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Review

Quorum sensing for carbon-neutral wastewater treatment: Mechanisms, challenges, technological pathways, and future prospects

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ABSTRACT

Global climate targets demand a rapid transition to carbon neutrality across all industrial sectors, including wastewater management. Wastewater treatment plants are historically energy-intensive and remain significant sources of potent greenhouse gases, primarily nitrous oxide (N_2O) and methane (CH_4). Recent biological interventions have targeted quorum sensing (QS)—a microbial communication mechanism regulating gene expression and community behavior—to optimize biological treatment efficiency. However, the highly context-dependent and sometimes paradoxical effects of QS on simultaneous greenhouse gas mitigation and energy recovery remain poorly resolved. Here we synthesize recent advancements to show that QS operates as a master biological regulator of both direct emissions and energy consumption in wastewater ecosystems. Evidence indicates that QS distinctly modulates N_2O production through concentration- and signal-dependent pathways, while actively suppressing CH_4 escape and enhancing aerobic granulation to cut aeration energy demands. Furthermore, targeted QS deployment in anaerobic digestion accelerates direct interspecies electron transfer, substantially boosting methane recovery to offset operational energy use. These insights reveal that manipulating microbial social networks presents a viable, albeit complex, biological lever for balancing emission reductions with energy optimization. Ultimately, precision control of QS systems offers a transformative technological pathway for achieving carbon-positive wastewater infrastructure.

1. Introduction

Carbon neutrality has become an international priority in response to urgent issues such as global climate change and energy transition. Wastewater treatment, an essential process for environmental protection and sustainable development, enhances energy efficiency and resource utilization, thereby playing a key role in achieving carbon-neutrality goals [1]. However, the wastewater treatment process itself is energy-intensive; it requires significant electricity and fuel and is associated with greenhouse gas (GHG) emissions, including carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4). The carbon footprints of wastewater treatment plants (WWTPs) are systematically classified into three categories based on the emission source: Scope 1—direct process emissions, Scope 2—energy-related indirect emissions, and Scope 3—extended indirect value chain emissions [2]. GHG emissions and energy consumption result from WWTP operations across various stages, including the biological treatment of sewage and the processing of sludge [3]. Reducing energy consumption and carbon emissions, and enhancing energy recovery, are crucial for WWTPs to achieve carbon neutrality.

Quorum sensing (QS) is a communication mechanism among microorganisms that allows bacteria to adapt to environmental changes by sensing signaling molecules and coordinating biological processes, thereby enhancing the secretion of extracellular polymeric substances (EPSs) and biofilm formation, etc. [4]. QS

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plays a crucial role in biological wastewater treatment, as it enhances treatment efficiency, reduces energy consumption, chemical use, and GHG emissions, and promotes resource recovery for sustainable operations [5–7]. Specifically, QS supports carbon neutrality in wastewater treatment by (1) regulating the activity of functional microorganisms (e.g., denitrifying communities), which enhances the expression of key functional genes and enzyme activity, thereby reducing GHG emissions during biological treatment [8]; (2) promoting sludge flocculation and granulation, which improves settling efficiency and reduces aeration energy consumption [9–12]; (3) facilitating microbial aggregation and metabolic coordination, which advances anaerobic digestion (AD) and CH_4 recovery [13,14]; and (4) optimizing microbial community structure and enhancing the competitive advantage of beneficial consortia, which ensures the stable operation of low-carbon treatment processes [15]. These synergistic effects collectively reduce the operational carbon footprint, contributing to energy-positive wastewater treatment.

This review provides an innovative theoretical framework that integrates QS regulation technology with environmental sustainability in wastewater treatment, aiming to reduce GHG emissions and energy consumption, optimize treatment efficiency, enhance energy (CH_4) recovery, and strike an environmental-economic balance. Compared with previous research [16,17] this study provides a comprehensive review of the latest advancements in QS for biological wastewater treatment and highlights the critical role of QS in achieving carbon neutrality from a broad, forward-looking perspective on environmental sustainability. First, this review provides an overview of QS and its fundamental roles in wastewater treatment. Second, we examine the dual impact of QS on GHG emissions, covering its multipathway regulation of N_2O production and inhibition, as well as its dual role in CH_4 emissions. Third, we analyze the potential for energy savings, highlighting QS mechanisms such as improved sludge flocculability, reduced membrane fouling, and enhanced granulation. Fourth, we discuss the application prospects of QS for CH_4 recovery, focusing on its ability to enhance AD processes. Finally, we outline the limitations of applying QS to carbon-neutral wastewater treatment and propose future research directions and challenges. Through this comprehensive analysis of the mechanisms and applications of QS in wastewater treatment, we offer insights and technical knowledge to aid green transformation and carbon neutrality.

2. Fundamentals of quorum sensing

QS is mediated by the synthesis, secretion, and receptor-based detection of signaling molecules known as autoinducers [4]. The LuxI-LuxR system is a canonical model of QS that involves a density-dependent autoinduction cycle: At low cell densities, basally expressed LuxI synthase produces trace acyl-homoserine lactones (AHLs; e.g., 3-Oxohexanoyl-Homoserine Lactone [$3OC_6$-HSL]) that diffuse extracellularly; upon reaching critical cellular thresholds, the accumulated AHLs ($\geq$10 nM) bind to and allosterically activate the transcription factor LuxR [18]. The resultant LuxR-AHL complex initiates *lux* operon transcription, driving bioluminescence (*luxAB*) while upregulating LuxI to establish a self-reinforcing amplification loop [18]. This archetypal AHL-mediated mechanism provides a fundamental framework for diverse QS systems for wastewater treatment using functional bacteria. To date, many signaling molecules that facilitate bacterial communication have been found, including AHLs, autoinducing peptides (AIPs), autoinducer-2 (AI-2), diffusible signal factor (DSF), second messenger 3′-5'cyclic diguanosine monophosphate (c-di-GMP), the quinolones [2-heptly-3-hydroxy-4-quinolone (PQS) and 2-heptyl-4-quinolone], and an autoinducer in *Escherichia coli*. This section presents the QS regulation mechanisms mediated by these signaling molecules and their roles in wastewater treatment.

2.1. AHL-QS

AHLs are signaling molecules found in Gram-negative bacteria and are central to the LuxI/R system. The LuxI/R system is composed of LuxI (AHL synthase) and LuxR (AHL receptor). Homologs of LuxI/R have been identified in many species, such as lasI/R and RhlI/R in *Pseudomonas aeruginosa*, TofI/R in *Burkholderia glumae*, and FllI/R in *Methanosaeta harundinacea* 6Ac [4,19,20].

Pseudomonas aeruginosa is a well-established model organism for investigating QS-regulated bacterial behaviors (Fig. 1a; Supplementary Text S1). Notably, long-chain AHLs, such as 3-Oxododecanoyl-homoserine lactone ($3OC_{12}$-HSL), require the assistance of an efflux pump for their transmission [21]. Researchers have investigated the inhibitory effects of various efflux pump inhibitors (astragaloside IV, eugenol, and baicalin) on *P. aeruginosa* biofilms and QS activity to expand the QS inhibitor (QSI) library and the available pathways [22]. In a laboratory-scale membrane bioreactor (MBR), astragaloside IV delayed membrane contamination and reduced filtration energy by approximately 60% [10]. Laboratory-scale studies have shown that regulating the AHL-mediated QS system is important for removing chemical oxygen demand, nitrogen, phosphorus, and heavy metals [23]. In Li et al.'s study, cell adhesion and ammonia removal were linked to the AHL side chain length and β-position substituents. Adding $3OC_6$-HSL or hexanoyl-homoserine lactone (C_6-HSL) boosted biomass growth, microbial activity, extracellular proteins, and nitrified particle formation [24]. AHL signaling molecules, such as decanoyl-homoserine lactone (C_{10}-HSL) and dodecanoyl-homoserine lactone (C_{12}-HSL), also play important roles in biofilm development (adhesion) in full-scale WWTPs [25].

2.2. AIP-QS

Gram-positive bacteria generally exhibit AIP-mediated QS mechanisms (Fig. 1b; Supplementary Text S2), as exemplified by *Staphylococcus aureus* [26]. Bacteria regulate QS by secreting modified small-molecule polypeptides, which require ATP-binding cassette transporters for extracellular release [27]. Once extracellular AIPs reach a threshold concentration, they bind to the two-component phosphoprotein kinase signal recognition system in the cell membrane, triggering phosphorylation and activating downstream gene expression [28].

AIP is crucial for biofilm formation in *S. aureus*, but unlike in *P. aeruginosa*, biofilm formation is induced at low densities, and separation occurs at high densities [29]. The specific mechanism is described in Supplementary Text S2. Additionally, some signal peptides (bacteriocins) act as antibiotics, helping control competition in mixed-species systems. Bacteriocins, including nocardithiocin in *Nocardia*, a common destroyer of activated sludge treatment systems, may play a role in the filamentous bulking of activated sludge [30]. Numerous genes involved in AIP synthesis have been identified in AD, and AIPs have been found in both methanogens and bacteria [31,32]. AIPs appear to function as interspecific communication signals between methanogens and syntrophic bacteria, thereby jointly regulating methanogenesis [31,32].

2.3. AI-2-QS

In the 1990s, researchers found that AI-2 induces QS in *Vibrio harveyi* [33]. The homology of *luxS*, which encodes AI-2 synthase, was subsequently identified in various Gram-negative and Gram-

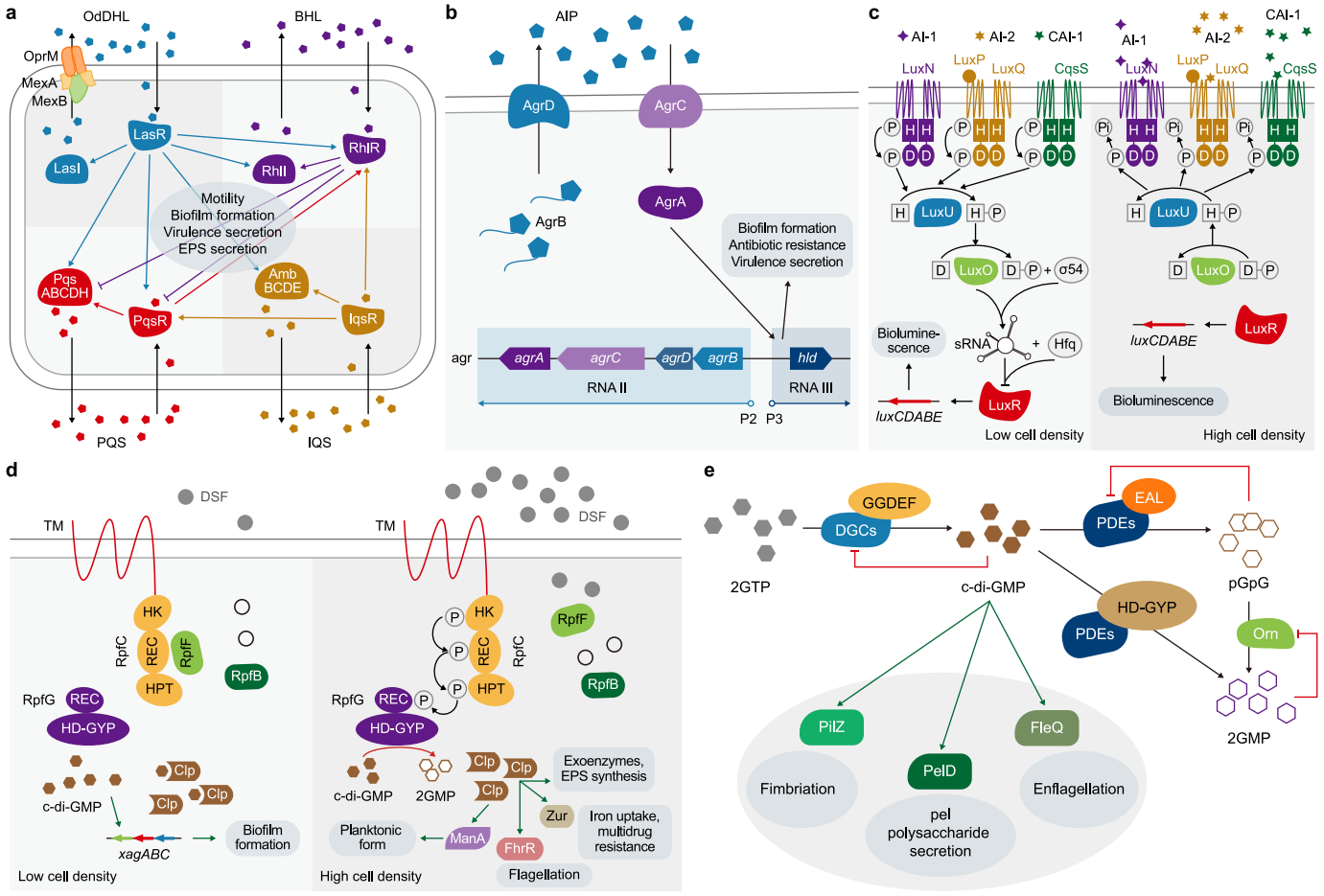


Fig. 1. Regulation diagram of the *N*-acyl-homoserine lactone (AHL)-mediated quorum sensing system in *Pseudomonas aeruginosa* (**a**), the autoinducing peptide (AIP)-mediated quorum sensing system in *Staphylococcus aureus* (**b**), the autoinducer-2 (AI-2)-mediated quorum sensing system in *Vibrio harveyi* (**c**), the diffusible signal factor (DSF)-mediated quorum sensing system in *Xanthomonas campestris* pv. campestris (**d**), and the second messenger 3′-5′cyclic diguanosine monophosphate (c-di-GMP)-mediated quorum-sensing system in *P. aeruginosa* (**e**). EPS: extracellular polymeric substances; PQS, 2-heptly-3-hydroxy-4-quinolone; IQS, 2-(2-hydroxyphenyl)-thiazole-4-carbaldehyde; TM, transmembrane domain; DSF, diffusible signal factor; HK, histidine kinase domain; REC, receiver domain; HPT, histidine phosphotransfer domain; HD-GYP and EAL domain, c-di-GMP-degrading enzyme; Clp, cyclic AMP receptor-like protein; Orn, oligoribonuclease; DGC, diguanylate cyclase; PDE, phosphodiesterase.

positive bacteria [34]. Therefore, AI-2 is believed to promote interspecific bacterial communication and regulate the expression of functional genes [34]. *V. harveyi* also produces AI-1 and CAI-1 via LuxN and CqsA (Fig. 1c; Supplementary Text S3) [35].

Studies have shown that the exogenous addition of QSIs (e.g., farnesol and quorum-quenching [QQ] bacteria) can suppress AI-2 levels and reduce biofouling in MBRs, as well as energy consumption [5,36]. However, in *Vibrio cholerae*, bacterial biofilm formation is facilitated at low cell densities [37]. In anaerobic (An)-MBRs, AHL and AI-2 are closely linked to biological properties, including organic matter removal and CH_4 production, and CH_4 production is positively correlated with long-chain AHLs [38]. Co-fermentation of Δ*luxSlsrR E. coli* (deletion of the *luxS* and *lsrR* genes) with waste-activated sludge for 15 days has been shown to enhance acetate consumption by *Methanosarcina* and boost CH_4 production [39]. Notably, AI-2 is crucial for resistance gene transfer [40], aerobic granulation [41], and the promotion of partial nitrification [42].

2.4. DSF-QS

DSF was first discovered in the Gram-negative bacterium *Xanthomonas campestris* pv. *campestris* (Xcc) [43], and structurally similar molecules have since been reported in many bacteria, such as *P. aeruginosa* (PDSF) [44] and *Burkholderia cenocepacia* (BDSF) [45]. Xcc senses and transduces DSF via the RpfC-RpfG two-component system (Fig. 1d; Supplementary Text S4), which regulates target genes and bacterial phenotypes [46].

At low cell densities, DSF-QS positively regulates biofilm formation; at high cell densities, it promotes biofilm dispersion [46]. The exogenous addition of BDSF reportedly reduces the transcription levels of *lasR*, *rhlR*, and *pqsR* in *P. aeruginosa* and thus lowers AHL and PQS levels, inhibiting QS activity and biofilm formation [45]. Laboratory-scale research has shown that adding *cis*-2-decenoic acid could disperse biofilms and decrease EPS production in an MBR [47], which extended the MBR operational lifespan by 56% without hindering microbial growth [48]. However, further investigation is needed on the environmental risks and long-term effects of *cis*-2-decenoic acid [48]. Additionally, RpfF plays a central role in anaerobic ammonium oxidation (anammox) communication and correlates with the synthesis genes of many bacterial signaling molecules (AHL and c-di-GMP), suggesting that selective and targeted modulation of bacterial communication can control community behavior and accelerate anammox reactor initiation [49]. DSF can also regulate the cyclic adenosine monophosphate (AMP) receptor-like protein, a c-di-

GMP controller, to balance EPSs and amino acids in anammox communities, thereby boosting metabolism, ammoxidation, and nitrogen removal [50].

2.5. c-di-GMP-QS

The bacterial second messenger c-di-GMP, a key regulator of growth and development, coordinates the transition from motility to quiescence (Fig. 1e; Supplementary Text S5). Low c-di-GMP levels promote motility, while high concentrations favor biofilm formation [51]. Cell extracts of *P. aeruginosa* biofilms reportedly contain 75–110 pmol mg^{-1} of c-di-GMP, whereas planktonic cells contain less than 30 pmol mg^{-1}, which suggests that reduced c-di-GMP levels may aid biofilm dispersal [51,52].

c-di-GMP, which regulates exopolysaccharide biosynthesis and promotes cell aggregation, also plays an important role in biofilm and granular sludge formation [53]. High intramembrane c-di-GMP levels stimulate EPS production and accelerate membrane contamination [54]. Particle size and EPS secretion are positively correlated with intracellular c-di-GMP levels during aerobic granular sludge (AGS) formation and disintegration. In a laboratory-scale sequencing batch reactor (SBR), nitrate may upregulate c-di-GMP via denitrification-derived nitric oxide (NO) and facilitate EPS secretion and AGS formation. However, excess NO may lead to particle disintegration by downregulating c-di-GMP and EPS [55]. Research involving a laboratory-scale upflow anaerobic sludge blanket reactor (UASB) has shown that the addition of 50 mg L^{-1} nano zero-valent iron [56] or 25 mg L^{-1} of the carbon-based material fullerene [57] increases c-di-GMP synthesis protein abundance and decreases degradation protein abundance. This indirectly enriches c-di-GMP, favors sludge particle formation, and enhances ammonium (NH_4^+) removal efficiency [57].

