Journal of Applied Phycology
https://doi.org/10.1007/s10811-026-03888-8

REVIEW

Microalgae cultivation in aqueous phases of hydrothermal biomass processing: Composition, constraints, and integration into circular biorefineries

Hilal Kabakcı[1] · **Anıl Tevfik Koçer**[1,2] · **Didem Balkanlı**[1]

Received: 14 January 2026 / Revised: 22 April 2026 / Accepted: 28 April 2026
© The Author(s) 2026

Abstract

Hydrothermal biomass processing, notably hydrothermal carbonization, hydrothermal liquefaction and hydrothermal gasification, generates an aqueous phase enriched in dissolved organic carbon, nitrogen, phosphorus, and inorganic ions. Although often regarded as a problematic effluent due to high chemical oxygen demand and the presence of inhibitory organics, this aqueous phase also represents a concentrated nutrient stream suitable for biological upgrading. Microalgae cultivation in hydrothermal aqueous phases has therefore emerged as a promising strategy to couple wastewater remediation with biomass production in integrated circular biorefineries. This review synthesizes current knowledge on how feedstock composition and hydrothermal process severity govern aqueous-phase chemistry, with particular emphasis on the formation and fate of short-chain organic acids, ammonium and nitrogenous organics, phenolics, and furanic intermediates. Microalgae cultivation studies in hydrothermal aqueous phases are critically evaluated, with particular focus on strain-specific tolerance, dilution strategies, nutrient and organic-carbon removal performance, and biochemical responses associated with mixotrophic growth. Across the literature, successful cultivation is most frequently achieved at moderate aqueous-phase loadings, where inhibitory compounds are sufficiently attenuated while nutrient availability remains adequate to sustain growth comparable to standard culture media. Under these conditions, systems commonly achieve high removals of nitrogen and phosphorus alongside substantial reductions in organic load, while producing biomass suitable for downstream valorisation. Key barriers to scale-up include variability in aqueous-phase composition, residual toxicity from phenolics, furans, and nitrogen heterocycles, and operational constraints in light-limited, high-ionic-strength media. Emerging solutions focus on process optimization and reactor design strategies that enable efficient coupling of detoxification and biomass production. Overall, this review links hydrothermal operating conditions to aqueous-phase chemistry and microalgal physiology, providing design guidance for integrated hydrothermal–microalgal platforms targeting nutrient recovery, effluent polishing, and sustainable biomass generation.

Keywords Microalgae cultivation · Hydrothermal Aqueous Phase · Nutrient recovery · Wastewater remediation · Circular biorefinery

Introduction

Thermochemical conversion processes represent a cornerstone of modern biomass valorisation technologies for sustainable energy production. These processes decompose complex organic matter under elevated temperatures in oxidative or anoxic environments, generating fuels and value-added chemicals through a cascade of dehydration, decarboxylation, and reforming reactions (Swaminaathan et al. 2024). Among these, hydrothermal processes have emerged as a distinct class capable of converting wet biomass without the need for energy-intensive drying.

✉ Didem Balkanlı
didem.balkanli@yildiz.edu.tr

[1] Faculty of Chemical and Metallurgical Engineering, Department of Bioengineering, Yildiz Technical University, Davutpasa Campus, Esenler, 34220 Istanbul, Türkiye

[2] Health Biotechnology Joint Research and Application Center of Excellence, Esenler, 34220 Istanbul, Türkiye

Published online: 19 May 2026

Operating under subcritical or supercritical water conditions, they exploit water's tuneable physicochemical properties, such as reduced dielectric constant and enhanced ionic product to promote hydrolysis, depolymerization, and condensation reactions (Ruiz et al. 2021; Lachos-Perez et al. 2022). This distinctive capacity positions hydrothermal systems at the forefront of sustainable biorefinery research, linking waste treatment, nutrient recovery, and renewable fuel synthesis within a single framework.

In hydrothermal systems, water acts simultaneously as solvent, reactant, and catalyst, enabling the conversion of biomass into energy-rich products such as biofuels, chemicals, and hydrochar under elevated temperatures and pressures. The process yields a complex mixture of phases, among which an aqueous phase rich in water-soluble organic and inorganic ions is invariably formed (Zhang et al. 2023; Qiu et al. 2025). This aqueous fraction typically contains short-chain organic acids, alcohols, phenols, furans, ammonia, phosphate, and trace metals derived from the feedstock matrix (Illoussamen et al. 2026). The composition depends strongly on the feedstock type and process severity, protein- and nitrogen-rich substrates produce alkaline, nitrogenous waters, while lignocellulosic materials yield acidic, oxygenated fractions (Feng et al. 2025).

