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Review

Photocatalytic/photoelectrocatalytic disinfection mediated the dissemination of antimicrobial resistance in aquatic environments

Yiwei Cai[1,2], Guiying Li[1,2], Po-Keung Wong[1,2], Huijun Zhao[1,2] and Taicheng An[1,2]

Photocatalytic (PC) and photoelectrocatalytic (PEC) disinfection are promising technologies for inactivating antibiotic-resistant bacteria (ARB) and degrading antibiotic resistance genes (ARGs). However, their role in the spread of antimicrobial resistance (AMR) is complex and ambiguous. This review provides a comprehensive summary of the dual role of PC/PEC technologies in controlling AMR dissemination. The significant effect of PC/PEC in eliminating ARB and destroying ARGs through mechanisms such as oxidative damage to cell membranes, proteins, and genetic material is first summarized. Furthermore, although optimal lethal treatment can inhibit horizontal gene transfer by inactivating donor/recipient cells and degrading genetic vectors, sub-lethal or non-optimal PC/PEC exposures may enhance ARGs transfer. Finally, key future research perspectives are highlighted, with emphasis on enhancing reactive oxygen species efficiency, mitigating dissolved organic matter fouling and mass-transfer constraints, and developing integrated strategies to ensure these technologies mitigate rather than exacerbate AMR spread.

Addresses

[1] Key Laboratory of Environmental Catalysis and Health Risk Control, Guangdong-Hong Kong-Macao Joint Laboratory for Contaminants Exposure and Health, Institute of Environmental Health and Pollution Control, Guangdong University of Technology, Guangzhou 510006, China

[2] Guangdong Basic Research Center of Excellence for Ecological Security and Green Development, Guangdong Technology Research Center for Photocatalytic Technology Integration and Equipment Engineering, School of Environmental Science and Engineering, Guangdong University of Technology, Guangzhou 510006, China

Corresponding author: An, Taicheng (antc99@gdut.edu.cn)

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Introduction

The overuse and misuse of antibiotics in human healthcare, agriculture, and aquaculture have greatly promoted the development and spread of antibiotic-resistant bacteria (ARB) and antibiotic resistance genes (ARGs) in various environments, particularly in water systems [1,2]. ARGs can spread between bacteria through horizontal gene transfer (HGT), including transformation, conjugation, and transduction. This enables the spread of antimicrobial resistance (AMR) beyond established vertical genetic routes and significantly exacerbates its environmental risk [3]. Traditional water disinfection methods, including chlorination, ultraviolet (UV) irradiation, and ozonation, have been widely used to inactivate pathogenic microorganisms [4,5]. However, the effectiveness of these methods in removing ARGs may be limited, and they might even induce bacterial stress responses due to sub-lethal damage to bacteria, thereby promoting HGT [6]. Therefore, there is an urgent need to develop alternative disinfection strategies that not only inactivate bacteria but also reduce the spread of ARGs.

Photocatalytic (PC) and photoelectrocatalytic (PEC) disinfection processes represent promising alternatives to traditional methods [7,8]. Compared to conventional disinfection methods such as chlorination and UV irradiation, PC and PEC processes offer several distinct advantages. These include strong oxidative capability through reactive oxygen species (ROS) generation with possible benefits for achieving both ARB inactivation and degradation of intracellular and extracellular ARGs (eARGs), minimal formation of toxic disinfection by-products, and the potential ability to utilize solar energy as a renewable light source. These advanced oxidation processes (AOPs) primarily utilize light-induced semiconductor materials to generate highly oxidative ROS, which can effectively inactivate a broad spectrum of microorganisms [9,10]. Our previous research has demonstrated that in-situ PEC can generate bactericides for the immediate inactivation and rapid degradation of Gram-negative bacteria [11]. A recent work has also demonstrated complete 7 log inactivation of *Staphylococcus aureus* within 8 minutes using an S-scheme

