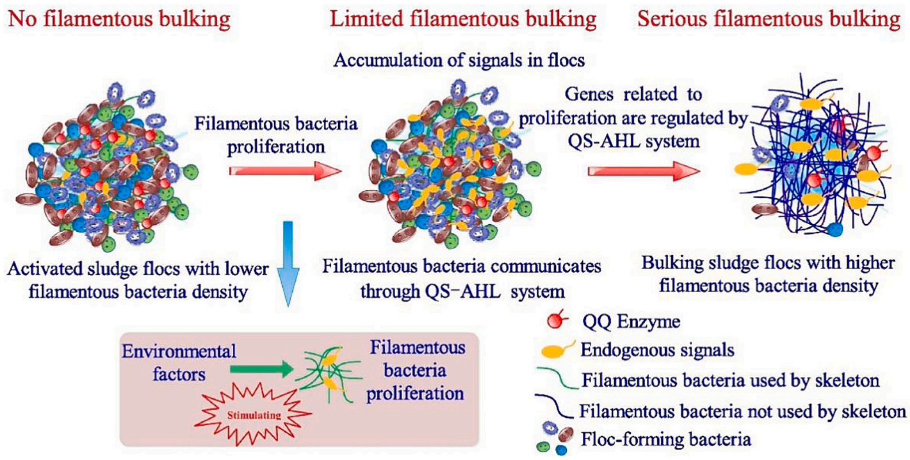

Fig. 4. Filamentous bulking mechanism based on QS (Shi et al., 2021).Copyright,2022, Elsevier.

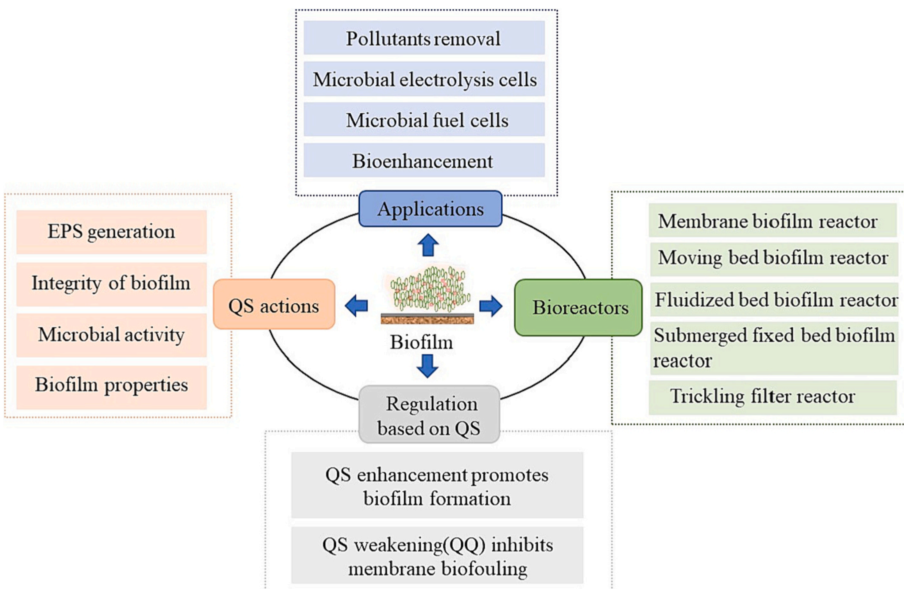

Fig. 5. An overview of quorum sensing in biofilms and its applications.

2022; Piculell et al., 2016). The addition of C10-HSL and C12-HSL significantly increased the oxidation rate of anoxic ammonia in oxygen-limited autotrophic nitrification/denitrification process (Clippeleir et al., 2011). The addition of Fulvic acid stimulated the secretion of C8-HSL of anammox biofilm, promoted the activity of anammox bacteria, and thus improved the denitrification rate and efficiency (Liu et al., 2020). The addition amount of AHLs affects the efficiency of QS enhancement to improve the processing performance of membrane bioreactor. Hu et al. (2016b) showed that compared with the blank control, the addition of 50 nM AHLs significantly increased the degradation rates of COD and ammonia, while the addition of 1000 nM AHLs reduced the COD removal rate and the nitrification of ammonia nitrogen by about 7 % and 2.6 %, respectively. This may be due to the high concentration of AHLs inhibiting the activity of functional microorganisms in the reactor. Microbial fuel cells (MFCs) can generate electricity while treating wastewater with high organic strength, and the addition of signal molecules promotes the formation of anode biofilms and improves power production, which will contribute to the wide application of MFCs (Christwardana et al., 2019; Monzón et al., 2015). And the addition of boron to MFC promotes the synthesis of AI-2, which increases the power generation potential by nearly 15 mV (Sun et al., 2021). Microbial electrolysis cells(MECs)is a new green energy technology that efficiently recycle hydrogen. The regulation of signal molecules on the electrical signal during the formation of anode biofilm can significantly improve the hydrogen production capacity and energy recovery capacity, and the promotion effect of short chain AHL is more significant (Liu et al., 2015). And the addition of C4-HSL to the biocathode of MEC improved sulfate reduction efficiency and biocathode stability, revealing the potential of QS in enhancing MEC's treatment of sulfate-containing wastewater (Shi et al., 2023). The application of QS in membrane bioreactors has expanded from water treatment to the generation of additional energy, indicating that signal molecules are a promising multifunctional regulator, and more applications such as special wastewater treatment need to be explored in the future.

