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Microalgae-bacteria consortia for organic pollutants remediation from wastewater: A critical review

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ABSTRACT

Organic pollutants (OPs) discharged via wastewater can severely impact public health, natural habitat, and environment in long term. The microalgae-bacteria consortia (MBC) demonstrates its potential as a sustainable bioremediation method for organic pollutants remediation from wastewater. The overarching goal of this study is to review (i) the formation of microalgae and bacteria consortia, (ii) the mechanism of MBC in OCs removal, (iii) the effects of operating conditions on the treatment efficiency, and (iv) the omics approach of MBC for removing OCs in wastewater. The review provides further insights into the application of omics techniques to identify microalgae-bacteria interaction in the consortia. Transcriptomics and metabolomics have elucidated the response of MBC to the impact of culturing conditions and presence of OCs in wastewater. Metagenomics identifies the four dominating-algal strains and observing microbial dynamics during ciprofloxacin treatment. The data of omics approach provide a strong support for upscaling MBC for OCs remediation in wastewater.

1. Introduction

There has been an increasing demand for clean water worldwide as freshwater accounts for only 1 % of all water on earth [1]. The drinkable water resource is deteriorating because of excessive usage for industrial purposes and pollution from wastewater. For example, the textile, food processing, pharmaceutical industries consume excessive clean water to produce a kilogram of products and subsequently release a considerable volume of wastewater into the environment. Organic pollutants (OPs) are unavoidable by-products that are generated from the manufacturing processes of raw materials and semi-finished products. These toxic OPs (i.e., pharmaceuticals, pesticides, herbicides, polyaromatic hydrocarbons, surfactants, and phenolic compounds) can severely impact the natural habitat and environment in the long term [2]. Hence, it is critically important to remove OPs in wastewater to a safe level before discharging.

Various technologies have been in practice for that purpose, such as hydrolysis, thermal degradation, and advanced oxidation processes, which ultimately end up OPs in biogas, compost, and biochar [3,4]. However, those technologies are known to associate with secondary pollution, high energy requirements, and therefore being costly. For example, the incineration of OPs having high moisture content can release dioxins [4]. In this sense, bioprocess technologies such as microalgae and bacteria are sustainable approach for sustainable and widespread application [5]. It is worthy to note that the microalgae-bacteria consortia (MBC) is more prominent than a solely bacterial or algal system [6]. In the MBC, microalgae can produce oxygen that is used by bacteria for their respiration, while CO_2 released by bacterial respiration can be subject to photosynthesis by microalgae [7], in which leverage the benefit of MBC for wastewater treatment purpose. Though the benefit of MBC is substantial, its application is constrained by a complex matrix of wastewater (e.g., pH, nutrient level,

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interferences). A pretreatment stage such as thermal, chemical, enzymatic, and fungal is required to transform the waste into a suitable medium for the proliferation of MBC. At a higher vision, MBC can contribute to a circular economy and the sustainable development of food industries via the production of valuable by-products such as biogas and biomass.

Recently, there have been reviews on the cultivation of MBC-based anaerobic digestion for wastewater treatment [8,9]. Fallahi *et al.* [10] and Aditya *et al.* [6] reviewed the nutrient removal capacity (e.g., nitrogen and phosphorus) of MBC in different wastewater matrices, such as domestic, industrial, and agro-industrial wastewater. Eheneden *et al.* [11] review the metabolic pathways and microbial responses of MBC on the antibiotic removal in wastewater treatment. In turn, Zhao *et al.* [12] focus on the symbiosis of MBC for a specific application in heavy metals remediation. The application of MBC in carbon capture and swine wastewater treatment were also reported [13,14].

However, a comprehensive review on a wide range of OPs remediation from wastewater have not been conducted yet, especially looking into omics of the MBC, to understand the mechanistic interaction of MBCs in wastewater. There is a critical need to investigate the formation of MBC, remediation mechanisms of MBC that stressed by OPs in wastewater. In addition, the viable usage of the MBC requires an insightful understanding of the wastewater matrix, operating conditions, the interaction of microalgae and bacteria, as well as molecular biology.

This review focuses on (i) the formation of MBC, (ii) the mechanism of MBC in OPs removal, (iii) the effects of operating conditions on OPs remediation, and (iv) the omics investigation of MBC for OPs removal in wastewater. This review presents the entire pathways of OPs removal in wastewater treatment using MBC from formation of the consortium to operational parameters and omics approaches.

2. Effects of organic pollutants to formation and interaction of microalgae-bacteria consortium

The consortium of algae and bacteria has been reported in three main forms of commensalism, mutualism, and parasitism. Commensalism is the relationship of two species that one strain gains nutrients and supports from the other with neither damages nor benefits. On the other hand, mutualism is a relationship with a benefit exchange of two species. For example, this relationship is demonstrated in the synthesis and delivery of vitamin B_{12} in the consortium of *Chlamydomonas reinhardtii*-heterotrophic bacteria. The green algae is responsible for producing two enzymes for vitamin B_{12}: vitamin B_{12}-independent (METE) and dependent (METH) methionine synthases; while heterotrophic bacteria are responsible for the delivery of vitamin B_{12} [15]. The last form of MBC is parasitism which is the relationship in which one species gains benefits but compromises their partner's growth.

The endosymbiotic theory proposes that cyanobacteria integration as plastid in eukaryotic algae. Algae allow bacteria to reside on their cellular surface in extracellular interaction zones (phycosphere), in which bacteria live as commensal and mutual creatures on algae [5]. Bacteria are also attached to algae and vice versa in the *Phaeodactylum tricornutum*-bacteria consortium, which fosters carbon fixation at a rate enhanced by two-thirds compared to a single algal culture [16]. In MBC, microalgae can provide a living habitat and nutrients such as carbohydrates, proteins, and lipids for bacteria. On the other hand, extracellular metabolites generated by bacteria, such as hormones and vitamins, are essential for algal growth [17]. On this basis, the mutual growth of algae and bacteria can enhance the degradation of antibiotics, which results in the improvement of antibiotic removal by the MBC.

2.1. Effects to physical forms

2.1.1. Granular MBC

Granular MBC is one of the most popular physical forms of MBC in which microalgae attach bacteria to their surface to generate a granular shape. Granular MBC is a dynamic biological process that commences with an initial linkage of bacteria and microalgae through fluid dynamic shear force. This linkage creates a sphere in which bacteria and microalgae attach to each other. The structure of the spheres is compact with a smooth surface and yellowish-brown appearance. Extracellular polymer substances (EPS) play an integral part in generating granules [18]. These substances can support microorganisms entangle with the others by establishing a gel-like network of cross-linked chains. The exoprotein in EPS can promote the attachment of microorganisms via hydrophobicity and aromatic stacking. Additionally, the generation of a gel-like network by EPS can contribute to the stability of MBC suspension, which can prevent the settlement of MBC. The granular MBC size can develop from 100 to 5500 μm, and one microalgae cell can attach up to eight bacteria cells [19].

The symbiotic relationship of bacteria and microalgae enhances granular MBC establishment and proliferation. The irregular, loose structure, and the green appearance of granular MBC result from the formation of an MBC sphere with slow and environmentally sensitive bacteria at the core of the granular [20]. The development of granular MBC stops when the association and dissociation of bacteria and microalgae reach equilibrium [21].

The formation of granular MBC can be affected by the presence of OPs, Wang *et al.* [22] indicated that the protein concentrations of microalgae increased when there are antibiotics and surfactants presented. It can be ascribed to the increment of protein synthesis to deal with oxidative stress and ensure microalgae growth in the consortia. However, these proteins did not contribute to antibiotic degradation, mainly in the cell metabolism pathways [22].

2.1.2. Biofilm MBC

The formation of MBC biofilm initiates with microalgae's attachment onto a surface of a bacterial biofilms. The adhesion of microalgae is affected by several factors such as physical attributes (free energy, surface roughness, and contact angle), pH, and the occurrence of bacteria on the surface. The attachment of microalgae onto the surface of the bacterial biofilms is reversible because microalgae can be easily detached [23]. The external conditions, microbial density, and substratum material should be considered to improve microalgae attachment. Biofilm thickening is the place where bacteria and microalgae proliferate [24]. The autotrophic activity of microalgae improves biofilm thickness on the external layer, and also enhances heterotrophic activity of bacteria and microalgae. Furthermore, extracellular polymer released by microorganisms on the surface improves the thickness and stability of biofilm [23]. In the biofilm of MBC, algae require light for their growth, while bacteria reside and grow in the biofilm by the oxygenic provision of algae. The biofilm MBC can keep the oxygen supply inside without requiring external oxygen provision.