Managing this liquid by-product has become a central challenge in hydrothermal biorefinery design. It can represent both a valuable nutrient stream suitable for microbial or algal cultivation and a potential pollutant requiring remediation (Durak et al. 2024). Accordingly, recent studies have explored physicochemical and biological strategies to recover carbon, nitrogen, and phosphorus from the aqueous phase or to reuse it directly as a growth medium for microalgae (Fig. 1).

Microalgae have attracted considerable attention as third-generation biomass feedstocks due to their ability to overcome many of the limitations associated with first- and second-generation biomass resources (Özçimen et al. 2018). First-generation biomass, derived from food crops such as corn and sugarcane, is constrained by competition with food supply, extensive land and freshwater requirements, and ethical concerns related to food security (Oliveira et al. 2024). Second-generation biomass, primarily composed of lignocellulosic materials such as agricultural residues and forestry waste, partially alleviates the food-versus-fuel conflict; however, it is limited by recalcitrant structures, complex pretreatment requirements, low conversion efficiencies, and high processing costs (Olivito et al. 2026). In contrast, third-generation biomass such as microalgae offers significant advantages, including rapid growth rates, high photosynthetic efficiency, and superior CO_2 fixation capacity (Şerbetçioğlu Sert et al. 2018; Koçer et al. 2020). Moreover, microalgae cultivation can be performed on non-arable land and using non-potable water or wastewater streams, thereby avoiding competition with agricultural resources while enabling simultaneous carbon capture and nutrient recovery (Gupta et al. 2024). In addition to these advantages, microalgae have been extensively investigated for a wide range of applications, including biofuel production, wastewater remediation, CO_2 sequestration, and the synthesis of high-value products such as nutraceuticals, pharmaceuticals, and bioplastics, underscoring their multifunctional role in integrated and sustainable biorefinery systems (Garcia-Perez et al. 2023; Karacaoğlu et al. 2025). These features position

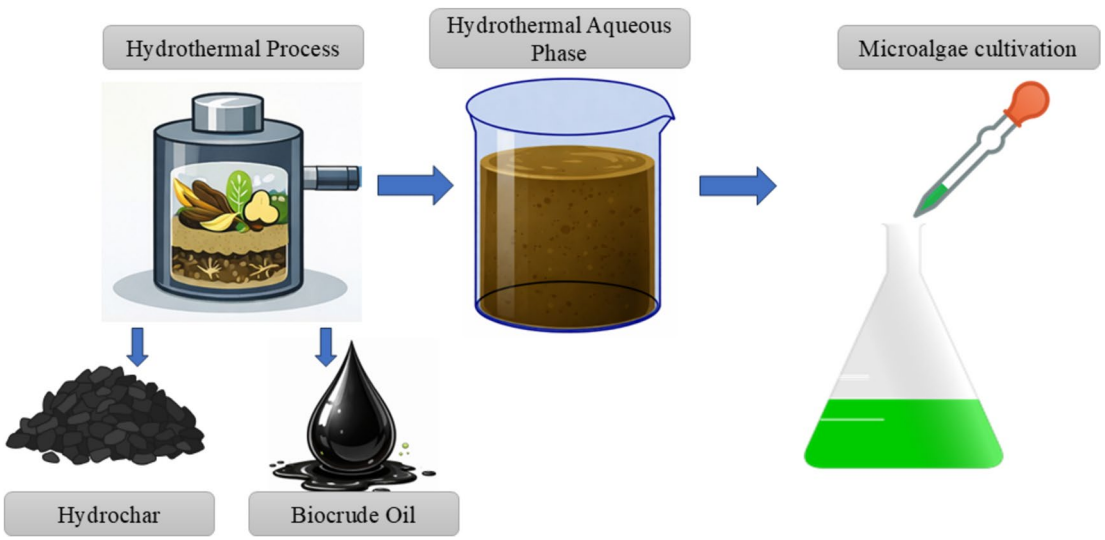


Fig. 1 Schematic representation of hydrothermal biomass processing and subsequent reuse of the hydrothermal aqueous phase for microalgae cultivation

microalgae as a highly sustainable and scalable feedstock for advanced biorefinery applications within circular bioeconomy frameworks (Xu et al. 2024).

Numerous studies have investigated strategies to enhance microalgal growth and the accumulation of target biomolecules. Nutrient modulation, particularly nitrogen and phosphorus control, plays a critical role in regulating biomass productivity and biochemical composition (Yang et al. 2025a; Minhas et al. 2026). In addition, optimization of environmental parameters such as light intensity, carbon availability, and cultivation mode (photoautotrophic, mixotrophic, and heterotrophic) significantly influences growth performance and metabolite accumulation (Dias et al. 2025). The use of waste-derived media, including industrial effluents and hydrothermal aqueous phases, has gained increasing attention as a cost-effective approach to supply essential nutrients while reducing environmental impact (Dias et al. 2025). These strategies highlight the adaptability of microalgae to diverse cultivation conditions and their strong potential for integration into circular biorefinery systems (Wang et al. 2025).