3. QS-driven reduction of Scope 1 emissions: direct GHG control

Scope 1 emissions from a WWTP include direct GHG releases occurring within the facility's physical boundaries, generated by activities owned or controlled by the plant [58]. These emissions are dominated by N_2O and CH_4, two potent GHGs with 100-year global warming potentials (GWP-100) of 265–298 and 28–36 times that of CO_2, respectively [58,59]. N_2O is predominantly emitted as an intermediate byproduct of nitrification/denitrification reactions in biological nitrogen removal (BNR) processes; CH_4 primarily originates from AD systems and escapes to the atmosphere via uncollected biogas or digester leaks [58]. Consequently, developing targeted mitigation strategies for these dominant Scope 1 emission sources is critical for accelerating carbon neutrality in wastewater treatment.

3.1. N_2O emission reduction mechanism

3.1.1. QS during nitrogen removal

Biological nitrogen removal in wastewater treatment involves nitrification and denitrification as the two core processes, along with several enhanced derivative pathways (e.g., nitrite shunt, anammox). QS has been shown to play a pivotal regulatory role in nitrification, denitrification, and anammox (Fig. 2a) [49]. In Gram-negative nitrogen-cycling bacteria (e.g., ammonia-oxidizing bacteria [AOB], nitrite-oxidizing bacteria [NOB], and denitrifiers), AHLs serve as key signaling molecules [60]. The conventional nitrification–denitrification pathway involves an AOB-mediated oxidation of NH_4^+ to nitrite (NO_2^-), followed by an NOB-mediated oxidation of NO_2^- to nitrate (NO_3^-), and a subsequent stepwise reduction of NO_3^- to nitrogen (N_2) by denitrifying bacteria. Anammox autotrophically converts NH_4^+ to N_2 using NO_2^- as an electron acceptor under anoxia. Its integration with partial nitrification (suppressing NOB while enabling AOB to generate NO_2^-) forms partial nitritation-anammox (PN/A) systems that reduce oxygen demand and eliminate organic carbon requirements compared to conventional processes [61].

Ammonia oxidation. *Nitrosospira multiformis* (AOB) possesses the NmuI/R system, producing tetradecanoyl-homoserine lactone (C_{14}-HSL) and 3-Oxotetradecanoyl-homoserine lactone ($3OC_{14}$-HSL). Intriguingly, its receptor NmuR exhibits a higher affinity for exogenous C_{12}-HSL, suggesting a sophisticated QS system that may regulate environmental adaptation and nitrogen cycling [62].

Nitrite oxidation. *Nitrobacter winogradskyi* (NOB) employs the NwiI/R system to produce C_{10}-HSL and mono-unsaturated $C_{10:1}$-HSL. These two signal molecules mediate cell-density perception and, potentially, biofilm formation [63]. Shared C_{10}-HSL production with an AOB such as *Nitrosomonas europaea* indicates possible cross-kingdom QS, which synchronizes coupled nitrification and prevents NO_2^- accumulation [64].

Denitrification. *Paracoccus denitrificans* utilizes the PdeI/PdeR system to synthesize hexadecanoyl-homoserine lactone (C_{16}-HSL). PdeR responds to endogenous C_{16}-HSL and diverse exogenous long-chain AHLs (C_{12}-HSL, C_{14}-HSL, octadecanoyl-homoserine lactone [C_{18}-HSL]) and regulates aggregation and biofilm formation via an autoinducing feedback loop [65–67]. Crucially, *P. denitrificans* employs a unique "signal hijacking" strategy: It internalizes environmental long-chain AHLs via membrane vesicles, preferentially delivering them to conspecific cells. This privatizes signals, enabling premature QS activation at low cell densities and conferring a competitive advantage [67].

Anammox. In *Candidatus* Jettenia caeni, HdtS-type synthases (JqsI-1/2) produce four AHL signaling molecules: $3OC_6$-HSL, C_6-HSL, 3-Oxooctanoyl-homoserine lactone ($3OC_8$-HSL), and octanoyl-homoserine lactone (C_8-HSL). These molecules bind to the putative receptor JqsR to directly regulate *hzsA* (encoding hydrazine synthase)—a functional biomarker that controls nitrogen removal efficiency. Homologous systems in *Ca.* Brocadia and *Ca.* Kuenenia indicate QS ubiquity in anammox bacteria [68].

Additionally, QS performs concentration and structure-dependent regulatory roles in nitrogen removal from wastewater systems (see Supplementary Table S1). Specific signal molecules enhance denitrification: Short-chain AHLs (C_4/C_6/C_8-HSL) and optimized long-chain AHL ratios (C_{14}/$3OC_{14}$-HSL >1.0) upregulate functional genes (*hzsA/hzo/nirS*) to activate anammox or denitrification pathways while facilitating microbial cooperation (e.g., denitrifiers supply NO_2^- to anammox bacteria under high C/N ratio) [69–73]. Conversely, certain QS signals (e.g., C_{12}-HSL >80 nM) and specific QS systems (e.g., Las/Rhl in aerobic denitrifiers) suppress keystone bacteria (*Candidatus* Kuenenia) or directly repress denitrification gene expression (*napA/nirS/nosZ*) [74,75]. This functional contradiction may arise from three parallel, dependent mechanisms:

(1) Concentration dependence. Identical molecules (e.g., C_{12}-HSL) enhance denitrification at low concentrations but inhibit anammox at elevated levels [75].
(2) Environmental modulation. Different C/N ratios shift dominant nitrogen removal pathways by altering signal molecule ratios (e.g., C_{14}/$3OC_{14}$-HSL) [70].
(3) Strain specificity. Low temperatures (10 °C) induce C_8-HSL secretion in psychrotolerant strains to improve ammonium removal, whereas aerobic denitrifiers employ QS networks (e.g., via iron chelation) to inhibit their own denitrifying enzymes [74,76].

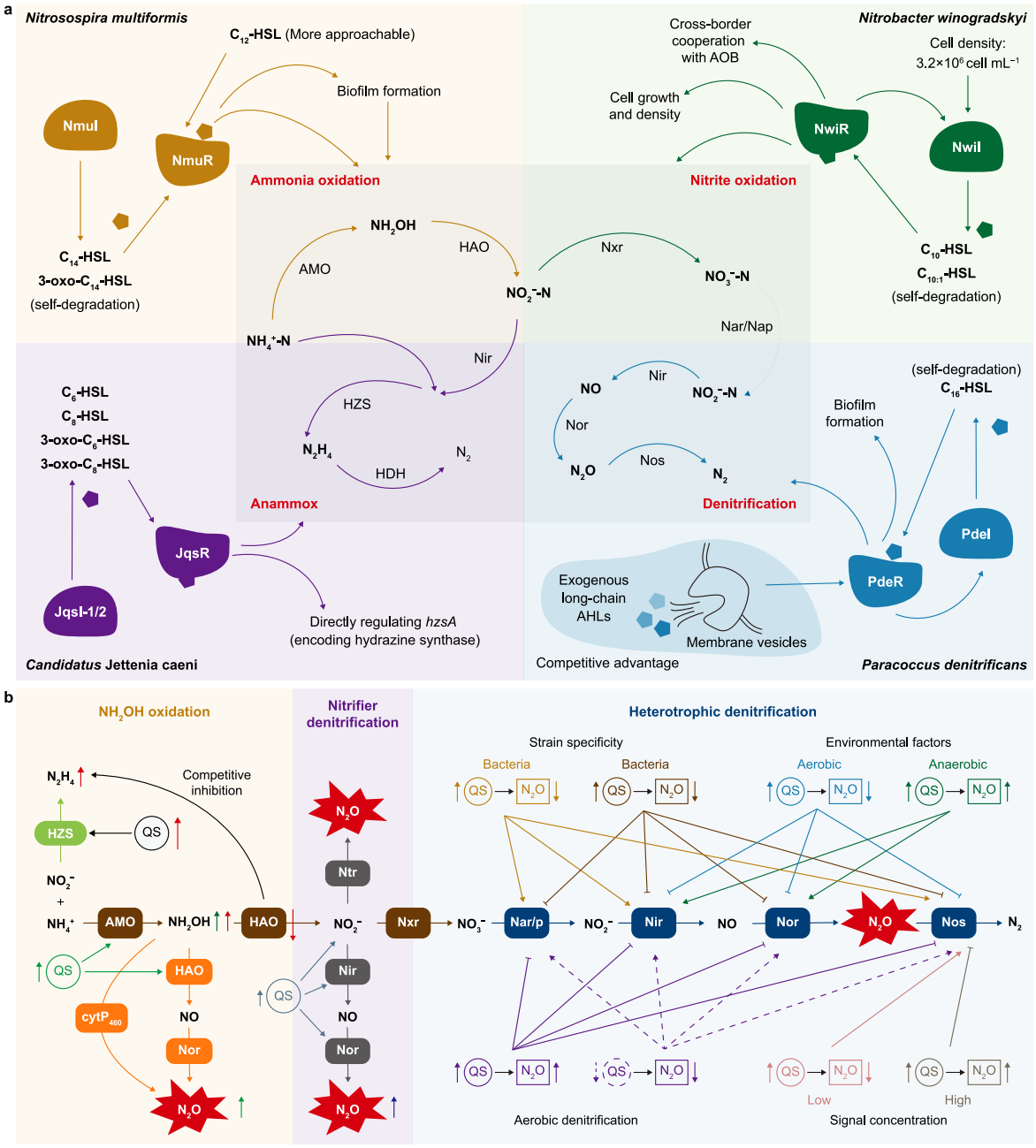


Fig. 2. a, The quorum sensing (QS) regulation of different functional bacteria during nitrogen removal, including ammonia oxidation, nitrite oxidation, denitrification, and anammox. **b**, The regulating effect of QS on N_2O emission. HSL, homoserine Lactone; AOB, ammonia-oxidizing bacteria; AHL, *N*-acyl-homoserine lactone; AMO, ammonia monooxygenase; HAO, hydroxylamine oxidoreductase; Nxr, nitrite oxidoreductase; Nar, nitrate reductase; Nap, periplasmic nitrate reductase; Nir, nitrite reductase; Nor, nitric Oxide reductase; Nos, nitrous oxide reductase; HZS, hydrazine synthase; HDH, hydrazine dehydrogenase; QS, quorum sensing.

Thus, QS-based strategies require precise calibrations of signal types, dosages, and environmental parameters (temperature, C/N, dissolved oxygen [DO]). The targeted quenching of signals or application of QSIs (e.g., acylases and curcumin) can alleviate metabolic repression [77,78]. The contradictory phenomenon underscores the dynamic complexity of microbial communication networks in nitrogen removal systems and the need for integrated multiomics approaches to decipher QS topology for precision optimization [79,80]. In addition, the concentration of AHLs reflects the dynamic equilibrium between QQ and QS in mixed microbial systems. Engineering applications could target the QQ–QS equilibrium to optimize the denitrification process, rather than directly adding expensive signaling molecules [81]. Moreover, strategically constructed synthetic microbial communities that modulate this equilibrium can significantly enhance nitrogen removal efficiency [82], representing a promising direction for future research.

3.1.2. QS-regulated N_2O emissions

N_2O, a potent greenhouse gas and ozone-depleting substance, is ubiquitously generated during biological nitrogen removal in wastewater treatment systems. Its production primarily stems from three microbial pathways (Fig. 2b) [83,84]: (1) NH_2OH oxidation: Abiotic and enzymatic decomposition of NH_2OH yields

N_2O; (2) Nitrifier denitrification: AOB reduce NO_2^- to N_2O using electron donors (NH_4^+, NH_2OH); (3) Heterotrophic denitrification: Incomplete reduction of NO_3^-/NO_2^- by heterotrophs leads to N_2O accumulation.

As a central regulator of microbial metabolism, QS modulates N_2O emissions from nitrogen removal systems by targeting key enzymatic activities and gene expression in N_2O production pathways.

(1) Effects of QS on NH_2OH oxidation and the nitrifier denitrification pathway

In the NH_2OH oxidation pathway, C_8-HSL upregulates ammonia monooxygenase (AMO) and hydroxylamine oxidoreductase (HAO) activity, leading to NH_2OH accumulation and incomplete oxidation. Concurrently, it enriches aerobic denitrifiers (e.g., *Pseudomonas* spp.), collectively resulting in a 43.2% increase in N_2O emissions [8]. During partial nitrification, boron-activated AI-2 QS suppresses NOB activity but maintains AOB activity, resulting in NO_2^- accumulation that may indirectly enhance N_2O production via AOB-mediated NH_2OH decomposition or denitrification [42]. Although anammox directly converts NH_4^+ to N_2 with minimal N_2O yield, its application is challenging because the key metabolic intermediate hydrazine (N_2H_4) competitively inhibits HAO when externally supplied ($\leq$10 mg N L^{-1}) as an anammox enhancer. This inhibition triggers substantial NH_2OH accumulation, which subsequently elevates N_2O production [61]. Notably, the gene *hzsA* (encoding N_2H_4 synthase) is regulated by QS, suggesting that targeted QS manipulation could mitigate N_2H_4-induced N_2O emissions while maintaining anammox efficiency [68].

Research has demonstrated that 25 nmol L^{-1} of C_6-HSL elevates AOB abundance from 0.2% to 1.6% in the nitrifier denitrification pathway, concomitantly promoting NO_2^- accumulation (0.2–0.4 mg L^{-1}) and enhancing denitrification enzyme (NirK/NorB) activities. These collective effects increase N_2O release from AOB denitrification by 5.7% [8]. Although the literature on QS regulation of AOB denitrification remains scarce, compelling evidence indicates that QS mediates NO_2^- accumulation that is a key inducer of N_2O formation in this pathway [84]. This mechanistic link establishes NO_2^--driven N_2O production as a promising research direction for targeted QS interventions.

(2) Effects of QS on the denitrification pathway

Research has shown that QS predominantly regulates N_2O emissions through a coordinated denitrification process involving multiple pathways, with significant strain specificity and context dependence [8,85]. QS exhibits phylogenetically distinct strategies for N_2O mitigation. In *Propionibacterium freudenreichii*, QS upregulation of substrate transporters and denitrifying enzymes (Nar/Nir/NosZ) elevates the NosZ/NorB ratio by 14.5%, driving electron transfer optimization that reduces N_2O emissions by 74% [85]. Conversely, in *Pseudomonas fluorescens* 2P24, the QS regulator MupR binds to promoters of denitrification genes (*narH, nirQS, norBC*), thereby suppressing denitrification activity and minimizing N_2O emissions under high cell density [86].

Paradoxically, other studies indicate that QS can simultaneously suppress aerobic denitrification and promote N_2O accumulation [74,77,87]. Kellermann et al. explained this duality using *Pseudomonas* spp., in which high cell-density conditions triggered QS-mediated repression of denitrification genes (*napA-nosZ*), ultimately leading to increased N_2O emissions; denitrification was restored in *rhlI/lasI* mutants, but N_2O accumulation was reinduced by AHL supplementation. Mechanistically, QS downregulates CyaY (Fe-S cluster assembly protein) and impairs the NosR-mediated activation of NosZ, thereby uncoupling enzyme abundance from function and triggering N_2O accumulation [87]. This mechanistic insight supports QS inhibition strategies. Natural QSIs, such as curcumin, relieve QS repression and boost periplasmic nitrate reductase (NAP) and nitrite reductase (NIR) activities by 260 $\pm$ 6% and 350 $\pm$ 7%. Co-application with *P. aeruginosa* SD-1 further enhances these activities by 88% and 74%, respectively, and upregulates key genes (*napA*, *nirS*, *norB*, and *nosZ*) twofold to threefold, thereby converting 77% of nitrogen to N_2 via aerobic denitrification. Although enhanced *nosZ* expression is indicative of N_2O mitigation potential, QSI safety and scalability need to be validated [78]. Wang et al. reduced N_2O emissions in anaerobic soils by 61% using penicillic acid (QSI), which concurrently suppressed *narG* and enhanced *nosZ*. The researchers also confirmed QSI's environmental safety, supporting its agricultural potential [88].

The role of QS in regulating N_2O emissions exhibits marked context dependency dictated by environmental conditions and signal concentration. Oxygen availability switches QS function: Under aerobic conditions, C_6-HSL suppresses N_2O accumulation in *Paracoccus denitrificans* by uniformly inhibiting *nirS, norC*, and *nosZ* expression (approximately 50% suppression) and thereby constraining both production and reduction pathways. Anaerobiosis reverses this effect, causing C_6-HSL to stimulate N_2O production via the upregulation of *nirS* and *norC* expression while leaving *nosZ* unaffected [89]. Signal concentration dictates biphasic responses: C_{12}-HSL (25 nmol L^{-1}) activates dissimilatory nitrate reduction to ammonium in anaerobic/anoxic/oxic (A/A/O) systems, competing with denitrification for electron donors while enhancing *nosZ* activity. This dual action elevates nitrogen removal efficiency by 21.3% while reducing N_2O emissions by 49.5% [8]. In another study, low doses of C_{12}-HSL (5 nmol L^{-1}) were found to reduce GHG emissions by lowering N_2O production and the system's GWP by 46.8% [90]. Higher concentrations have been shown to reverse the effects: C_8-HSL (50 nmol L^{-1}) reduces Nos enzyme abundance, thereby impairing N_2O-to-N_2 reduction and causing net accumulation. Similarly, high-dose C_{12}-HSL (50 nmol L^{-1}) promotes N_2O synthesis despite partial compensation via increased Nos abundance, resulting in increased net emissions [90]. Therefore, it is essential to establish dose–response relationships for key signaling molecules (e.g., AHLs) across various wastewater matrices to identify the critical environmental thresholds that trigger pathway shifts.