Regarding OPs, both microalgae and bacteria can remediate the OPs by themselves. Microalgae also connect with other microorganisms to accommodate bacteria while bacteria supply growth factors for microalgae. Both types of microorganisms release the removal of OPs is further leveraged by the MBC biofilm. Biofilm in the MBC can be developed via photo-rotating biological contactor [25]. In detail, biofilm act as a host for various removal mechanisms, such as adsorption to biofilm, biodegradation, photodegradation and volatilization [26]. The biofilm of MBC can degrade OPs via nutrient transfer between algae and bacteria [27]. Bacteria oxidize OPs, while microalgae bind these substances to their carbon skeleton via the photosynthesis process [27]. Bacteria can resist to antibiotics by co-metabolism; nevertheless, algae have the higher antibiotic capabilities than bacteria [28].

2.1.3. Floc MBC

The floc MBC relates to a weak interaction between microbes and microalgae in flexible shapes and loose configurations [19]. Specifically, various aerobic bacteria facilitate microbial flocculation of bacterial

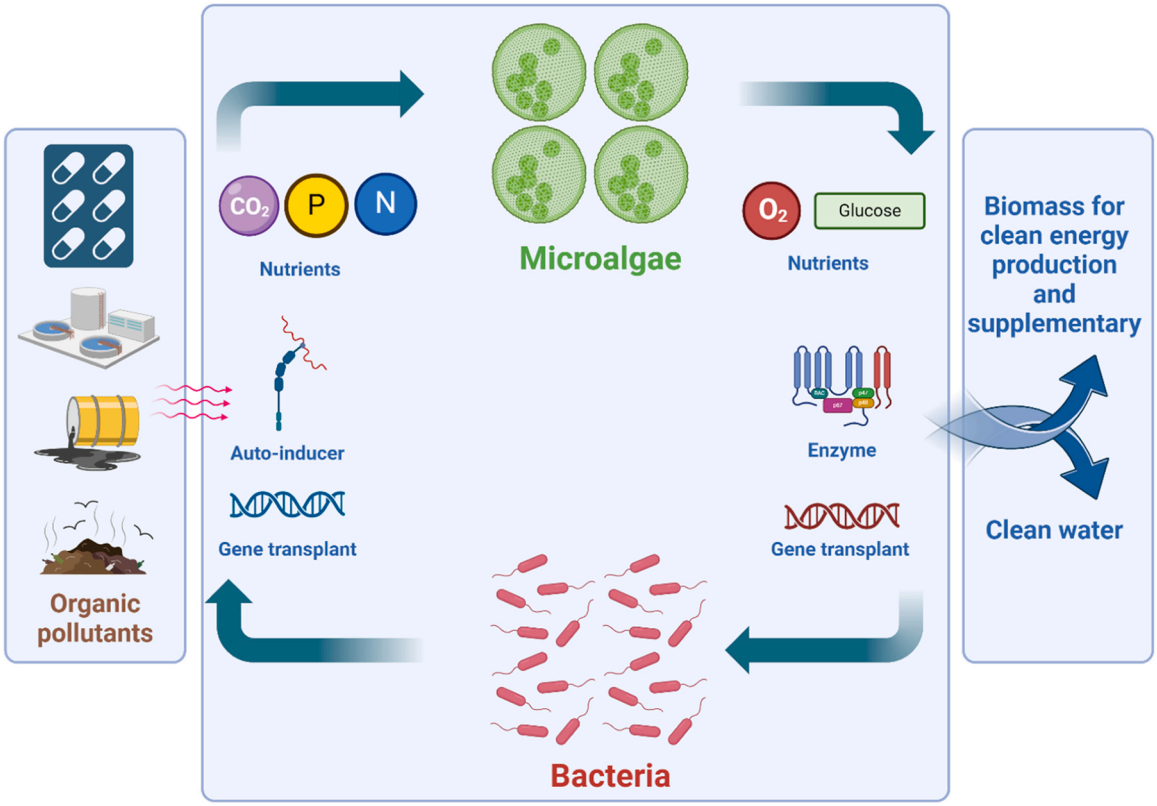

Fig. 1. The interaction between microalgae and bacteria in removing OPs from industrial wastewater.

cells. The formation of floc MBC starts with bacteria-secreted extracellular polymer in the medium. The bacteria flocculation is promoted with increasing extracellular polymer secretion, which is linked with the space availability within bio-floc [29]. Bacteria adhere to the microalgae surface to generate a greater biofilm, which promotes the attachment of microalgae around biofilm until the floc size is proper for gravity auto-flocculation [29]. Moreover, the flocculation process is influenced by changes in microalgal surface attributes such as pH, dissolved oxygen, nitrogen, and magnesium content [30]. When floc-forming bacteria considerably outweigh filamentous ones, pinpoint floc generation occurs. Contrastingly, the figure for filamentous bacteria is significantly larger than that of floc-forming bacteria, leading to the generation of filamentous bulking [31].

To date, there are very rare studies about the effects of OPs on the formation of MBC floc. Zhou *et al.* [32] reported self-suspended MBC particles that can increase tetracycline degradation up to 74 %, due to 20.4 % increase in EPS production in the MBC. The floc of MBC should also act as the host for OPs degradation, such as granular and biofilm. The floc always tends to float on the upper part, whereas the granular has a better settleability [33]. Floc has a smaller size, looser, and less compacted structure than the granular resulting in less internal micro-environments. Therefore, floc is likely less pronounced than granular for OPs remediation, similar with other conventional pollutants.

2.2. *Effects to interactions*

The interaction of microalgae and bacteria in the MBC is sophisticated due to their high level of biodiversity. That complicated interaction has been unveiled by advanced techniques, like a next-generation sequencing methods, providing critical understanding into the cellular activity of the MBC, at the level of molecules and genes [34,35]. The effect of OPs to MBC interaction results in two different ways to respond by the MBC: short-term response and long-term response.

Regarding short-term responses, OPs can induce oxidative stress, changes in photosynthesis, and other metabolism processes, including protein, lipid, and nucleic acid synthesis [36]. Bacteria adapt to OPs toxicity via the adjustment of enzyme activities, sequestration, bioaccumulation, target site amplification, efflux pump mechanisms, cell walls, and cell membrane modification. Organic pollutants activate SOS mechanisms in bacteria by causing the expression of DNA protective proteins. These proteins ensure DNA integrity and correct error parts, which enhance viability and enable continuous replication [11]. Laughlin *et al.* [37] proposed that the oxidative stress induced by OPs can increase the production of antioxidant enzymes, such as superoxide dismutase and glutathione reductase. By using enzymatic functionality, bacteria can ensure their proliferation and develop pathways for antibiotic degradation. Organic pollutants can disrupt the electron transport chains (ETC) across the thylakoid membrane of microalgae, activating the generation and build-up of free radicals in ETC. This effect can interfere with ATP production by acting as an obstacle to electrochemical potential from PS II to PS I or ATP synthase [11]. The maximal electron transport rates in PS II and PS I in *Microcystis aeruginosa* declined from 71 % to 24.3 %, respectively, when erythromycin concentration was 25 mg/L.

Regarding long-term response, MBC can change their community structure to adapt to OPs stress. When OPs present, the species with high resistance and lower abundance can become popular over time. For instance, the most substantial shift in microbial community structure is initiated at the genus level, followed by alteration in the family one during the elimination of erythromycin, sulfamethoxazole, and tetracycline [38]. Oxytetracycline and sulfamethoxazole encourage the proliferation of polyphosphate-accumulating bacteria during the removal of sulfamethoxazole and oxytetracycline [39]. Additionally, the adaptive response to OPs causes the occurrence of genes for the survival of bacterial communities. The bacterial response to OPs is related to the chemoreceptors in cell membranes and two-component regulatory systems. These systems are capable of modifying the components of cell

surfaces, which activate antibiotic efflux pump systems and produce enzymes that metabolize OPs. As a result, the biofilm formation is stimulated, which facilitates the flocculation of bacteria to resist OPs [40].

Overall, the short-term effect of OPs enhances protoplasmic responses of microalgae and bacteria cells, while long-term OPs effects alter the whole MBC structures [41]. It is noted that to change the community structure of MBC, the dose of OPs might need to be at a relatively high level, for example, up to 100 mg/L of sulfamethoxazole and tetracycline [38,41]; because at low OPs dose such as 1 mg/L of oxytetracycline and ofloxacin, they supports the growth of MBC. In addition, the required exposure time to change the MBC community structure is also expected to be up to 10d [11].