In recent years microalgae cultivation in the aqueous phase of hydrothermal processes has emerged as an innovative strategy for coupling waste remediation with biomass production. The approach addresses two goals simultaneously:

(i) Reducing the load of dissolved organic compounds, nitrogen, and phosphorus in hydrothermal effluents, and
(ii) Generating algal biomass rich in lipids, carbohydrates, and proteins for biofuels and other high-value bioproducts (Belete et al. 2019; Zora Tarhan et al. 2021).

Compared to conventional cultivation media, the aqueous phase offers a unique advantage as it inherently contains bioavailable carbon, nitrogen, and phosphorus species derived from biomass conversion, thereby reducing the need for external nutrient supplementation. This not only lowers operational costs but also enhances resource efficiency by closing nutrient loops within the biorefinery system. Previous studies demonstrated that various microalgae species can grow in suitably diluted hydrothermal effluents while achieving nutrient removal efficiencies above 80% (Koçer et al. 2023; Wang et al. 2026).

This review aims to provide a comprehensive and systematic evaluation of hydrothermal aqueous phases and their potential for integration into microalgae-based circular biorefinery systems. Particular emphasis is placed on understanding the composition and variability of AP generated from different hydrothermal technologies, and how these characteristics influence downstream biological processes. The review further examines key factors affecting microalgae cultivation, including nutrient availability, inhibitory compounds, and process optimization strategies. In addition, recent advances in aqueous phase valorization, as well as the associated engineering and economic challenges for scale-up, are critically discussed. By integrating thermochemical and biological perspectives, this work aims to provide a clearer framework for linking upstream hydrothermal processing with downstream biotechnological applications, thereby supporting the development of more efficient and sustainable circular biorefinery systems.

Hydrothermal process of biomass

Hydrothermal processes are governed by the physical state of water under specific thermodynamic conditions. Subcritical water refers to liquid water maintained between 100 °C and 373 °C under pressurized conditions that prevent vaporization, whereas supercritical water exists beyond its critical point (T_c = 373 °C; P_c = 22.1 MPa) (Lachos-Perez et al. 2022). Within this continuum, temperature and pressure modulate water's dielectric constant, viscosity, and ionic product, profoundly influencing reaction (Kumar et al. 2018; Ruiz et al. 2021). Based on operating regimes and target products, hydrothermal technologies are typically classified as hydrothermal carbonization (HTC) for 180–250°C, hydrothermal liquefaction (HTL) for 250–370°C, and hydrothermal gasification (HTG) for temperatures exceeding 400°C. Each pathway triggers a network of reactions - hydrolysis, depolymerization, dehydration, decarboxylation, condensation, aromatization, and hydrogenation - yielding solids (hydrochar), liquids (bio-oil and aqueous phase), and gases (CO_2, CH_4, H_2) (Lachos-Perez et al. 2022). Among these products, the aqueous phase (also termed the aqueous phase or process water) has gained increasing attention as both an environmental liability and a potential nutrient reservoir for biological reuse.

Hydrothermal technologies themselves represent a major advancement in integrated waste treatment and resource recovery. Through controlled reactions in hot compressed water, these processes convert diverse organic feedstocks including agricultural residues, food waste, sewage sludge, and microalgae into carbonaceous solids (hydrochar), bio-oil, and gases such as CO_2 and CH_4 (Illoussamen et al. 2026). Their ability to process wet biomass without prior drying renders them particularly attractive for sustainable waste management. Beyond producing renewable fuels, hydrothermal systems provide a means to recycle nutrients and mitigate environmental pollution, aligning with the principles of the circular bioeconomy (Nguyen et al. 2023). Ongoing research continues to refine process efficiency, product selectivity, and downstream valorisation, extending

the potential of hydrothermal treatment from waste conversion to a fully integrated waste-to-resource platform.

Aqueous phases of hydrothermal treatment of biomass

The aqueous phase generated during hydrothermal processes exhibits highly variable composition depending on feedstock type, process temperature, residence time, and target product (Jagadale et al. 2024; Nazari et al. 2025). It typically contains a complex mixture of dissolved organic compounds, inorganic nutrients, and trace metals, reflecting the incomplete conversion of biomass and the redistribution of heteroatoms during thermochemical reactions (Shah et al. 2026). The aqueous phase therefore represents both an opportunity for resource recovery and a challenge for environmental management (Nguyen et al. 2023). Although hydrothermal processes transform a substantial fraction of organic matter into value-added solids and oils, the remaining liquid phase retains numerous compounds that can be further valorised through biological or catalytic routes (Koçer et al. 2023).