(3) The balance of BNR efficiency and N_2O emissions

The positive correlation between enhanced BNR efficiency and reduced N_2O emissions is often invalidated, and this is also the case in QS-mediated systems. In A/A/O reactors, C_6-HSL, C_8-HSL, and C_{12}-HSL uniformly elevate ammonium removal rates by 19.7–22.0%, but they exert divergent effects on N_2O: C_8-HSL causes emissions to surge by 43.2% due to AMO-triggered NH_2OH accumulation and aerobic denitrifier enrichment; and C_6-HSL increases N_2O release by 5.7% by stimulating AOB proliferation and NirK/NorB activity; whereas C_{12}-HSL reduces N_2O by 49.5% by activating electron shunting and enhancing NosZ activity [8]. Yan et al. reported that C_6-HSL-driven QS in integrated processes (chemical oxygen demand oxidation/partial nitritation/denitrification/anammox) enriched the functional bacteria (AOB: +159%; anammox bacteria: +198.8%; denitrifying bacteria: +94.5%) and boosted extracellular protein secretion at the cost of an 85.1% increase in N_2O emissions [91]. Fang et al. corroborated this trade-off through modeling: Reducing DO from 0.4 to 0.2 mg L^{-1} decreased N_2O emissions but slowed ammonium removal by 25% [92]. To reconcile BNR efficiency with N_2O mitigation, future researchers should investigate the molecular interactions between QS signals,

functional gene expression, and electron transport; define the environmental thresholds governing pathway switching; and develop concentration-adapted signaling strategies or engineered strains.

3.2. QS-mediated CH_4 escape mechanism

CH_4, a potent greenhouse gas, is primarily generated during AD and sludge storage; approximately 86.4% of CH_4 emissions from WWTPs originate from anaerobic treatment tanks [93]. QS primarily regulates CH_4 emissions via three mechanisms: enhancing CH_4 oxidation, suppressing methanogenesis, and improving the efficiency of microbial processes involving CH_4.

3.2.1. Regulating CH_4 oxidation

CH_4 oxidation by methane-oxidizing bacteria (MOB) is a common method for CH_4 mitigation. Puri et al. first identified AHL-based QS in aerobic MOB, which operates via a positive feedback loop (MbaI-MbaR-N-3-hydroxydecanoyl-L-homoserine lactone [3-OH-C_{10}-HSL]) that activates a nonribosomal peptide synthetase (NRPS) secondary metabolite cluster. This mechanism likely coordinates resource allocation and ecological competition at high cell densities, and it offers novel insights into the chemical ecology of methanotrophic consortia. However, no direct evidence that links QS to enhanced CH_4 oxidation is available. NRPS-derived products (e.g., siderophores or antimicrobial peptides) may bolster population resilience under competition/stress, indirectly sustaining CH_4 consumption [94]. It is essential to validate this by testing ΔNRPS mutants in simulated sediment environments, as confirming that NRPS products confer ecological fitness could enable targeted engineering of QS systems to optimize MOB persistence. Strategies for directly enhancing oxidation efficiency should focus on CH_4 metabolic pathways (e.g., CH_4-oxidation enzyme expression) rather than on the QS–NRPS axis. Puri et al. identified orphan LuxR-type receptors (MmsR; 67% homology to *Methylomonas tundripaludum* MbaR) in *Methylomonas* that exhibit broad-spectrum signal sensitivity, potentially "eavesdropping" on competitor density to preemptively activate stress adaptations and thereby stabilize MOB niches [95]. *Methylobacter*, a methane-oxidizing bacterium, exhibits reduced oxidation rates due to EPS accumulation, which is promoted by its secretion of three AHL signaling molecules: C_6-HSL, C_8-HSL, and C_{10}-HSL [96]. These insights suggest that QS regulation could enhance CH_4 oxidation rates and reduce emissions.

3.2.2. Affecting nitrate/nitrite-dependent anaerobic methane oxidation

An alternative approach for CH_4 oxidation is nitrate/nitrite-dependent anaerobic methane oxidation (n-DAMO), in which specialized archaea and bacteria couple CH_4 consumption to denitrification under anaerobic conditions; this causes CH_4 emissions to dissolve, eliminating external carbon requirements [97]. Given the extremely slow growth of n-DAMO microorganisms, accelerating their granulation is crucial for enhancing reactor performance and startup efficiency. EPS content has been found to exhibit a significant positive correlation with granule size and serve as a decisive factor in n-DAMO granule formation [98]. Notably, n-DAMO archaea, which are equipped with complete AHL-QS systems (synthesis and sensing), dominate the high expression of key EPS biosynthesis genes, suggesting a potential regulatory role of AHLs in EPS synthesis. Furthermore, coupling n-DAMO archaea with the anammox process promotes the formation of larger and denser granular sludge. Anammox bacteria, as primary producers of c-di-GMP, likely enhance granulation by elevating intracellular c-di-GMP levels [98]. A recent study showed that the exogenous addition of 0.2 μM C_6-HSL significantly enhanced the metabolic activity and proliferation of anammox bacteria and n-DAMO archaea, promoting the use of CH_4 as an electron donor in nitrogen removal. This caused nitrate and nitrite removal rates to increase by 65.6% and 48.5%, respectively, indicating a potential suppression of CH_4 emissions [99]. This discovery provides a key scientific basis and potential regulatory targets for engineering and optimizing n-DAMO-based processes, specifically by accelerating granulation to improve treatment efficiency/stability, reduce biomass loss, and mitigate CH_4 leakage risks.

3.2.3. Suppressing methanogenesis

Direct suppression of methanogenesis during production offers a more immediate mitigation pathway. Cheng et al. demonstrated this using AHLs in microbial electrolysis cells to treat γ-HCH. Adding C_4-HSL or 3OC_6-HSL increased cytochrome production, diverting electrons to dechlorinators (e.g., *Pseudomonas*) over methanogens (e.g., *Methanosarcinales*), thereby stimulating dechlorination while suppressing CH_4. Notably, quenching endogenous AHLs with acylase intensified methanogenesis inhibition, highlighting the vital role of native QS in sustaining CH_4 production [100]. Similarly, AiiM lactonase (QQ enzyme) led to restructured communities (increasing Gram-positive and decreasing Gram-negative bacteria), ultimately inhibiting CH_4 yield by > 400% [101]. Thus, whether modulation occurs via exogenous AHLs (QS) or quenching endogenous signals (QQ), the overarching goal is to achieve an optimal AHL equilibrium and maximize microbial community function. Given its high calorific value, CH_4 is mainly recovered as an energy source, a topic further discussed in Section 5.

4. QS-driven reduction of Scope 2 emission: energy consumption optimization

High energy consumption is a critical barrier to sustainable wastewater treatment. Aeration during the biological treatment stage is the most energy-intensive process in WWTPs—accounting for 40–75% of total energy use—followed by sludge treatment, pumping, and chemical dosing [102]. Conventional energy-saving strategies in wastewater treatment have primarily focused on physical equipment upgrades and process parameter optimization, such as adopting high-efficiency pumps and DO-based aeration control [103]. However, external, hardware-based approaches fail to address the microbial biochemical reaction system, which is central to the treatment process, and its intrinsic efficiency [104]. QS interventions follow the transformative strategy of targeting collective microbial behaviors and metabolic coordination at the source, thereby fundamentally enhancing the efficiency of biochemical reactions and offering a novel pathway to significantly reduce energy consumption per unit of pollutant removal. This section comprehensively reviews the potential of QS to optimize microbial processes in key treatment units (e.g., aeration, sludge management, membrane filtration) and the associated mechanisms that lead to direct reductions in electricity consumption and Scope 2 GHG emissions. Specifically, we discuss how QS manipulation can enhance sludge flocculation and granulation to minimize aeration [105] and mitigate membrane biofouling to reduce the energy demands of filtration and aeration [106].

4.1. QS in wastewater treatment: from improved flocculation to energy reduction

QS regulates sludge flocculation and optimizes sludge structure and performance, enhancing wastewater treatment efficiency and

reducing energy consumption [9]. The adhesive quality of EPSs enables them to adsorb pollutants and improve sludge flocculation and sedimentation [107]. Liu et al. reported that sludge aggregation becomes difficult after EPS extraction and that the overall effect of EPS (mainly influenced by tightly bound (TB)-EPS) may promote or hinder aggregation depending on the cell separation distance [108]. The genes that encode EPS synthesis are often regulated by QS [109], and many researchers have achieved EPS regulation by modulating QS [110,111]. In a laboratory-scale SBR study, C_8-HSL and C_6-HSL increased the EPS content and chemical composition of sludge, thereby affecting the particle size, irregularity, and internal mass-transfer resistance of activated sludge flocs, ultimately enhancing nutrient removal efficiency [9].

4.1.1. The regulatory role of QS in sludge bulking

During sludge flocculation, filamentous bacteria act as a skeleton, supporting flocculating bacteria that attach to them via EPS secretion, grow, and ultimately form sludge flocs [112]. Overgrown filamentous bacteria can cause sludge bulking, which impairs settleability, effluent quality, and energy efficiency [113]. During proliferation, bacteria evolve QS-related genes that reshape EPS architecture and composition [112,114,115]. Shi et al. found that filamentous bacteria with evolved *hdtS* genes exhibit a surge in C_6-HSL synthesis, which triples and densifies the EPS protein content during sludge bulking, thereby shielding hydrophobic groups, reducing hydrophobicity, and impairing bacterial aggregation [112]. As a QSI, vanillin effectively suppresses both filamentous [112] and nonfilamentous bulking [114] and has demonstrated broad applicability for bulking control through QS interference. Additionally, studies have shown that silver nanoparticles (AgNPs) may perform a concentration-dependent role in QS modulation. A low concentration of AgNPs (1 mg L^{-1}) triggers the AHL-QS system in filamentous bacteria (comprising the synthetic gene *hdtS* and the sensing genes *traR* and *lasR*), stimulating the production of arginine and tyrosine, which, in turn, form a repulsive electrostatic barrier and impair sludge aggregation [116]. In contrast, at high organic loading rates, a high dosage of AgNPs (10 mg L^{-1}) acts as a QSI, helping maintain the surface and electrostatic barriers of sludge aggregates, preserve the gel properties of exopolysaccharides, and control nonfilamentous bulking [115].

Interestingly, exogenous signaling molecules can effectively counteract sludge bulking. Treatment of filamentous bulking sludge with $3OC_6$-HSL, C_{12}-HSL, and $3OC_{14}$-HSL has been shown to induce significant 1.9-, 2.0-, and 1.6-fold reductions in the sludge volume index (SVI), respectively, by stimulating tryptophan production, thereby increasing hydrophobicity and enhancing sludge aggregation and settling. Furthermore, upon assimilation by QS bacteria, they triggered a positive feedback loop that boosted AHL and EPS production, while competitive exclusion of filamentous bacteria stabilized the microbial community and further improved settleability [15]. It has been reported that SVI reductions significantly decrease the energy demand for aeration [117]. Aziz et al. demonstrated that adding flocculant (10 g L^{-1} polyaluminum chloride) could reduce the SVI from 334.4 to 27.5 mL g^{-1}, thereby lowering aeration demand from 667 L to 330 L per cycle and achieving 50.5% energy savings [118]. The role of AHLs in fungal (*Penicillium*) sludge bulking is complex. Exogenously added heptanoyl-homoserine lactone (C_7-HSL) activates the mitogen-activated protein kinase pathway, thus stimulating hyphal synthesis and further increasing the SVI. In contrast, C_{12}-HSL and C_{14}-HSL suppress yeast-to-hyphal transition by downregulating the genes involved in cell wall remodeling and hyphal tip growth. The resulting shortening of hyphae prevents excessive penetration from microbial aggregates, thereby controlling sludge bulking and reducing SVI by 6.1% and 39.7%, respectively [119]. QS exerts dualistic effects, promoting beneficial aggregation or inducing sludge bulking, mediated by specific signal molecules and influenced by microbial evolution and environmental factors. This functional duality underscores the need for context-dependent QS manipulation to optimize sludge treatment processes.

4.1.2. The potential role of QS in oxygen transfer efficiency

By directly regulating microbial behavior and EPS secretion, QS offers a novel approach to modulating oxygen transfer efficiency (OTE), a critical determinant of aeration energy consumption in wastewater treatment. For instance, in partial nitrification systems, an enhanced secretion of C_8-HSL increases oxygen transfer resistance within the sludge layer, reducing OTE. Paradoxically, this suppression benefits the partial nitrification process by inhibiting NOB activity and promoting nitrite accumulation [120]. Besides QS-mediated regulation, EPS concentration and composition significantly affect OTE, thereby influencing aeration energy consumption [121]. OTE decreases as the concentration of total suspended solids (TSS) increases, necessitating a greater energy input to maintain DO levels. Compared to conventional activated sludge (CAS) systems, MBRs often operate at higher TSS levels but achieve higher OTE due to favorable biomass properties, such as lower EPS content and smaller floc sizes, which partially offset the negative impact of high TSS on mass transfer [122]. EPS synthesis is highly influenced by aeration intensity; excessive levels not only waste energy but also accelerate endogenous microbial respiration, reducing active biomass and impairing sludge activity [121]. Thus, balancing sludge properties (e.g., EPS levels) with aeration energy is crucial for energy-efficient wastewater treatment (Fig. 3a). QS manipulation is a promising strategy for precise control of EPS synthesis, enabling stable sludge performance with reduced aeration energy. Future studies should quantify the role of QS in regulating EPS composition, systematically examine EPS dynamics under different aeration intensities, and develop QS-based aeration control strategies. Furthermore, establishing quantitative relationships between EPS properties and OTE would provide a theoretical basis for optimizing the energy efficiency of biological treatment systems and ultimately achieving significant energy savings without compromising treatment performance.

4.2. Mitigation of biofilm fouling to reduce energy consumption

Integrating membrane filtration and CAS in an MBR improves treatment efficiency and reduces its footprint, but requires higher energy (0.8 versus 0.4 kWh m^{-3} for CAS) for fouling control [123,124].Membrane fouling markedly reduces aeration efficiency, and biofouling of fine-pore diffusers can increase energy use by up to 50% over two years [104]. Therefore, suppressing biofilm formation can reduce energy and material consumption in MBR systems and enhance OTE, leading to additional energy savings.

From economic and operational stability perspectives, employing QQ bacteria to mitigate membrane fouling is advantageous over chemical inhibitors or free QQ enzymes. QQ bacteria can self-replicate and continuously produce multiple QQ enzymes, thereby sustaining antifouling effects. Furthermore, when immobilized within functional carriers, they exhibit enhanced activity and stability while enabling carrier recovery and reuse, thereby promoting environmental friendliness and cost-effectiveness [125]. To date, many studies have explored the control effects of QQ regulation strategies on biofouling and have reported remarkable results [17,126], demonstrating effective reductions in energy consumption (Table 1). However, this technology remains largely confined to laboratory-scale research, primarily because of activity loss in QQ bacteria during long-term operations, the physical degradation of immobilization carriers (e.g., swelling,

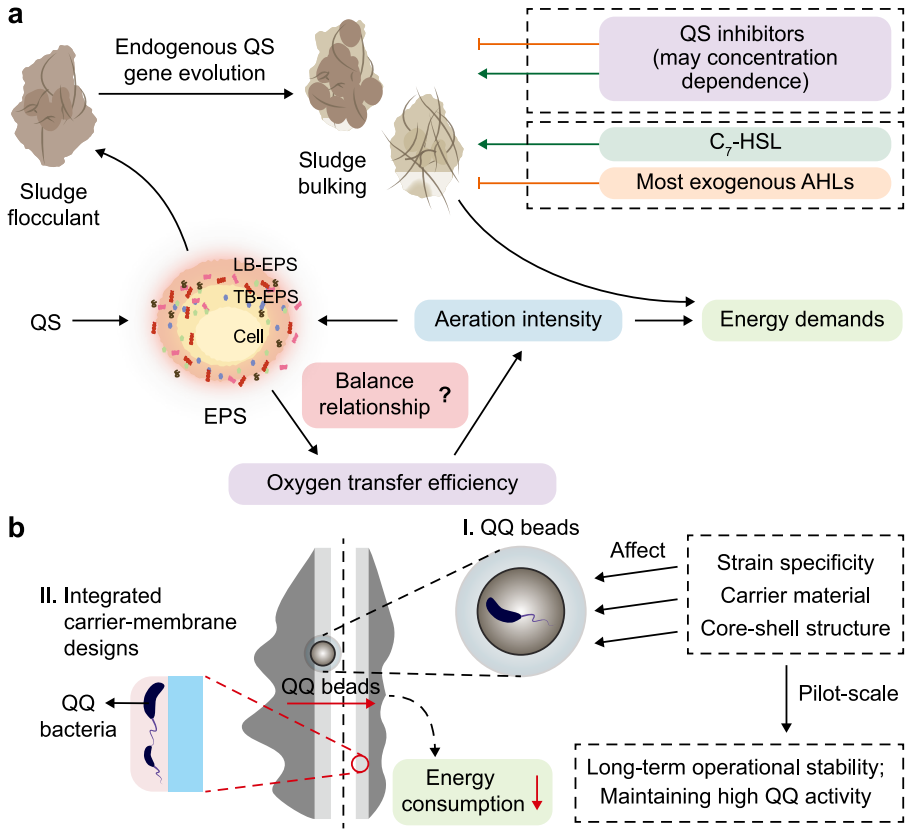


Fig. 3. a, The multifaceted role of quorum sensing (QS) regulation in sludge bulking, and the yet-to-be-elucidated balance among extracellular polymeric substances (EPS), oxygen transfer efficiency, and aeration intensity. Question marks indicate relationships that remain to be established. **b**, QS inhibition alleviates membrane fouling by screening quorum-quenching (QQ) bacterial strains, optimizing carrier materials and structures, and developing *in situ* QQ membranes, thereby enhancing long-term operational stability and maintaining high-efficiency QQ activity in the future. LB, loosely bound; TB, tightly bound; HSL, homoserine Lactone; AHL, *N*-acyl-homoserine lactone.

strength reduction, alginate leakage), and a decline in biological performance (e.g., reduced QQ efficiency and invasion by exogenous microorganisms). Recent studies have thus focused on enhancing the durability and applicability of QQ bacteria in real MBR environments through material improvements and optimization of encapsulation processes (Supplementary Table S2).

Studies have shown that the use of composite carrier materials, such as polyvinyl alcohol-sodium alginate (PVA-SA), core-shell structures, and electrospun fiber coatings, significantly enhances the activity of QQ bacteria and improves the mitigation of membrane fouling. These findings suggest that the carrier's physical structure (e.g., porosity, core-shell configuration) plays a critical role in protecting QQ bacteria and delaying the decline of their activity [127–129]. However, significant variation in the duration of QQ bacterial activity has been observed across studies. For instance, some systems maintained 76–95% of their initial activity after 40–45 days [128–131], while others declined to 40–50% within a comparable timeframe [132,133]. These discrepancies may be due to differences in bacterial strains, carrier material stability, encapsulation technique effectiveness, and operational conditions (Fig. 3b). For example, when *Brucella* sp. ZJ1 was encapsulated in PVA/SA; its activity decreased by 60% and 50% after 40 and 54 days of operation in 7 L and 20 L reactors, respectively [132,133]. In contrast, *Delftia* sp. JL5 encapsulated in PVA/SA retained over 90% of its activity after 30 days [131], and *Bacillus* sp. SDC-U1 also exhibited stable activity after 40 days [134]. Interestingly, the fungal QQ strain *Vanrija* sp. MS1 exhibited a 31% increase in activity after 85 days of operation when immobilized in fluidizing spherical PVA-SA beads, with enhanced performance under acidic conditions [135]. Overall, it is evident that species-specific characteristics significantly influence the QQ efficacy in MBRs.