2.2.1. Nutrient transfer

Nutrient transfer between microalgae and bacteria influences their proliferation rate through supplying nutrients or nutrient competition between them. The nutrient interaction between microalgae and bacteria should be considered because it impacts the formation and stability of MBC (Fig. 1).

In MBC, microalgae use the organic nutrients and other trace elements to produce macromolecules, such as polyphosphates, proteins, carboxylic acids, and polysaccharides through the photosynthesis process, then these molecules play a role as naturally occurring reducing and capping agents for the bacterial deterioration and production of valuable products such as nanoparticles [42]. The addition of OPs, such as antibiotics, at low doses improves the growth of MBC, as previously mentioned. In terms of nutrient transfer, the low dose of OPs stimulates the carbohydrate production of microalgae (up to 17 %), which then mutually assists the growth of bacteria [43].

Microalgae also connect with other microorganisms to accommodate bacteria while bacteria supply growth factors for microalgae. Both types of microorganisms release digestive enzymes, including sulfatase, glucosidase, galactosidase, and phosphatase, to degrade macromolecules. The macromolecules are broken down into smaller molecules and then are taken up by the passive and active transport processes of MBC. After that, these molecules are used by MBC to synthesize a range of factors such as vitamins, hormones, and siderophores by bacteria, while amino acids and other cofactors by microalgae [14]. After that, these synthesized molecules are released to MBC through a diffusion mechanism. For instance, Kong et al., 2023 presented that ammonia-oxidizing bacteria employed the hydrolysate of extracellular protein from *Chlorella*, while *Chlorella* used nitrite, which is reduced and released by ammonia-oxidizing bacteria to culture [44]. *M. aquaticum* was reported to use indole acetic acid as a nitrogen source, which is released into culture through the diffusion mechanism of *Chlamydomonas*. This consumption reduces the chlorophyll degradation; thus reaching mutual symbiosis [45]. On that basis, the low dose of OPs will promote the production of those products, similar to carbohydrates, to benefit bacteria; however, it is noted that the excessive OPs can inhibit both microalgae and bacteria cells, then ultimately compromise the nutrient transfer process in MBC.

2.2.2. Cell-to-cell communication

Cell-to-cell interaction is vital in consortium systems and influences different physiological processes like nutrient uptake, bio-formation, and stability of the consortia [46]. The cell-to-cell communication in MBC can be conducted by quorum sensing which is the process bacteria release signaling molecules such as auto-inducers and acyl homoserin lactones to communicate with others in the consortia [47]. These signaling molecules assist bacteria in presenting coordinated gene expression in a population-reliant behavior.

Microalgae can identify auto-inducers and acyl homoserin lactones and show positive or negative responses. For instance, *Pseudoalteromonas* sp. AS25, with 10^2 cells/mL, releases algicidal substances such as urocanic acids that can prevent the growth of *Skeletonema costatum* in their consortium [48]. Oxidase and acylase can inactivate the homoserine lactone rings, thereby negatively influencing bacteria behavior [35]. In another study, investigating MBC sludge demonstrated that the content of acyl-homoserine lactones directly impacts the ability of microbial attachments and consortium stability. Most MBC are *Acinetobacter*, *Flavobacterium,* and *Chryseobacterium,* which increase the generation of acyl homoserin lactones and extracellular polymeric substances (EPS) [48]. Chen *et al.* [49] showed the increasing production of indoleacetic acid (signaling molecules) in the MBC of bacteria and *C. vulgaris* under light and dark environments. This result verifies that indoleacetic acid can boost the MBC performance and promote the algae growth and lipid production [49].

Regarding the effect of OPs, studies have not investigated the specific change of cell-to-cell communication. However, the general trend is that the increase of OPs presented in the culture would compromise the overall activities of MBC, including cell-to-cell communication.

2.2.3. Gene transfer

Gene transfer refers to the horizontal transfer of a gene in consortia, which has a vital role in evolutionary processes [50]. Horizontal gene transfer (HGTF) is the exchange of genetic materials between bacteria and algae. Anti-organic pollutant genes, such as antibiotic-resistant genes are contained in mobile genetic elements, including plasmids and integrons. There are three ways of HGTF: transduction, conjugation, and transformation. Gene conjugation is the main path of HGTF in which bacteria and algae directly contact each other for DNA transfer. Transduction refers to the transfer of DNA through bacteriophages. The transformation is the process in which short DNA fragments are received by naturally competent bacteria [51].

A couple of substances that participated in the gene transfer of MBC in wastewater, such as eustigmatophyte operon, α-amylase, and α-glycosides. Yurchenko *et al.* [52] also indicated the signal of eustigmatophyte operon transfer between *Phycorickettsia* and bacteria is due to the close relation of eustigmatophyte operon in microalgae to bacteria. It was reported the transfer of α-amylase gene from actinobacterium to the genomes of *Porphyridium purpureum* via conjugation [53]. This transfer can provide the hydrolysis of α-glycosides for *Porphyridium purpureum*, which improves the polysaccharide hydrolysis. The increased polysaccharide hydrolysis can boost the consumption and metabolism of carbohydrates in MBC, increasing the capability of nutrients in wastewater.

Similar to the cell-to-cell communication, there have not been a clear understanding of the effect of OPs on the gene transfer in MBC, which requires further investigation.

3. Mechanism of organic pollutants remediation from wastewater by MBC

Most of the current research focus on the single role of microalgae and bacteria in the degradation of OPs, there is no collective report in an algal-bacterial community. The following sections are dedicated to the sole role of microalgae and bacteria. Basically, the remediation of OPs happens via three main mechanisms in MBC, including biosorption, bioaccumulation, and biodegradation. From one hand, the metabolic potential of microorganisms to biologically transform OPs is essential for the bioremediation process. On the other hand, the success and type of process in bioremediation depends on the bioavailable fractions of OPs. To what extent the OPs are subject to which mechanisms depending on characteristic of the OPs themselves, such as hydrophobicity, chemical structure, toxicity.

3.1. Bacterial remediation

Organic pollutants are degraded via different stages and mechanisms, including biosorption, bioaccumulation, and biodegradation. The adsorption onto the cell wall is an extracellular process, while

bioaccumulation is an intracellular one. Biodegradation is subject to both external and internal processes.

3.1.1. Biosorption

The term "sorption" is used for both absorption (phase change in substance level) and adsorption (surface adherence at the molecular level). Biosorption is a biphasic process of adsorption that can be either metabolic-dependent and independent. Metabolic-dependent adsorption is slow and strongly related to the metabolic energy [54]. In contrast, metabolic-independent adsorption is a physical process in which functional groups on the bacterial cell wall interact with organic pollutant molecules based on van der Waals, electrostatic, and hydrophobic interactions. Organic pollutants are transferred from the aqueous phase to attach to the cell wall surface.

The extent of this process in pollutant removal is determined by the chemical characteristics of the specific pollutants and extracellular components of bacterial cells, consisting of cell walls, EPS, and biosurfactant secretion. The presence of negatively charged functional groups (such as carboxyl, hydroxyl, and phosphoryl) in cell walls causes the accumulation of negative charges on bacterial surfaces, which attracts cationic groups of pollutants through electrostatic interactions [55]. Surface complexation is the main mechanism of cells to bind with carboxyl groups, while electrostatic interactions are applicable for amino groups. There are other studies in which hydrophobic interaction and van der Waals forces are involved in the biosorption of OPs [56–58].

The EPS has a functional role not only for the structural stability of MBC but also for the surface properties and ecological functions [59]. In addition to the cell surface, EPS has a sorption role in MBC. Various functional groups (such as proteins and polysaccharides) with different charges in the structural constituents of EPS cause a complex natural structure with wide affinities and specificities to adsorb OPs [60]. However, EPS is generally considered a negatively charged substance that contributes to the adsorption of positively charged OPs [61]. Different field factors (such as bioavailability, adsorption, and mass transfer) in the biosorption of OPs can be modified by biosurfactant secretion. For instance, higher polycyclic aromatic hydrocarbons (PAHs) having four- and five-ring PAHs are low in water solubility, which causes a low rate of adsorption. Biosurfactants in bacterial mediums provide more hydrophilicity for OPs, which alters bioavailability [62].

3.1.2. Bioaccumulation

Bioaccumulation occurs when OPs penetrate inside the cells by crossing cell membranes and accumulate within cells without changing their chemical structure [55]. Bioaccumulation was a preferred metabolic pathway for antibiotic uptake [63]. OPs are transported by two kinds of passive and active transmembrane transport processes. In passive transport, the mechanisms of simple (free) diffusion and alienation diffusion are based on the concentration gradient of OPs between the inside and outside of cells.