heterojunction catalyst under simulated solar light [12]. In addition, another finding confirms that new forms of effective bactericidal agents, such as halide radicals, can be generated in situ through a PC or PEC process for use in high-performance bactericidal systems [13,14]. In addition, the strong oxidative potential of ROS can degrade eARGs, thereby reducing the frequency of HGT [15]. Our previous research has clarified that during prolonged PEC inactivation, the leakage of cytoplasm and biomolecules (such as bacterial building blocks like nucleic acids and proteins) is significant. Furthermore, extending PEC treatment allows the leaked DNA to be further degraded and eventually mineralized, which indirectly inhibits the occurrence of HGT processes [16]. However, the interaction between disinfection processes and HGT is complex and ambiguous. Increasing evidence indicates that the impact of disinfection processes on microbial communities and the ARG pool is not merely 'removal' or 'inactivation'. Especially under sub-lethal conditions, bacteria activate a series of physical responses to deal with environmental oxidative stress, which may act as a "booster" for HGT [17,18]. For example, our recent research has confirmed that sub-lethal PC enhances the transformation process of ARGs in water [19]. This 'double-edged sword' effect makes it harder to assess the environmental safety of PC/PEC disinfection technologies.

Herein, this review aims to comprehensively summarize the current knowledge regarding PC and PEC processes in controlling the spread of AMR. We mainly focus on recent advances in ARB and ARG elimination, discuss the dual role of these processes in promoting or inhibiting HGT, and elucidate the related regulatory mechanisms involved. Finally, we provide perspectives to future research needs and technological improvements.

Advance in photocatalysis/photoelectrocatalysis in antibiotic-resistant bacteria inactivation and antibiotic resistance genes removal

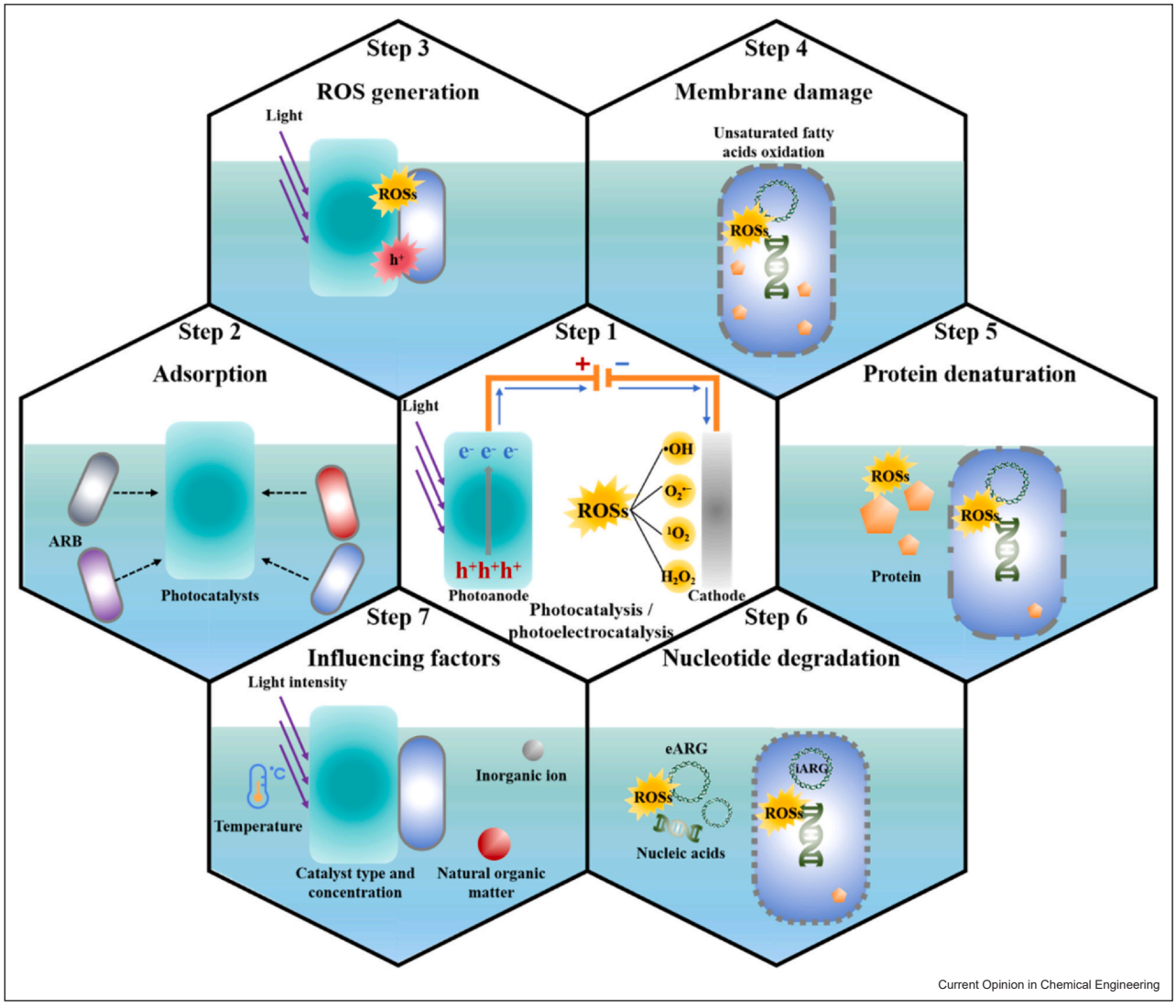
PC typically uses semiconductor materials that can create electron-hole pairs when exposed to suitable light. These charge carriers join in redox reactions to produce ROS, leading to the inactivation of ARB and the further decomposition of ARGs. PEC works as an improved version of PC by applying an electric voltage to the system [16]. This helps separate the charges more effectively and increases ROS production.