Core-shell structures hold promise in further enhancing the long-term stability of QQ bacteria. For instance, Yi et al.'s triple-layer microcapsule system consisted of an SA gel core that encapsulated BH4 bacteria, a chitosan intermediate layer for toxic isolation, and a semi-interpenetrating network hydrogel shell composed of SA and polyacrylamide. This system retained approximately 80% of its initial activity after 100 days of operation [136]. Similarly, Iqbal et al. designed a core-shell configuration with a PVA-SA hydrogel sheet (encapsulating BH4 bacteria) as the core and a 3D-printed porous polylactic acid hard shell. Compared with the control group, this design extended reactor operation by 1.9 times, even when aeration energy consumption was reduced by 50%, and maintained nearly 100% QQ activity for more than 160 days [128]. These results highlight the shell's critical role in protecting the encapsulated agents, although the extent of protection varies across systems. Notably, QQ applications involving core-shell encapsulation have predominantly focused on BH4 bacteria, and the efficacy of this strategy for other QQ strains remains largely unexplored. To facilitate scalable applications, researchers should aim to elucidate the mechanistic principles underlying the maintenance of QQ activity within core-shell structures, particularly the balance between carrier mechanical strength and retention of biological activity. Moreover, integrated carrier membrane designs, such as functionalized membranes with built-in QQ capabilities, have recently emerged as promising alternatives, as they enable *in situ* and long-term fouling control [137–139].

Table 1
Effect of QQ on membrane contamination and energy consumption in MBR.

Scale	Method	Effects	Energy consumption	Energy consumption calculation formula	Reference
Pilot-scale	QQ beads (*Rhodococcus* BH4)	Under the same aeration conditions, the increase in TMP was 500% slower in the QQ-MBR than in the control MBR, and remained 70% slower even at one-third of the aeration rate.	Traditional MBR requires approximately 0.5 kWh m^{-3} for filtration and aeration, while QQ-MBR needs only 0.2 kWh m^{-3}, representing a 60% reduction.	Filtration energy and aeration energy were calculated according to equations (1) and (2).	[192]
Lab-scale	A patterned QQ membrane	The patterned QQ membrane increased the operating time by 2.2-fold relative to the non-patterned membrane.	The specific filtration energy consumption of the patterned QQ membrane was reduced to less than half compared to the non-patterned membrane.	Filtration energy and aeration energy were calculated according to equations (1) and (2).	[193]
Lab-scale	Membrane reciprocation and QQ bacteria (*Rhodococcus* BH4)	Compared to traditional MBRs, the operating time of QQ-MBR is extended by six times.	This method achieves an 81% energy savings.	Filtration energy demand was calculated according to equation (3). $E_{s,a} = \frac{wRT_1}{28.97ne}\left[\left(\frac{p_2}{p_1}\right)^n - 1\right]\frac{1}{MF}$ $E_{s,a}$, specific aeration energy demand (Wh m^{-3}); w, weight of air flowrate (kg s^{-1}); R, universal gas constant for air (8.314 J mol^{-1} K^{-1}); T_1, absolute inlet temperature (K); p_1, absolute inlet pressure (atm); p_2, absolute outlet pressure (atm); e, efficiency (0.7); n, specific heat ratio (n = 0.283); 28.97, molecular weight of dry air; M, membrane area (m^2); F, membrane flux (m^3 m^{-2} s^{-1}). $E_{s,r} = \frac{2\Pi\tau r}{60MF}$ $E_{s,r}$, specific membrane reciprocation energy demand (Wh m^{-3}); τ, torque; r, reciprocation frequency (rpm).	[106]
Lab-scale	QQ beads (*Candida albicans* entrapping polymer beads)	Under the same aeration intensity, QQ-MBR's operation time increased 24.4-fold. At lower aeration (1.2 L min^{-1}), QQ-MBR lasted twice as long as conventional MBR (2.0 L min^{-1}).	Compared to conventional MBR, vacant-QQ MBR reduced aeration energy by 25%, whereas the QQ-MBR achieved a 40% reduction, indicating an additional 15% saving from the biological QQ effect.	Filtration energy demand was calculated according to equation (3). $E_{s,a} = \frac{E_a}{\eta V} = \frac{P_w t_t}{\eta V}$ $E_{s,a}$, specific aeration energy consumption (Wh m^{-3}); E_a, aeration energy consumption (Wh m^{-3}); V, volume of permeate (m^3); η, efficiency (0.6); t_t, total MBR operating time (h); P_w, useful power input (W); the variable P_w was calculated by the velocity gradient (G) that is expressed by the Q_a and the P_w. $G = \sqrt{\frac{Q_a\left(P_1 \ln\left(\frac{P_2}{P_1}\right)\right)}{3.61\mu V}} = \sqrt{\frac{P_w}{\mu V}}$ G, velocity gradient (s^{-1}); Q_a, air flow rate (m^3 h^{-1}); P_1, absolute pressure at the reactor surface (kPa); P_2, absolute pressure at the point of air injection (kPa); μ, absolute viscosity (Kg m^{-1} s^{-1});	[194]
Lab-scale	Hybridization of physical cleaning and QQ	A significant improvement in fouling control was accomplished when QQ was coupled with physical cleanings, particularly in the filtration or relaxation mode.	When the aeration rate decreased from 103 to 52 s^{-1}, the specific filtration energy consumption increased by 42% in the QQ-MBR, compared with a 2.8-fold increase in the control. At 52 s^{-1}, the QQ-MBR reduced aeration energy consumption by 27% relative to operation at 103 s^{-1}.	The energy consumption of the compressor used for air supply was measured using an energy meter (KEM2500, KORINS, Korea) Filtration energy and aeration energy were calculated according to equations (1) and (2).	[195]
Lab-scale	QQ bacteria (*Rhodococcus* BH4) combined with high-dose chloride binding	The TMP of the conventional MBR reached 50 kPa after approximately 50 days, while that of QQ-MBR increased to approximately 20 kPa during the same period.	The specific filtration energy was reduced from 14.7 to 3.8 Wh m^{-3}, saving about 74% of the energy required for filtration.	Filtration energy and aeration energy were calculated according to equations (1) and (2).	[196]

Note.
1. Abbreviations: QQ, quorum quenching; MBR, membrane bioreactor; TMP, transmembrane pressure.
2. Equation (1): $E_{f,q} = E_{f,f}\frac{\int_0^t P_{TMP,QQ}\,dt}{\int_0^t P_{TMP,conventional}\,dt}$, $E_{f,q}$, specific filtration energy of QQ-MBR (kWh m^{-3}); $E_{f,f}$, specific filtration energy in the full-scale MBR, 0.071 (kWh m^{-3}); t, filtration time (h); P_{TMP}, transmembrane pressure

difference (Pa). Equation (2): $E_{s,a} = E_{f,a}\frac{D_p}{D_f}$, $E_{s,a}$, specific aeration energy (kWh m^{-3}); $E_{f,a}$, specific aeration energy in the full-scale MBR, 0.521 kWh m^{-3}; D_p, specific aeration demand in the pilot-scale MBR (m^3 m^{-2} h^{-1}); D_f, specific aeration demand in the full-scale MBR (m^3 m^{-2} h^{-1}). Equation (3): $E_{s,f} = \frac{1}{\eta_f}\int_0^{t_f} P_{TMP}dt$, $E_{s,f}$, specific filtration energy demand (Wh m^{-3}); η, efficiency (0.6); t_f, filtration time (h); P_{TMP}, transmembrane pressure difference (Pa).

4.3. Enhancement of granular sludge performance for energy savings

Aerobic and anaerobic granular sludge (AnGS) have high bioactivity and excellent settling properties [140] and outperform CAS with 50% energy savings, footprint reduction, clarifier elimination, and flow returns [141,142]. With pumping and mixing energy reduced, aeration becomes the dominant energy consumer (e.g., increasing from 44% to 67%), making it the focus of further energy optimization [142]. The slow, unstable granulation that occurs during startup requires extended or intensified aeration, leading to high energy use. Accelerating the sludge granulation process to shorten startup time is therefore an effective energy-saving strategy for both AGS and AnGS [143]. This section focuses on how QS enhances granulation speed and stability, thereby reducing energy input.

During the transition from flocs to particles, the dominant species shifts from potential signal quenchers (30% reduction) to producers (3-fold increase) [144], and this shift correlates strongly with QS in complex microbial communities [145]. The addition of the AHL-degrading enzyme acylase reduces AHL content in AGS, thereby weakening microbial attachment [146]. Conversely, supplementation with boron, a fundamental component of the AI-2 signaling molecule, enhances tryptophan production, thereby increasing AGS growth rate, hydrophobicity, and overall SBR performance [147]. Similarly, in the anaerobic sludge granulation process, AI-2 and C_4-HSL promote filamentous bacteria's participation in particle growth and performance, whereas DSF has a negative effect [148]. Ma et al. analyzed AHL levels in 10 industrial anaerobic particle bioreactors and identified C_8-HSL and C_{10}-HSL as potential universal QS signal molecules that promote anaerobic granulation by regulating EPS synthesis [149].

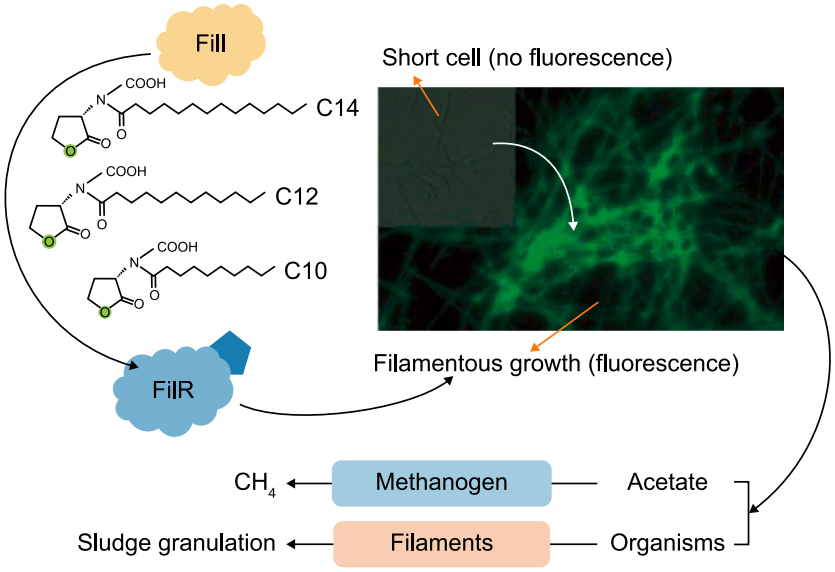
In Zhang et al.'s study, AHL mainly affected AGS performance by promoting adenosine triphosphate (ATP) synthesis, regulating EPS secretion, and regulating microbial activity [150]. Stable particles had higher ATP levels (1.8 μmol per g volatile suspended solids [VSS]) than disintegrated particles (0.8 μmol per g VSS), suggesting that particle stability can be improved by enhancing microbial ATP synthesis [150]. Substrate metabolic efficiency is the main factor affecting ATP content [151]. Research has shown higher levels of AHL accumulation (C_8-HSL, 3OC_8-HSL, 3OC_{12}-HSL) in starch-fed granules than in acetate-fed ones, which greatly improved the activity of the starch hydrolase α-amylase and promoted substrate degradation, EPS production, and sludge granulation and stability [152]. Microbial communities in AGS are crucial for treatment efficiency and system stability. Reactors with shorter sludge retention times (SRTs) exhibit enhanced nitrogen removal and granulation than those with longer SRTs, largely due to the enrichment of AHL- and EPS-producing bacteria such as Xanthomonadaceae, Rhothrobacteriaceae, and Hyphomonadaceae [140]. The exogenous addition of AHL can enrich for AHL-producing genera such as *Aeromonas* and *Pseudomonas* and further induce sustained AHL release, thereby accelerating granulation, improving particle characteristics, and enhancing long-term structural stability [153].

DSF and c-di-GMP also drive sludge granulation by stimulating EPS secretion. Alginate-like exopolysaccharide, regulated by c-di-GMP, reportedly accelerates aerobic sludge granulation [154]. Conversely, DSF finely modulates the extent and progression of granulation by antagonizing c-di-GMP [155]. The regulatory role of c-di-GMP is considered the main mechanism behind nonfilamentous sludge bulking in AGS [156]. DSF can thus be employed to restore deteriorating AGS systems by reducing c-di-GMP levels and EPS content, thereby improving settleability. In contrast, salicylic acid acts as a DSF inhibitor; it diminishes DSF concentration,

a

Anaerobic digestion process	Signal molecules
Hydrolysis/Acidogenesis	AHLs, AIP, AI-2, DSF, c-di-GMP
Acetogenesis	AHLs, AIP, DSF, c-di-GMP
Methanogenesis	AHLs, AIP?, PQS?, c-di-GMP?

b QS system in *Methanosaeta harundinacea* 6Ac



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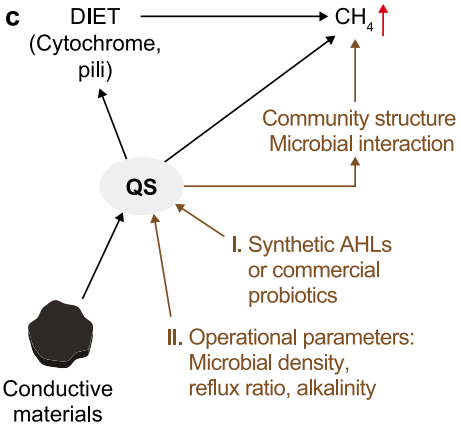

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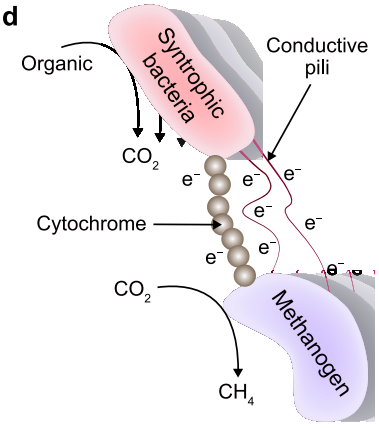

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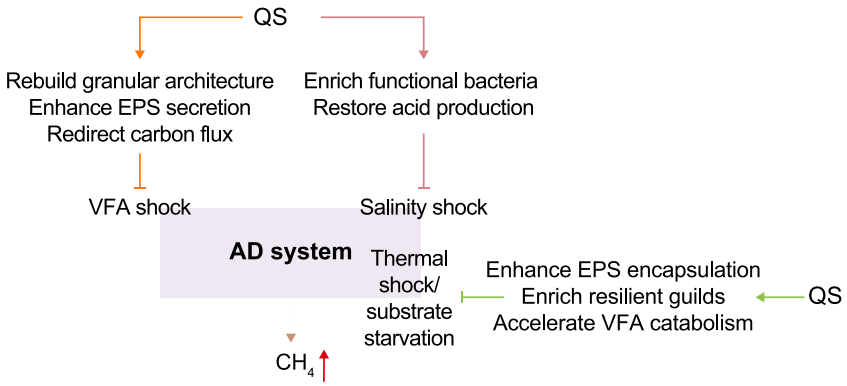

Fig. 4. a, Anaerobic digestion (AD) process and signal molecules at each stage. **b**, The quorum-sensing (QS) system of *Methanosaeta harundinacea* 6Ac and its regulation of the physiological behavior of archaea. **c**, Regulatory strategies of QS on methanogenesis. **d**, The direct interspecies electron transfer (DIET) mechanism between methanogens and syntrophic bacteria. **e**, Effect of QS on the shock resistance of AD. AHL, *N*-acyl-homoserine lactone; AIP, autoinducing peptide; AI-2, autoinducer-2; DSF, diffusible signal factor; c-di-GMP, 3′-5'cyclic diguanosine monophosphate; PQS, 2-heptly-3-hydroxy-4-quinolone; C10, *N*-carboxyl-C_{10}-HSL; C12, *N*-carboxyl-C_{12}-HSL; C14, *N*-carboxyl-C_{14}-HSL; VFA, volatile fatty acid. Question marks indicate relationships that remain to be established.

leading to c-di-GMP accumulation and enhanced granule maturation [157]. Under anaerobic conditions, c-di-GMP concentration is a major driver of granulation: Elevated c-di-GMP levels increase EPS production and reduce bacterial motility, facilitating particle formation [158].

Anammox bacteria regulate c-di-GMP to promote aggregation and granulation as an adaptive strategy against adverse environmental stresses, including low temperature, aerobic conditions, and low pH [159], a mechanism analogous to that observed under aerobic regimes [155]. Similarly, AHL signaling molecules can promote sludge granulation under unfavorable conditions [160,161]. For example, in phenolic wastewater treatment, AHLs (e.g., C_4-HSL and 3-Oxodecanoyl-homoserine lactone [3OC_{10}-HSL]) can regulate the content and composition of EPS and bacterial communities, thereby promoting AGS formation [161]. The precise regulation of microbial aggregation behavior through QS is expected to overcome current limitations in AGS technology—specifically in stability, energy consumption, and scalability—thereby positioning it as a core process in future approaches to low-carbon wastewater treatment. Research must bridge the gap from mechanistic understanding to engineering applications to ensure robust scientific and technological support for achieving carbon neutrality in WWTPs.

5. QS-augmented methanogenesis for carbon offsetting

AD is a cost-effective strategy for organic waste disposal and energy recovery. It produces biogas, a recognized renewable energy source, and effectively promotes carbon neutrality by reducing GHG emissions and offsetting energy consumption with CH_4 in WWTPs [13]. For example, a poultry rendering plant (wastewater flow: 4.5 million L day^{-1}) diverts 2 million kg of CH_4 per year via covered retention ponds, offsetting 50,000 tons of CO_2 equivalent in its carbon footprint. The system generates 14,000–68,000 m^3 of biogas per week, yielding 40,000–170,000 kWh of electricity per week [162]. This meets the plant's operational energy demand and supplies surplus power to the grid, amplifying its climate mitigation benefits.