In active transport, the transport proteins are involved in the membrane at the expense of energy. This process, which is selective and specific, can be against the concentration gradient. Passive and active diffusion was observed for the transmembrane transport processes of naphthalene and fluoranthene across the membrane of *Pseudomonas putida* PpG1064 and *Rhodococcus* sp. BAP-1, respectively [64].

Accumulation causes the changes in the permeability and disruption of the cell membrane. This phenomenon was seen in the bioaccumulation of levofloxacin [65]. The accumulation process may further bind OPs to cellular constituents such as proteins, which may cause an increase in antioxidant responses [60]. The intracellular presence of OPs can induce antioxidant response and degradation to restore cell balance, in which biodegradation can be considered a pre-step [61]. Bioaccumulation and biotransformation were observed for 5-methyl--benzotriazol, benzotriazol, and lidocaine [66].

3.1.3. Biodegradation

The metabolization of the biodegradation process breaks down the complex OPs into intermediate metabolites, which can be continually transformed into simpler structural components**.** Biodegradation of OPs occurs in the cells through two main mechanisms: metabolic degradation and cometabolism. OPs act as a carbon source for cells in metabolic degradation, while cells need a main substrate source to degrade OPs in the co-metabolization process [67]. Metabolization of OPs is diverse, such as aerobic and anaerobic conditions, prokaryotic and eukaryotic organisms, and aromatic and aliphatic hydrocarbons. A wide variety of biodegradation enzymes, belonging to the classes of hydrolases, transferases, and isomerases, are responsible for the reactions of oxidation/reduction, ring cleavage, side chains metabolization, oxygen addition to the double bonds, hydrolysis, and dehalogenation [55]. For instance, PAHs degradation is facilitated when bacterial dioxygenase is applied to oxygenate the benzene rings in the culture medium of *Pseudomonas aeruginosa* WJ6 [68].

Biodegradation comprises of internal and external degradation. OPs are absorbed and transmitted through the cell walls before being degraded and metabolized in the biotransformation processes, so called internal degradation. The OC characteristics are commonly classified based on their solubility. OPs are degraded by intracellular enzymes. Cytochrome P450 family (CYP) epoxidases and transferases are the main enzymes in intracellular reactions, such as hydroxylation, C═C bond epoxidation, reduction, dealkylation, and dehalogenation [55]. Other biodegradation processes are complex OPs and co-metabolization, in which OPs are fragmented as a "non-growth-substrate" accompanied by a "growth-substrate." The main enzymes involved in these reactions belong to oxygenases [55].

Regarding external degradation, insoluble OPs are fragmented in the external environment before they are chelated with EPS to transform them into soluble complexes to facilitate their transmission into cells, then the intermediates are metabolized [61]. The main extracellular enzymes include oxidoreductases, oxygenases, laccases, and peroxidases. Several OPs have complex structures with low solubility and high molecular mass, which hinders their chelation with EPS. Hydrolytic enzymes, such as cellulases, hemicellulase, lipases, and proteases, are released to break down the major chemical bonds of the macromolecules [55].

3.2. Algal remediation

Algal can remove or transform OPs via several different pathways. Key OPs removal mechanisms by algal remediation include biosorption, bioaccumulation and enzymatic biotransformation. Algal biosorption results from the extracellular interactions of cell walls and extracellular polysaccharides with OPs. Functional groups, such as hydroxyl and amino groups, are responsible for attraction and complexation with charged groups of OPs. The main mechanisms on the cell surface sorption are ion exchange, complexation, chelation, and microprecipitation.

Bioaccumulation of OPs is carried out to transfer organic compounds inside algal cells. Three main pathways that are accounted for bioaccumulation are energy-independent diffusion, passive-assisted diffusion, and active uptake [60].

The internal and external biotransformation of OPs produces less harmful by-products. In internal biotransformation, OPs are broken down in two-phase enzymatic reactions. In phase I, redox enzymes, such as hydroxylases, carboxylases, and decarboxylases, are involved in oxidation-reduction and hydrolysis reactions. The hydrophilicity of OPs was improved by adding and revealing hydrophilic functional groups. In Phase II, various groups of OPs with electrophilic sites are coupled with glutathione, further catalyzed by glutathione-S-transferases. This reaction leads to the opening of the pollutant's epoxide rings and the subsequent expulsion of the pollutants from the cell [60].

In the external biotransformation, enzymes, such as laccase glycoproteins, are externally secreted to degrade several OPs [69].

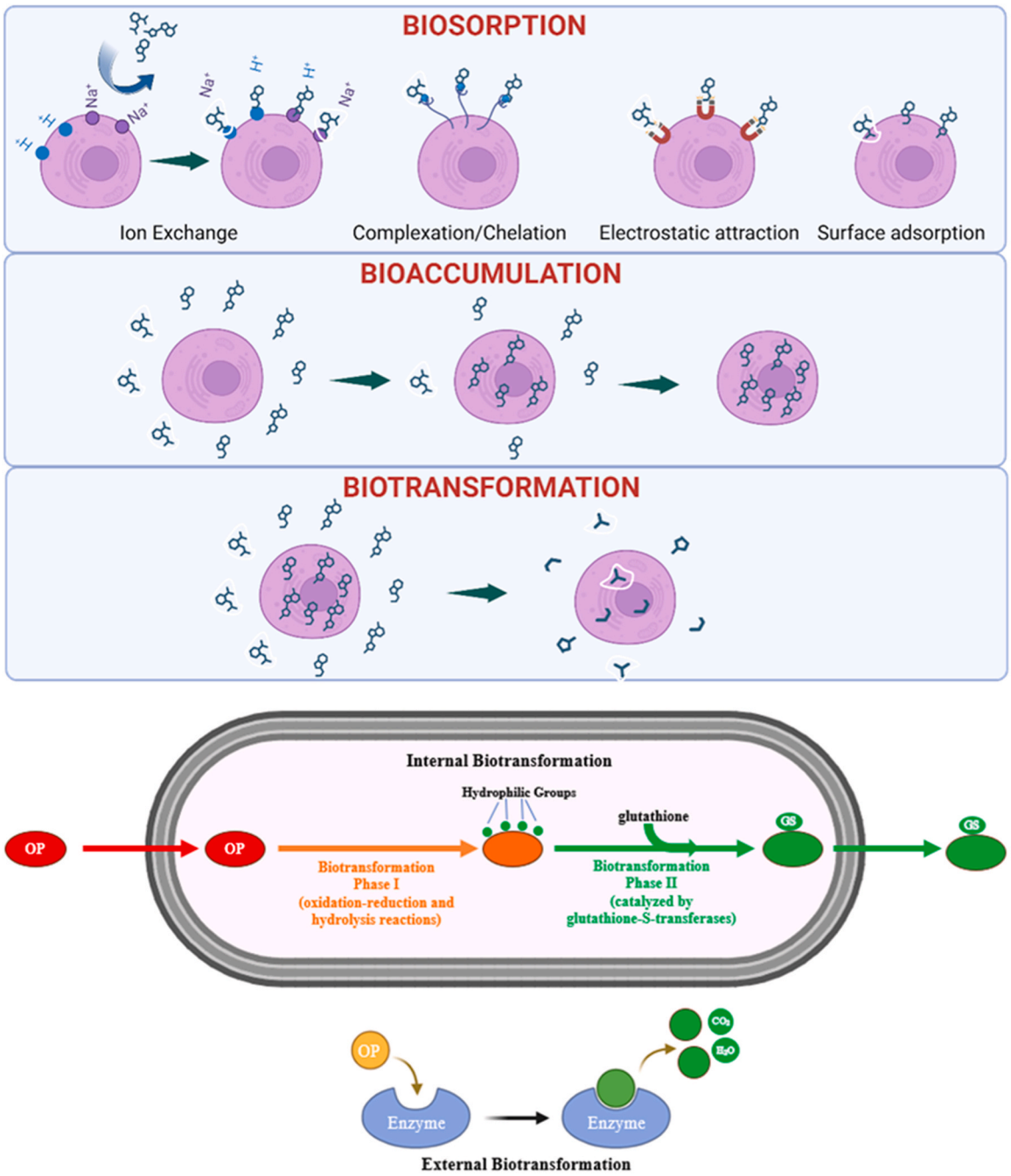

Fig. 2. The removal mechanism of OPs in wastewater using microorganisms.

