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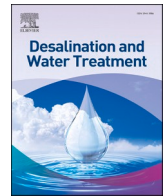
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Autotrophic vs. heterotrophic microalgae: Juxtaposition of performances in treating organic-rich effluent

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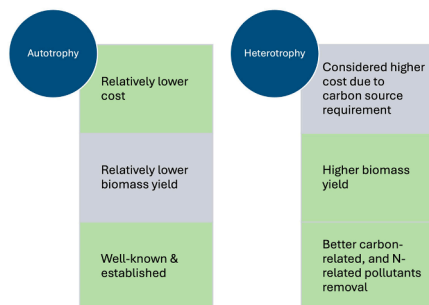
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GRAPHICAL ABSTRACT

Microalgae for wastewater treatment

Which one is better???



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ABSTRACT

Microalgae-based wastewater treatment is an alternative to physico-chemical and bacteria-based technologies. Microalgae-based wastewater treatment showed enormous potential, not only exhibiting excellent pollutant removal efficiencies but also unlimited opportunities for resource recovery. Despite its promising future, the question of selecting autotrophy or heterotrophy regimes for optimal organic pollutant removal remains. This current work juxtaposes the performance of autotrophic and heterotrophic cultures in treating organic-rich wastewater to shed light on the unsolved puzzle. This review paper details the autotrophy and heterotrophy growth regimes for microalgae, as well as highlights the source of organic-rich wastewater and its characteristics. A clear comparison between both regimes was then discussed with recent references. Heterotrophic cultures showed better parameter removal performances, especially carbon-related and N-related compounds, while the removal of P-related compounds is considerably similar. Heterotrophic regimes also resulted in higher biomass yield with higher P content as compared to autotrophy. Despite their superiority, heterotrophic regimes continuously require additional carbon sources, posing a cost-related limitation. In contrast, autotrophic culture has an added value of carbon sequestration, making it beneficial for climate mitigation and lowering operational costs. Future research should concentrate on techno-economic and cost-benefit analyses to further refine the currently discussed topic.

1. Introduction

Microalgae, known for their ability to adapt to changing environmental situations, can flourish by adopting numerous trophic modes due to their metabolic flexibility [1–3]. Autotrophic and heterotrophic culturing are the main methods used in the commercial production of microalgae [4,5]. During heterotrophic cultivation, microalgae depend on exogenous organic compounds, such as glucose or residual sugars, to acquire energy and carbon [6]. This technique enables the manipulation of growth conditions and has the potential to result in increased biomass production, rendering it appropriate for large-scale manufacturing. Conversely, autotrophic cultures utilize light as an energy source and carbon dioxide (CO₂) as their supply of carbon [7]. This approach replicates the inherent photosynthetic mechanism, rendering it highly sustainable and ecologically benign. Nevertheless, autotrophic culturing frequently necessitates a more elaborate infrastructure to ensure sufficient illumination and carbon dioxide, which might pose a constraint in large-scale operations [8]. Both approaches present unique benefits, and the selection between them typically relies on the specific objectives of the production process, such as the amount of biomass produced, the nutrient composition, and the cost-efficiency.

When comparing both methods, it becomes evident that heterotrophic production is preferable for producers due to the cost efficiency [8, 9]. Scaife et al. [10] found that in an autotrophic culture employing a thin layer technique, the highest cell density reached was 40 g/L with biomass productivity of 3.3 g/L.d. However, other research has demonstrated that microalgae grown heterotrophically can achieve productivity ten times higher [11]. The disparity becomes even more evident when comparing lipid productivities. Heterotrophic growth allows for the attainment of high cell densities, which can surpass 75 g/L, as it is not constrained by limitations in light availability [12]. This value appears to be significantly higher when compared to the usual quantities found in photosynthetic production, which range from 0.5 to 4 g/L [13].

Contrary to the earlier remark, the market has disclosed a completely different outcome. The global algae market was valued at \$20.94 billion in 2022, with over 80 % of the value attributed to production in open ponds (autotrophy) and a minimal contribution from cultivation in closed fermenters [14]. Open ponds are frequently employed since they are more affordable and need less effort to maintain [15]. Open ponds mimic the natural living environments of microalgae, which are considered better for mass production [16].

In the era of circular economy and as the effort of valorization of waste, the cultivation of microalgae using wastewater offered a new vision [17,18]. Microalgae present in wastewater have the potential to offer numerous advantages, including the elimination of coliform bacteria, nitrogen, phosphorus, and heavy metals, as well as the decrease of organic substances in the wastewater [19]. The cultivation of

microalgae from wastewater harnesses the nutrients present in the wastewater to facilitate its growth. This approach enables a decrease in production costs and greenhouse gas emissions while also yielding economically valuable biomass [20]. Research on wastewater treatment is growing significantly, alongside autotrophy and heterotrophy microalgae (Fig. 1).

SCOPUS database revealed that articles related to [wastewater treatment] grew noticeably over the last 15 years, reaching a peak of nearly 25,000 articles in 2024 (Fig. 1a). Amongst the [wastewater treatment] findings, articles on [autotrophy microalgae] and [heterotrophy microalgae] also grew eminently and highly correlated with wastewater treatment based on the co-occurrence map (Fig. 1b). Publication on [heterotrophy microalgae] gained exponential growth in 2012, while [autotrophy microalgae] in 2013. One of the articles [8] presented an extensive production cost analysis and concluded that heterotrophic production of microalgae biomass was not significantly different from autotrophic production. It also highlighted that energy and glucose contributed about 78 % of the overall costs in heterotrophic cultivation. With wastewater offering alternative sources of glucose and nutrients, will heterotrophic cultivation become superior?

Many researchers are already shedding some light on the autotrophy vs. heterotrophy production cost of microalgae, discussing the production of microalgae using wastewater and comparing the biomass characteristics produced under autotrophy vs. heterotrophy conditions. Nevertheless, a clear juxtaposition between autotrophy and heterotrophy regimes in terms of treating organic-rich effluent performance is still missing. The current work thoroughly discussed the comparison between autotrophy and heterotrophy regimes for treating organic-rich wastewater. Firstly, this review detailed the auto and heterotrophy cultivation regimes of microalgae, sources of organic-rich effluents, and algae-based treatment technologies. These are followed by comprehensive performance juxtaposition between autotrophy and heterotrophy cultures. Finally, the author's perspectives are presented as the bottom lines, research limitations, and future approaches to provide future research directions.

2. Autotrophic culture

Autotrophic microalgae, found abundantly in diverse aquatic ecosystems, represent a microscopic wonder with profound implications for the planet's biological diversity. Through photosynthesis, these microorganisms convert solar energy into chemical energy by using chlorophyll and other pigments to capture light [24,25]. This energy is then used to drive the synthesis of organic molecules, such as sugars and lipids, which serve as the building blocks for cellular processes and growth [26,27]. From photosynthesis, microalgae generate energy and also contribute to the production of oxygen, which plays a crucial role in

the maintenance of oxygen levels in aquatic ecosystems [28]. As primary producers, autotrophic microalgae hold a pivotal position at the base of the ecological pyramid, influencing the dynamics of entire ecosystems. The significance of their photosynthetic prowess extends beyond ecological realms, impacting global oxygen levels and contributing to

the regulation of atmospheric carbon dioxide.