Many recent studies have confirmed that PC and PEC can successfully inactivate different types of ARB [20–22]. For instance, a new continuous-flow groundwater disinfection system using an In_2S_3/ $Mo_{4/3}B_{2-x}Tz$ photocatalyst was shown to remove 8.06 log of methicillin-resistant *S. aureus* within 15 minutes under visible light, even with low oxygen levels [20]. In addition, our recent study elucidated that modified graphitic carbon nitride, containing two dopants and nitrogen defects, showed improved and sustained ability to inactivate both Gram-negative *Escherichia coli* (resistant to gentamicin, cefotaxime, and polymyxin) and Gram-positive methicillin-resistant *S. aureus* [21]. We also successfully removed both tetracycline and tetracycline-resistant *E. coli* at the same time using a UVA-driven PEC system with TiO_2 nanotube arrays [23]. This evidence indicates that PC/PEC technologies hold great promise in controlling the prevalence of ARB in aquatic environments [24].

Recently, researchers have expanded to evaluate the potential of these technologies for simultaneously removing ARB and ARGs in aquatic environments. Several reports show that both ARB density and ARG abundance drop significantly after PC or PEC treatment. For instance, Wang et al. [25] observed a 7 log inactivation of sulfadoxine and ampicillin-resistant *E. coli* as well as complete degradation of intracellular ARG *sul1* starting from an initial concentration of 1.6×10^8 copies mL^{-1} after 80 minutes of COF-Ti_3C_2/visible-light treatment. Similarly, a novel supramolecular photocatalyst, SA-PDI@C60, has been reported to achieve 99.7% inactivation of *E. coli* carrying kanamycin resistance genes (*kanR*) and degradation of *kanR* by 5.80 log (from $1 \times 10^{5.8}$ mL^{-1} to < LOD) within 1 hour under sunlight irradiation [26]. Our previous research has also reported that some natural minerals possess the potential of photocatalysts, and they also exhibit excellent performance in ARB inactivation or ARGs degradation under sunlight irradiation [27]. Relevant evidence also indicates that hematite nanoparticles at environmental concentrations can reduce eARGs in aquatic environments by 3–5 orders of magnitude under visible light irradiation [28]. Therefore, PC and PEC show strong potential for killing ARB and degrading ARGs, indicating they could be widely used in future water pollution control.