Water, acting as both reaction medium and reactant, facilitates hydrolysis and rearrangement reactions that generate a broad suite of water-soluble products, including short-chain organic acids (formic, acetic, lactic), furanic compounds (furfural, 5-hydroxymethylfurfural), phenolics, aldehydes, ketones, nitrogen-containing organics, and low-molecular-weight aromatics (Xu et al. 2022). In addition, significant quantities of ammonium, phosphate, potassium, calcium, and sodium ions leach into solution, originating from proteins, nucleic acids, and mineral phases in the feedstock (Belete et al. 2019).

Managing and converting the aqueous phase has therefore become a focal point of modern hydrothermal research. Several valorization strategies have been proposed:

(i) Recirculation of the aqueous phase to improve aqueous phase efficiency and promote secondary hydrothermal reactions (Mau et al. 2019; He et al. 2022),
(ii) Microalgae cultivation for nutrient recovery and biomass production (Koçer et al. 2023), and,
(iii) Chemical upgrading via adsorption, catalytic oxidation, or nutrient precipitation (Nguyen et al. 2023).

The choice of strategy depends strongly on the feedstock: recirculation is generally feasible for lignocellulosic and carbohydrate-rich materials, whereas sludge-derived or protein-rich effluents often exhibit high ammonia and heterocyclic content that limit reuse without pretreatment (Xu et al. 2022).

While these variations are often attributed to feedstock characteristics, the type of hydrothermal process itself also plays a decisive role in shaping the composition and properties of the aqueous phase (Nguyen et al. 2023). Significant differences emerge when comparing HTC, HTL, and HTG systems. Aqueous phases derived from HTC, typically operating at moderate temperatures (180–250 °C), are generally characterized by acidic conditions and high concentrations of short-chain organic acids such as acetic and formic acids (Libra et al. 2011). These compounds originate from partial hydrolysis and dehydration reactions and can serve as potential carbon sources, although their accumulation may also lead to inhibitory effects depending on concentration (Ghaziaskar et al. 2019). In contrast, HTL processes (250–370 °C) produce aqueous phases enriched in nitrogen-containing compounds, particularly ammonium and heterocyclic organics, due to extensive protein decomposition (Shah et al. 2026). These aqueous phases are typically neutral to alkaline and contain higher total nitrogen levels, which can enhance microalgal growth but may also introduce toxicity constraints (Basar et al. 2023). HTG, operating under supercritical conditions (>374 °C), results in more complete conversion of organic matter into gaseous products, leading to aqueous phases with comparatively lower organic content but retained inorganic nutrients (Sarker et al. 2022). As a result, HTG-derived aqueous phases are generally less suitable as carbon-rich media but may offer advantages in terms of reduced inhibitory compound concentrations (Liao et al. 2022). Overall, these differences clearly demonstrate that the selection of hydrothermal technology directly determines the chemical characteristics and biological suitability of the aqueous phase, thereby critically influencing downstream microalgae cultivation performance.

Chemical composition of aqueous phase

The composition of the hydrothermal aqueous phase reflects the degradation pathways of carbohydrates, proteins, and lipids under subcritical conditions and varies depending not only on feedstock characteristics but also on the hydrothermal process employed. Short-chain organic acids, chiefly acetic, formic, lactic, and propionic acids, dominate in most reports, often representing more than 70% of the identified organics. These acids arise mainly from deamination of amino acids and decarboxylation of carbohydrates through intermediates such as glycine and glyceraldehyde (Xu et al. 2022). Increasing temperature (200–250 °C) and residence time enhance their formation, with total concentrations reaching 2–20 g L^{-1} (Sindhuwati et al. 2026). These compounds are particularly abundant in HTC-derived aqueous phases, where mild processing conditions favor partial hydrolysis and the accumulation of oxygenated intermediates. Dicarboxylic acids including malonic, succinic, methylsuccinic, and glutaric acids are also produced from carbohydrate fragmentation and amino-acid oxidation.

Nitrogen-containing compounds are among the most abundant heteroatom species in the aqueous phase. Ammonia typically predominates at lower temperatures through the deamination of amino acids and peptides, while higher temperatures favour the formation of heterocyclics such as indoles, pyroles, pyrazines, and aminophenols via Maillard reactions between sugars and amino acids (Xu et al. 2022). The concentration of these nitrogenous species correlates strongly with the protein content of the feedstock; sludge and algae derived APs often exhibit NH_4^+, N concentrations above 5 g L^{-1} (Belete et al. 2019; Zora Tarhan et al. 2021). Such nitrogen enrichment is particularly pronounced in HTL systems, where elevated temperatures promote extensive protein degradation and nitrogen mineralization. Under alkaline conditions, nitrogen heterocycles are stabilized, whereas sulfur from amino acids oxidizes predominantly to sulfate (SO_4^{2-}) (Xu et al. 2022).