Central to the flourishing of autotrophic microalgae is the availability of light, their primary energy source for photosynthesis. The intensity, duration, and spectral quality of light are critical factors that influence the efficiency of this process [29]. From open ponds to closed

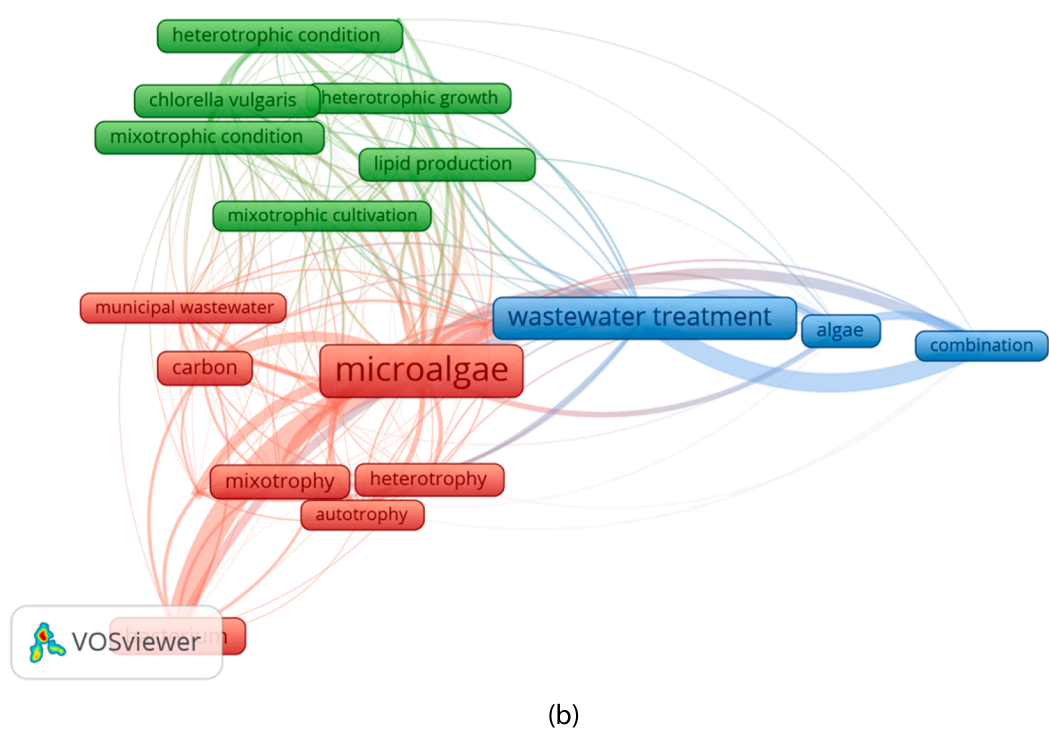
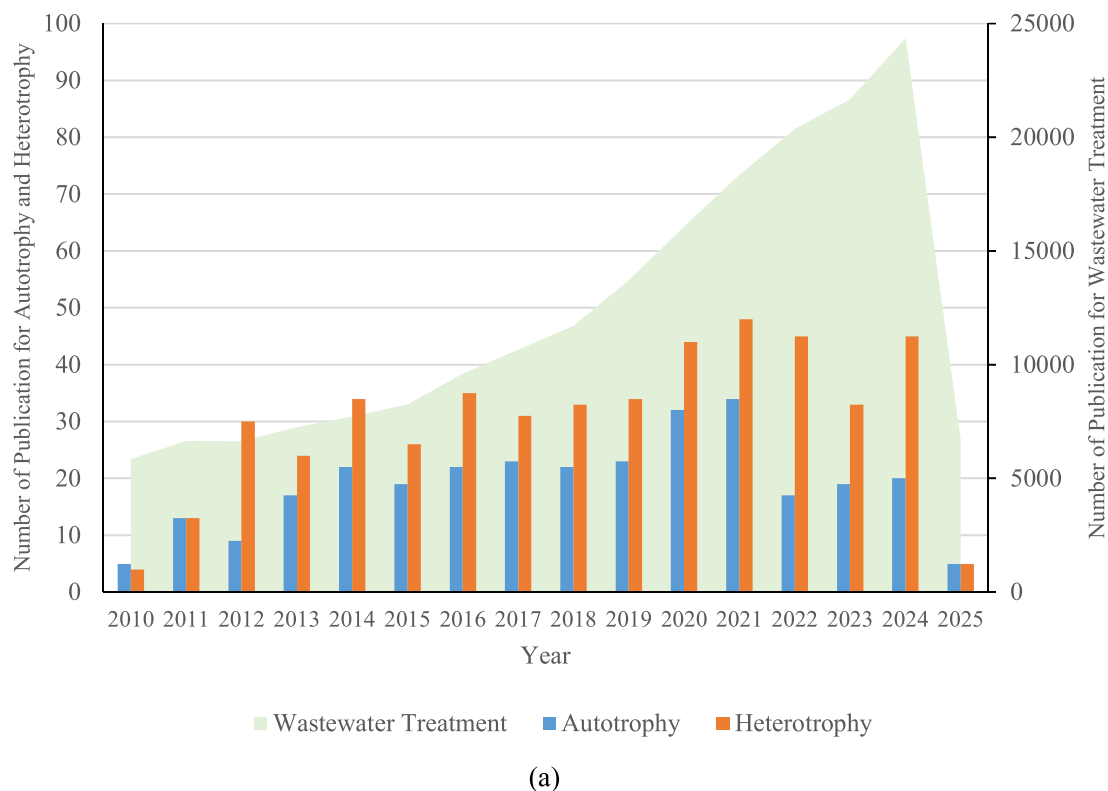


Fig. 1. (a) Number of publications in the SCOPUS database over the last 15 years, and (b) Co-occurrence map from the extracted article for [wastewater treatment] and [microalgae] metadata (n = 1249) (Constructed by following previous literature [21–23]).

photobioreactors, the choice of cultivation system becomes a crucial consideration, impacting factors such as light penetration, temperature control, and scalability [30].

In addition to light, autotrophic microalgae exhibit distinct nutritional requirements essential for their growth and productivity. Autotrophic organisms use carbon dioxide from their surroundings to perform photosynthesis. Autotrophic microalgae development and metabolic processes depend on the availability of a sufficient and regulated supply of carbon dioxide. The effective delivery of carbon dioxide in autotrophic microalgae growing systems has been the subject of much research and is essential to achieving ideal growth conditions in photobioreactors [31,32]. Autotrophic microalgae require key nutrients such as nitrogen, phosphorus, and trace minerals for healthy growth and biomass production. The availability of these nutrients directly impacts the productivity and quality of the biomass [30]. Nitrogen, often supplied in the form of nitrates or ammonium, is a critical component of proteins and nucleic acids. Phosphorus, another key nutrient, is sourced from phosphate compounds and is essential for energy transfer processes within the microalgae's cells. Micronutrients, including elements such as iron, zinc, and manganese, serve as cofactors for enzymes, influencing a range of metabolic reactions [33].