Nevertheless, as mentioned in Section 2.2.1, the mutual interaction of MBC is not limited to a simple O_2/CO_2 exchange in which aerobic bacteria use photosynthetically to produce O_2 from microalgae, and in return, CO_2 is provided by the bacteria for carbon uptake. Besides, complementary exchanges exist when bacteria growth-promoting factors and algal metabolites are released into the medium [70]. The secreted metabolites, released by microalgae and other OPs, are assimilated by heterotrophic bacteria [71]. The mechanism of OPs removal by MBC is presented in Fig. 2.

4. Factors affecting the organic pollutants remediation of microalgae-bacteria consortium

The MBC has been employed to treat OPs in wastewater since this process offers advantages such as the utilization of natural sunlight and the energy-saving benefits from avoiding mechanical aeration [72]. The collaborative synergy between microalgae and bacteria contributes to effective wastewater treatment and enhancing resilience to environmental fluctuations. Hence, it is crucial to optimize the large-scale implementation of microalgae-bacteria treatment systems. The key factors, such as lighting conditions, pH, temperature, and co-occurrence of ions are discussed in this section.

4.1. Light intensity

The growth of phototrophic microalgae relies on the availability of light, which serves as the energy source for transforming inorganic carbon, typically CO_2, into organic carbon [72]. When light intensity is below the saturation point, photosynthetic activity correlates with light intensity. However, at elevated light intensities, based on the specific

microalgal species and other cultivation factors (e.g., temperature), the photosynthetic receptor system may suffer damage, leading to photoinhibition and, consequently, hindering microalgal growth [72].

Hence, adequate light pose a significant influence on nutrient uptake, metabolic processes, and oxygen production, creating favorable conditions for both microalgae and bacteria [72]. The synergistic effects between microalgae and bacteria, driven by optimal light conditions, contribute to the stability and resilience of the consortium [73]. Additionally, considerations such as light penetration in wastewater and potential interference from turbidity or light-absorbing substances highlight the need for careful system design and optimization. Finding the right balance in light intensity is crucial for maximizing the potential of microalgae-bacteria consortia in sustainable wastewater treatment [74]. Besides, the distribution of light in terms of uniformity and depth of penetration also needs to be considered to avoid the self-shading effect, which occurs when upper layers shad the cells in the layers below. Even though there are reports that confirm microalgal growth in light deficiencies [75], adequate light penetration may be challenging in full-scale granular reactors. Solutions have been offered to mitigate the effects of self-shading on algal growth through geometry optimization, lessening effects of mixing-induced light-dark cycles [76], higher nutrient availability [77], and short and intense light flashes [78].

Some previous studies express that pollutants removal efficiencies were observed to increase from 71 % to 89 %, respectively, with increasing light intensities from 50 to 300 μmol m^{-2} s^{-1}, resulting in biomass productivity increasing from 0.33 to 0.93 gDW/m^2/d in the biofilm photobioreactor (BPBR) [73]. The findings of Kumar *et al.* [79] indicated that higher light intensity is associated with increased lipid production rather than carbohydrate and protein production, similar to the elevated light intensity at 300 μmol m^{-2} s^{-1}, which had a beneficial impact on the carbon and protein contents in the biomass. Fan *et al.* [80] reported that increasing the light intensity from 70 to 210 μmol m^{-2} s^{-1} led to enhanced treatment performance of the microalgal-bacterial granular sludge (MBGS) process in removing organic matter in wastewater. At the highest light intensity (210 μmol photons m^{-2} s^{-1}), the highest organic removal efficiency of 70.5 % was achieved. Accordingly, this improvement could be attributed to the increased biomass growth, bioactivities, chlorophyll, and EPS of MBGS [80].

Overall, the light intensity provided for the MBC is important in that increasing light intensity improves the production of pigments, lipids, protein, fatty acids, and carbohydrates of microalgae. While the change of light intensity mostly impacts the metabolism of microalgae (e.g., *Scendesmus* and *Chlorella* sp.) [79], the structure of bacteria community of MBC was also changed consequently. There is also evidence that light favors aerobic bacteria's proliferation, inhibiting anaerobic bacteria's growth [80]. It has been clearly shown in the metagenomics data which phylum *Protebacteria* was the most abundant bacteria in MBC, increasing from 60.2 % to 80.4 %. In contrast, *Proteiniclasticum* decreased from 29.1 % to 8.3 % when the light intensity increased in MBC. There is no direct evidence of the effect of light intensity on OPs removal by MBC, however, it can be interpreted that increasing light intensity supports the growth of MBC and the production of enzymes and proteins for OPs remediation.

4.2. Acidity or basicity

The pH of wastewater significantly influences the removals of a microalgae-bacteria consortium in removing OPs. It could directly affect the enzymatic activities and growth of microalgae and bacteria [81]. Nutrient availability, pollutant toxicity, microbial community composition, and biochemical pathways for pollutant degradation are pH-dependent factors that can impact the treatment performance of the consortium [82]. Identifying and maintaining the optimal pH range is essential for maximizing pollutant removal efficiency. Avoiding pH fluctuations is crucial to ensure the stability and effectiveness of the microorganisms involved in practical applications.

Most microalgal species can typically grow in a pH range of 7.0–9.0 [81,82]. Nevertheless, certain microalgae could exhibit alkalophilic characteristics, while others are acidophilic. For instance, *Spirulina platensis* can flourish well in environments with pH levels between 9.0 and 10.0 [83], whereas *Chlorococcum littorale* prefers acidic environments with pH values ranging from 5.0 to 6.0 [84]. Furthermore, the pH of the wastewater can be influenced by the concentration of supplied CO_2 due to the chemical equilibria established among CO_2, H_2CO_3, HCO^{3-}, and CO_3^{2-} [85]. An increase in the CO_2 concentration within the gaseous input stream reduces pH values within the culture system. The provision of CO_2 in the microalgal cultures can prevent any adverse effects on microalgal cells due to a decline in the wastewater pH [85]. Furthermore, the uptake of carbon dioxide via algal photosynthesis raises pH levels and can cause phosphate precipitation. It has been documented that phosphate precipitation typically takes place within the pH range of 9–11 [86]. Additionally, the pH level plays a crucial role in influencing the removal of ionic pollutants. The removal process primarily occurs through surface biosorption, where electrostatic interaction is the determining factor. For example, the highest removal capability of tetracycline from wastewater using *Desmodesmus* sp. and *Klebsiella pneumoniae* when the pH of culture was 7 [87].

4.3. Temperature

Temperature is critical in OPs remediation as it supports heterotrophs' growth and metabolic activity [88]. The heterotrophic bacteria typically use enzymes to degrade OPs and the temperature has an impact on the activity of these enzymes, given each enzyme having an optimal temperature range for maximum enzyme activity [89]. At lower temperatures, enzyme activity slows down, reducing the rate of OPs degradation, while enzymes may denature, reducing activity at higher temperatures [88–90]. The optimal temperatures could promote faster growth and higher biomass production, which enhances the rate of organic degradation [88,90]. The suitable temperature range for most algae species is between 20 and 30 °C. Increased temperatures within the optimal range positively impact photosynthesis and cell division, attributable to activities associated with the Calvin cycle.

The temperature could affect the algal photosynthesis due to the intricate kinetics of the ribulose-1,5-bisphosphate (Rubisco) enzyme, which functions in both carboxylase and oxygenase pathways [91]. However, above 30°C, the enzyme's affinity for CO_2 decreases, leading to reduced photosynthetic activity. The decreased photosynthetic activity reduces produced O_2, which is utilized for the OPs degradation by the aerobic bacteria [91].

4.4. Co-occurrence ions

The impact of co-occurrence ions is diverse in the organic removal processes of a microalgae-bacteria consortium. These ions could influence nutrient availability, affecting the growth of microalgae and bacteria crucial for organic matter degradation. Co-occurrence ion-based changes in ionic strength and pH may alter the stability and activity of enzymes, impacting the metabolic processes of the consortium [81,82]. Several ions might exert toxic effects, inhibiting microbial activities and reducing overall organic contaminant removal efficiency [92]. As the surface of the algal cell wall typically has a negative charge, it plays a crucial role in the adsorption of positively charged pollutants through electrostatic interaction [93]. Positively charged pollutants could induce toxicity in the algal cells through various mechanisms, such as obstructing functional groups within enzyme active sites, disrupting cellular metabolism, displacing essential metal cofactors in functional units, generating free radicals causing the disruption of biomolecules like proteins, lipids, and nucleic acids [94].

On the other hand, wastewater treatment using algal-bacterial aerobic granular sludge in a photo sequencing batch reactor can effectively remove OPs while increasing K^+ and Mg^{2+} from 11 % and 13–19 % and

Table 1
The treatment conditions and removal efficiency of OPs in wastewater.