Oxygenated compounds such as alcohols, aldehydes, ketones, phenols, and cyclic oxygenates, derive from saccharide fragmentation and lignin depolymerization. Alcohols and ketones form through dehydration of polyols and carbohydrate intermediates, while phenols originate from lignin and protein aromatics (Feng et al. 2025). Furfural and 5-hydroxymethylfurfural (5-HMF) are common intermediates from hemicellulose and cellulose hydrolysis and may polymerize into hydrochar precursors (Xu et al. 2022). These intermediates are typically more concentrated in HTC and HTL systems, whereas under HTG conditions they are largely converted into gaseous products or further degraded.

Minor fractions of hydrocarbons are also detected. Long-chain alkanes and alkenes appear at low concentrations owing to lipid decarboxylation, whereas benzene derivatives and polycyclic aromatic hydrocarbons (PAHs) arise from condensation and aromatization reactions of small oxygenates during HTC, particularly in sewage-sludge systems rich in proteins and fats (Shah et al. 2026).

The recirculation of aqueous phase during successive HTC cycles influences both hydrochar yield and aqueous chemistry. For lignocellulosic or protein-poor substrates, recycling enhances acid concentration and promotes carbon conversion efficiency, whereas in protein-rich materials such as brewer's spent grain or sludge, elevated ammonia and nitrogen heterocycles can suppress char formation or alter surface functionality (Mau et al. 2019). Similar recirculation effects have also been reported in HTL systems, where accumulation of nitrogen-rich intermediates can significantly alter aqueous phase composition and downstream process performance (Hong et al. 2021).

Overall, the hydrothermal aqueous phase is dominated by low-molecular-weight organic acids and nitrogenous compounds, accompanied by minor oxygenates, phenols, and hydrocarbons. Their relative abundance is governed not only by feedstock composition, process temperature, and pH, but also by the selected hydrothermal pathway (HTC, HTL, or HTG) and the extent of secondary reactions occurring in the aqueous phase. A comparative summary of the chemical composition of hydrothermal aqueous phases reported in the literature is presented in Table 1.

Physical properties of aqueous phase

The physical characteristics of hydrothermal aqueous phases vary considerably depending on feedstock composition, reaction temperature, residence time, and process configuration, as well as the type of hydrothermal process employed (HTC, HTL, or HTG). Observable properties such as colour, turbidity, viscosity, and density are direct reflections of the extent of biomass degradation and the nature of soluble and suspended products.

The colour of the aqueous phase typically ranges from light yellow to dark brown. Lignocellulosic materials and carbohydrate-rich residues tend to produce darker liquors due to the formation of humic-like substances, polymerized phenolics, and Maillard reaction products (Xu et al. 2019). Conversely, aqueous phases derived from microalgal or sludge feedstocks often display greenish or olive hues, attributed to residual chlorophyll derivatives and nitrogenous pigments (Leng et al. 2022). Darker coloration is particularly evident in HTC systems due to the accumulation of polymerized intermediates, whereas HTL-derived aqueous phases may appear less opaque but more concentrated depending on nitrogen-rich compound formation (Zhong et al. 2024).

Turbidity and suspended solids are largely influenced by the inorganic ash and cell-wall components of the initial biomass. Diatomaceous feedstocks yield more turbid liquors due to the presence of fine silica frustules, while lignocellulosic and algal residues generally produce clearer supernatants after sedimentation or centrifugation (Belete et al. 2019). Turbidity tends to increase with higher process severity, as intensified hydrolysis and condensation reactions release fine particulate char and colloidal carbon species (Mau et al. 2019). This effect is often more pronounced in HTC and HTL systems, whereas HTG-derived aqueous phases generally exhibit lower turbidity due to more complete conversion of organics into gaseous products (Watson et al. 2017).

Viscosity and density are affected by both temperature and the concentration of dissolved organic matter. At subcritical conditions, elevated levels of organic acids and polymeric degradation intermediates slightly increase dynamic viscosity compared with pure water (Yabalak et al. 2023). Aqueous phases derived at higher temperatures (>250 °C) often exhibit reduced viscosity due to enhanced depolymerization and lower molecular weight organics (Watson et al. 2020; Illoussamen et al. 2026). Accordingly, HTC-derived aqueous phases tend to exhibit higher apparent viscosity due

Table 1 Representative chemical composition of hydrothermal aqueous phases derived from various biomass types