The excellent antibacterial and ARGs degradation potential mentioned above may be attributed to the disinfection mechanism. The disinfection mechanism of PC/PEC technologies is a complex process and involves several pathways (Figure 1), mainly including the oxidative damage of ROS, the direct action of photogenerated holes, and the auxiliary effects of other physical and chemical factors [29,30]. Among them, ROS plays the most important role. ROS generated during the PC process mainly includes $^{\bullet}OH$, $O_2^{\bullet-}$, H_2O_2, and $^1O_2$ [9]. These reactive molecules, particularly $^{\bullet}OH$, are often strongly oxidizing and can effectively damage various components of bacterial cells. For the cell membrane, ROS can oxidize unsaturated fatty acids in the membrane to form lipid peroxides [31]. This

Figure 1



Bacterial inactivation processes and mediated mechanism of photocatalytic/photoelectrocatalytic disinfection.

damages the integrity of the membrane, leading to the leakage of intracellular substances (such as potassium ions and nucleic acids) (Figure 1). For proteins, ROS can oxidize amino acid residues (such as tyrosine and cysteine), leading to protein denaturation and inactivation of enzymes (such as ATP synthase) [16]. This disrupts cell metabolism and leads to the death of the cells (Figure 1). For nucleic acids, ROS can attack the phosphate backbone and base pairs, causing strand breaks and base oxidation of DNA (including intracellular ARGs) and RNA [32], and this destroys genetic information, including ARGs, and prevents cell proliferation (Figure 1). Therefore, PC removes ARGs through both direct and indirect pathways. ROS directly damages ARGs by breaking DNA strands and modifying bases, making the genes nonfunctional. Indirectly, killing host bacteria reduces the number of cells that can spread ARGs. In addition, the degradation of extracellular DNA (eDNA) will restrict the uptake of ARGs by other bacteria through the transformation process in HGT.

In PEC systems, the applied electric field improves the separation of photogenerated charges and changes where ROS are formed [33]. On the anode, photogenerated holes accumulate and directly oxidize organics and cell components. On the cathode, O_2 is converted into $O_2^{\bullet-}$, which can turn into H_2O_2 and $^{\bullet}OH$. The electric field helps concentrate these ROS near the electrode and

around microbial cells, making them more effective. Besides ROS and hole damage, the adhesion between catalysts and cells is also important. Materials with good hydrophilicity and high surface energy can adhere to cells better (Figure 1), bringing ROS closer to the targets and improving oxidative damage [25,34]. In addition, our previous research also elucidated that different types of ARB exhibit varying sensitivities to PC inactivation, which is due to the different intensity of the stress response mechanism of antibiotic resistance action targets [35].

Although these results are encouraging, the removal of ARB and ARGs can be affected by many factors. These include substances in the water (like natural organic matter and inorganic ions), light intensity, the type and amount of catalyst, and treatment time. Therefore, it is important to optimize these conditions to achieve the best removal performance of ARGs.

Dissemination of antimicrobial resistance during photocatalytic/photoelectrocatalytic disinfection

Although PC and PEC processes can effectively inactivate bacteria and degrade ARGs, their impact on the horizontal transfer of ARGs remains unclear. Increasing evidence suggests that these disinfection processes can either inhibit or promote HGT, depending on the treatment conditions and bacterial physiological state.