The development and production of autotrophic microalgae are also significantly influenced by the temperature of the growing environment and the water quality. Ensuring that autotrophic microalgae cultures are healthy and growing robustly requires maintaining appropriate water quality that is free of pollutants and regulating temperature within an ideal range [24,34]. The pH of the growth medium emerges as a critical parameter affecting nutrient availability and enzymatic activities [35]. Autotrophic microalgae thrive within specific pH ranges, and maintaining optimal conditions is imperative for the proper functioning of cellular processes. The pH of the growth medium is carefully controlled and monitored throughout the cultivation process to provide a conducive environment for microalgal growth [30].

The choice of autotrophic microalgae strains is a key consideration, as different species exhibit varying growth characteristics and metabolic capabilities. For instance, *Chlorella sp.*, known for its rapid growth and high lipid content, holds promise in biofuel production [36]. *Spirulina sp.*, a cyanobacterium often categorized with microalgae, is valued for its protein-rich composition and nutritional benefits [37]. *Dunaliella salina*, recognized for its ability to accumulate high concentrations of beta-carotene, finds applications in the nutraceutical and cosmetic industries [38]. The intended application often influences the selection of a specific strain, whether it be biofuel production, wastewater treatment, or the synthesis of valuable compounds for pharmaceutical or nutraceutical purposes. As the field of autotrophic microalgae cultivation advances, researchers explore genetic engineering and metabolic engineering approaches to enhance desirable traits. This includes efforts to increase lipid production for biofuel applications, improve nutrient utilization efficiency, and modify metabolic pathways for the synthesis of specific high-value compounds [24,39]. These endeavors aim to tailor autotrophic microalgae to meet the growing demands of various industrial sectors, from renewable energy to sustainable agriculture and beyond.

3. Heterotrophic culture

Algae are widely used in many different industries and have historically been grown autotrophically by using sunlight to power photosynthesis. Because heterotrophic cultivation has made it possible for microalgae to survive in the absence of light, it has created new opportunities. A class of microorganisms known as heterotrophic microalgae gets its carbon and energy from organic sources [40]. Heterotrophic microalgae need outside organic substances for growth and survival, in contrast to autotrophic microalgae, which can make their food through photosynthesis [28]. These microalgae are essential to many ecosystems and have attracted much interest recently because

of their possible uses in sectors like bioremediation and the production of biofuel. To fully utilize heterotrophic microalgae and create sustainable solutions, it is essential to understand their traits and needs.

Heterotrophic microalgae require particular conditions to be cultivated in order to achieve maximum productivity and growth. Some general variables are significant in the production of heterotrophic microalgae (including the type of carbon source, nutrient availability, nitrogen source, etc.), which vary based on the species of microalgae and the intended application [41]. A unique class of tiny organisms known as heterotrophic microalgae differs from autotrophic organisms in that they produce their energy through the uptake of external organic carbon sources [42]. Understanding these microbes' unique cultivation requirements in detail is essential to realizing their full potential. Providing them with an adequate source of nutrients is essential to their growth and determines their metabolic processes. This source of nutrients frequently consists of a variety of organic substances, from basic sugars to more intricate substrates like yeast extract [8,43]. The heterotrophic microalgae's metabolic pathways are directly impacted by the nuances of nutrient availability, which in turn influences cellular activities and eventually determines the productivity of the algae. Since these microbes cannot use sunlight for photosynthesis, the availability of a carbon supply is equally important as that of a nutrition source. The lifeblood of heterotrophic microalgae is glucose, glycerol, or other organic carbon molecules, which power a variety of metabolic activities [44].

Furthermore, because nitrogen is an essential component of proteins and nucleic acids, the development of these microbes requires careful selection and the provision of a nitrogen source. To satisfy the unique nitrogen needs of the concerned microalgae species, nitrate, ammonium, or other organic nitrogen molecules are used [33]. The complex metabolic pathways and nutrition availability of heterotrophic microalgae interact dynamically, demonstrating the organisms' flexibility (adaptation) to a wide range of environmental niches. Controlling the temperature is another essential component of the growing process.

Although the ideal temperature for growth varies depending on the species, many heterotrophic microalgae strains thrive best in environments that are between 20 and 30 °C [45]. Furthermore, the pH of the growth medium critically affects nutrient availability and enzymatic activity. The medium's pH, which is normally kept in the neutral to slightly acidic range, is a carefully regulated parameter that guarantees the ideal growing circumstances for the microalgae [46]. Because they promote nutrient uptake and keep cells from settling, aeration and mixing are essential steps in the culture process. Sufficient aeration guarantees that the microalgae are exposed to the components required for growth, and appropriate mixing keeps the growth media homogeneous [47,48]. A crucial component of a good cultivation process is the routine monitoring and management of culture conditions, which include nutrient concentrations, pH levels, and cell density [49]. This makes it possible to adjust in real-time to maximize productivity and growth, guaranteeing that the microorganisms are flourishing in a setting that caters to their particular requirements.

Heterotrophic microalgae are a broad category of strains and species that each have distinct qualities that make them useful for both scientific research and practical uses in industry. Several strains that have been the subject of substantial research are *Chlorella sp.*, *Schizochytrium sp.*, *Aurantiochytrium sp.*, and *Cryptocodium sp.* [50–53]. These strains are renowned for their unique characteristics. Because of its high lipid content and quick development, *Chlorella sp.* has potential applications in the manufacturing of biofuels [54,55]. *Schizochytrium sp.* and *Aurantiochytrium sp.* are members of the *Thraustochytriaceae* family and are very desirable candidates for use in pharmaceutical and nutraceutical applications due to their abundance of omega-3 fatty acids [56]. Because of its capacity to generate the powerful antioxidant astaxanthin, *Cryptocodium sp.* is used in the food and cosmetics sectors [57]. The intended application is for biofuel production, medicines, nutraceuticals, or other biotechnological endeavors that influence the choice of a

particular strain. In order to increase the productivity of these strains and modify their characteristics for particular industrial uses, researchers are still investigating and characterizing novel strains and utilizing genetic engineering and synthetic biology. The possibility of finding new strains with special traits and uses is growing as our knowledge of heterotrophic microalgae grows, spurring innovation in the environmentally friendly production of valuable substances and the reduction of environmental problems.

4. Source and characteristics of organic-rich effluent

Organic-rich effluent is stated to originate from three sources: industrial effluent, agricultural runoff, and home sewage [58]. Recent studies in industrial sources have identified various contributors to this effluent, such as chemical industries [59], food processing [60], pulp and paper mills [61], textile industries [62], petroleum refineries [63], and coal mining activities [64]. A study conducted in Korea found that chemical fiber manufacturing produces various organic compounds as byproducts, such as suspended organic solids, biological oxygen demand, chemical oxygen demand, total nitrogen, and 1,4-Dioxane [65]. This effluent is produced as a result of the water utilized in the manufacturing process [66]. In another research, wastewater from restaurants was reported to contain organic-rich effluent as a result of the use of oil, fats, grease, and cleaning chemicals [67].