Process Type	Feedstock/Source	Organic Content	Inorganics Content	Reference
HTC	Microalgae	Short-chain organic acids TN: 67–123 g L^{-1}	Not quantified	(Khoo et al. 2020)
HTC	Olive mill waste	TOC: 17.3–35.1 g L^{-1} TN: 0.4–0.7 g L^{-1}	Not quantified	(Dahdouh et al. 2024)
HTC	Lipid-extracted *P. oculatum*	TOC: 20.9 g L^{-1} NH_3: 2.2 g L^{-1} NO_3^-: 0.22 g L^{-1}	Na: 6700 ppm K: 2500 ppm	(Tsarpali et al. 2021)
HTC	Sewage sludge	Acetic Acid: 2 g L^{-1} NH_4^+: 3–5 g L^{-1}	Not quantified	(Xu et al. 2022)
HTC	Olive pomace	Formic acid: 2.1 g L^{-1}, Acetic acid: 1.6 g L^{-1} TN: 2–3 g L^{-1}	Not quantified	(Zora Tarhan et al. 2021)
HTL	*Chlorella sp.*	TOC: 14–35 g L^{-1} TN: 7.8–23.4 g L^{-1}	Not quantified	(Leng et al. 2022)
HTL	Sewage sludge	TOC 12.8 g L^{-1} TN: 7.5 g L^{-1}	Not quantified	(Shah et al. 2020)
HTL	Wood waste	Acetic acid: 20–55 g L^{-1}	Not quantified	(Sindhuwati et al. 2026)
HTG	Apricot tree resin	TOC: 0.5–12.5 g L^{-1}	Not quantified	(Selvi Gökkaya 2025)
HTG	Rice straw	TOC: 0.014–0.022 g L^{-1}	Na: 90–100 ppm K: 110–4150 ppm Mg: 130–290 ppm Ca: 150–190 ppm	(Liu et al. 2024)
HTG	Microalgae	Phenols: 35 mg g^{-1} TOC reduction: 90% TN: 0.42–4.29 g L^{-1}	Na: 182–12100 ppm K: 93.7–878 ppm Mg: 4.52–7.30 ppm Ca: 11.6–128 ppm	(Onwudili et al. 2013)

to the presence of polymerized intermediates, whereas HTG systems typically yield lower-viscosity liquids.

Electrical conductivity (EC), though primarily a chemical parameter, also reflects the physical ionic strength of the medium. Typical EC values range from 3 to 35 mS cm^{-1}, increasing with salt and nutrient release from mineral-bound feedstocks such as sludge or manure (Ahn et al. 2024; Szkadłubowicz et al. 2025). Elevated EC values are frequently observed in HTL-derived aqueous phases due to higher concentrations of dissolved nitrogen species, while HTC systems may exhibit moderate conductivity depending on feedstock composition.

These physical attributes influence the subsequent handling and potential reuse of the aqueous phase. For instance, darker, more viscous liquors may require dilution or filtration before microalgae cultivation, while high turbidity can hinder light penetration in algal cultivation systems. Understanding these physical characteristics, and their dependence on both feedstock and hydrothermal processing route, is therefore crucial for designing downstream separation, pretreatment, and reuse strategies within integrated hydrothermal biorefineries (Nguyen et al. 2023).

Table 2 summarizes representative physical properties of aqueous phases generated during hydrothermal processing of different biomass feedstocks. Across studies, pH values span a broad range, reflecting both feedstock composition and process severity. Hydrothermal carbonization of lignocellulosic and carbohydrate-rich materials typically yields acidic aqueous phases (pH ≈ 3–5), consistent with the accumulation of organic acids, whereas protein-rich substrates and hydrothermal liquefaction processes tend to produce near-neutral to mildly alkaline aqueous phases due to enhanced nitrogen mineralization and ammonium formation.

Electrical conductivity varies widely, particularly in systems involving sludge or aqueous-phase recirculation, indicating substantial accumulation of dissolved inorganic ions and soluble organic species. Elevated conductivity and persistent dark coloration are commonly associated with increased process severity or recirculation, reflecting higher dissolved solids, chromophoric compounds, and refractory organics. Collectively, these physical properties impose additional constraints on downstream biological reuse, as pH, salinity, and optical density directly influence microalgal growth, light penetration, and nutrient bioavailability.