Photocatalytic/photoelectrocatalytic disinfection controlling antibiotic resistance gene transfer mechanism

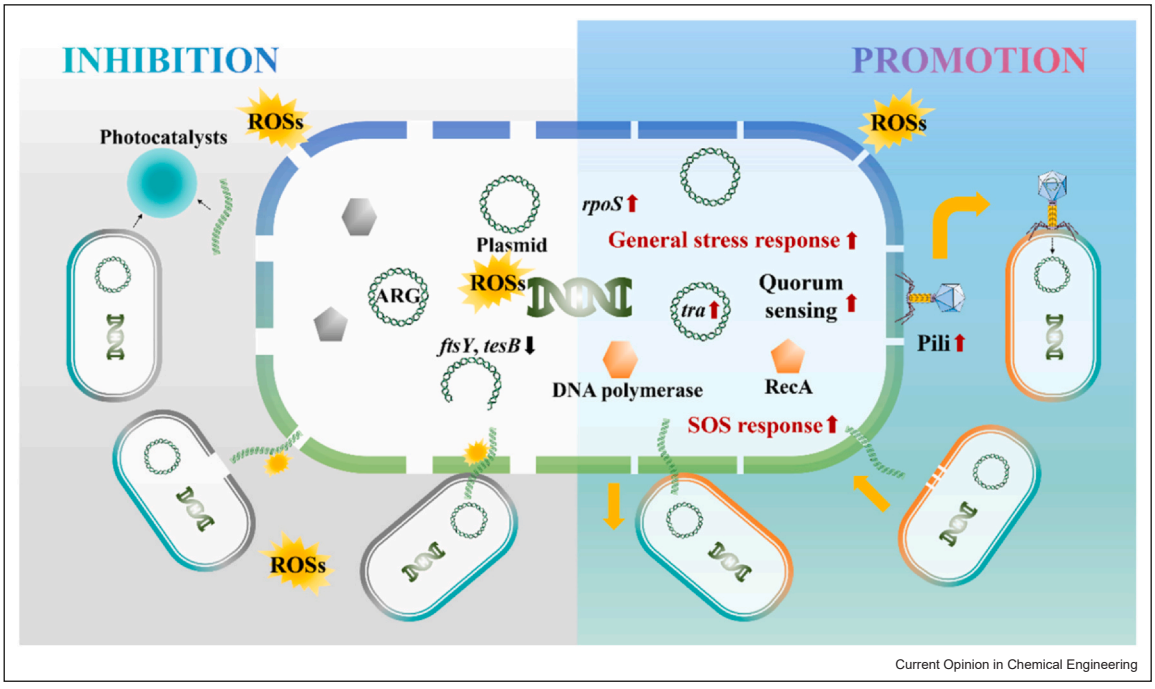
When conditions are optimal, PC can suppress HGT by killing bacterial cells and degrading free DNA. The ROS produced during this process creates strong oxidative stress that damages cell membranes, proteins, and genetic materials. This leads to bacterial death and the destruction of both plasmid and genomic DNA. For example, one study showed that C/O-g-C_3N_4 activating peroxydisulfate PC effectively inactivated ARB and inhibited the transformation of ARGs [36]. This suppression was attributed to the inactivation of donor cells and the degradation of ARG. Solar photo-Fenton process has also been proven to effectively remove free plasmid DNA harboring ARGs in wastewater, thereby reducing the risk of their transformative transfer [15]. In addition, our recent research indicates that PC can inhibit the emergence of multidrug-resistant bacterial populations in aquatic environments by restricting the conjugation of ARGs [37]. In PEC systems, the use of an external electric field further increases ROS production and improves contact between bacteria and the catalyst surface. This enhances the disruption of HGT. As reported by Liu et al. [38], a PEC-assisted Fenton system not only inactivated ARB but also reduced the transformation frequency of eARGs by destroying plasmids. Thus, appropriate PC/PEC conditions indeed demonstrate potential in controlling the spread of AMR.