3.2.2. QQ inhibits membrane biofouling

Signal molecular degradation enzymes have high purification cost, poor stability and limited pollution control time, and the addition of QQ microorganisms makes it a better way to control membrane biofouling (Huang et al., 2019a; Liu et al., 2024b; Oh and Lee, 2018). Some typical QQ methods for controlling membrane biofouling are listed in Table 2. The facultative QQ bacteria (FQQ) were obtained by anaerobic screening of the aerobic QQ bacteria. FQQ significantly control the membrane biofouling in anaerobic membrane bioreactors (AnMBR) and has no effect on COD removal and methane production (Xu et al., 2020). Waheed et al. (2017) fixed the QQ alliance composed of AHLs and AI-2 degrading bacteria in alginate beads, proving that the alliance could effectively control membrane biofouling at both stable and changing organic loading rates (OLR). Nahm et al. (2016) has developed QQ bacteria capture tablets, which have a larger surface area and stronger QQ effect than QQ beads and are suitable for membrane bioreactors (MBR) with hollow fiber membrane. The two silicon reinforced core-shell beads coated with BH_4 have high compressive strength, and the QQ beads still have more than 70 % QQ activity after 5 months of continuous operation in the MBR of a laboratory-scale system (Li et al., 2023a). Electrostatic spinning nanofibers coated on the surface of BH_4 coated gel beads have high mass transfer performance and selectivity, which is conducive to the durability of QQ activity and good physical washing effect (Pang et al., 2023). The mass transfer and stability of immobilized QQ bacteria continue to improve, protecting the target bacteria to better play the quenching role, thus becoming a sustainable and cost-effective membrane biofouling control strategy, but the complexity of packaging may limit its practical application.

Methods such as addition of QS inhibitors, biostimulation and degrading signaling molecules by ROS have also been studied because of their advantages. Continuous addition of γ-caprolactone (GCL) with similar structure to AHL can stimulate the enrichment of AHL-degrading bacteria, but the cost of adding GCL cannot be ignored (Yu et al., 2022). Other biological stimulants such as gamma-heptalactone, D-xylonic acid-1, 4-Lactone, acetamide and urea have all been shown to promote the inactivation of AHLs (Yu et al., 2022). The strategy of combining biostimulation and bioaugmentation has good potential in membrane biofouling control and engineering applications. The application of electric fields in MBR can significantly degrade C8-HSL to control membrane biofouling and remove some emerging pollutants such as atrazine and estrone (Borea et al., 2018). The combination of UV catalysis and QQ can simultaneously control membrane biofouling, improve COD removal efficiency and disinfect wastewater, and its comprehensive performance shows great application potential (Mehmood et al., 2021).

Membrane biofouling will cause frequent cleaning and replacement of membranes and require higher aeration intensity, which will greatly increase the energy consumption and operation cost (Weerasekara et al., 2014; Yi et al., 2023). Jahangir et al. (2012) showed that when the QQ container was put into the 0.8 L laboratory sized MBR, the aeration rate could be reduced by 0.5–1.0 LPM to save energy. Weerasekara et al. (2014) evaluated the combined effects of QQ and physical washing on pollution control and energy saving at different aeration intensities. The results show that the filtration performance of QQ-MBR is not significantly affected even at low aeration intensity, and QQ-MBR can save 27 % of aeration energy. By comparing the sludge characteristics, pollutant removal efficiency and membrane biofouling of QQ-MBR and Control-MBR under three different aeration intensities, Yi et al. (2023) proved that QQ beads could reduce the aeration intensity required by the operation of MBR while controlling membrane biofouling, and would not adversely affect the treatment efficiency. The role of QQ in controlling membrane biofouling and reducing aeration energy consumption will greatly reduce the operating costs of membrane processes.