Studies indicate that the pH and electrical conductivity of the hydrothermal aqueous phase tend to increase slightly upon recirculation within hydrothermal processing systems. This behavior is generally attributed to the accumulation of inorganic ions and soluble degradation products. Nevertheless, despite these incremental changes, the pH of the

Table 2 Representative physical properties of hydrothermal aqueous phases (aqueous phases) derived from various biomass types

Process Type	Feedstock/Source	Process Conditions (°C)	pH	Electrical Conductivity (mS cm^{-1})	Turbidity/Appearance	Reference
HTC	Microalgae	180–250	2.95–4.50	—	Amber, odorous	(Khoo et al. 2020)
HTC	Lipid-extracted microalgae	180	~7.5	—	Amber, clear to slightly turbid	(Tsarpali et al. 2021)
HTC	Orange and olive pomace	250	4.2–4.5	3.7–6.9	Dark, acidic	(Zora Tarhan et al. 2021)
HTC	Sludge	200	6.9 ± 0.01	22 ± 0.4	Dark brown	(Mau et al. 2019)
HTC	Septage	180–260	6.0–8.0	10–25	Brown, opaque	(McGaughy and Reza 2018)
HTL	Microalgae + sewage sludge	300–350	7.0–8.2	—	Dark brown, concentrated	(Leng et al. 2022)
HTC	Incineration fly ash	180	11.84	65.8	Dark brown	(Chen et al. 2025)
HTC	Sewage sludge	180	7.52	16.50	Dark brown	(Chen et al. 2025)
HTC	Sewage sludge	210	5.7	2.27	-	(Szkadłubowicz et al. 2025)
HTC	Sewage sludge	200	5.38	2.09	-	(Szkadłubowicz et al. 2025)
HTC	Sewage sludge	200	8.74	29	-	(Ahn et al. 2024)

recirculated aqueous phase typically remains within a range comparable to that of the original feedstock, suggesting a degree of buffering capacity in the system. Conductivity on the other hand increases within the system and then stabilizes within recirculations (Ahn et al. 2024).

Microalgae cultivation in hydrothermal aqueous phases

The reuse of hydrothermal aqueous phase as a nutrient source for microalgae cultivation has attracted increasing attention as an integrated strategy for waste valorisation and nutrient recovery. These aqueous streams are typically enriched in dissolved organic carbon, nitrogen, phosphorus, and trace elements, enabling algal growth while simultaneously providing wastewater remediation potential (Nguyen et al. 2023). In contrast to conventional wastewaters dominated by inorganic nutrients, hydrothermal aqueous phase often contains substantial fractions of reduced nitrogen species and low-molecular-weight organic acids, which can promote mixotrophic or hetero-mixotrophic growth and alter growth behaviour and kinetics relative to photoautotrophic cultivation.

HTL-derived aqueous phases generally contain higher concentrations of nitrogen heterocycles, phenolics, and other reduced organic compounds than HTC-derived waters, primarily due to increased process severity and the greater extent of biomass decomposition. This results in elevated inhibitory pressure on photosynthetic microorganisms and necessitates stronger dilution, nutrient balancing, or pre-conditioning prior to cultivation (Lachos-Perez et al. 2022). As a result, cultivation performance in hydrothermal aqueous phase is governed not solely by nutrient availability but by the interplay among organic loading, nitrogen speciation, ionic strength, and residual inhibitory compounds. This section summarizes cultivation strategies, growth behaviour and kinetics, biochemical responses, and transformations of hydrothermal aqueous phase during cultivation, with emphasis on the conditions under which hydrothermal aqueous phase functions as a viable nutrient resource rather than a growth-limiting medium.

Although HTC-, HTL-, and HTG-derived aqueous phases contain broadly similar classes of compounds, the primary distinction among these processes lies in the concentration and distribution of these components, which are governed by process severity. In particular, the higher reaction temperatures and pressures in HTL typically lead to more extensive biomass decomposition, resulting in elevated concentrations of phenolic compounds and nitrogen-containing species that are often associated with inhibitory effects on microalgal growth (Basar et al. 2023). In contrast, HTC-derived aqueous phases are generally characterized by lower concentrations of such inhibitory compounds and are therefore often considered less restrictive for cultivation, although this depends strongly on feedstock type and operational conditions (Wei et al. 2025). From a microalgal cultivation perspective, these differences mainly affect the extent of dilution or pre-conditioning required to mitigate inhibitory effects while maintaining nutrient availability (Tsarpali et al. 2021). HTL-derived streams generally require more stringent conditioning due to higher organic and nitrogen loads, whereas HTC-derived streams tend to be less restrictive under comparable conditions, although this depends strongly on feedstock composition and process parameters (Wei et al. 2025).

Growth behaviour and cultivation performance in hydrothermal aqueous phase

Microalgae cultivation in hydrothermal aqueous phases differs fundamentally from cultivation in synthetic media or municipal wastewaters, as growth is governed by the combined effects of dissolved organic carbon, reduced nitrogen species, elevated ionic strength, and residual inhibitory compounds formed during thermochemical conversion. Consequently, cultivation strategies reported in the literature emphasize toxicity mitigation, organic loading control, and exploitation of mixotrophic metabolism rather than maximization of volumetric productivity alone (Belete et al. 2019). Most studies employ suspended cultures in laboratory-scale batch or semi-batch systems using diluted hydrothermal aqueous phase as a partial or sole nutrient source, reflecting the need to precisely control aqueous chemistry and assess tolerance thresholds (Shah et al. 2020; de Castro e Silva et al. 2024).