The cascade process of methanogenesis (hydrolysis, acidogenesis, acetogenesis, and methanogenesis) involves various microorganisms [13]. Past research has shown that efficient biotransformation for AD relies on the symbiotic relationships between bacteria and methanogens [163]. Efficient intra- or interspecific communication among microorganisms is crucial and closely related to the bacterial QS system [32]. QS systems among bacteria have been extensively studied [164], and those in methanogenic archaea have been explored using a wide range of bioinformatics techniques [31]. This section summarizes established QS regulatory systems in methanogens and recent studies on QS signaling molecules that regulate the efficiency of methanogenesis in each anaerobic system. The findings reveal the mechanisms by which QS regulates CH_4 production and facilitates the accurate and efficient implementation of carbon neutrality.

5.1. QS systems governing methanogenic consortia in AD

Previous studies have simultaneously detected signaling molecules such as AI-2, AHLs, AIP, PQS, DSF, and c-di-GMP in anaerobic systems, indicating that QS is prevalent in these systems (Fig. 4a) [31,32,165]. AHLs can regulate the community structure of both bacteria and methanogens [166], while c-di-GMP and DSF can regulate flagellar motility and biofilm matrix components, thereby contributing to biofilm formation and spread. Additionally, c-di-GMP and DSF are involved in the biosynthesis of bacterial type IV pili; they promote cell aggregation and affect syntrophic interactions during CH4 generation (e.g., direct interspecies electron transfer [DIET]) [32,165]. However, most signal-molecule–related genes are associated with syntrophic bacteria, and only one specific AHL-QS system, regulated by FilI-FilR, has been validated in methanogens [19]. Zhang et al. discovered FilI-FilR, homologs of LuxI–LuxR, in *Methanosaeta harundinacea* 6Ac (Fig. 4b) and identified three AHL-like signaling molecules (carboxylated AHLs) produced by the FilI protein: *N*-carboxyl-C_{14}-HSL, *N*-carboxyl-C_{12}-HSL, and *N*-carboxyl-C_{10}-HSL. These molecules can stimulate the transformation of 6Ac from short cells to filamentous bacteria, alter carbon metabolism pathways, promote acetate conversion, and increase CH_4 production. The filamentous bacteria simultaneously provide attachment points for other microorganisms, thereby facilitating AnGS formation [19]. This QS system has been identified in many methanogens, demonstrating the universality of QS in prokaryotes [32,167]. The only c-di-GMP-related protein found in archaea occurs in the uncultivated methanogen MRE50 [168]. Du et al. found that homologs of c-di-GMP synthase (diguanylate cyclase) and hydrolase (phosphodiesterase) exist in 62.3% (43/69) of methanogens. The researchers postulated that c-di-AMP may be a derivative of c-di-GMP and a potential second messenger in archaea [32]. Substantial experimentation is required to validate this proposal. Research on QS in methanogens remains nascent, and the related genomic basis and mechanistic underpinnings have not been fully elucidated [32]. However, preliminary evidence suggests that QS has significant potential to enhance methanogenesis and advance carbon neutrality. Despite this functional significance, most research on QS has focused exclusively on bacterial systems [164], leaving methanogen-specific signaling mechanisms largely unexplored. Elucidating the various archaeal–bacterial cross-kingdom signal networks is thus a critical avenue for future research that can aid in optimizing syntrophic partnerships and maximizing bioenergy recovery.

5.2. Methanogenic amplification via QS tactics

5.2.1. QS-directed assembly of functional consortia

Studies have demonstrated that AHLs (C_4–C_8) enhance wastewater treatment and methanogenesis by restructuring bacterial and archaeal consortia [166]. Stage-specific AHLs positively correlated with syntrophic guilds have been identified, revealing how microbial social networks dynamically orchestrate AD processes [167,169]. This establishes that modulating signal-molecule composition or concentration may enable directional regulation of microbial behavior to optimize CH_4 yield and carbon neutrality.

While exogenous additives (e.g., commercial probiotics, synthetic AHLs; Table 2) incur prohibitive costs, endogenous QS manipulation via operational parameters allows for sustainable enhancement (Fig. 4c). Microbial density control (2.5–12.5% of the functional bacteria inoculum) can regulate endogenous AHLs and enrich syntrophic acetogen-methanogen partnerships, in turn boosting propionate and butyrate acid conversion via EPS-mediated aggregation [169]. Yan et al. found that a reflux ratio of

100–200% and an alkalinity of 1800–2200 mg L^{-1} were optimal for stimulating the growth and metabolism of specific methanogens and acetic acid bacteria through various AHLs, and this indirectly promoted the AD process and improved microbial aggregation [170,171]. Among the 10 detected endogenous signal molecules, $3OC_6$-HSL and $3OC_{14}$-HSL were positively correlated with genes involved in CH_4 metabolism and ATP synthesis. These molecules stimulated the metabolism and growth of acetoclastic methanogens (*Methanosaeta*), hydrogenotrophic methanogens (HMs; *Methanospirillum* and *Methanolinea*), and syntrophic acetic acid bacteria. *Methanobacterium*, a kind of HM, was positively induced by C_{14}-HSL, C_{10}-HSL, $3OC_{12}$-HSL, and $3OC_8$-HSL, which indicates that the social behaviors of HMs are regulated by various AHLs [171]. These findings provide operational levers for endogenous signal amplification, transforming reactor management into a QS programming tool.

5.2.2. QS-orchestrated DIET enhancement

DIET is a microbial electron-exchange mode that enables direct cell-to-cell electron transfer through biological conductive structures (e.g., multi-heme cytochromes and conductive pili; Fig. 4d) and enhances CH_4 production in AD by facilitating syntrophic partnerships [172,173]. However, establishing direct bioelectric connections may prolong the methanogenesis lag phase [173]. Conductive materials (e.g., biochar, metal oxides, and activated carbon) are therefore employed as exogenous electron mediators for mediated interspecies electron transfer (MIET) [163]. For instance, the addition of 10 g L^{-1} Fe_3O_4 has been shown to enhance the conductivity of anaerobic sludge and electron-transfer activity, thereby creating favorable conditions for MIET [174]. Emerging evidence reveals that these materials have a more profound regulatory function beyond electron shuttling: they modulate microbial QS systems and optimize DIET partnerships concurrently (Fig. 4c) [175,176]. Research has shown that Fe_3O_4 can influence methanogenic fermentation processes by altering the relative abundance of functional genes (e.g., QS genes) and metabolic pathways [177]. Similarly, granular activated carbon (GAC) can trigger the QS system, leading to the development of more DIET functional partners and genes than in a non-GAC system, thereby improving CH_4 production [31]. In addition, adding biochar (2–15 g L^{-1}) has been found to decrease the lag time for CH_4 formation by 27.5–64.4%, increase CH_4 yield by 22.4–40.3%, and enrich DIET-associated microorganisms such as Anaerolineaceae and *Methanosaeta* [178]. Research on the dircet regulation of DIET by QS is limited. In 2019, Yin et al. noted, “Inducing the formation of DIET-dependent biofilms and particles through stimulation of QS systems (e.g., administered signaling molecules) may be a potential strategy to regulate methanogenic efficacy” [163]. Since the bioelectric connection between microorganisms is closely related to cell aggregation [179], QS-induced biofilms or anaerobic particles can increase microbial density and shorten cell–cell distances [180,181]. Du et al. showed that adding a conductive filter to a UASB led to increased biomass, biofilm growth, methanogen enrichment, and CH_4 production, all of which were linked to high AHL concentrations and AHL-related gene expression [32].

The addition of AHLs enriches certain methanogens, including those involved in DIET, suggesting a link between QS and DIET [166,182,183]. Specific syntrophic partners are reportedly involved in QS, including *Syntrophobacter*, *Smithella*, and *Geobacter* [32]. Yin et al. conducted a metagenomic analysis of 12 anaerobic samples to evaluate QS-based cooperation between syntrophic partners in methanogenesis and various identified QS-related genes. Among these, DSF and c-di-GMP-related genes from syntrophic bacteria influenced the expression of type IV pili genes, which are crucial for DIET [165]. Later, Zhao et al. reported that QS regulation (via the addition of 10 μg L^{-1} C_4-HSL and C_6-HSL) upregulated the expression of genes associated with conductive pili and c-Cyts cytochrome (by 12.7- and 10.3-fold, respectively), enhancing DIET, improving CH_4 yield and system stability, and shifting the microbial communities toward DIET-favoring taxa such as *Methanosaeta* and *Geobacter* [14]. Interestingly, loading AHL on biochar reduced the effect of AHL on AD performance, while the co-addition of separated biochar and AHL further enhanced the effect of AHL and improved DIET [184]. Exogenous AHL can also increase the abundance of *Geobacter* and *Methanothrix* after a temperature shock, thereby potentiating the DIET pathway [185]. However, QS signal molecules are expensive, and any exogenous additions should be cost-effective and considered in terms of carbon neutrality. Although many systems are syntrophic, QS regulation of DIET has been limited to *Methanosaeta* and *Geobacter* to date. Further research is required to clarify the QS regulation mechanisms at both the individual and population levels.

Table 2
Effects of QS or QQ regulation on the anaerobic digestion process.

Exogenous addition	Effect and mechanism	Applicable scene	Reference
QS			
C_4-HSL	Promoted the methanogenic metabolic pathways of AnGS and had positive effects on methanogenesis.	Methane production phase.	[197,198]
C_6- or C_8-HSL	Induced the enrichment of *Actinomyces* and accelerated hydrolysis and acidification in AnGS.	Pre-treatment/complex substrate degradation stage.	[197]
$3OC_6$-HSL	Maximized the increase in methanogenic activity by 30.8% and promoted the methanogenic metabolic pathways of AnGS.	Methane production phase.	[197]
C_{12}-HSL was added on the fifth day of fermentation (30 days in total)	Improved cumulative CH_4 yield by 47.7% (310.7 ± 2.5 mL g^{-1}); strengthened the hydrogenotrophic methanogenesis pathway by enriching *Methanobacterium* and improved substrate hydrolysis, acidification, and organic acid utilization.	Late hydrolysis and acidogenesis phase (VFA accumulation period).	[198]
AHLs mixture (C_6-, C_8-, C_{10}-, and $3OC_6$-HSL)	Increased the total number of bacteria and archaea, altered the microbial community structure, accelerated the growth of methanogenic archaea, and promoted CH_4 synthesis.	Multiple signals can be coordinated to cover multiple stages of AD.	[13]
QQ			
Escherichia coli mutant:Δ*luxSlsrR* (quenching AI-2)	Improved CH_4 production from acetate by increasing the abundance of *Methanosarcina*, promoted Firmicutes enrichment, and increased methanogenesis rates.	Methanogenesis phase.	[39]
AHL-type QQ bacteria (0.5, 1, 5 and 10 mg of strain per g of heads)	5 mg of strain per g of heads dosage maximized cumulative methane yield with 48.7% enhancement, promoted glucose consumption and carbon conversion efficiency, and altered the microbial community structure during the steps of acetogenesis and methanogenesis.	Hydrolysis, acetogenesis, and methanogenesis phase.	[199]

Abbreviations: QS, quorum sensing; QQ, quorum quenching; AnGS, anaerobic granular sludge; VFA, volatile fatty acid; AD, anaerobic digestion.

5.3. Augmented process robustness through QS regulation

AD performance is inherently vulnerable to external stressors, such as pH fluctuations, shock loading, temperature shifts, toxicants, and salinity, which trigger volatile fatty acid (VFA) accumulation, reactor instability, and elevated operational costs and energy consumption [186]. QS offers a targeted microbial "rewiring" strategy to enhance system resilience and CH_4 yield, thereby advancing carbon-neutral waste valorization (Fig. 4e).

As critical intermediates in methanogenesis, VFAs require precise concentration control for optimal AD efficiency [180]. For instance, 50 mM acetate disrupts the AI-2 QS system of *Methanosarcina barkeri*, inhibiting cell aggregation and methanogenesis [187]. This QS-VFA sensitivity nexus highlights a fundamental mechanism of microbial governance. Zhang et al. used exogenous C_6-HSL to restore acid-shocked UASB reactors subjected to shock loading; this resulted in the granular architecture being rebuilt, EPS secretion being enhanced, and carbon flux being redirected from VFA production to methanogenesis [180]. Liu et al. activated AI-2 QS with 1 mg L^{-1} boronic acid in a UASB, thereby stimulating syntrophic acetate oxidizers and hydrogenotrophic methanogens to resolve VFA overload [188]. In addition to acid stress, QS provides cross-protective adaptations against multifaceted environmental challenges in anaerobic digestion systems. High salinity disrupts sludge structure, impairs microbial activity, and reduces VFA production. Under saline inhibition, C_4-HSL-mediated QS signaling upregulates halotolerant Bacteroidetes and butyrogenic bacterial consortia [189], thereby preserving acidogenic functionality despite osmotic stress. In cases of thermal shock and substrate starvation, a mixture of exogenous AHLs (C_4-HSL, C_6-HSL, C_8-HSL, and $3OC_8$-HSL) rapidly restores AnGS viability and methanogenic activity through tripartite mechanisms: (i) enhancing EPS-dependent cell encapsulation, (ii) enriching resilient functional guilds, and (iii) accelerating post-perturbation VFA catabolism [182,190]. Conversely, when pentachlorophenol toxicity occurs, AI-2 quenching suppresses acetogenesis while favoring hydrogenotrophic methanogenesis, a strategic metabolic rerouting that curtails VFA accumulation and enhances methane yield [191]. These findings demonstrate the role of QS as a master regulator of microbial stress resilience, dynamically tuning community structure and metabolic flux to sustain anaerobic bioconversion under physicochemical perturbations.

Despite promising advancements, the engineering of QS-enhanced AD systems is constrained by critical knowledge gaps, one of which is a central paradox concerning signal specificity: while AI-2 quenching enhances methanogenesis under toxic stress [191], AI-2 activation conversely promotes recovery from acid stress [188]. This raises the need to determine how competing QS systems (e.g., AHLs versus AI-2) prioritize stress responses within complex consortia. Furthermore, a mechanistic understanding of the metabolic regulation behind the identified correlations between QS dynamics and community shifts remains lacking, particularly the specific enzymes and pathways modulated by QS during VFA degradation. Translational implementation faces significant barriers due to the economic unsustainability of exogenous signal addition, necessitating innovative solutions such as engineered autoinducer-synthesizing syntrophic consortia or matrices endowed with signal-recycling capabilities.

6. Conclusion and future prospects

In this study, we systematically reviewed the role of QS and related biotechnologies in accelerating the carbon neutrality of WWTPs, focusing on three integrated objectives: mitigation of direct GHG emissions (Scope 1), reduction of energy-related emissions (Scope 2), and enhancement of AD for CH_4 recovery. Using a multidimensional assessment framework encompassing emission-reduction efficiency, energy-saving potential, and carbon-offset capacity, we discussed how QS mediates complex microbial behaviors that govern N_2O and CH_4 metabolism, thereby enabling energy conservation by regulating sludge performance and enhancing CH_4 recovery. Notably, QS is not a universally beneficial tool but a context-dependent regulator whose impact, whether positive or negative, is determined by the specific treatment process, microbial community, and operational objective. Regarding direct GHG mitigation, QS enhancement shows promise in reducing N_2O emissions by optimizing anaerobic denitrification, whereas its inhibition (via QQ) may be warranted during nitrification. Specific QS signals can be enhanced during AD to boost CH_4 yield and process stability, thereby contributing directly to energy neutrality. For operational energy optimization, the strategy varies: QS enhancement can improve sludge settleability and granulation, reducing aeration demands, whereas QQ is the established approach for combating membrane biofouling and certain forms of sludge bulking. Therefore, the key to future applications lies in understanding and leveraging this duality. Through the precise management of microbial ecology, a dynamic balance can be achieved between emission reduction, energy optimization, and energy recovery, providing a novel and promising microbially engineered pathway for wastewater treatment systems to achieve carbon neutrality.

Although key advancements have been made in signal manipulation, electron-transfer facilitation, and microbial community steering, critical system-specific bottlenecks also exist, including high contextual dependence and resulting variable efficacy, contradictory effects on metabolic pathways (e.g., N_2O accumulation), and limited long-term stability of exogenous interventions. QS-based strategies demonstrate dual potential for emission reduction and energy-saving and recovery; however, scalable implementation will require integrated approaches that combine synthetic biology, advanced materials, and systems engineering, supported by rigorous techno-economic and life-cycle assessments. We recommend prioritizing the following directions for future research:

(1) QS-based strategies for regulating GHG emissions

Researchers should aim to establish dose–response relationships for key signaling molecules (e.g., AHLs) under real-world wastewater conditions, identify critical environmental thresholds that trigger pathway shifts, and fine-tune the QS/QQ balance to steer electron flow, optimize nitrogen removal, and minimize N_2O emissions. Integrated multi-omics, metabolic flux analysis, and advanced microcharacterizations of EPS properties (porosity, hydrophobicity, and thickness) can help determine how QS regulates carbon/electron fluxes, key enzyme activities (e.g., NOS, NirK, pMMO, and Mcr), and CH_4 diffusion barriers. The findings would provide a theoretical basis for designing controllable emission-reduction strategies and would validate whether QS-driven resource reallocation can serve as a universal mechanism for mitigating GHG emissions.

(2) QS-based strategies for regulating energy consumption

To address the dual role of QS in sludge aggregation and

bulking, a quantitative library linking signal molecules, microbial communities, and sludge properties should be established. Machine-learning–assisted strategies can optimize signal-molecule selection and dosing across diverse water-quality conditions. Further, elucidating the influence of QS on EPS composition under different aeration intensities would help clarify its impact on OTE. An integrated model linking EPS properties, OTE, and energy consumption will enable QS-mediated targeted regulation of EPS that reduces aeration demand without sacrificing treatment performance. Robust, high-performance QQ carriers with enhanced stability must also be developed and evaluated under real conditions to ensure their long-term efficacy and ecological safety in full-scale applications.