3.3. Signaling in granular sludge

3.3.1. QS promotes granule formation

Granular sludge can be used to high salinity wastewater, high concentration organic wastewater, and industrial wastewater. Its characteristics include regular shape, dense structure, synchronous nitrogen and phosphorus removal, good sedimentation, and low energy consumption (Li et al., 2015a; Li et al., 2023b). The long start-up time of granule formation and the poor long-term stability limit its wide application (Zhang et al., 2021b). A range of strategies to promote more stable granule production have been investigated, including granule culture under suitable operating conditions, granule core strengthening, and regulation of EPS (Huang et al., 2019c; Lee et al., 2010; Zhang et al., 2019e). In essence, these strategies also promote the formation of granules by changing the growth state of related microorganisms, promoting the flocculation of microorganisms, and the concentration and composition of EPS (Lee et al., 2010; Li et al., 2023b). However, these strategies have the problems of complicated operation and low efficiency.

Granule is essentially microspheres formed by self-immobilization of microorganisms mediated by QS (Lin et al., 2020). As shown in Fig. 6, when QS is high in the system, microorganisms gradually flocculate to form granule with anaerobic cores and aerobic outer layers (Li et al., 2014; Lin et al., 2020). Direct addition of signal molecules can increase the activity of substrate degrading enzymes and induce the secretion of endogenous signal molecules, change the structure of microbial community, and thus accelerate the formation of granules (Li et al., 2015b; Xue et al., 2023; Zhang et al., 2023). During the nitrification process, it is difficult to achieve rapid granulation because the nitrifying microorganisms grow slowly. Li et al. (2015a) greatly accelerated the granulation of nitrifying sludge by adding signal molecules at the initial start-up stage, among which the addition effect of 3-oxo-C6-HSL was the most significant. Ding et al. (2015) added strains that produce AHLs and AI-2 as sustainable strategies speed up anaerobic granulation, and the results showed that interspecific QS regulation was more effective than intraspecific QS regulation. Filamentous bacteria can promote the formation of granules by immobilizing other microorganisms, but their excessive

Table 2
QQ methods and their effects in membrane reactors.

QQ methods	Additives	Reactor	Indicators	Result	Ref
Adding enzymes	Acylase	MBR	COD removal	≈	(Sun et al., 2021)
	Acylase	Nanofiltration	Flux profiles	+	
Adding QS inhibitors	Vanillin	RO	Biofilm formation	–	(Sun et al., 2021)
	Rhodococcus sp. BH_4	MBR	COD removal	≈	(Sun et al., 2021)
	Immobilized BH_4	MPBR	TMP	–	(Güneş and Taşkan, 2022)
	The facultative QQ bacteria	AnMBR	AHL, EPS	–	(Xu et al., 2020a)
	Immobilized facultative QQ consortium	AnMBR	COD removal and methane yield	≈	(Xu et al., 2020)
Degrading signaling molecules by reactive (ROS)	Long-wave UV	MBR	TOC, COD, TN and TP removal	≈	(Sun et al., 2021)
	TiO_2 nanoparticles under UV irradiation	UASB	COD removal	+	(Mehmood et al., 2021, Zhang et al., 2022b)
	Electric field	EMBR	Phenol removal	+	(Sun et al., 2021, Yu et al., 2020)
	Electric field	EMBR	C8-HSL	–	(Borea et al., 2018)

Notes: "+": Increase; "–": Decrease; "≈": No significant difference.

growth will make the granules easily disintegrate (Li et al., 2015b). The addition of the supernatant of AHL producing bacteria can promote the formation of the dense structure of the granules, reduce the growth of filamentous bacteria on the surface of the granules, and avoid the problem that the direct adding bacteria is easy to lose during long-term operation (Zhang et al., 2020). In a word, the enhancement of QS results in fast granule growth, compact structure, no excessive growth of filamentous bacteria, and high granule stability. And it is worth considering the reasonable increase of signal molecule concentration and the appropriate addition time.