Microorganisms	Substances	Conditions	Removal efficiency (%)	References
Desmodesmus sp. and *Klebsiella pneumoniae*	Tetracyclines	Optimal ratio: 1:2 of *Desmodesmus* sp.: *K. pneumoniae* Temperature: 25 °C pH 7 10 % inoculum	95	Jingrui *et al.* [87]
Ochrobactrum sp.	Erythromycin A	pH: 9.3 Temperature: 32 ℃	97	Zhang *et al.* [98]
Acinetobacter sp.	Sulfamethoxazole	Sulfamethoxazole concentration: 5 – 240 mg/L Temperature: 25 °C pH: 7	100	WangWang [99]
Chlorella vulgaris	Levofloxacin	Levofloxacin concentration: 200 mg/L NaCl concentration: 1 % Time: 11 d Light/dark ratio of 16:8 Light intensity: 45–50 μmol/m^2.s Temperature: 25 °C	91	Xiong *et al.* [65]
Chlorella sorokiniana and *Brevundimonas basaltis*	Cephalexin	pH = 8.0 Temperature: 23 °C Light/dark cycles: 16:8 Light intensity: 235 μmol /m^2s Time: 7 days	96	da Silva Rodrigues *et al.* [100]

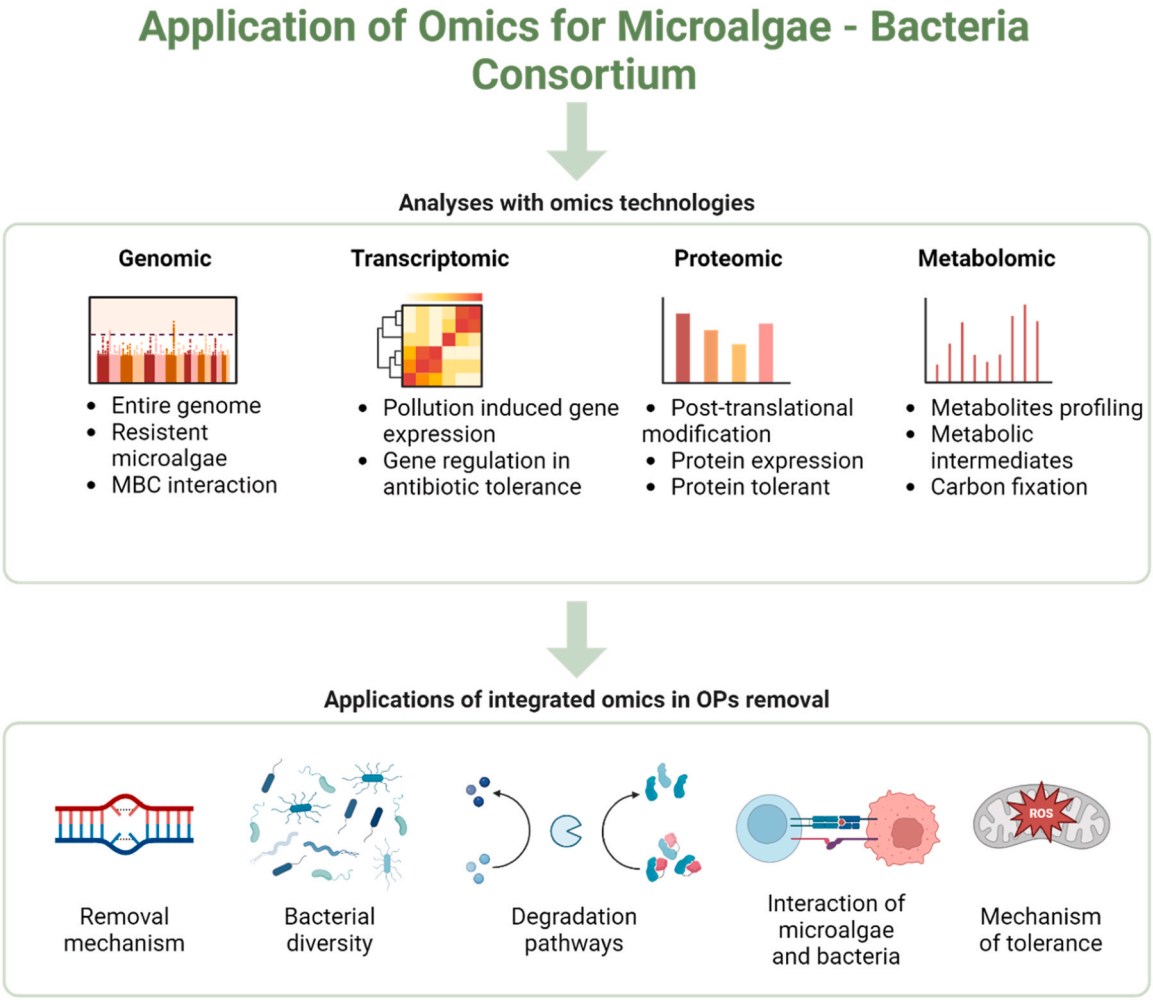

Fig. 3. Multi-omics approach in organic pollutant treatment in wastewater.

26 %, respectively [95]. This trend indicated that metals could be beneficial for the microalgae-bacteria consortium in removing OPs in the wastewater. Additionally, copper ions (Cu^{2+}) co-occur due to some industrial discharges. These ions could act as cofactors for enzymes produced by bacteria in the consortium, enhancing their ability to break down complex OPs [96]. Co-occurrence ions also aid in sedimentation

Table 2
The metagenomic research in microalgal-bacterial consortium.

Microalgal species/ Consortia	Insights	OPs	Wastewater	References
Scenedesmus obliquus FACHB−12-Phycisphaeraceae and *Rhizobiaceae*	Removal mechanism and identification of bacteria composition	Ciprofloxacin	Pharmaceutical	Wang *et al.* [108]
Scenedesmaceae, Rhodocyclaceae, and Burkholderiaceae	Degradation pathways and adaptation capacity	Sulfamethoxazole	Synthetic water	Hu *et al.* [109]
Sphaeropleales, Hapalosiphon, and Rhodopseudomonas, Azotobacter	Identifying bacteria diversity and DNA extraction efficiency	Phenols	Olive washing water	Maza-Márquez *et al.* [110]
Scenedesmus and Chlorella	Identifying the reduction of antibiotic and bacteria diversity	Tetracycline and Sulfadiazine	Pharmaceutical	Liu *et al.* [111]
Microalge-bacteria granules	Identifying the resistomes and microbial composition	Antibiotics	Wastewater	Ovis-Sánchez *et al.* [112]

and organic matter removal as they affect aggregates' formation in bioflocculation [72]. Furthermore, these ions can influence the competitive and mutualistic interactions between microorganisms, shaping the balance within the consortium [97]. Therefore, understanding the specific ions and their concentrations is essential for optimizing the performance of microalgae-bacteria consortia in environmental applications such as wastewater treatment. The effect of cultivation conditions on the removal rate of OPs in wastewater is summarized in Table 1.

5. Omics application in wastewater treatment

During the last decades, omics has gained an important position in biological science. The use of omics technologies has improved our understanding of the interactions among microorganisms and external environments to an extent that was unimaginable just a decade ago. Furthermore, omics technologies are important tools for the extensive study of microbial molecules, including proteins, DNA, RNA, and metabolites [5]. The application of omics techniques in investigating algal metabolomics, transcriptomics, genomics, and proteomics (called "algomics") is critical in assisting researchers in exploring microalgae's biology, and physiology which can be a prerequisite for using microalgae in industry and agriculture [101].

Gaining insights into microalgal suitability based on wastewater ingredients can be obtained through algomics to improve the effectiveness of bioremediation. In this case, omics techniques can shed light on how microalgae are affected by various wastewater conditions. As sustainable bioremediation of wastewater is dependent on specific microalgae-bacteria consortia, omics techniques are needed to gain further insight into microbial compositions, the response of microalgal and bacterial cells to nutrients and contaminants, and the contribution of genes, metabolites, and proteins to bioremediation. Based on this new understanding, bioremediation approaches can be found to improve wastewater treatment efficiency and the sustainability of wastewater treatment [102]. The roles of the multi-omics approach are presented in Fig. 3.