(3) QS-based strategies for enhancing CH_4 production efficiency

Future efforts should focus on enhancing endogenous QS and DIET via substrate-induced metabolic regulation, signal-anchored conductive materials (e.g., AHL-grafted biochar), and enriched syntrophic consortia to overcome the cost and sustainability limitations of exogenous signal or enzyme addition. The aforementioned approaches can diminish reliance on external inputs while promoting CH_4 production. Additionally, considering the role of QS in improving system robustness under stress conditions such as VFA accumulation, researchers should clarify how QS restructures microbial interaction networks and, accordingly, develop robust engineered consortia capable of maintaining stable QS communication and metabolic function during disturbances.

CRediT authorship contribution statement

Wen-Qian Wang: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization, Validation. **Yong-Mei Wang:** Writing – review & editing, Conceptualization, Formal analysis, Investigation. **Xiao-Chi Feng:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization, Project administration. **How Yong Ng:** Writing – review & editing, Supervision. **Nan-Qi Ren:** Funding acquisition.

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.

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Appendix A. Supplementary data

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References

[1] A.M. Abdelrahman, S. Kosar, H. Gulhan, B. Cicekalan, G. Ucas, E. Atli, H. Guven, H. Ozgun, I. Ozturk, I. Koyuncu, J.B. van Lier, E.I.P. Volcke, M.E. Ersahin, Impact of primary treatment methods on sludge characteristics and digestibility, and wastewater treatment plant-wide economics, Water Res. 235 (2023) 119920.
[2] Q. Zhang, C.W.Y. Wong, R. Klassen, Carbon neutrality: operations management research opportunities, J. Oper. Manag. 70 (3) (2024) 344–354.
[3] A. Capodaglio, G. Olsson, Energy issues in sustainable urban wastewater management: use, demand reduction and recovery in the urban water cycle, Sustainability 12 (1) (2020) 266.
[4] J. Lee, L. Zhang, The hierarchy quorum sensing network in Pseudomonas aeruginosa, Protein Cell 6 (1) (2015) 26–41.
[5] K. Lee, S. Lee, S.H. Lee, S.-R. Kim, H.-S. Oh, P.-K. Park, K.-H. Choo, Y.-W. Kim, J.-K. Lee, C.-H. Lee, Fungal quorum quenching: a paradigm shift for energy savings in membrane bioreactor (MBR) for wastewater treatment, Environ. Sci. Technol. 50 (20) (2016) 10914–10922.
[6] J. Lee, Y.-J. Won, D.-C. Choi, S. Lee, P.-K. Park, K.-H. Choo, H.-S. Oh, C.-H. Lee, Micro-patterned membranes with enzymatic quorum quenching activity to control biofouling in an MBR for wastewater treatment, J. Membr. Sci. 592 (2019) 117365.
[7] C. Jiang, X. Wang, H. Wang, S. Xu, W. Zhang, Q. Meng, X. Zhuang, Achieving partial nitritation by treating sludge with free nitrous acid: the potential role of quorum sensing, Front. Microbiol. 13 (2022).
[8] K. Cheng, W. Sang, X. Jin, D. Jia, Q. Zhang, F. Gan, L. Zou, S. He, Clarifying the mechanism of AHLs-regulated quorum sensing in reducing N2O emission from the aerobic tank in wastewater treatment plant, Process Saf. Environ. Prot. 201 (2025).
[9] X. Yan, S. Zheng, Z. Huo, B. Shi, J. Huang, J. Yang, J. Ma, Y. Han, Y. Wang, K. Cheng, J. Feng, J. Sun, Effects of exogenous N-acyl-homoserine lactones on nutrient removal, sludge properties and microbial community structures during activated sludge process, Chemosphere 255 (2020) 126945.
[10] W.-Q. Wang, X.-C. Feng, Y.-M. Wang, H.-T. Shi, X. Zhang, C.-Y. Jiang, N.-Q. Ren, Effects of astragaloside IV on membrane biofouling in a membrane bioreactor from the perspective of extracellular polymeric substances and the bacteria community structure, Biochem. Eng. J. 197 (2023) 108983.
[11] Y. Xue, H. Ma, Y.-Y. Li, Anammox-based granulation cycle for sustainable granular sludge biotechnology from mechanisms to strategies: a critical review, Water Res. 228 (2023) 119353.
[12] B.T. Wong, K.Y. Show, D.J. Lee, J.Y. Lai, Carbon balance of anaerobic granulation process: carbon credit, Bioresour. Technol. 100 (5) (2009) 1734–1739.
[13] Y. Mit Prohim, R.D.A. Cayetano, P. Anburajan, N. Tang Thau, S. Kim, H.-S. Oh, Enhancement of biomethane recovery from batch anaerobic digestion by exogenously adding an N-acyl homoserine lactone cocktail, Chemosphere 312 (2023) 137188.
[14] S. Zhao, S. Zhu, S. Liu, G. Song, J. Zhao, R. Liu, H. Liu, J. Qu, Quorum sensing enhances direct interspecies electron transfer in anaerobic methane production, Environ. Sci. Technol. 58 (6) (2024) 2891–2901.
[15] D. Dong, Q. Liu, X. Wang, H. Hu, B. Wu, H. Ren, J. Wang, Regulation of exogenous acyl homoserine lactones on sludge settling performance: monitoring via ultrasonic time-domain reflectometry, Chemosphere 303 (Pt 2) (2022) 135019.
[16] S. Zhao, Y. Dai, R. Wang, Q. Guo, G. Song, L. Song, J. Bian, K. Zhao, R. Liu, Y.-Y. Li, Broad influence of quorum sensing in environmental biotechnology: from mechanisms to applications, ACS ES&T Eng. 5 (2) (2025) 284–302.
[17] B. Xu, Q. Su, Y. Yang, S. Huang, Y. Yang, X. Shi, K.H. Choo, H.Y. Ng, C.H. Lee, Quorum quenching in membrane bioreactors for fouling retardation: complexity provides opportunities, Environ. Sci. Technol. (2024).
[18] W.C. Fuqua, Stephen C. Winans, Greenberg E. Peter, Quorum sensing in bacteria: the LuxR-LuxI family of cell density-responsive transcriptional regulators, J. Bacteriol. 176 (1994) 6.
[19] G. Zhang, F. Zhang, G. Ding, J. Li, X. Guo, J. Zhu, L. Zhou, S. Cai, X. Liu, Y. Luo, G. Zhang, W. Shi, X. Dong, Acyl homoserine lactone-based quorum sensing in a methanogenic archaeon, ISME J. 6 (7) (2012) 1336–1344.
[20] M.S. Jang, E. Goo, J.H. An, J. Kim, I. Hwang, Quorum sensing controls flagellar morphogenesis in Burkholderia glumae, PLoS One 9 (1) (2014) e84831.
[21] I. Alav, J.M. Sutton, K.M. Rahman, Role of bacterial efflux pumps in biofilm formation, J. Antimicrob. Chemother. 73 (8) (2018) 2003–2020.
[22] W.-Q. Wang, X.-C. Feng, H.-T. Shi, Y.-M. Wang, C.-Y. Jiang, Z.-J. Xiao, Y.-J. Xu, X. Zhang, Y. Yuan, N.-Q. Ren, Biofilm inhibition based on controlling the transmembrane transport and extracellular accumulation of quorum sensing signals, Environ. Res. 221 (2023) 115218.
[23] T. Zeng, L. Wang, X. Ren, N.A. Al-Dhabi, H. Sha, Y. Fu, W. Tang, J. Zhang, The effect of quorum sensing on cadmium- and lead-containing wastewater treatment using activated sludge: removal efficiency, enzyme activity, and microbial community, Environ. Res. 252 (Pt 2) (2024) 118835.
[24] A.J. Li, B.L. Hou, M.X. Li, Cell adhesion, ammonia removal and granulation of autotrophic nitrifying sludge facilitated by N-acyl-homoserine lactones, Bioresour. Technol. 196 (2015) 550–558.
[25] J. Wang, Q. Liu, B. Wu, F. Zhao, S. Ma, H. Hu, X. Zhang, H. Ren, Quorum sensing signaling distribution during the development of full-scale municipal wastewater treatment biofilms, Sci. Total Environ. 685 (2019) 28–36.
[26] B.H. Gless, M.S. Bojer, P. Peng, M. Baldry, H. Ingmer, C.A. Olsen, Identification

of autoinducing thiodepsipeptides from staphylococci enabled by native chemical ligation, Nat. Chem. 11 (5) (2019) 463–469.
[27] J.D. Shrout, R. Nerenberg, Monitoring bacterial Twitter: does quorum sensing determine the behavior of water and wastewater treatment biofilms? Environ. Sci. Technol. 46 (4) (2012) 1995–2005.
[28] M. Kleerebezem, L.E.N. Quadri, O.P. Kuipers, W.M. De Vos, Quorum sensing by peptide pheromones and two-component signal-transduction systems in gram-positive bacteria, Mol. Microbiol. 24 (5) (1997) 895–904.
[29] K.-F. Kong, C. Vuong, M. Otto, Staphylococcus quorum sensing in biofilm formation and infection, Int. J. Med. Microbiol. 296 (2–3) (2006) 133–139.
[30] Y.F. Tsang, S.N. Sin, H. Chua, Nocardia foaming control in activated sludge process treating domestic wastewater, Bioresour. Technol. 99 (9) (2008) 3381–3388.
[31] H. Dang, N. Yu, A. Mou, L. Zhang, B. Guo, Y. Liu, Metagenomic insights into direct interspecies electron transfer and quorum sensing in blackwater anaerobic digestion reactors supplemented with granular activated carbon, Bioresour. Technol. 352 (2022) 127113.
[32] Q. Du, Q. Mu, G. Wu, Metagenomic and bioanalytical insights into quorum sensing of methanogens in anaerobic digestion systems with or without the addition of conductive filter, Sci. Total Environ. 763 (2021) 144509.
[33] B.L. Bassler, M. Wright, R.E. Showalter, M.R. Silverman, Intercellular signalling in Vibrio harveyi: sequence and function of genes regulating expression of luminescence, Mol. Microbiol. (1993).
[34] M.J. Federle, B.L. Bassler, Interspecies communication in bacteria, J. Clin. Investig. (2003).
[35] C.S. Pereira, J.A. Thompson, K.B. Xavier, AI-2-mediated signalling in bacteria, FEMS Microbiol. Rev. 37 (2) (2013) 156–181.
[36] H. Park, J.-U. Jang, J. Park, H. Park, K.-H. Choo, J. Jeon, H. Yeo, C.-H. Lee, K. Lee, Exploring novel quorum quenching strain: enhanced disrupting autoinducer-2 bacterial communication to combat biofouling in membrane bioreactor for wastewater treatment, Chem. Eng. J. 486 (2024) 150173. Lausanne, Switzerland : 1996.
[37] J. Zhu, J.J. Mekalanos, Quorum sensing-dependent biofilms enhance colonization in Vibrio cholerae, Dev. Cell (2003).
[38] S.S.A. Shah, H. Park, H.-J. Park, J. Kim, N. Mameda, K.-H. Choo, The relationship between quorum sensing dynamics and biological performances during anaerobic membrane bioreactor treatment, Bioresour. Technol. 363 (2022) 127930.
[39] S. Sabidi, Y. Hoshiko, T. Maeda, Quorum quenching of autoinducer 2 increases methane production in anaerobic digestion of waste activated sludge, Appl. Microbiol. Biotechnol. 106 (12) (2022) 4763–4774.
[40] C. Liu, S.G. Goh, L. You, Q. Yuan, S. Mohapatra, K.Y.-H. Gin, B. Chen, Low concentration quaternary ammonium compounds promoted antibiotic resistance gene transfer via plasmid conjugation, Sci. Total Environ. 887 (2023), 163781-163781.
[41] Y. Xiong, Y. Liu, Involvement of ATP and autoinducer-2 in aerobic granulation, Biotechnol. Bioeng. 105 (1) (2010) 51–58.
[42] H. Hu, Y. Liu, F. Luo, X. Zhang, Y. Wang, Z. Ye, J. Chen, T. Li, Stable and rapid partial nitrification achieved by boron stimulating autoinducer-2 mediated quorum sensing at room & low temperature, Chemosphere 304 (2022) 135327.
[43] C.E. Barber, J.L. Tang, J.X. Feng, M.Q. Pan, T.J. Wilson, H. Slater, J.M. Dow, P. Williams, M.J. Daniels, A novel regulatory system required for pathogenicity of Xanthomonas campestris is mediated by a small diffusible signal molecule, Mol. Microbiol. 24 (3) (1997) 555–566.
[44] D.G. Davies, C.N. Marques, A fatty acid messenger is responsible for inducing dispersion in microbial biofilms, J. Bacteriol. 191 (5) (2009) 1393–1403.
[45] Y. Deng, C. Boon, S. Chen, A. Lim, L.H. Zhang, Cis-2-dodecenoic acid signal modulates virulence of Pseudomonas aeruginosa through interference with quorum sensing systems and T3SS, BMC Microbiol. 13 (2013) 231.
[46] Y. Deng, J.E. Wu, F. Tao, L.-H. Zhang, Listening to a new language: DSF-based quorum sensing in gram-negative bacteria, Chem. Rev. 111 (1) (2011) 160–173.
[47] W. Song, J. Ryu, J. Jung, Y. Yu, S. Choi, J. Kweon, Dispersive biofilm from membrane bioreactor strains: effects of diffusible signal factor addition and characterization by dispersion index, Front. Microbiol. 14 (2023), 1211761-1211761.
[48] W. Song, C. Kim, J. Lee, J. Han, Z. Jiang, J. Kim, S. An, Y. Park, J. Kweon, Low-biofouling membrane bioreactor: effects of cis-2-Decenoic acid addition on EPS and biofouling mitigation, Chemosphere 358 (2024), 142110-142110.
[49] X. Tang, Y. Guo, B. Jiang, S. Liu, Metagenomic approaches to understanding bacterial communication during the anammox reactor start-up, Water Res. 136 (2018) 95–103.
[50] Y. Guo, Y. Zhao, X. Tang, T. Na, J. Pan, B.S.L. Huazhang Zhao A, Deciphering bacterial social traits via diffusible signal factor (DSF) -mediated public goods in an anammox community, Water Res. (2021).
[51] M. Valentini, A. Filloux, Biofilms and cyclic di-GMP (c-di-GMP) signaling: lessons from Pseudomonas aeruginosa and other bacteria, J. Biol. Chem. 291 (24) (2016) 12547–12555.
[52] A.B. Roy, K. Sauer, Diguanylate cyclase NicD-based signalling mechanism of nutrient-induced dispersion by Pseudomonas aeruginosa, Mol. Microbiol. (2014).
[53] D. Perez-Mendoza, J. Sanjuan, Exploiting the commons: cyclic diguanylate regulation of bacterial exopolysaccharide production, Curr. Opin. Microbiol. 30 (2016) 36–43.
[54] H. Chen, Y. Tian, Z. Hu, C. Wang, P. Xie, L. Chen, F. Yang, Y. Liang, C. Mu, C. Wei, Y.-P. Ting, G. Qiu, Y. Song, Bis-(3′-5′)-cyclic dimeric guanosine monophosphate (c-di-GMP) mediated membrane fouling in membrane bioreactor, J. Membr. Sci. (2022).
[55] D. Wu, B. Zhao, P. Zhang, Q. An, Insight into the effect of nitrate on AGS granulation: granular characteristics, microbial community and metabolomics response, Water Res. 236 (2023) 119949.
[56] Z. Wang, X. Liu, S.-Q. Ni, X. Zhuang, T. Lee, Nano zero-valent iron improves anammox activity by promoting the activity of quorum sensing system, Water Res. 202 (2021).
[57] S. Ismail, C. Zou, Z. Wang, J. Zhan, C. Cao, Y. Wang, M. Abdalla, X. Zhuang, S.-Q. Ni, Fullerene (C60) supplementation stimulated Anammox granules at low doses and inhibition occurred at high doses: Phenomenon and mechanism, ACS ES&T Eng. 4 (2) (2024) 375–387.
[58] Z. Wu, H. Duan, K. Li, L. Ye, A comprehensive carbon footprint analysis of different wastewater treatment plant configurations, Environ. Res. 214 (Pt 2) (2022) 113818.
[59] H. Nie, X. Liu, Y. Dang, D. Sun, Early activated quorum sensing enhanced a nosZ-deficient strain of Pseudomonas aeruginosa for stably recovering nitrous oxide from incineration leachate in microbial electrolysis cell, Bioresour. Technol. 360 (2022) 127394.
[60] S. Mukherjee, B.L. Bassler, Bacterial quorum sensing in complex and dynamically changing environments, Nat. Rev. Microbiol. 17 (6) (2019) 371–382.
[61] H. Wang, B. Chen, Y. Shi, L. Yang, X. Chen, Competitive inhibition of hydrazine on hydroxylamine oxidation by ammonium-oxidizing bacteria and its stimulative impact on associated N2O production, Chem. Eng. J. 516 (2025).
[62] J. Gao, A. Ma, X. Zhuang, G. Zhuang, An N-acyl homoserine lactone synthase in the ammonia-oxidizing bacterium Nitrosospira multiformis, Appl. Environ. Microbiol. 80 (3) (2014) 951–958.
[63] E.O. Burton, H.W. Read, M.C. Pellitteri, W.J. Hickey, Identification of acyl-homoserine lactone signal molecules produced by Nitrosomonas europaea strain Schmidt, Appl. Environ. Microbiol. 71 (8) (2005) 4906–4909.
[64] B.L. Mellbye, P.J. Bottomley, L.A. Sayavedra-Soto, Nitrite-oxidizing bacterium Nitrobacter winogradskyi produces N-Acyl-Homoserine lactone autoinducers, Appl. Environ. Microbiol. 81 (17) (2015) 5917–5926.
[65] N. Wang, J. Gao, S. Xiao, G. Zhuang, Overexpression of pdeR promotes biofilm formation of Paracoccus denitrificans by promoting ATP production and iron acquisition, Front. Microbiol. 13 (2022) 966976.
[66] <Environmental Adaptability and Quorum Sensing Iron Uptake Regulation During Biofilm Formation by Paracoccus denitrificans.pdf>.
[67] K. Morinaga, T. Yamamoto, N. Nomura, M. Toyofuku, Paracoccus denitrificans can utilize various long-chain N-acyl homoserine lactones and sequester them in membrane vesicles, Environ Microbiol Rep 10 (6) (2018) 651–654.
[68] X. Tang, Y. Guo, T. Zhu, H. Tao, S. Liu, Identification of quorum sensing signal AHLs synthases in Candidatus Jettenia caeni and their roles in anammox activity, Chemosphere 225 (2019) 608–617.
[69] Z. Liu, T. Zeng, J. Wang, Z. Wang, D. Zhao, J. Wei, Y. Peng, L. Miao, AHL-mediated quorum sensing drives microbial community succession and metabolic pathway in algal-bacterial biofilm system, Water Res. 282 (2025) 123702.
[70] J. Li, J. Li, J. Meng, K. Sun, Understanding of signaling molecule controlled anammox through regulating C/N ratio, Bioresour. Technol. 315 (2020) 123863.
[71] Y. Zhang, J. Zhang, J. Li, P. Wei, R. Luo, H. Han, Fast start-up of ANAMMOX biofilm processes at low temperatures by economical quorum sensing regulation: the importance of endogenous N-acyl-homoserine lactones from enhanced inoculated sludge, Environ. Res. 214 (Pt 3) (2022) 114097.
[72] Z. Peng, J. Qin, Y. Zhao, Y. Li, F. Hu, Z. Bai, H. Yang, B. Jin, J. Ji, Comparison of the performances and mechanisms of anammox bacteria in-situ self-enrichment under heterotrophic and autotrophic conditions by inoculating ordinary activated sludge, Bioresour. Technol. 422 (2025) 132213.
[73] L. Liu, S. Xu, F. Wang, Z. Yan, Z. Tian, M. Ji, Effect of exogenous N-acyl-homoserine lactones on the anammox process at 15 °C: nitrogen removal performance, gene expression and metagenomics analysis, Bioresour. Technol. 341 (2021) 125760.
[74] M. Toyofuku, N. Nomura, E. Kuno, Y. Tashiro, T. Nakajima, H. Uchiyama, Influence of the Pseudomonas quinolone signal on denitrification in Pseudomonas aeruginosa, J. Bacteriol. 190 (24) (2008) 7947–7956.
[75] X. Zhang, H. Zhang, N. Zhang, Y. Ma, N. Liu, G. Han, Q. Wang, Impacts of exogenous quorum sensing signal molecule-acylated homoserine lactones (AHLs) with different addition modes on Anammox process, Bioresour. Technol. 371 (2023) 128614.
[76] T. Yang, X. Wang, H. Chen, M. Wang, Y. Wang, H. Chen, H. Dai, Transcriptome analysis expands underlying mechanisms of quorum sensing mediating heterotrophic nitrification-aerobic denitrification process at low temperature, Bioresour. Technol. 414 (2024) 131581.
[77] X. Cui, X. Ruan, J. Yin, M. Wang, N. Li, D. Shen, Regulation of las and rhl quorum sensing on aerobic denitrification in Pseudomonas aeruginosa PAO1, Curr. Microbiol. 78 (2) (2021) 659–667.
[78] X. Ruan, J. Yin, X. Cui, N. Li, D. Shen, Bioaugmentation and quorum sensing disruption as solutions to increase nitrate removal in sequencing batch reactors treating nitrate-rich wastewater, J. Environ. Sci. (China) 98 (2020)