The content of signal molecules can be increased by proper operation to accelerate granulation. Alternating OLR strategy and sludge retention time (SRT) control strategy are based on QS to promote sludge granulation (Lin et al., 2020). The change of OLR promotes the secretion of AHL, AI-2 and *c*-di-GMP, induce microorganisms to secrete more EPS with large molecular weight, which promotes the maturation and maintains the stability of aerobic granules (Zhang et al., 2017). The changes of SRT will also affect the sludge concentration and lead to the change of cell density, thus affecting the content of AHLs (Li et al., 2022). Zhang et al. (2019d) established AGS reactors with different SRTs and proved that the aerobic granules formed at 6d SRT had the most compact structure and high granulation rate. Direct addition of AHL to promote granulation is expensive and unsustainable (Ma et al., 2019; Zhang et al., 2020). AHL-producing strains regulate AHL release according to the environment, but the addition of strains will cause bacteria to be washed away and produce excess sludge (Zhang et al., 2020). Stimulating the continuous release of endogenous AHL by adding AHL supernatant of strains with high AHL production capacity is an economical and feasible strategy to continuously promote granulation, but the optimal dosage and time of AHL supernatant remains to be studied (Zhang et al., 2020). Using stored granules directly as seeds may be an easier way to jump-start a granule system (Gao et al., 2021; Lin et al., 2020). Appropriate addition of exogenous AHL can significantly improve the bioactivity recovery ability of long-term stored granules and contribute to the rapid recovery of granules (Gao et al., 2021). Indirectly promoting the secretion of endogenous signaling molecules is a more economical and sustainable strategy than directly addition, but the possible adverse effects on sludge characteristics should also be noted.

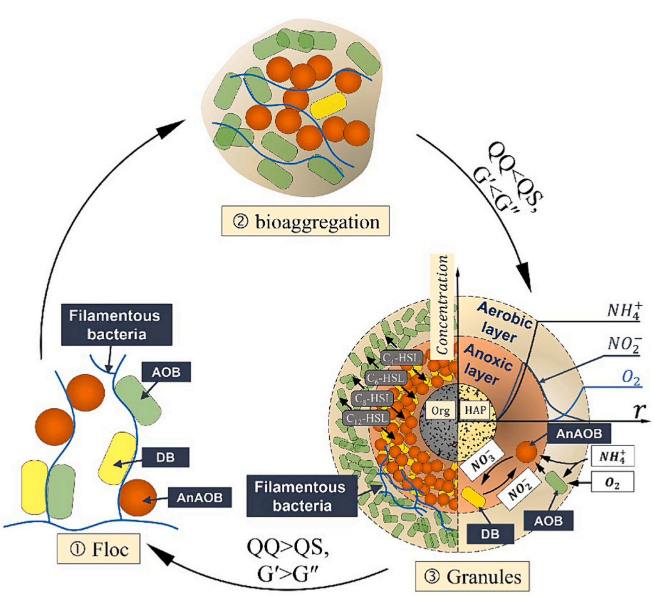

Fig. 6. Granule formation mechanism based on QS/QQ (Xue et al., 2023). Copyright,2023, Elsevier.

3.3.2. QS improves granule performance

QS plays an important role in improving granule performance and provides a new idea for the long-term stable and efficient operation of granule. The addition of AHLs promoted the accumulation of EPS in the sludge, which provided a rigid net for functional microorganisms and contributed to the formation of aerobic granules with stable structure and high pollutant removal efficiency (Yue et al., 2020; Zhang et al., 2019d). The size of aerobic granules is closely related to nitrogen removal efficiency (Li et al., 2023b). Stable granule structure provides a suitable microbial niche, and autotrophic and heterotrophic microorganisms coexist and interact on the granules, which is conducive to promoting the treatment of pollutants (Zhang et al., 2019d). The addition of C8-HSL can not only effectively solve the problem that anaerobic anammox granules are easy to flotation under high load conditions, but also significantly improve the sedimentation performance of granules and the removal efficiency of TN (Zhang et al., 2019). And the addition of 3-oxo-C6-HSL to the autotrophic nitrification sludge significantly increased the bacterial adhesion and ammonia degradation effect of nitrification granular sludge (Li et al., 2015a). At the same time, low-phosphorus manipulation has also been validated to stimulate the secretion of AHL and AI-2, enabling aerobic granules to have higher organic loads and faster sedimentation rates (Zhang et al., 2017). The addition of different signal molecules plays different roles in improving the properties of granules. Therefore, operations that can stimulate the secretion of multiple signaling molecules at the same time would be a better choice. In the future, more studies are needed to explore the possibility of improving the overall performance of granules by adjusting QS to achieve a reasonable distribution of microorganisms on the granules.