Another investigation revealed that wastewater contains effluent high in organic matter originating from the fluorescent whitening chemical. This study stated that 82 % of wastewater contains Total Organic Carbon (TOC) [68]. Additional harmful chemical compounds, such as acetic acid and methanol, have been discovered to originate from an important business [69]. The pollutants discussed in this study are produced in petrochemical refineries, coal gasifiers, and during the paper production process using the kraft method. These organic compounds are known to be harmful and pose a threat to both the environment and human health. Additionally, they can originate from operations conducted in potato-starch manufacturing facilities and the conversion of substances such as formaldehyde into minerals [69].

Water that contains effluents rich in organic matter has numerous notable properties, particularly elevated levels of biochemical oxygen demand (BOD) and chemical oxygen demand (COD). In addition, a study has shown that the Rhone River has been experiencing pollution since 1976 due to the presence of organic pollutants. Furthermore, the river frequently includes high concentrations of suspended solids, including sediment, organic particles, and debris. In 1989, the concentration of suspended silt in the Rhone River downstream varied from 6 to 23 mg/L, as reported by Santiago et al. [70].

Organic-rich effluents exhibit diverse hues and smells due to the existence of organic molecules such as dyes, pigments, and sulfides [71, 72]. Eutrophication is a phenomenon that occurs when organic matter is abundant in water bodies, leading to the growth of algae, depletion of oxygen, and negative impacts on aquatic ecosystems [73,74]. As the abundance of nutrients causes algae to multiply, they use oxygen during the process of decomposition, resulting in a decrease in oxygen levels in the water. The loss of aquatic resources can result in significant repercussions for the biodiversity of aquatic ecosystems, leading to disturbances in the ecological equilibrium and compromising the overall quality of water. Another property of effluent that is rich in organic matter is its high concentration of nutrients. These effluents consist of several sources, including home sewage, detergents, and cleaning chemicals. Moreover, the discharge resulting from agricultural activities, which involve the use of fertilizers and animal waste, has a substantial role in the accumulation of nutrients [75,76]. Moreover, nutrient-dense waste products arise from sectors such as food processing, chemical manufacturing businesses, and metropolitan regions, where nutrients can be transported into water bodies through rainwater runoff. Quality of water Nutrient contamination leads to degradation by fostering excessive algal growth, so compromising the overall quality of

water. This proliferation can result in unpleasant smells, unattractive layers, and problems with the taste and odor of drinking water [77]. In addition, the breakdown of algae can produce toxins that are detrimental to human health and exacerbate the deterioration of water quality. Table 1 displays the attributes of wastewater produced by different industrial activities.

5. Effluent treatment by algae-based technologies

Nutrient-rich wastewater, such as from agriculture, aquaculture, domestic, and food production, has been eyed for resource reclamation recently. The organic contents in wastewater leached from its respective processing steps normally will gradually degrade into dissolved nutrients in the form of ammonia, nitrites, nitrates, phosphates, and organic

Table 1
Source and characteristics of organic-rich effluent.

No	Industry	Characteristics*	Reference
1	Pulp and paper	BOD up to 152 (kg/ton) COD up to 539 (kg/ton) SS up to 140 (kg/ton)	[78]
2	2,4 D manufacturing facility	BOD 330 (mg/L) COD 40,000 (mg/L) DOC 7486 (mg/L)	[79]
3	Textile and dyeing industries	TOC 8467 (mg/L) TDS 3685 (mg/L) BOD 105.8 (mg/L) COD 720 (mg/L) Color 656 (Pt-Co) Nitrate 42.3 (mg/L) Nitrite 10.3 (mg/L) Phosphate 0.9 (mg/L) Sulfate 201.3 (mg/L) TSS 1214 (mg/L)	[80]
4	Battery	BOD 6.0 ± 0.6 (mg/L) COD 256 ± 62 (mg/L) DO 1.6 ± 0.3 (mg/L) TDS 1868 ± 463 (mg/L)	[81]
5	Iron/metal galvanizing	BOD 6.0 ± 0.7 (mg/L) COD 460 ± 476 (mg/L) DO 1.7 ± 0.7 (mg/L) TDS 1827 ± 489 (mg/L)	[81]
6	Tanking/car wash	BOD 5.9 ± 0.8 (mg/L) COD 918 ± 294 (mg/L) DO 2.0 ± 0.2 (mg/L) TDS 2330 ± 700 (mg/L)	[81]
7	Iron/steel	BOD 5.9 ± 0.8 (mg/L) COD 310 ± 251 (mg/L) DO 1.2 ± 0.5 (mg/L) TDS 3654 ± 891 (mg/L)	[81]
8	Vinasse	BOD > 60 (mg/L) COD 1500–1900 (mg/L) Color 1.092 (Pt-Co) DOC 480–550 (mg/L) TOC 550–660 (mg/L)	[82]
9	Sewage	COD 262 (mg/L) Toal P 4.7 (mg/L PO ₄ ³⁻) Total N 42 (mg/L TKN) Total solid 1971 (mg/L)	[83]
10	Vinasse	COD 20,731 (mg/L) Total N 187,5 (mg/L TKN) Total P 133 (mg/L PO ₄ ³⁻) Total solid 18,170 (mg/L)	[83]
11	Glycerol	COD 1108,230 (mg/L) Total N 0 (mg/L TKN) Total P 0 (mg/L PO ₄ ³⁻) Total solid ND (mg/L)	[83]
12	Rice Wastewater	COD 5353 (mg/L) Total N 104.6 (mg/L TKN) Total P 124.5 (mg/L PO ₄ ³⁻) Total solid 1971 (mg/L)	[83]

* BOD: biological oxygen demand; COD: chemical oxygen demand; DO: dissolved oxygen; DOC: dissolved organic carbon; SS: suspended solid; TKN: total Kjeldahl nitrogen; TOC: total organic carbon; TSS: total suspended solids

compounds in water, subsequently leading to environmental problems such as eutrophication if discharged abruptly [84]. Hence, aligned with global continuous awareness of sustainability, the reclamation of those valuable nutrients has become a center of discussion to this date. Algae-based technology is considered one of the promising approaches, as it is known for its efficiency in removing organic matter through biological mechanisms while producing valuable microalgal biomass [85]. While nitrogen and phosphorus elements in wastewater generally disrupt the ecological cycle, both are essential in algae cultivation. Hence, integrating wastewater treatment with algae cultivation is a novel approach to maximizing resources [86]. However, raw wastewater usually has a high content of suspended solids with turbidity that may hinder sufficient light penetration for microalgae growth. Hence, this treatment was usually used as the primary treatment. Three major mechanisms involved in pollutant removal of microalgae are biosorption, bioaccumulation, and biotransformation [87].

Biomass produced rich in lipids, proteins, and carbohydrates is useful to be utilized in the production of biofuels, biofertilizers, animal feed, and bioplastic production [87,88]. Biofuels produced from microalgal biomass normally have lower carbon footprints, where most of the carbon content comes from fatty acids, than regular petroleum diesel [86]. This serves as an additional advantage in energy production sectors, as conventional biomass cultivation and conversion are considered costly to apply [85]. This is a simultaneous resolution of a dual challenges approach, where two environmental issues, water pollution, and energy demand, were addressed at one time. Table 2 summarizes some of the recent studies on algae-based treatments for various types of wastewaters, consisting of single strain and algae co-culture applications.