179–185.
[79] J.H. Yang, D.Q. Huang, Y.C. Geng, Y.R. Ling, N.S. Fan, R.C. Jin, Role of quorum sensing-based regulation in development of anaerobic ammonium oxidation process, Bioresour. Technol. 367 (2023) 128228.
[80] Q. Liu, D. Dong, Y. Jin, Q. Wang, F. Zhao, L. Wu, J. Wang, H. Ren, Quorum sensing bacteria improve microbial networks stability and complexity in wastewater treatment plants, Environ. Int. 187 (2024) 108659.
[81] Z. Feng, Y. Sun, T. Li, F. Meng, G. Wu, Operational pattern affects nitritation, microbial community and quorum sensing in nitrifying wastewater treatment systems, Sci. Total Environ. 677 (2019) 456–465.
[82] Y. He, H. Yun, L. Peng, J. Ji, W. Wang, X. Li, Deciphering the potential role of quorum quenching in efficient aerobic denitrification driven by a synthetic microbial community, Water Res. 251 (2024) 121162.
[83] P. Wunderlin, J. Mohn, A. Joss, L. Emmenegger, H. Siegrist, Mechanisms of N2O production in biological wastewater treatment under nitrifying and denitrifying conditions, Water Res. 46 (4) (2012) 1027–1037.
[84] C. Ma, M.M. Jensen, B.F. Smets, B. Thamdrup, Pathways and controls of N(2)O production in nitritation-anammox biomass, Environ. Sci. Technol. 51 (16) (2017) 8981–8991.
[85] M. Wu, Z. Zhang, X. Zhang, L. Dong, C. Liu, Y. Chen, Propionibacterium freudenreichii-Assisted approach reduces N(2)O emission and improves denitrification via promoting substrate uptake and metabolism, Environ. Sci. Technol. 56 (23) (2022) 16895–16906.
[86] J. Li, M. Nie, H. Ma, X. Tao, Y. Sun, X. Tu, P. Zhang, L.Q. Zhang, R. Jia, Y.X. He, N. Zhang, H. Ge, Quorum sensing coordinates carbon and nitrogen metabolism to optimize public goods production in Pseudomonas fluorescens 2P24, Adv. Sci. (Weinh.) 12 (12) (2025) e2412224.
[87] R. Kellermann, S.H.W. Vick, K. Lindtveit, D.A. Milligan, L.L. Bergaust, Cell density dependent restriction of N2O reductase in denitrifying Pseudomonas spp., a potential driver of N2O emissions in natural systems, FEMS Microbiol. Lett. 370 (2023).
[88] Q. Wang, J. Wei, B. Wan, Q. An, J. Gao, G. Zhuang, The regulation effect of preventing soil nitrogen loss using microbial quorum sensing inhibitors, Environ. Res. 246 (2024) 118136.
[89] Y. Cheng, Y. Zhang, Q. Shen, J. Gao, G. Zhuang, X. Zhuang, Effects of exogenous short-chain N-acyl homoserine lactone on denitrifying process of Paracoccus denitrificans, J. Environ. Sci. (China) 54 (2017) 33–39.
[90] W. Sang, Z. Ge, Q. Zhang, F. Gan, N. Wan, L. Zou, A new strategy for greenhouse gas emission reduction in the anaerobic/anoxic/oxic biological treatment process using exogenous N-acyl-homoserine lactones, a quorum-sensing signaling molecules, Water Sci. Technol. 90 (10) (2024) 2764–2783.
[91] X. Yan, K. Xu, R. Zhu, L. Zhang, G. Li, K. Ma, X. Li, Y. Han, Effects of N-hexanoyl-L-homoserine lactone-based quorum sensing on performance, sludge properties, N2O generation, and microbial community structure in the SCONDA process, J. Environ. Chem. Eng. 13 (3) (2025).
[92] F. Fang, H. Li, X. Jiang, X. Deng, P. Yan, J. Guo, Y. Chen, J. Yang, Significant N(2)O emission from a high rate granular reactor for completely autotrophic nitrogen removal over nitrite, J. Environ. Manag. 266 (2020) 110586.
[93] S. Masuda, S. Suzuki, I. Sano, Y.Y. Li, O. Nishimura, The seasonal variation of emission of greenhouse gases from a full-scale sewage treatment plant, Chemosphere 140 (2015) 167–173.
[94] A.W. Puri, A.L. Schaefer, Y. Fu, D.A.C. Beck, E.P. Greenberg, M.E. Lidstrom, Quorum sensing in a methane-oxidizing bacterium, J. Bacteriol. 199 (5) (2017).
[95] D.L. Aaron W. Puri, a Amy L. Schaefer, Zheng Yu, Mitchell W. Pesesky, E. Peter Greenberg, Mary E. Lidstrom, Interspecies chemical signaling in a methane-oxidizing bacterial community, Appl. Environ. Microbiol. 85 (7) (2019).
[96] M.S. Zhang, C.F. Chiu, Y.N. Wang, Analysis of microbial methane oxidation capacity of landfill soil cover using quorum sensing, Environ. Res. 268 (2025) 120781.
[97] R. Ma, Z. Hu, J. Zhang, H. Ma, L. Jiang, D. Ru, Reduction of greenhouse gases emissions during anoxic wastewater treatment by strengthening nitrite-dependent anaerobic methane oxidation process, Bioresour. Technol. 235 (2017) 211–218.
[98] Z.C. Zhao, R.L. Li, S.Q. Fan, Y. Lu, B.F. Liu, D.F. Xing, N.Q. Ren, G.J. Xie, Deciphering the formation of granules by n-DAMO and Anammox microorganisms, Environ. Res. 255 (2024) 119209.
[99] D. Xu, T. Liu, Y. Lu, Y. Li, J. Guo, Intensifying nitrogen removal capacity of membrane biofilm reactor coupling n-DAMO and Anammox processes by dosing signaling molecules, ACS ES&T Water (2025).
[100] J. Cheng, X. Su, M. Liu, Z. Lu, J. Xu, Y. He, Simultaneous regulation of biocathodic gamma-HCH dechlorination and CH(4) production by tailoring the structure and function of biofilms based on quorum sensing, Environ. Pollut. 335 (2023) 122357.
[101] P.D.T. Nguyen, N.A. Mustapha, K. Kadokami, R. Garcia-Contreras, T.K. Wood, T. Maeda, Quorum sensing between Gram-negative bacteria responsible for methane production in a complex waste sewage sludge consortium, Appl. Microbiol. Biotechnol. 103 (3) (2019) 1485–1495.
[102] N. Tsalas, S.K. Golfinopoulos, S. Samios, G. Katsouras, K. Peroulis, Optimization of energy consumption in a wastewater treatment plant: an overview, Energies 17 (12) (2024).
[103] T. Temesgen, M. Han, Advancing aerobic digestion efficiency using ultrafine bubbles in wastewater treatment, J. Water Proc. Eng. 55 (2023).
[104] M. Garrido-Baserba, P. Asvapathanagul, H.D. Park, T.S. Kim, G.A. Baquero-Rodriguez, B.H. Olson, D. Rosso, Impact of fouling on the decline of aeration efficiency under different operational conditions at WRRFs, Sci. Total Environ. 639 (2018) 248–257.
[105] Y. Wang, J. Wang, Z. Liu, X. Huang, F. Fang, J. Guo, P. Yan, Effect of EPS and its forms of aerobic granular sludge on sludge aggregation performance during granulation process based on XDLVO theory, Sci. Total Environ. 795 (2021) 148682.
[106] J. Kim, E. Bae, H. Park, H.J. Park, S.S.A. Shah, K. Lee, J. Lee, H.S. Oh, P.K. Park, Y.C. Shin, H. Moon, V. Naddeo, K.H. Choo, Membrane reciprocation and quorum quenching: an innovative combination for fouling control and energy saving in membrane bioreactors, Water Res. 250 (2024) 121035.
[107] L. Karygianni, Z. Ren, H. Koo, T. Thurnheer, Biofilm matrixome: extracellular components in structured microbial communities, Trends Microbiol. 28 (8) (2020) 668–681.
[108] X.-M. Liu, G.-P. Sheng, H.-W. Luo, F. Zhang, S.-J. Yuan, J. Xu, R.J. Zeng, J.-G. Wu, H.-Q. Yu, Contribution of Extracellular Polymeric Substances (EPS) to the sludge aggregation, Environ. Sci. Technol. 44 (11) (2010) 4355–4360.
[109] S. Schäper, W. Steinchen, E. Krol, F. Altegoer, D. Skotnicka, L. Søgaard-Andersen, G. Bange, A. Becker, AraC-like transcriptional activator CuxR binds c-di-GMP by a PilZ-like mechanism to regulate extracellular polysaccharide production, Proc. Natl. Acad. Sci. 114 (24) (2017).
[110] H. Wang, P. Wu, D. Zheng, L. Deng, W. Wang, N-Acyl-Homoserine lactone (AHL)-mediated microalgal-bacterial communication driving chlorella-activated sludge bacterial biofloc formation, Environ. Sci. Technol. 56 (17) (2022) 12645–12655.
[111] Y. Ren, F. Pei, X. Cao, W. Zhang, R. Du, J. Ge, W. Ping, Purification of exopolysaccharides from Lactobacillus rhamnosus and changes in their characteristics by regulating quorum sensing genes via polyphenols, Int. J. Biol. Macromol. 240 (2023) 124414.
[112] H.-X. Shi, J. Wang, S.-Y. Liu, J.-S. Guo, F. Fang, Y.-P. Chen, P. Yan, New insight into filamentous sludge bulking: potential role of AHL-mediated quorum sensing in deteriorating sludge floc stability and structure, Water Res. 212 (2022) 118096.
[113] X. Lu, G. Yan, L. Fu, B. Cui, J. Wang, D. Zhou, A review of filamentous sludge bulking controls from conventional methods to emerging quorum quenching strategies, Water Res. 236 (2023).
[114] H.-X. Shi, J. Wang, S.-Y. Liu, J.-S. Guo, F. Fang, Y.-P. Chen, P. Yan, Potential role of AHL-mediated quorum sensing in inducing non-filamentous sludge bulking under high organic loading, Chem. Eng. J. 454 (2023) 140514.
[115] W.-X. Liu, J. Wang, S.-Y. Liu, Y.-P. Chen, F. Fang, P. Yan, Potential role of quorum quenching activity of silver nanoparticles in controlling non-filamentous bulking within activated sludge process, Chemosphere (2023).
[116] H.-X. Shi, S.-Y. Liu, J.-S. Guo, F. Fang, Y.-P. Chen, P. Yan, Potential role of AgNPs within wastewater in deteriorating sludge floc structure and settleability during activated sludge process: filamentous bacteria and quorum sensing, J. Environ. Manag. 349 (2024) 119536.
[117] A. Seid-Mohammadi, G. Asgari, M. Rafiee, M.T. Samadi, F. Nouri, M. Pirsaheb, F. Asadi, The formation of aerobic granular sludge for the treatment of real landfill leachate using a granular sequencing batch reactor at a constant volume, Environ. Qual. Manag. 32 (3) (2022) 135–146.
[118] S.Q. Aziz, H.A. Aziz, M.S. Yusoff, Powdered activated carbon augmented double react-settle sequencing batch reactor process for treatment of landfill leachate, Desalination 277 (1–3) (2011) 313–320.
[119] Z. Feng, X. Lu, C. Chen, Y. Huo, D. Zhou, Transboundary intercellular communications between Penicillium and bacterial communities during sludge bulking: inspirations on quenching fungal dominance, Water Res. 221 (2022) 118829.
[120] M. Li, D. Li, L. Hu, D. Deng, Z. Li, H. Li, J. Zhang, Mechanisms of signaling molecules regulating microbial community succession and metabolic pathways in partial nitrification of a composite zeolite-biofilm under low salinity, Chem. Eng. J. 479 (2024).
[121] L. Xing, J. Yang, Y. Zhang, B.J. Ni, C. Yang, C. Yuan, A. Li, Model-based evaluation of the impacts of aeration on tightly bound and loosely bound extracellular polymeric substance production under non-steady-state conditions, Sci. Total Environ. 852 (2022) 158566.
[122] M. Capodici, S.F. Corsino, D. Di Trapani, M. Torregrossa, G. Viviani, Effect of biomass features on oxygen transfer in conventional activated sludge and membrane bioreactor systems, J. Clean. Prod. 240 (2019).
[123] J.-U. Jang, J. Park, H. Kim, S. Lee, K.-H. Choo, K. Lee, Harnessing gravity-driven membranes in activated sludge bioreactors: enhancing energy efficiency and mitigating biofouling via quorum quenching, npj Clean Water 8 (1) (2025).
[124] X.D. Hao, J. Li, M.C.M. van Loosdrecht, T.Y. Li, A sustainability-based evaluation of membrane bioreactors over conventional activated sludge processes, J. Environ. Chem. Eng. 6 (2) (2018) 2597–2605.
[125] H. Lee, S. Min, D. Chae, C. Kim, H.S. Oh, K. Lee, J. Lee, K.H. Choo, C.H. Lee, P.K. Park, Effect of the type and concentration of multivalent cations on the durability of polymeric media for degrading quorum sensing signaling molecules in membrane bioreactors, Water Res. 282 (2025) 123637.
[126] Y. Wang, X. Feng, H. Shi, W. Wang, C. Jiang, Z. Xiao, Y. Xu, N. Ren, New insights into biofilm control and inhibitory mechanism analysis based on the novel quorum quenching bacterium Acinetobacter pittii HITSZ001, J. Membr. Sci. 663 (2022) 121012.
[127] H. Pang, J. Huang, X. Li, K. Yi, S. Li, Z. Liu, W. Zhang, C. Zhang, S. Liu, Y. Gu, Enhancing quorum quenching media with 3D robust electrospinning