However, improper, sub-lethal, or weaker natural PC may not restrict the spread of ARGs in aquatic environments and could even exacerbate the AMR problem. Sub-lethal PC or PEC can activate bacterial stress responses, such as the SOS response, which increases the expression of genes related to DNA repair and recombination. As a result, the frequency of conjugation and transformation may rise. For instance, we have shown that sub-lethal PC may induce ARB to enter a viable but non-culturable (VBNC) state, and that they can resume physiological metabolism after stress removal [39]. VBNC cells maintain metabolic activity and gene expression, but they cannot form colonies on standard culture media. This state allows bacteria to evade detection by conventional plate-count methods. Importantly, VBNC bacteria can revive under favorable conditions, regaining culturability and full metabolic function. When these cells revive, they may still be able to spread and acquire ARGs [6]. We have also confirmed that sub-lethal PC promotes the horizontal transfer of ARGs through dual mechanisms — conjugation and transformation [40]. Another of our studies also found that the promotion of ARG conjugative transfer was observed during the early stage of lethal PC disinfection [35]. Therefore, PC is likely to have a 'reverse-hormetic effect' on the horizontal transfer of ARGs, meaning that sub-lethal, mild, or transient treatments promote the spread of antibiotic resistance. It is also worth noting that beyond engineered PC systems, natural photochemical processes occurring in sunlit surface waters may also influence the fate of ARGs. On one hand, photoactive minerals such as sphalerite, pyrrhotite, hematite, and goethite can generate low levels of ROS under light irradiation [41–43]. On the other hand, dissolved organic matter (DOM) can act as a photosensitizer, producing reactive intermediates that may also contribute to the degradation of eARGs [44,45]. However, these natural photosensitization processes typically generate relatively low levels of ROS, which may induce sub-lethal oxidative stress in bacteria rather than complete inactivation, potentially influencing ARG dissemination in natural aquatic environments. Further research is needed to assess the ecological implications of these natural PC processes on the environmental dissemination of antimicrobial resistance.

Effects of photocatalysis/photoelectrocatalysis on antibiotic resistance gene transfer

PC and PEC can both inhibit and promote the transfer of ARGs. This depends on various factors like the disinfection system used, the state of the microbes, and the characteristics of the ARGs themselves.

Figure 2



Effects of photocatalytic/photoelectrocatalytic disinfection on ARG transfer.

Inhibitory effects of photocatalysis/photoelectrocatalysis on antibiotic resistance gene transfer

PC and PEC processes can inhibit ARG transfer through several key mechanisms: First, ROS generated during these processes cause significant oxidative damage. ROS can break the phosphodiester bonds and directly oxidize nucleobases in ARG sequences (Figure 2), leading to gene degradation and loss of transfer capability [46,47]. In addition, plasmids, transposons, and integrons are the main vectors for ARGs horizontal transfer, among which plasmids play a dominant role in conjugation [48]. PC/PEC treatment damages these carriers by directly oxidizing their nucleic acid structures. For example, PC can break plasmid DNA strands (Figure 2), preventing bacterial replication and transfer. Research has confirmed that after photocatalyzed treatment with H_2O_2 + O_3, the structure of microbial plasmids is extensively degraded [49]. Second, both donor and recipient bacteria can be inactivated [50]. ROS generated by PC/PEC systems can damage bacterial cell membranes, denature proteins (inactivation of transfer-related enzymes), and destroy nucleic acids. This kills ARG-carrying bacteria and reduces the number of participants in HGT (Figure 2). Third, photocatalysts exhibit excellent adsorption performance [25,47]. As noted previously, photocatalysts can adsorb both free ARGs and microorganisms, preventing contact between donor and recipient bacteria (Figure 2). Fourth, ARG transfer-related genes are also downregulated [40,51]. Under exposure to high levels of ROS, the PC/PEC system inhibits the expression of HGT-related genes (Figure 2), such as conjugative transfer regulators *ftsY* and *tesB* as well as the recombinase *recA*, which is essential for ARGs transformative transfer.