To summarize Table 2, the removal of P-related compounds is generally similar, while the removal of carbon-related and N-related compounds is distinct. Depending on the source of wastewater, used species, and operational conditions, autotrophy cultures achieved removal of COD removal, ranging from 29 % to 99 %, as compared to 75–97 % for heterotrophy. TN removal ranges between 56 % and 97 % in autotrophy and between 35 % and 93 % in heterotrophy. For TP, autotrophy achieved removal ranging from 70 % to 100 %, while heterotrophy ranged between 75 % and 96 %. Significant differences were observed in terms of the biomass yield, in which it was higher in heterotrophy conditions (0.8–17.99 g/L), as compared to autotrophy (0.24–0.7 g/L) and mixotrophy (1.24–2.79 g/L).

According to Afonso et al. [85], utilization of algae monoculture is a highly demanding process; alternative approaches such as consortium or microalgae-bacteria culture are preferred. Besides, the usage of a single microalgae strain in most water treatment studies without involving bacteria and other symbiotic microorganisms will hinder the real application of the treatment [93]. The application of microalgae and bacteria consortiums gained attention due to their symbiotic interaction that helped enhance the efficiency of the treatment process, facilitating sedimentation through floc formation, cutting aeration costs, and also minimizing emissions of greenhouse gases [107]. Degradation of organic matter by bacteria produces CO₂ and nutrients that are needed for algae photosynthesis, while the later process generates oxygen needed for bacterial growth [92,108]. The treatment works through bioaccumulation, biosorption, and biodegradation mechanisms [107]. As studied by Foladori et al. [93], no external aeration is possible with co-culture cultivation of algae and bacteria, where photosynthesis acts as the sole oxygen generation. In a respected study, besides excellent organic matter removal, outstanding removal TSS of effluent was also due to the excellent settle ability of biomass forming dense aggregates. This performance contradicts the usual finding that single algae species are used in the treatment, which is difficult to sediment and separate. Microalgae also provide other benefits to bacteria, such as providing a habitat for them, encouraging their growth through the secretion of extracellular metabolites, and also providing protection from adverse conditions. The structure and stability of the consortium are maintained

by the adhesion of bacteria to the algae surface [104].

6. Performance comparisons

This section is constructed based on the presented data in Table 2 and illustrated in Fig. 1 in the boxplot graph [109]. It can be seen that most of the previous studies utilized the autotrophy regime for wastewater treatment as compared to heterotrophy. This might be subject to the long-known performance of autotrophic microalgae in treating wastewater and its potential to produce secondary resources. In general, the performance of pollutant removal between autotrophy and heterotrophy regimes is similar. Pollutant removal depends on some critical factors, including used species and operational parameters. Besides autotrophy and heterotrophy growth regimes, mixotrophy growth regimes also offer new alternatives, in which light and dark periods were accompanied by the changing of carbon source.

Removal of carbon-related parameters (BOD, COD, TOC) (Fig. 2a) is considerably higher in heterotrophic culture. The mean and median of the carbon-related compounds removal are higher for heterotrophy, as compared to autotrophy. This phenomenon occurred due to the direct utilization of organic carbon in heterotrophic regimes, while autotrophic culture fixed inorganic carbon (CO₂) through photosynthesis. Autotrophic culture relies on light availability as an energy source for photosynthesis, limiting some of the metabolic activities when the light is absent. This was then related to the continuous performance of pollutant breakdown to be higher in heterotrophic culture. Due to the lack of the number of data, the mean and median for mixotrophy culture cannot be determined.

Diving deeper into the performance of nutrient-related compound removal (Fig. 2b and c) and biomass yield (Fig. 2d), a clear comparison can be seen by analyzing data on *S. acuminatus* GT-2 [98]. The heterotrophy growth regime produced significantly higher biomass yield while also showing higher P recovery inside the biomass. These results were subjected to the efficient utilization of carbon sources in heterotrophic conditions, leading to a continuous supply of ATP, which is important for P accumulation and cell growth. In autotrophic conditions, energy is more sporadic, depending on light availability and photosynthesis efficiencies. *C. sorokiniana* also showed a significant increment in biomass yield and higher TN and TP removal while growing under heterotrophic conditions as compared to autotrophy [97]. The mean and median of N-related compounds are also higher in the heterotrophy regime, as compared to the autotrophy (Fig. 2b). N and P utilizations were highly correlated with biomass yield. In this case, *C. sorokiniana*'s better heterotrophic performance may also be subjected to better utilization of carbon sources. Heterotrophic growth reduced the need for energy for the photosynthesis apparatus, which then redirected toward other metabolic activities, including P accumulation and cell growth. Heterotrophic conditions may also trigger a stress response to an unfavorable condition, leading to the action of survival strategies such as P accumulation. This statement is proven by analyzing Fig. 2c, in which the removals mean and median of P-related compounds (TP, PO₄, PO₄-P) are averagely higher in heterotrophic conditions as compared to autotrophy.

Discussing the mixotrophy regime, Cheng et al. [105] highlight the differences between heterotrophy and mixotrophy cultures' performance in removing N. Mixotrophic conditions showed higher removal of TN by *Chlorella pyranoidosa* FACHB-10. This result was obtained due to the availability of dual nitrogen removal mechanisms in mixotrophic cultures. N removal in heterotrophic conditions solely relied on the organic carbon metabolism to uptake nitrogen. The balance of C and N was reported to be better in mixotrophic culture because of the availability to use both organic and inorganic carbons. *C. sorokiniana* also showed significantly higher biomass and lipid yields in the mixotrophy regime as compared to heterotrophy. Due to dual energy sources, mixotrophy culture showed a higher biomass production as compared to the other regimes (Fig. 2d). Previous research mentioned a lower lipid

Table 2
Treatment of organic-rich wastewater using alga-based technology.