This section investigates four main omics techniques, including metagenomics, transcriptomics, proteomics, and metabolomics. Metagenomics is an analytical approach that investigates microorganisms' diversity and metabolic activities by DNA sequencing techniques [103]. The drawback of metagenomics is that it does not provide information on the adaptation of MBC to the change of environmental stress, such as the variation in OPs concentration. Transcriptomics is the research of the entire transcriptome of a cellular system, such as coding and non-coding messenger RNAs, as well as regulatory RNAs as catalytic RNAs and miRNA. A transcriptome contrasts with the genome as transcripts are dynamic, showing high variability under different situations. Transcriptomics is employed to analyze the toxicity of antibiotics and herbicides for algae [104]. However, transcriptomics does not determine the key RNA coding for proteins, which are responsible for adapting MBC to the variation in OPs concentration. Proteomics is the research of the entire protein compounds of a living system at specific conditions and times. Proteomics employs identifying the variation of key proteins in the adaptation process of MBC. Unlike DNA and RNA, protein analysis is restricted by the amount of samples because they cannot be produced by artificial replication [102]. Metabolomics relates to a comprehensive examination of metabolites in cellular processes, including metabolic intermediates, secondary metabolites, hormones, and signaling molecules, to determine the overall picture of cellular physiology. Metabolomics shows valuable information on the microalgal and bacterial carbon flux in wastewater and the varied metabolites impact the development, productivity and MBC interactions [13]. However, metabolomics does not provide information about creatures that are better adapted to environmental stress.

5.1. Metagenomics approaches

Genes related to OPs decomposition and antibiotic resistance are commonly determined as functional genes via functional metagenomics [105]. An urban resistome was detected through metagenomics before and after treating wastewater, concentrating on antibiotic resistance genes [106]. Based on this approach, strategies can be established to reduce the development of antibiotic resistance gene diversity and dynamics [107]. Table 2 shows the application of metagenomics in identifying the interactions between microalgae and bacteria for OPs removal.

Wang *et al.* [108] employed the metagenomics approach to identify the ciprofloxacin removal mechanism by MBC. The main components of the consortium were *Rhizobiaceae, Rhodocyclaceae, Phycisphaeraceae*, *Thermoactinomycetaceae,* and *Cellulomonadaceae*. The presence of nitrogen fixation bacteria can be associated with an improvement in antibiotic treatment ability. The degradation of ciprofloxacin may relate to the biological oxidation processes of microalgal cells, including dihydroxylation, decyclopropyl, hydroxylation, dealkylation, defluorination, piperazine epoxidation, and de-carbonylation processes [108].

Hu *et al.* [109] employed metagenomics to determine the variation of MBC under the presence of sulfamethoxazole coupled with the degradation pathway of these antibiotics. Sulfamethoxazole degradation is the intracellular process in which the S-N linkage of sulfamethoxazole is disintegrated into 4-amino benzene sulfonic acid and 3-amino-5-methylisoxazole because the sulfur atom of the sulfamethoxazole molecules is the most susceptible position. 4-amino benzene sulfonic acid can be converted to a carbon source of pyruvate via the serially biological processes of microorganisms. The presence of sulfamethoxazole leads to variations in the composition of microorganisms in the consortia. *Proteobacteria* population decreased, while the amount of *Scenedesmaceae* was high at elevated concentrations of sulfamethoxazole (10 mg/L). The metagenomics results indicate over-expression of catalase and superoxide dismutase genes as these enzymes act as antioxidants of microorganisms in quenching the reactive oxygen species produced by increased sulfamethoxazole in the wastewater environment [109].

The metagenome sequencing method assesses the changes in the structure of microbial communities in the environment. Kadri *et al.* [113] identified the bacterial communities of algal-bacterial consortia and purple photosynthetic bacteria in piggery wastewater treatment via 16 s rDNA. Regarding algal-bacterial communities, the consortia

Table 3
The application of transcriptomics in identifying the interaction in MBC during wastewater treatment.

Microalgal species/ Consortia	Insights	OPs	Wastewater	References
C. pyrenoidosa and bacteria	The improved deterioration of tetracycline using microalgae-bacteria consortiums	Tetracycline	Industrial wastewater	Qi *et al.* [120]
Chlorella sp.-Cupriavidus necator	The cooperation mechanism for phenol deterioration	Phenol	Industrial wastewater	Yi *et al.* [119]
S. obliquus	The effect of tetracycline on the algal photosynthesis	Tetracycline	Pharmaceutical	Chen *et al.* [121]
Chlorella strain	The mechanism for phenol tolerance	Phenol	Industrial wastewater	Zhou *et al.* [122]
Fermentative bacteria and microalgae	The sulfamethoxazole degradation pathway	Sulfamethoxazole	Mariculture wastewater treatment	Fan *et al.* [117]
Cyanobacteria Synechococcus sp	The effect of sulfamethoxazole on the cyanobacteria	Sulfamethoxazole	Industrial wastewater	Zhang *et al.* [123]
Desmodesmus sp	Elucidating the change in metabolism pathways of new algae in sewage treatment	Mixture OPs	Sewage	Wang *et al.* [118]

showed the occurrence of *Actinobacteria, Cyanobacteria, Chloroflexi, Firmicutes, Epsilonbacteraeota, Patescibacteria,* and *Proteobacteria*, in which *Cyanobacteria* and *Proteobacteria* are the main species. Regarding purple photosynthesis bacteria, the consortia revealed the occurrence of phyla *Acidobacteria, Chloroflexi, Epsilonbacteraeota, Firmicutes, Patescibacteria, Proteobacteria, and Synergistetes*, in which *Proteobacteria* and *Synergistetes* made up 83.8 % and 5.3 % respectively [114]. Similarly, Ovis-Sánchez *et al.* [112] used a similar approach to determine the taxonomic profile of the microalgae bacteria consortium in wastewater treatment processes. The identified strains include *Pseudomonas aeruginosa, Enterococcus faecium, Klebsiella pneumoniae, Staphylococcus aureus, Enterobacter spp., Acinetobacter baumannii, and Escherichia coli.*, in which *E. coli* constitutes the majority. The main microalgal composition of the consortia is *Chlorella,* and diatoms such as *Thalassiosira* and *Phaeodactylum* and cyanobacteria such as *Synechocystis*.

5.2. Transcriptomic approaches

The transcriptomic takes into account (i) the internal elements including the different stages of cell development, signaling pathways, and metabolic state and type, and (ii) external elements such as nutritional conditions and environmental stressors [115].

Regarding the effects of internal elements on gene expression patterns, when algae cell grows, transcription elements bind to gene promoter regions, initiating the transcription of genes involved in metabolism. In addition, several epigenetic modifications affect gene expression via managing DNA accessibility to transcriptional machinery, including DNA acylation and histone modifications [116].

The effect of external stressors on gene expression tends to be rapid and transient. For instance, toxic substances and nutritional changes can affect signaling pathways which have a role in regulating gene expression, with signaling cascades triggering the activation or inactivation of target genes via signal transduction. The transcriptomic research of MBC is presented in Table 3.

Fan *et al.* [117] employed transcriptomic approaches to elucidate the effect of sulfamethoxazole on MBC in mariculture wastewater treatment. This study found that genes involved Photosystem II, Cytochrome b6/f complex, Photosystem I, and ATP synthase were upregulated when the consortia were exposed to sulfamethoxazole. Regarding Photosystem II, PsbB, PsbJ, and PsbE genes, which are responsible for producing chlorophyll apolipoprotein CP47, D1 protein, and cytochrome subunit b559 were upregulated. Regarding Photosystem I, PsaA and PsaB genes, which have a role in generating chlorophyll apolipoprotein P700A1 and P700A2 were also upregulated. An increase in the D1 protein of the P680 and PsaC-encoded protein production can improve the number of binding sites and transport protein binding sites, which accelerates electron transport and ATP synthesis.

Jinhu Wang et al. (2022c) employed transcriptomic techniques to elucidate changes in gene expression of *Desmodesmus* sp, finding that 18,872 and 35,871 genes experienced upregulation and downregulation, respectively, when *Desmodesmus* sp was used to treat sewage wastewater. The changes in RNA expression were linked to the essential biological processes of creatures, including cellular protein modification, biosynthesis of small molecule metabolites, protein production, ubiquitin-mediated proteolysis, and oxidative phosphorylation [118]. Transcriptomic analyses of *Chlorella sp.* indicated that the expression of genes involved in photosynthesis-antenna protein synthesis, carbon fixation pathways, ribosomal protein synthesis and DNA replication changed significantly when *Chlorella* sp. was cultivated with *Cupriavidus necator* and exposed to phenol. Additionally, there was an upregulation of antenna proteins such as *Lhca2–5, Lhcb1, Lhcb2, Lhcb4, and Lhcb5*, which play a pivotal role in photosynthesis light harvesting of *Chlorella* sp. The enhanced expression of these genes boosted the photosynthesis of *Chlorella* sp. and generated more oxygen than a monoculture of *Chlorella* sp, which promoted the aerobic deterioration of phenol by *Cupriavidus necator*. Correspondingly, more carbon dioxide production, which coupled with the enhanced degradation of phenol, promoted the expression of genes related to the Calvin cycle in *Chlorella* sp. Additionally, the presence of phenol boosted the protein synthesis of ribosomes, which enhanced cell proliferation [119].