Promotional effects of photocatalysis/photoelectrocatalysis on antibiotic resistance gene transfer

The regulatory mechanisms underlying the enhanced HGT under PC/PEC also involve several bacterial response pathways. First, sub-lethal ROS exposure can trigger the SOS response, leading to the expression of recombinase RecA and error-prone DNA polymerases (Figure 2). This response facilitates DNA repair but also promotes homologous recombination and conjugative transfer [52,53]. In addition, sub-lethal PC/PEC treatments can trigger bacterial general stress responses, and bacteria will activate a series of regulatory mechanisms to adapt to adverse environments, thereby inadvertently promoting the HGT of ARGs (Figure 2). For example, sub-lethal stress can cause overproduction of global regulatory genes (such as *rpoS*). These genes not only help bacteria withstand stress but also increase the activity of transfer-related genes (such as *tra* genes on plasmids), thereby enhancing conjugative transfer [54,55]. Second, sub-lethal PC/PEC treatment can cause mild damage to the bacterial cell membrane, increasing

its permeability without causing cell lysis. This increased permeability allows more DNA (including eARG) to enter cells more easily (Figure 2), promoting the transformation process of ARGs [56,57]. At the same time, more permeable membranes facilitate formation of conjugation channels between donor and recipient bacteria and enhance plasmid transfer (Figure 2), increasing the frequency of conjugative ARG transfer [40,58,59]. In addition, there is evidence that extracellular ROS generated by moderate PC treatment can increase outer membrane permeability, which can facilitate phage infection. Increased pili synthesis induced by intracellular ROS provides more sites for phage recognition and invasion (Figure 2), thereby promoting phage-mediated transduction of ARGs [60]. Third, oxidative stress can affect bacterial communication systems like quorum sensing, which controls conjugative plasmid transfer [61]. For example, quorum-sensing C12-HSL accelerated the conjugative transfer of antibiotic resistance plasmids through membrane remodeling, oxidative stress, and RpoS-RMF crosstalk [62]. Fourth, ROS can also alter the activity of HGT-related genes, including those controlling conjugation machinery (like pilus formation) and DNA uptake systems [63,64].

Understanding these mechanisms is essential for developing next-generation disinfection methods that reduce AMR spread. For instance, ensuring complete bacterial inactivation and avoiding sub-lethal treatment levels can minimize stress responses that promote HGT.

Conclusions and perspective

PC and PEC disinfection processes show great potential to eliminate microbial contamination and reduce the abundance of ARB and ARGs in water. However, their dual role in either inhibiting or promoting the HGT of ARGs highlights the complexity of applying these technologies in the context of combating AMR.

To better use PC and PEC for controlling AMR dissemination, future research should focus on: (1) Enhancing the research on the mechanism of PC/PEC mitigation of ARGs horizontal transfer in complex aquatic environments, such as municipal wastewater, hospital effluents, industrial wastewater, and livestock wastewater. By simulating real engineered systems, we can better understand the interaction between the system and complex pollutants and microbial communities, and how these factors influence HGT; (2) Developing improved photocatalysts. We need to create more suitable catalysts that are highly efficient, durable, and reusable, improving their design and composition to boost performance and lower costs. Specific design priorities to address ARG dissemination risks include: (a) enhancing ROS generation efficiency to achieve rapid, complete bacterial inactivation and avoid sub-lethal stress responses; (b) mitigating fouling by DOM to maintain activity in real water matrices; (c) minimizing mass-transfer limitations to prevent localized sub-lethal ROS zones; (d) ensuring degradation of intracellular ARGs; (e) preventing catalyst leaching; and (f) using earth-abundant minerals to ensure cost-effectiveness and sustainability; (3) Establishing a comprehensive evaluation system for the ecological risks of PC/PEC disinfection. It is important to assess potential ecological risks, such as any toxic effects from treatment by-products or leftover catalyst materials, to ensure safe practical application. (4) Combining PC/PEC disinfection with other water treatment methods. Integrating these processes with existing technologies (like biological treatment or membrane filtration) could enhance overall performance and provide more reliable control over ARG spread.

In conclusion, while PC/PEC disinfection processes are promising tools for reducing the spread of AMR, they must be used wisely to avoid unintended problems. A deeper understanding of the underlying mechanisms and ecological impacts will be essential for the sustainable implementation of these technologies in water treatment systems.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

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

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