Wastewater	Regime	Species	Operational conditions	Findings*	References
Shrimp aquaculture	Autotrophy	<i>Chlorella vulgaris</i>	<ul style="list-style-type: none"> Conducted in 22.7 L tank, with aeration and LED lighting of 2.8 W/m² intensity for 21 d 	Removal NO ₃ ⁻ 59 % Removal P 74 %	[84]
Shrimp aquaculture	Autotrophy	<i>Tetraselmis suecica</i>	<ul style="list-style-type: none"> Conducted in 22.7 L tank, with aeration and LED lighting of 2.8 W/m² intensity for 21 days 	Removal NO ₃ ⁻ 35 % Removal P 37 %	[84]
Urine wastewater	Autotrophy	<i>Chlorella vulgaris</i>	<ul style="list-style-type: none"> Ratio human urine to normal water = 1:1 7 days exposure in a well-lit environment, in culture receptacles 	Removal Ca 49 % Removal Cl 61 % Removal K 59 % Removal Mg 73 % Removal N 62 % Removal P 55 %	[86]
Wastewater from vegetable cooking	Autotrophy	<i>Desmodesmus</i> sp. HXY3	<ul style="list-style-type: none"> Culture diluted to 20 % concentration using wastewater Cultured in a columned photobioreactor, incubated at 25 °C under 60 μM photons/m²s (12 h light: 12 h dark) for 12 days 	Removal TN 97 % Removal TOC 93 % Removal TP 81 %	[89]
Wastewater from vegetable cooking	Autotrophy	<i>Desmodesmus</i> sp. HXY7	<ul style="list-style-type: none"> Culture diluted to 20 % concentration using wastewater Cultured in a columned photobioreactor, incubated at 25 °C under 60 μM photons/m²s (12 h light: 12 h dark) for 12 days 	Removal TN 90 % Removal TOC 91 % Removal TP 93 %	[89]
Wastewater from vegetable cooking	Autotrophy	<i>Chlorella vulgaris</i> FACHB 8	<ul style="list-style-type: none"> Culture diluted to 20 % concentration using wastewater Cultured in a columned photobioreactor, incubated at 25 °C under 60 μM photons/m²s (12 h light: 12 h dark) for 12 days 	Removal TN 94 % Removal TOC 92 % Removal TP 96 %	[89]
Tannery wastewater (leather finishing stage)	Autotrophy	<i>Tetraselmis</i> sp.	<ul style="list-style-type: none"> Cultivated in photobioreactor at ambient temperature Continuous aeration (1 L/min) and 24 h light (3910 lux) 	Removal COD 57 % Removal P 98 % Removal TN 71 % Removal TOC 31 %	[90]
Dairy wastewater	Autotrophy	<i>Chlorella saccharophila</i> , <i>Chlamydomonas pseudococum</i> , <i>Scenedesmus</i> sp., and <i>Neochloris oleoabundans</i>	<ul style="list-style-type: none"> Illuminated with 12 h light/12 h dark (80 μmol/m²s) Cultivated in photobioreactor at 30 °C for 10 days at 120 rpm CO₂ bubbled at 150 mL/min into the mixture 	Removal COD 99 % Removal NH ₄ -N 100 % Removal NO ₃ -N 99 % Removal PO ₄ -P 99 %	[91]
Synthetic low C/N wastewater	Autotrophy	<i>Chlorella vulgaris</i>	<ul style="list-style-type: none"> Conducted in photobioreactor with 1:1 alga to sludge ratio for 6 days Continuous illumination (200 μmol/m²s) without external light at room temperature Aerated with 2 % CO₂ 	Removal COD 83 % Removal NH ₃ -N 76 % Removal TN 66 % Removal TP 100 %	[92]
Synthetic municipal wastewater	Autotrophy	<i>Chlorella vulgaris</i>	<ul style="list-style-type: none"> Photobioreactor illuminated at 650 μmolph/m²s of photosynthetic active radiation (PAR) for 12 h Culture mixed at 150 rpm continuously and bubbled with 1 L/min, operated at 20 °C with decreasing HRT (7, 5, and 3 days) 	Removal TN 56 % Removal TOC 50 % Removal TP 96 %	[88]
Municipal wastewater	Autotrophy	<i>Chlorella</i> sp.	<ul style="list-style-type: none"> Photo-sequencing batch reactor (PSBR) Light supplied by the cool-white lamp (8 led x 0.5 W) on 1 side of the reactor for 16 h 	Removal COD 87 % Removal TKN 98 %	[93]
Primary effluent from wastewater treatment plant	Autotrophy	<i>Chlorella vulgaris</i>	<ul style="list-style-type: none"> Light intensity of 0.98 W/cm² for 28 days; flask was stirred 4 times a day manually 	Removal COD 65 % Removal NH ₄ ⁺ -N 63 % Removal NO ₃ -N 64 % Removal TP 70 %	[94]
Livestock wastewater	Autotrophy	<i>Chlorella</i> sp. and <i>Coelastrella cogersae</i>	<ul style="list-style-type: none"> Conducted in a chamber with an irradiance of 70–100 μE/m²s) with 16 h light; 8 h dark photoperiod Continuous aeration of 100 L/h at 25 °C for 8 days 	Removal BOD 29 % Removal COD 29 % Removal TN 84 %	[95]
Synthetic wastewater	Autotrophy	<i>Chlorella sorokiniana</i>	<ul style="list-style-type: none"> Continuous air at a rate of 1 LPM (0 % and 0.04 % CO₂ conditions), 0.5 LPM (1–5 % CO₂ conditions), light intensities 3500 – 10,500 lux 	Biomass yield 0.7 g/L Total lipids yield 0.12 g/L	[96]

(continued on next page)

Table 2 (continued)

Wastewater	Regime	Species	Operational conditions	Findings*	References
Synthetic wastewater	Autotrophy	<i>Chlorella sorokiniana</i>	<ul style="list-style-type: none"> Modified BG–11, continuous illumination 36 $\mu\text{mol}/\text{m}^2\text{s}^1$, 25 °C 	Biomass yield 0.4 g/L Lipid content 30 % Removal TN 27.71 % Removal TP 75.65 %	[97]
Synthetic wastewater	Autotrophy	<i>Scenedesmus acuminatus</i> GT–2	<ul style="list-style-type: none"> BG–11, air 0.4 (lpm), 27 °C, continuous light illumination 	Biomass yield 0.24 g/L/d P recovery 0.11 mg/Lh	[98]
Aquaculture wastewater	Heterotrophy	<i>Chlorella</i> sp.	<ul style="list-style-type: none"> Co-culture with <i>Phaeodactylum tricornutum</i> 	Removal NH_4^+ -N 100 % Removal TN 93.26 % Removal TP 96.12 %	[99]
Hydroponic wastewater	Heterotrophy	<i>Chlorella</i> sp. G049	<ul style="list-style-type: none"> Cultured with 12.2 g/L of glucose and 15 mg/L of indole–3-acetic acid 6 days of incubation 	Removal COD 88.74 % Removal NH_4^+ 81.21 % Removal NO_3 93.79 % Removal PO_4 89.94 %	[100]
Hydroponic wastewater	Heterotrophy	<i>Chlorella</i> sp. AARL G049	<ul style="list-style-type: none"> Cultured with glucose and indole–3-acetic acid 6 days of incubation 	Removal COD 92.41 % Removal NH_4^+ 100 % Removal NO_3 96.77 % Removal PO_4 97.03 %	[101]
Municipal wastewater	Heterotrophy	<i>Scenedesmus</i> sp.	<ul style="list-style-type: none"> Glucose 20 g/L, pH 7–8, 8 days Co-culture with yeast 	Removal NO_3 -N 96 % Removal PO_4 -P 93 % Removal TAN 100 %	[102]
Synthetic municipal wastewater	Heterotrophy	<i>Tetradesmus obliquus</i>	<ul style="list-style-type: none"> Separated algae membrane oxygenated sludge reactors Without external aeration, with an internal reflux ratio of 5 and C/N ratio of 10 	Removal COD 97 % Removal NH_4^+ -N 99 % Removal TN 82 % Removal TP 96 %	[103]
Vinegar production wastewater	Heterotrophy	<i>Chlorella</i> sp.	<ul style="list-style-type: none"> Carried in 500 mL Erlenmeyer flask at 26 °C for 8 days Continuous shaking at 150 rpm, with $50 \pm 10 \mu\text{mol}/\text{m}^2\text{s}$ light intensity Bacteria (<i>Bacillus firmus</i> and <i>Beijerinckia fluminensis</i>) added after 24 h of algae cultivation 	Removal COD 77 % Removal TN 79 % Removal TP 75 %	[104]
Furfural wastewater	Heterotrophy	<i>Chlorella pyranoidosa</i> FACHB–10	<ul style="list-style-type: none"> Modified BG–11 medium with addition of 0.75 g/L NaNO_3 pH 7.2 Continuous shaking 120 rpm at 25 °C 	Biomass yield 1.52 g/Ld Removal COD 75.64 % Removal TN 35.32 % Removal TP 78.15 %	[105]
Synthetic wastewater	Heterotrophy	<i>Scenedesmus acuminatus</i> GT–2	<ul style="list-style-type: none"> BG–11, acetic acid and glucose, 27 °C 	Biomass yield 0.53 g/L/d P recovery 0.2 mg/Lh	[98]
Synthetic wastewater	Heterotrophy	<i>Scenedesmus incrassatulus</i>	<ul style="list-style-type: none"> pH 7.5, temperature 30 ± 1 °C; airflow 1 vvm, agitation 100–350 rpm, with glucose, culture period 6 d 	Biomass yield 17.99 g/L Total carotenoids 1.97 mg/gDW	[106]
Synthetic wastewater	Heterotrophy	<i>Chlorella sorokiniana</i>	<ul style="list-style-type: none"> Modified BG–11, Glucose 6 g/L, 25 °C 	Biomass yield 0.8 g/L Lipid content 31.35 % Removal TN 91.02 % Removal TP 97.44 %	[97]