5.3. Proteomic approaches

Proteomics is a powerful technique to explore metabolism processes as it relates to proteins. Determining protein and molecular profiles gives insight into the metabolic processes of microorganism cells and identifies vital proteins that play an integral part in biochemical processes [124]. The proteomic research of MBC is presented in Table 3.

Shen *et al.* [125] employed proteomic approaches (iTRAQ) to elucidate the effect of photosynthetic bacteria on the organic carbon utilization of microalgae in wastewater. Through proteomics, the differential expression of 262 proteins was observed, with an upregulation of 82 proteins and a downregulation of 180 proteins. When microalgae absorbed acetate, it was assimilated by acetyl-CoA synthase to form acetyl Co-A [126]. The presence of acetate can enhance the upregulation of microalgal acetyl-CoA synthetase, which promotes the acetate assimilation of microalgae in the consortia. Ribulose bisphosphate carboxylase/oxygenase (RuBisCO) is responsible for converting CO_2 into sugars in the Calvin cycle. The production of RuBisCO and phosphoribulokinase in microalgae decreased when photosynthetic bacteria were present, indicating that the presence of photosynthetic bacteria can decrease CO_2 assimilation and disrupt the Calvin cycle in microalgae [125].

Gao et al. [127] elucidated the carbon metabolism regulation of bacterial-microalgal consortia in mariculture wastewater treatment by determining the variation in protein profile using iTRAQ techniques. The proteomics approach enhanced the production of 40 proteins, while there was a downregulation of 171 proteins. Among 40 upregulated proteins, there were 7 essential enzymes which are needed in the Calvin cycle. The enhanced expression of these enzymes indicated an increase

Table 4
The insight investigation into OPs removal of MBC using a proteomic approach.

Microalgal species/ Consortia	Insights	OPs	Wastewater	References
Sphingomonas sp. strain TTNP3	Generating proteome map and identifying subunit of hydroquinone dioxygenase	Bisphenol A and nonylphenol	Industrial wastewater	Collado *et al.* [128]
Chlorella vulgaris F1068	Identifying the mechanism of nitrogen assimilation	Ammonium	Municipal sewage wastewater	Liu *et al.* [129]
Chlorella vulgaris	Elucidating the correlation of protein content with ecotoxicity	Chlorophenols	Toxic sludge extracts	Wang *et al.* [130]
Chlorella vulgaris and Scenedesmus obliquus	Identifying metabolism under sludge toxicity stress	Hydroquinone	Industrial sludge extract	Chen *et al.* [131]

in the growth rate of microalgae and biomass accumulation with increased bicarbonate. Moreover, the presence of bicarbonate enhanced the expression of proteins in Photosystem I and Photosystem II. The increased expression of magnesium chelatase (EC 6.6.1.1) in microalgae also illustrated, via proteomic approaches, which result showed the improvement of chlorophyll synthesis with bicarbonate presence, improving the photosynthesis process of microalgae in the consortia [127].

5.4. Metabolomic approaches

Metabolomics relate to a comprehensive examination of metabolites in cellular processes, including metabolic intermediates, secondary metabolites, hormones, and signaling molecules, to immediately determine the overall picture of cellular physiology. The research using metabolomic approaches is presented in Table 5.

Wang *et al.* [132] analyzed the metabolome to elucidate an increase in the amoxicillin tolerance capacity of *Prototheca zopfii* in the algal-bacterial consortium. Through the metabolomic approach, the intracellular metabolites of the monoculture and co-culture of algae showed a significant difference. There were 25 and 24 metabolic processes, respectively, that were varied in *Prototheca zopfii* cultivated with *P. aeruginosa* and *B. subtilis*. Carbon fixation in photosynthetic creatures, arginine biosynthesis, cysteine, methionine, alanine, nicotine, aspartate, nicotinamide, and glutamate metabolism were profoundly impacted. Additionally, arginine biosynthesis, pentose phosphate pathway, and aminoacyl-tRNA biosynthesis are significantly changed in *P. aeruginosa* and *B. subtilis* when they are cultivated with *Prototheca zopfii.* These findings indicated that the co-cultivation of *Prototheca zopfii* with *P. aeruginosa* and *B. subtilis* mainly affected the carbohydrate metabolism pathways. The changes in carbohydrate metabolism pathways of microalgae and bacteria could be the primary reasons for varying amoxicillin tolerance.

The promotion of carbohydrate metabolism increased the production of glucose 6-phosphate, ribulose 5-phosphate, and trehalose 6-phosphate in the consortia. These substances promoted energy metabolism and provided the materials for the anabolism of macromolecules such as alginate and poly-γ-glutamate. These substances also upregulated the Krebs cycle and increased the relative abundance of trehalose, leading to improved antibiotic elimination and evolution of antibiotic resistance respectively. The increased amino acid synthesis, especially glutamate, led to poly-γ-glutamate production which, along with alginate, play an important role in reducing the effects of amoxicillin on bacteria [132].

Chen *et al.* [133] compared the metabolomic profile to reveal the correlation between algal metabolism and nutrient deterioration of the MBC in wastewater treatment processes. There were 304 detected metabolites, such as carbohydrates, polyols, phosphates, fatty acids, benzenoids, amino acids, nucleosides, and other compounds. The significant distinction of metabolites in the monoculture and the consortium was 114 out of 304, and these metabolites were used as bio-indicators to elucidate the pattern of metabolic modulation. Through metabolomic analysis, the presence of bacteria can boost the production of protein and fatty acid via improving proline, asparagine, and glutamine synthesis and downregulating the energy production of the Kreb cycle. Additionally, the occurrence of bacteria decreased the entry of phosphate in microalgal cells since the production of protein related to phosphate transporters, such as ATP-binding cassette transporters, was inhibited [133].

6. Conclusion

This review highlights the potential of using MBC for remediation of OPs in wastewater. The MBC can have a variety of forms, interaction, and mechanisms, which offer benefits to that application purposes. The review consolidates the recent knowledge in using multi-omics techniques to determine the detailed interaction of microalgae and bacteria in the consortium. Transcriptomics and metabolomics demonstrate the response of the consortia to the change of nutrients and pollutants in wastewater. Multi-omics approaches provide a significant step forward to improve our understanding of microalgal-bacterial processes and to support the application of microalgae-bacteria consortia for remediating OPs in wastewater.

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Table 5
Identification of interaction among MBC using metabolomic approaches.

Microalgal species/ Consortia	Insights	OPs	Wastewater	References
Microalgae-bacteria symbiotic systems	Under the presence of antibiotics	Tetracycline and Sulfadiazine	Pharmaceutical	Cao *et al.* [134]
Chlorella pyrenoidosa/Rhodobacter capsulatus	Carbon source usage	Organic and inorganic carbon	Industrial wastewater	Shen *et al.* [125]
Synechococcus sp. and Chroococcus sp	Increase in monoacylglycerol and fatty acid production	Ciprofloxacin and erythromycin	Wastewater	FangLiu [135]
Microalgae-bacteria consortia	Effect of temperature	Nutrients	Wastewater	Zhang *et al.* [136]
Chlorella sorokiniana-bacteria	Correlation of metabolic regulation and nutrient deterioration	Organic chemicals	Wastewater	Chen *et al.* [133]
Pseudomonas aeruginosa, Bacillus subtilis, and Prototheca zopfii W1	Antibiotics tolerant capacity	Amoxicillin	Wastewater	Wang *et al.* [132]

CRediT authorship contribution statement

Chawalit Chaiwong: Writing – original draft. **Soroosh Danaee:** Writing – original draft. **Tan Phat Vo:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Peter J. Ralph:** Supervision, Investigation. **Unnikrishnan Kuzhiumparambil:** Writing – review & editing. **Mikael Kim:** Writing – review & editing. **Nature Poddar:** Writing – review & editing. **Bao Tran Pham:** Writing – original draft. **Phong H.N. Vo:** Writing – review & editing, Supervision, Conceptualization. **Huu Hao Ngo:** Supervision, Methodology, Investigation. **Mathieu Pernice:** Writing – review & editing, Supervision. **Chris Songsomboon:** Writing – review & editing, Supervision.

Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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