coating: a novel biofouling control strategy for membrane bioreactors, Water Res. 234 (2023) 119830.
[128] T. Iqbal, S.S.A. Shah, K. Lee, K.-H. Choo, Porous shell quorum quenching balls for enhanced anti-biofouling efficacy and media durability in membrane bioreactors, Chem. Eng. J. 406 (2021).
[129] S.S.A. Shah, J. Kim, H. Park, N. Mameda, K. Lee, H.Y. Ng, K.-H. Choo, Polysulfone-reinforced quorum quenching media with silica cage encapsulation: advancing biofouling control in anaerobic membrane bioreactors, J. Membr. Sci. 717 (2025).
[130] H. Yu, K. Lee, X. Zhang, K.H. Choo, Core-shell structured quorum quenching beads for more sustainable anti-biofouling in membrane bioreactors, Water Res. 150 (2019) 321–329.
[131] F. Xu, J. Liao, J. Hu, Y. Feng, Y. Huang, X. Feng, S. Li, Biofouling mitigation and microbial community dynamics in the membrane bioreactor by the indigenous quorum quenching bacterium Delftia sp, JL5, Bioresour Technol 388 (2023) 129753.
[132] J. Zhu, W. Xu, Y. Yang, X. Su, X. Xiao, F. Dong, H. Fu, C. Chen, J. Chen, F. Sun, Quorum quenching driven microbial community to biofouling control in membrane bioreactor for landfill leachate treatment, J. Membr. Sci. 722 (2025).
[133] R. Wang, Z. An, L. Fan, Y. Zhou, X. Su, J. Zhu, Q. Zhang, C. Chen, H. Lin, F. Sun, Effect of quorum quenching on biofouling control and microbial community in membrane bioreactors by Brucella sp. ZJ1, J. Environ. Manag. 339 (2023) 117961.
[134] H. Kim, A. Noori, M.H. Kim, C. Lee, J.-H. Ko, B.-K. Hwang, K. Lee, H.-S. Oh, Biofouling mitigation of a membrane bioreactor for industrial wastewater treatment by quorum quenching, J. Membr. Sci. 690 (2024).
[135] J. Park, H. Park, J.U. Jang, H. Kim, H. Park, T. Iqbal, H.S. Oh, K.H. Choo, K. Lee, Benefits of fungal-to-bacterial quorum quenching as anti-biofouling strategy in membrane bioreactors for wastewater treatment and water reuse, Bioresour. Technol. 403 (2024) 130848.
[136] K. Yi, J. Huang, H. Pang, S. Li, Z. Liu, X. Wang, W. Zhang, C. Zhang, S. Liu, Y. Gu, Semi-interpenetrating network hydrogels-based microcapsule for quorum quenching bacteria biocontainment to enhance biofouling control in membrane bioreactor, Chem. Eng. J. 486 (2024).
[137] S.S.A. Shah, K. Lee, H. Park, K.-H. Choo, Live membrane filters with immobilized quorum quenching bacterial strains for anti-biofouling, J. Membr. Sci. 641 (2022).
[138] H. Pang, J. Huang, X. Li, K. Yi, Z. Liu, X. Wang, W. Zhang, C. Zhang, S. Liu, Control of membrane biofouling in MBR for wastewater treatment by biohybrid membrane with superhydrophilic self-QQ function, J. Environ. Chem. Eng. 12 (6) (2024).
[139] B. Hou, X. Chen, D. Wang, R. Geng, X. Zhou, X. Xiao, X. Rong, Z. Wu, J. Wei, Modification of polyacrylonitrile ultrafiltration membrane with acylase for enhanced biofouling control based on quorum quenching, J. Water Proc. Eng. 59 (2024).
[140] Z. Zhang, Z. Yu, Z. Wang, K. Ma, X. Xu, P.J.J. Alvarezc, L. Zhu, Understanding of aerobic sludge granulation enhanced by sludge retention time in the aspect of quorum sensing, Bioresour. Technol. 272 (2019) 226–234.
[141] J. Ekholm, M. de Blois, F. Persson, D.J.I. Gustavsson, S. Bengtsson, T. van Erp, B.M. Wilén, Case study of aerobic granular sludge and activated sludge—Energy usage, footprint, and nutrient removal, Water Environ. Res. 95 (8) (2023).
[142] L. Strubbe, E.J.H.v. Dijk, P.J.M. Deenekamp, M.C.M.v. Loosdrecht, E.I.P. Volcke, Oxygen transfer efficiency in an aerobic granular sludge reactor: dynamics and influencing factors of alpha, Chem. Eng. J. 452 (2023).
[143] Z. Mu, X. Wang, H. Wang, G. Lv, N. Wang, Z. Li, Aeration-phase calcium addition for stabilizing aerobic granular sludge in treating municipal wastewater with low-strength municipal wastewater, ACS ES&T Water 5 (8) (2025) 4701–4714.
[144] C.H. Tan, K.S. Koh, C. Xie, J. Zhang, X.H. Tan, G.P. Lee, Y. Zhou, W.J. Ng, S.A. Rice, S. Kjelleberg, Community quorum sensing signalling and quenching: microbial granular biofilm assembly, npj Biofilms Microbiomes 1 (2015) 15006.
[145] C.H. Tan, K.S. Koh, C. Xie, M. Tay, Y. Zhou, R. Williams, W.J. Ng, S.A. Rice, S. Kjelleberg, The role of quorum sensing signalling in EPS production and the assembly of a sludge community into aerobic granules, ISME J. 8 (6) (2014) 1186–1197.
[146] Y.C. Li, J.R. Zhu, Role of N-acyl homoserine lactone (AHL)-based quorum sensing (QS) in aerobic sludge granulation, Appl. Microbiol. Biotechnol. 98 (17) (2014) 7623–7632.
[147] S.-H. Zhang, X. Yu, F. Guo, Z.-y. Wu, Effect of interspecies quorum sensing on the formation of aerobic granular sludge, Water Sci. Technol. 64 (6) (2011) 1284–1290.
[148] Y. Ding, H. Feng, W. Huang, D. Shen, M. Wang, A sustainable method for effective regulation of anaerobic granular sludge: artificially increasing the concentration of signal molecules by cultivating a secreting strain, Bioresour. Technol. 196 (2015) 273–278.
[149] H. Ma, X. Wang, Y. Zhang, H. Hu, H. Ren, J. Geng, L. Ding, The diversity, distribution and function of N-acyl-homoserine lactone (AHL) in industrial anaerobic granular sludge, Bioresour. Technol. 247 (2018) 116–124.
[150] Z. Zhang, R. Cao, L. Jin, W. Zhu, Y. Ji, X. Xu, L. Zhu, The regulation of N-acyl-homoserine lactones (AHLs)-based quorum sensing on EPS secretion via ATP synthetic for the stability of aerobic granular sludge, Sci. Total Environ. 673 (2019) 83–91.
[151] D. Wunsch, K. Trautwein, S. Scheve, C. Hinrichs, C. Feenders, B. Blasius, D. Schomburg, R. Rabus, Amino acid and sugar catabolism in the marine bacterium Phaeobacter inhibens DSM 17395 from an energetic viewpoint, Appl. Environ. Microbiol. 85 (24) (2019).
[152] Z. Zhang, L. Wang, Y. Ji, R. Cao, J. Zhou, M. Li, L. Zhu, X. Xu, Understanding the N-acylated homoserine lactones(AHLs)-based quorum sensing for the stability of aerobic granular sludge in the aspect of substrate hydrolysis enhancement, Sci. Total Environ. 858 (2023).
[153] B. Zhang, W. Li, Y. Guo, Z. Zhang, W. Shi, F. Cui, P.N.L. Lens, J.H. Tay, A sustainable strategy for effective regulation of aerobic granulation: augmentation of the signaling molecule content by cultivating AHL-producing strains, Water Res. 169 (2020) 115193.
[154] Y.-C. Yang, X. Liu, C. Wan, S. Sun, D.-J. Lee, Accelerated aerobic granulation using alternating feed loadings: Alginate-like exopolysaccharides, Bioresour. Technol. 171 (2014) 360–366.
[155] A. Tang, S. Fan, P. Zhang, A. Li, Role of diffusible signal factor in regulating aerobic granular sludge formation under temperature shocks, Bioresour. Technol. 412 (2024) 131369.
[156] S. Wang, G. Wang, P. Yan, Y. Chen, F. Fang, J. Guo, Non-filamentous sludge bulking induced by exopolysaccharide variation in structure and properties during aerobic granulation, Sci. Total Environ. 876 (2023) 162786.
[157] C. Li, A. Tang, S. Zhang, V. Mironov, A. Li, Bidirectional regulation of aerobic granular sludge through diffusible signal factor/bis(3′-5′)-cyclic dimeric guanosine monophosphate crosstalk: restoring stability and enhancing maturation at low temperatures, Bioresour. Technol. 434 (2025).
[158] C. Wang, G. Yu, F. Yang, J. Wang, Formation of anaerobic granules and microbial community structure analysis in anaerobic hydrolysis denitrification reactor, Sci. Total Environ. 737 (2020) 139734.
[159] Y. Guo, S. Liu, X. Tang, F. Yang, Role of c-di-GMP in anammox aggregation and systematic analysis of its turnover protein in candidatus jettenia caeni, Water Res. 113 (2017) 181–190.
[160] H. Peng, J. Guo, H. Li, Y. Song, C. Lu, Y. Han, Y. Hou, Granulation and response of anaerobic granular sludge to allicin stress while treating allicin-containing wastewater, Biochem. Eng. J. 169 (2021) 107971.
[161] S. Liu, Q. Wang, J. Liang, J. Li, Z. Shao, Y. Han, M. Arslan, M.G. El-Din, Z. Li, C. Chen, The potential effects of N-Acyl homoserine lactones on aerobic sludge granulation during phenolic wastewater treatment, Environ. Res. 251 (2024) 118654.
[162] N. Lovanh, J. Loughrin, G. Ruiz-Aguilar, K. Sistani, Methane production from a rendering waste covered anaerobic digester: greenhouse gas reduction and energy production, Energies 16 (23) (2023).
[163] Q. Yin, G. Wu, Advances in direct interspecies electron transfer and conductive materials: Electron flux, organic degradation and microbial interaction, Biotechnol. Adv. 37 (8) (2019) 107443.
[164] R.G. Abisado, S. Benomar, J.R. Klaus, A.A. Dandekar, J.R. Chandler, Bacterial quorum sensing and microbial community interactions, mBio 9 (5) (2018) e02331, 17, 2018 9.
[165] Q. Yin, M. Gu, S.W. Hermanowicz, H. Hu, G. Wu, Potential interactions between syntrophic bacteria and methanogens via type IV pili and quorum-sensing systems, Environ. Int. 138 (2020) 105650.
[166] L. Lv, W. Li, Z. Zheng, D. Li, N. Zhang, Exogenous acyl-homoserine lactones adjust community structures of bacteria and methanogens to ameliorate the performance of anaerobic granular sludge, J. Hazard Mater. 354 (2018) 72–80.
[167] Y. Zhang, J. Li, F. Liu, H. Yan, J. Li, X. Zhang, A.K. Jha, Specific quorum sensing signal molecules inducing the social behaviors of microbial populations in anaerobic digestion, Bioresour. Technol. 273 (2019) 185–195.
[168] U. Römling, M.Y. Galperin, M. Gomelsky, Cyclic di-GMP: the first 25 years of a universal bacterial second messenger, Microbiol. Mol. Biol. Rev. 77 (1) (2013) 1–52.
[169] T. Li, F. Guo, Y. Lin, Y. Li, G. Wu, Metagenomic analysis of quorum sensing systems in activated sludge and membrane biofilm of a full-scale membrane bioreactor, J. Water Proc. Eng. 32 (2019) 100952.
[170] H. Yan, J. Li, J. Meng, J. Li, A.K. Jha, Y. Zhang, X. Wang, Y. Fan, Insight into the effect of N-acyl-homoserine lactones-mediated quorum sensing on the microbial social behaviors in a UASB with the regulation of alkalinity, Sci. Total Environ. 800 (2021) 149413.
[171] H. Yan, J. Li, J. Meng, J. Li, A. Kumar Jha, Y. Zhang, Y. Fan, X. Wang, Effects of reflux ratio on the anaerobic sludge and microbial social behaviors in an expanded granular sludge bed reactor: from the perspective of acyl-homoserine lactones-mediated quorum sensing, Bioresour. Technol. 337 (2021) 125360.
[172] A.-E. Rotaru, P.M. Shrestha, F. Liu, M. Shrestha, D. Shrestha, M. Embree, K. Zengler, C. Wardman, K.P. Nevin, D.R. Lovley, A new model for electron flow during anaerobic digestion: direct interspecies electron transfer to methanosaeta for the reduction of carbon dioxide to methane, Energy Environ. Sci. 7 (1) (2014) 408–415.
[173] D.R. Lovley, Syntrophy goes electric: direct interspecies electron transfer, Annu. Rev. Microbiol. 71 (1) (2017) 643–664.
[174] Q. Yin, S. Yang, Z. Wang, L. Xing, G. Wu, Clarifying electron transfer and metagenomic analysis of microbial community in the methane production process with the addition of ferroferric oxide, Chem. Eng. J. 333 (2018) 216–225.
[175] Q. Gao, Q. Zhao, K. Wang, X. Li, H. Zhou, J. Ding, L. Li, Promoting methane production during anaerobic digestion with biochar: is it influenced by

quorum sensing? Chem. Eng. J. 483 (2024).
[176] Q. Yin, K. He, A. Liu, G. Wu, Enhanced system performance by dosing ferroferric oxide during the anaerobic treatment of tryptone-based high-strength wastewater, Appl. Microbiol. Biotechnol. 101 (9) (2017) 3929–3939.
[177] Z. Wang, W. Zhang, X. Xing, X. Li, D. Zheng, H. Bao, L. Xing, Effects of ferroferric oxide on propionate methanogenesis in sequencing batch reactors: microbial community structure and metagenomic analysis, Bioresour. Technol. 363 (2022) 127909.
[178] G. Wang, Q. Li, X. Gao, X.C. Wang, Synergetic promotion of syntrophic methane production from anaerobic digestion of complex organic wastes by biochar: performance and associated mechanisms, Bioresour. Technol. 250 (2018) 812–820.
[179] A. Doloman, M.S. Besteman, M.G. Sanders, D.Z. Sousa, Methanogenic partner influences cell aggregation and signalling of syntrophobacterium fumaroxidans, Appl. Microbiol. Biotechnol. 108 (1) (2024) 127.
[180] Y. Zhang, F. Liu, H. Liu, W. Zhang, J. Li, Exogenous N-hexanoyl-L-homoserine lactone assists in upflow anaerobic sludge blanket recovery from acetate accumulation via aceticlastic methanogens enrichment, Bioresour. Technol. 346 (2022) 126600.
[181] J. Li, F. Liu, J. Li, Y. Zhang, Regulation of endogenous acyl homoserine lactones by microbial density to enhance syntrophism of acetogens and methanogens in anaerobic digestion, Chem. Eng. J. 378 (2019) 122233.
[182] L. Lv, C. Feng, W. Li, Z. Ren, P. Wang, X. Liu, W. Gao, L. Sun, G. Zhang, Accelerated performance recovery of anaerobic granular sludge after temperature shock: rapid construction of protective barriers (EPS) to optimize microbial community composition base on quorum sensing, J. Clean. Prod. 392 (2023) 136243.
[183] H. Ma, S. Ma, W. Luo, L. Ding, J. Wang, H. Ren, Long-term exogenous addition of synthetic acyl homoserine lactone enhanced the anaerobic granulation process, Sci. Total Environ. 696 (2019) 133809.
[184] A.H. Li, B.C. Zhang, Z.W. He, C.C. Tang, A.J. Zhou, Y.X. Ren, Z. Li, A. Wang, W. Liu, Roles of quorum-sensing molecules in methane production from anaerobic digestion aided by biochar, J. Environ. Manag. 366 (2024) 121867.
[185] L. Lv, Z. Wei, C. Feng, J. Chen, W. Li, J. Bian, Z. Ren, G. Zhang, New insights into the persistent shock resistance of anaerobic granular sludge based on quorum sensing regulation: a novel gene regulatory mechanism, ACS ES&T Eng. (2024).
[186] S. Zhao, G. Song, S. Liu, J. Zhao, K. Zhao, S. Zhu, Y. Zeng, R. Liu, H. Liu, J. Qu, Anaerobic acidogenesis improvement and fermentation-type regulation by quorum sensing, ACS ES&T Eng. (2024).
[187] P. He, H. Duan, W. Han, Y. Liu, L. Shao, F. Lü, Responses of Methanosarcina barkeri to acetate stress, Biotechnol. Biofuels 12 (1) (2019).
[188] F. Liu, Y. Zhang, W. Shen, Z. Wu, J. Yang, Y. Zhang, J. Li, Y. Chen, Y. Zhang, Z. Yuan, Boron induced multiple quorum-sensing circuits in parallel to assist in anaerobic digestion recovery from volatile fatty acids accumulation, Chemosphere 362 (2024) 142640.
[189] Y. Chen, T. Chen, J. Yin, Impact of N-butyryl-l-homoserine lactone–mediated quorum sensing on acidogenic fermentation under saline conditions: insights into volatile fatty acids production and microbial community, Bioresour. Technol. 368 (2023) 128354.
[190] L. Lv, C. Feng, W. Li, G. Zhang, Z. Ren, X. Liu, X. Song, P. Wang, Exogenous N-acyl-homoserine lactones accelerate resuscitation of starved anaerobic granular sludge after long-term stagnation, Bioresour. Technol. 337 (2021) 125362.
[191] Y. Xiao, H. Yaohari, Z. Zhou, C.C. Sze, D.C. Stuckey, Autoinducer-2-mediated quorum sensing partially regulates the toxic shock response of anaerobic digestion, Water Res. 158 (2019) 94–105.
[192] S. Lee, S.K. Park, H. Kwon, S.H. Lee, K. Lee, C.H. Nahm, S.J. Jo, H.S. Oh, P.K. Park, K.H. Choo, C.H. Lee, T. Yi, Crossing the border between laboratory and field: bacterial quorum quenching for anti-biofouling strategy in an MBR, Environ. Sci. Technol. 50 (4) (2016) 1788–1795.
[193] J. Lee, Y.-J. Won, D.-C. Choi, S. Lee, P.-K. Park, K.-H. Choo, H.-S. Oh, C.-H. Lee, Micro-patterned membranes with enzymatic quorum quenching activity to control biofouling in an MBR for wastewater treatment, J. Membr. Sci. 592 (2019).
[194] K. Lee, S. Lee, S.H. Lee, S.R. Kim, H.S. Oh, P.K. Park, K.H. Choo, Y.W. Kim, J.K. Lee, C.H. Lee, Fungal quorum quenching: a paradigm shift for energy savings in membrane bioreactor (MBR) for wastewater treatment, Environ. Sci. Technol. 50 (20) (2016) 10914–10922.
[195] N.A. Weerasekara, K.H. Choo, C.H. Lee, Hybridization of physical cleaning and quorum quenching to minimize membrane biofouling and energy consumption in a membrane bioreactor, Water Res. 67 (2014) 1–10.
[196] N.A. Weerasekara, K.H. Choo, C.H. Lee, Biofouling control: bacterial quorum quenching versus chlorination in membrane bioreactors, Water Res. 103 (2016) 293–301.
[197] W. Dang, M. Li, W. Fu, K. Zhu, H. Liu, J. Yuan, W. Gao, G. Chen, Z. Wang, Effects of different N -acyl-serine lactone signaling molecules on the performance of anaerobic granular sludge, RSC Adv. 12 (9) (2022) 5439–5446.
[198] Y. Liu, W. Zhao, Y. Xi, S. Wang, J. Liang, Y. Zeng, W. Dong, K. Chen, H. Jia, X. Wu, Acyl homoserine lactone-based regulation strategy for improved methane production in anaerobic digestion of agricultural wastes, Appl. Energy 358 (2024) 122621.
[199] J. Liu, L. Wang, D. Lu, D. Wu, P. Zhang, Y. Zhou, Quorum quenching enhanced methane production in anaerobic systems – performance and mechanisms, Water Res. 235 (2023) 119841.