(continued on next page)

Table 2 (continued)

Wastewater	Regime	Species	Operational conditions	Findings*	References
Furfural wastewater	Mixotrophy	<i>Chlorella pyranoidosa</i> FACHB-10	<ul style="list-style-type: none"> Modified BG-11 medium with addition of 0.75 g/L NaNO₃ pH 7.2 Continuous shaking 120 rpm at 25 °C Fluorescent illumination at 120 μmol/m²s 	Biomass yield 1.24 g/L/d Removal COD 51.93 % Removal TN 51.2 % Removal TP 75.6 %	[105]
Synthetic wastewater	Mixotrophy	<i>Chlorella sorokiniana</i>	<ul style="list-style-type: none"> A cycle of 18 h of light and 6 h of dark period Continuous air at a rate of 1LPM (0 % and 0.04 % CO₂ conditions) and 0.5 LPM (1–5 % CO₂ conditions) during the light period Continuous acetic acid feeding during dark period 	Biomass yield 2.79 g/L Total lipids yield 0.75 g/L	[96]

* BOD: biological oxygen demand; COD: chemical oxygen demand; TAN: total ammoniacal nitrogen; TKN: total Kjeldahl nitrogen, TN: total nitrogen; TP: total phosphorus

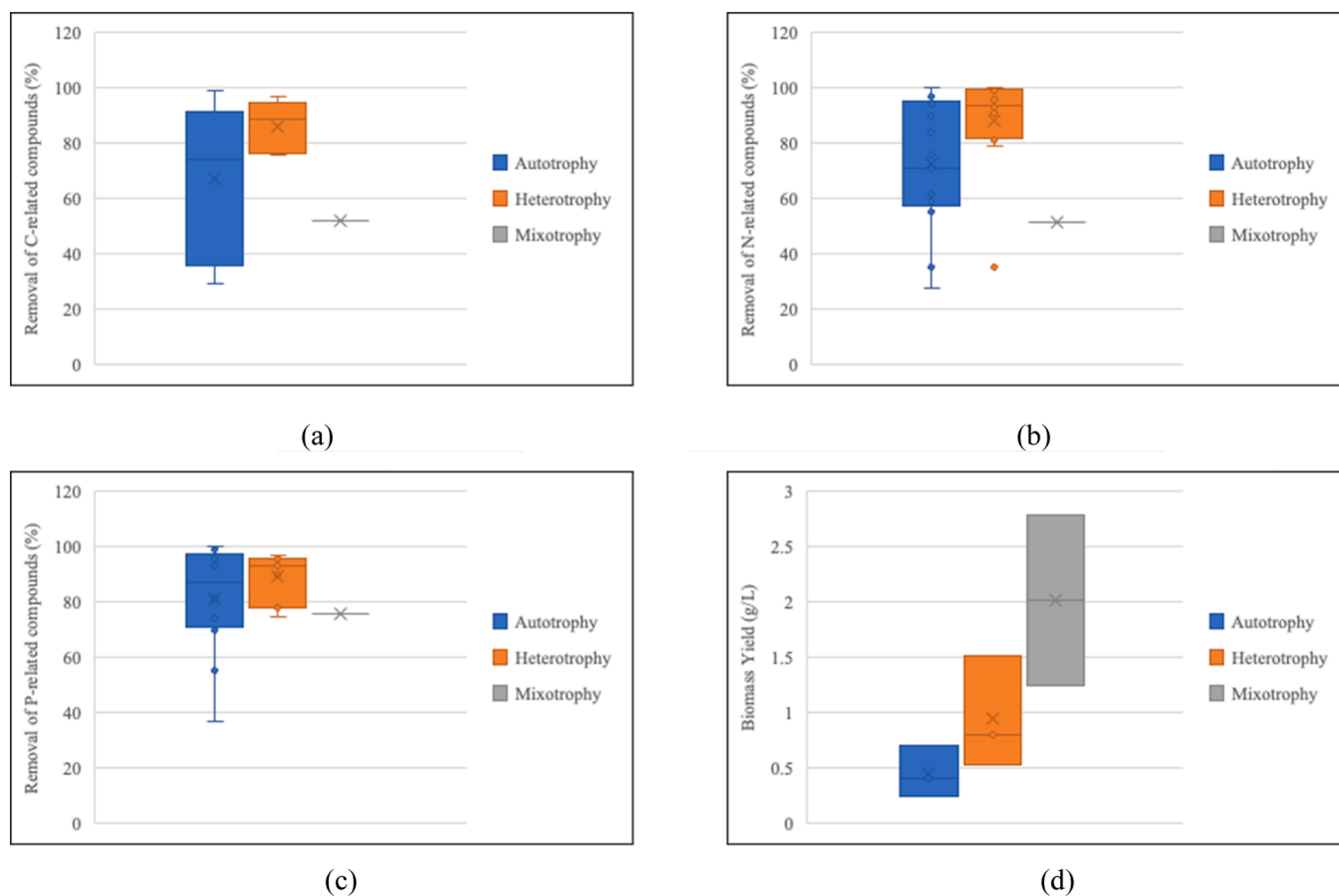


Fig. 2. Boxplot comparison of for removal of (a) C-related compounds [BOD, COD, TOC], (b) N-related compounds [NO₃, NH₄, NH₃, N, TN, TAN, TKN], (c) P-related compounds [PO₄, P, TP], and (d) Biomass yield.

content per biomass dry weight in mixotrophy culture as compared to heterotrophy; however, due to a significantly higher biomass yield, the lipid production per unit volume is increased.

To summarize, the heterotrophy regime showed better performance in pollutant removal from wastewater. Heterotrophy culture also showed a better biomass yield and lipid content as compared to autotrophy, while mixotrophy culture was actually superior among them. However, some considerations need to be considered in selecting an appropriate regime for wastewater treatment purposes, which are discussed in the following section.