The addition of AHL enhance the adaptability of granular sludge to the environment. Environmental factors such as the decrease of temperature, the easy change of pH of industrial wastewater with time, and substrate impact will affect the performance of granular sludge (Zhang et al., 2020; Zhang et al., 2019c). This may because of the ability of QQ activity to maintain higher levels in a wider range of environments than QS activity (Li et al., 2019b). Anaerobic anammox granules are highly sensitive to environmental changes (Zhang et al., 2019c; Zhang et al., 2019e). The addition of C6-HSL and C8-HSL significantly improved the activity, settling performance and low temperature denitrification performance of anammox granular sludge under high load and matrix impact conditions, thus expanding its treatment range (Zhang et al., 2021a; Zhang et al., 2019c). The fluctuating C/N culture strategy also stimulates the release of endogenous C4-HSL and C6-HSL, and improve the stability and activity of anammox granules under the influence of extreme pH (Zhang et al., 2021a). However, the actual wastewater situation is more complex, and the feasibility of enhancing the environmental adaptability of granular sludge by regulating QS needs to be further discussed.

4. Summary and research needs

Signal molecules, EPS and microorganisms are the three key parts of QS in shaping sludge forms, and the overall regulation of them needs to be carried out from the macro level. Utilizing the advantages of various signal molecules, exploring the optimal concentration and composition of EPS and optimizing the structure of microbial community are important ways to improve the efficiency of wastewater treatment.

QS affects the physical structure and properties of ASFs, and QQ inhibits the bulking of filamentous bacteria, but whether the reduction of signal molecules will affect the performance of flocs and the activity of other functional microorganisms has not been thoroughly studied, and the long-term stability of QQ in practical applications has not been evaluated. Future research is needed to develop more economical and efficient QQ analogues and inhibit filamentous bulking by optimal combination. The effect of AHL on microorganisms is comprehensive. How to accurately manipulate AHL to form efficient ASFs and whether other signaling molecules can play a synergistic role are worthy of further discussion. To optimize the wastewater treatment process, more research is required to ascertain the relationship between QS and ASF performance within a larger variety of operating conditions.

Studies have shown that it is possible to increase the effectiveness of biofilm treatment by optimizing QS and utilizing QQ to decrease membrane biofouling. It should be noted that the impact of QQ on sludge is complex, to achieve satisfactory wastewater treatment efficiency, the application of QQ strategy needs more comprehensive consideration. To guarantee the activity of QQ bacteria, it is also essential to optimize their type and ideal concentration, as well as the composition and material of the medium used to fix them. This will lower operating costs and complexity and facilitate the earliest possible implementation of the QQ strategy in practice. Additionally, in order to investigate the possibility of cooperative control of membrane biofouling, more thorough research on the blockage of other signaling molecules is required.

The formation of granules is an adaptive response of microorganisms. From adding purified AHL to adding AHL producing strain to adding AHL supernatant, the operation of exogenous AHL has been developing towards economy and sustainability. However, the factors considered in the operation are still incomplete. The possible effects and effectiveness of exogenous addition in harsh environment still need to be further discussed. The granules have a layered structure, and the microbial niche on the granules is closely related to its ability to remove pollutants. It may also be discussed to achieve the ideal distribution of microorganisms in the granule by adjusting QS to comprehensively improve the performance. Operating parameters also affect QS in the granule sludge, therefore, the operating parameters in the pelletizing process still need to be further optimized to reduce energy consumption or achieve energy reuse in the pelleting process, which is of great significance for the operation of actual wastewater treatment plants.

5. Conclusions

QS shapes sludge forms by influencing the concentration and composition of EPS and microbial community. QS enhancement can be used to accelerate the formation of sludge form and improve sludge performance. QQ can be applied to control filamentous bulking and membrane biofouling. These strategies have the advantages of efficiency, economy and environmental protection, and are a promising technology for improving activated sludge process. However, the current research is still limited to the laboratory scale, and the effectiveness and impact of QS regulation on pilot scale and industrial scale still need more comprehensive research. The diversity, effectiveness, sustainability of these strategies also needs to be optimized. In addition, a more comprehensive analysis of the possible impacts is needed to accelerate its application in practical wastewater treatment.

CRediT authorship contribution statement

Xia Wang: Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kaixin Yi:** Writing – review & editing, Resources, Methodology, Formal analysis, Conceptualization. **Haoliang Pang:** Writing – review & editing, Validation, Methodology, Formal analysis. **Zhexi Liu:** Writing – review & editing, Visualization, Methodology. **Xue Li:** Writing – review & editing. **Wei Zhang:** Writing – review & editing. **Si Liu:** Software, Methodology. **Jinhui Huang:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Chen Zhang:** Writing – review & editing.

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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