7. The bottom lines, limitations, and approaches

Heterotrophic and autotrophic growth of algae represent two different approaches to cultivating algae for wastewater treatment, each with its own set of benefits and drawbacks depending on the target expectations in terms of biomass quality, water purity, or economic sustainability [8,110]. The choice between heterotrophic and autotrophic algae cultivation for treating organic-rich wastewater depends on factors such as cost considerations, availability of resources, desired environmental outcomes, and specific project objectives. Each approach has its strengths and limitations, and the most suitable option will vary depending on the context and requirements of the wastewater treatment

application. When properly implemented and managed, algae-based wastewater treatment can be a sustainable and effective approach to mitigating water pollution and promoting resource recovery.

Heterotrophic algal growth results in a significant increase in biomass concentration compared to phototrophic conditions, as they do not rely on photosynthesis and exhibit higher growth rates. Their growth is supported by a variety of organic substrates, including waste materials, aiding in the breakdown of organic pollutants and reducing biochemical oxygen demand (BOD) levels [111]. This makes heterotrophic microalgae suitable for waste bioremediation and the production of valuable biomass for various applications.

The utilization of alternative carbon sources such as food and agricultural waste and wastewater for the heterotrophic cultivation of microalgae is suggested to achieve economically feasible generation of high-volume, low-value products like biofuels. The growth of microalgae in a heterotrophic manner leads to a notable enhancement in biomass concentration when compared to conditions of phototrophic nature, rendering them suitable for the remediation of waste and the generation of valuable biomass for diverse applications [112]. Heterotrophic algae demonstrate versatility in treating different types of wastewater, including municipal, industrial, and agricultural effluents, making them suitable for a wide range of applications [113]. Another advantage is their versatility in treatment technologies, as they can be integrated into various types of treatment systems, including conventional activated sludge systems, biofilm reactors, or even in combination with phototrophic algae in hybrid systems [114,115]. When used in conjunction with other treatment processes, heterotrophic algae can enhance treatment efficiency and overall pollutant removal.

On the other hand, autotrophic algae rely on photosynthesis, and their growth is dependent on inorganic carbon dioxide and sunlight, which are abundant and renewable resources. During photosynthesis, autotrophic algae release oxygen as a byproduct. This oxygenation of the wastewater can help improve its overall quality by increasing dissolved oxygen levels [116]. In terms of efficiency, autotrophic algae have the added advantage of carbon sequestration, which can help mitigate climate change and make them more sustainable in the long term. They can utilize wastewater and CO₂ as a growth matrix, leading to the production of valuable biological products such as biofuels, bioplastics, cosmetics, pharmaceuticals, and nutraceuticals [117,118]. Both heterotrophic and autotrophic algae contribute to the reduction of eutrophication in receiving water bodies by the efficient extraction of nutrients like nitrogen and phosphorus from wastewater [40].

Autotrophic cultivation generally has lower ongoing costs, even if it may require initial investments in infrastructure. Heterotrophic cultivation may have higher operational costs due to the need for additional organic carbon sources, which may come from waste materials but could also compete with food or feed production [8,119]. On the other hand, heterotrophic algae can be less energy-intensive compared to conventional wastewater treatment technologies. Both approaches have the potential to reduce nutrient and organic pollutant levels in wastewater effluent, thus benefiting the environment. By extracting added-value products from microalgae biomass, also the economic potential of microalgae systems is maximized. This approach aligns with the concept of a circular economy, where resources are used efficiently and waste is minimized [120]. Utilization of phototrophic algae represents the predominant method in algae-based wastewater treatment, along with being commonly employed in pilot-scale experiments. However, autotrophic wastewater treatment exhibits constrained efficacy in organic matter removal, so the pretreatment of the incoming wastewater directed toward the algal bioprocess is necessary [121].

Algae-based wastewater treatment relies entirely on the capacity of algae to take up and store nutrients in the biomass. Consequently, the efficacy of nutrient removal is directly linked to the productivity of biomass. This mechanism of nutrient removal constrains the utilization of algae in treating wastewater with low nutrient concentrations. The hydraulic retention time in algal-based wastewater treatment systems is

considerably prolonged (i.e., > 10 days), in stark contrast to the short duration (several hours) observed in bacteria-based processes [121].

Despite this, microalgae-based wastewater treatment offers a sustainable and eco-friendly approach to removing pollutants and improving water quality. The enormous potential of microalgae systems takes into account their ability to address multiple types of pollutants in wastewater [104,122]. Microalgae are capable of removing nutrients, organic pollutants, heavy metals, and oxygenate wastewater, making them an effective treatment option [123,124]. Moreover, microalgae are a promising tool for the safe, cost-effective, and efficient elimination of pesticide contaminants from the aquatic environment, so far supported mainly by the results of laboratory and pilot experiments [125]. Technological challenges and limitations, such as the need to consider co-existing micropollutants and the effects of environmental conditions, must be addressed for the large-scale implementation of microalgae bioremediation.

Using algae for wastewater treatment can offer several potential environmental and resource benefits; its sustainability depends on various factors and requires careful consideration of both environmental and economic aspects. Despite its promise to address environmental challenges and produce valuable resources, algal-based wastewater treatment faces significant barriers related to operational efficiency, scalability, and treatment effectiveness, which need to be addressed for widespread implementation. Incorporating the co-cultivation of microalgae with specific bacteria species may serve as a technological advancement to enhance the degradation of pollutants from organic-rich wastewater. The complex nature of wastewater, coupled with the ecological traits of algae, poses techno-economic challenges for the implementation of processes on the scale-up to an industrial level [121]. Switching to solar-powered devices for mixing and aeration and process control automation may also serve as a cost-reduction strategy. Further research is needed to assess the economic and environmental feasibility, focusing on the techno-economical aspect and its cost-benefit analysis to upscale microalgal processes for resource recovery from wastewater [126].

8. Conclusion

Microalgae-based technologies for wastewater treatment are, without doubt, performing excellently in terms of pollutant removal. These findings shed light on the ongoing debate about choosing between autotrophy and heterotrophy growth regimes. This study concluded that heterotrophic cultures are superior in terms of biomass productivity and carbon-related and N-related compound removal from wastewater, while the removal of P-related compounds is generally similar. The bottom lines of carbon source requirements in heterotrophy regimes need to be a major consideration, especially for operational cost estimation. Co-cultivation of microalgae with bacterial species could enhance wastewater pollution breakdown, while transitioning to solar-powered devices for mixing, aeration, and process control automation could reduce costs. Techno-economic and cost-benefit analyses are suggested as future research directions to give clearer guidance on this discussed topic.

CRedit authorship contribution statement

Said Nor Sakinah Mohd: Writing – original draft. **Wibowo Yudha Gusti:** Writing – original draft. **Ahmad Azmi:** Writing – original draft. **Čížková Mária:** Writing – original draft. **Kurniawan Setyo Budi:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Data curation, Conceptualization. **Imron Muhammad Fauzul:** Writing – review & editing, Writing – original draft, Resources. **Ismail Azimah:** Resources. **Jusoh Hajjar Hartini Wan:** Resources.

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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