Across reactor types, three operational parameters consistently dominate cultivation performance: dilution ratio, organic carbon loading, and nitrogen speciation. The dilution requirements for aqueous phases derived from HTC, HTL and HTG are significantly influenced by feedstock composition and the inherent tolerance of the cultivated microalgal species. When comparing identical feedstocks, HTL-derived aqueous phases generally necessitate more extensive dilution (0.5–3% v/v) compared to HTC-derived streams (1–5% v/v), primarily due to the higher concentrations of recalcitrant nitrogen-containing heterocyclics and hydrophobic hydrocarbons generated under more severe HTL conditions (Durak 2023; de Castro e Silva et al. 2024). Raw effluents from both processes frequently exhibit chemical oxygen demand exceeding 100,000 mg L^{-1} (Belete et al. 2019; Kulikova et al. 2023), necessitating substantial dilution prior to cultivation. This behaviour is further supported by experimental studies using lignocellulosic HTC process waters. For example, cultivation of *Chlorella minutissima* and *Botryococcus braunii* in HTC aqueous phases derived from orange and olive pomace required dilution levels of 50×–400× (corresponding to approximately 0.25–2% v/v aqueous phase), and although growth was sustained, maximum growth rates remained relatively low (up to ~0.13 g L^{-1} day^{-1}) compared to synthetic media, reflecting the presence of inhibitory compounds such as HMF and furfural (Zora Tarhan et al. 2021). Similarly, the use of HTL-derived aqueous phase has been shown to significantly suppress microalgal growth, with growth rates decreasing from approximately 0.74–1.08 to 0.38–0.44 day^{-1} upon initial exposure, indicating strong inhibitory effects of dissolved organic compounds (Ramírez-Romero et al. 2025). Accordingly, successful cultivation is typically reported at low hydrothermal aqueous phase fractions, with species such as *Chlorella vulgaris, Chlorella* sp., and *Coelastrella* sp. achieving growth comparable to standard media at approximately 1–10% aqueous phase, depending on feedstock origin and hydrothermal severity (Tsarpali et al. 2021). In contrast, higher fractions (>20–30%) frequently result in growth inhibition due to the combined effects of toxic compounds, elevated ionic strength, and reduced light penetration. Taken together, these findings indicate that dilution ratios below ~5–15% (v/v) generally provide the most stable operational window.

High organic loading further constrains cultivation performance. Microalgae cultivated in hydrothermal aqueous phase commonly operate under mixotrophic or hetero-mixotrophic regimes due to the presence of readily assimilable organic acids (e.g., acetate and formate) in combination with reduced nitrogen species. Moderate organic loading (typically ~500–2000 mg L^{-1} COD) can enhance biomass productivity; however, excessive organic concentrations (>2500–3000 mg L^{-1} COD) often lead to oxygen depletion, respiratory dominance, extended lag phases, and growth inhibition (Leng et al. 2018; Garcia-Perez et al. 2023). In addition, the dark coloration of hydrothermal aqueous phases increases optical density, reducing light penetration and compressing the effective photic zone, and therefore limiting photosynthesis (Kulikova et al. 2023).

Nitrogen speciation, particularly the predominance of ammonium, represents another critical determinant of cultivation performance. While ammonium provides a readily assimilable nitrogen source, its concentration must be carefully controlled. Across studies, optimal growth is generally observed at ammonium concentrations below ~100 mg L^{-1} NH_4^+-N, whereas higher levels (>150–200 mg L^{-1}) can induce toxicity, partly due to free ammonia formation under alkaline conditions. At even higher concentrations (200–500 mg L^{-1}), significant inhibition of Photosystem II (PSII) activity has been reported, resulting in reduced photosynthetic efficiency and suppressed biomass productivity (Leng et al. 2018; Chernova et al. 2019).

Long-term and continuous operation remains comparatively underexplored due to concerns regarding chronic exposure to residual inhibitors and the accumulation of recalcitrant organics (Leng et al. 2022). In response, selection-based adaptive strategies and co-cultivation approaches have been proposed to improve tolerance and process stability. The selection-based adaptive strategies enable progressive physiological and genetic adaptation under sustained stress conditions without targeted genetic modification, thereby enhancing tolerance to HTL aqueous phase toxicity and allowing higher reuse fractions without growth suppression (Ramírez-Romero et al. 2025). In parallel, fungal–microalgal co-cultivation can facilitate partial detoxification and improve nutrient removal through combined adsorption and biodegradation mechanisms (Chen et al. 2020). Overall,

hydrothermal aqueous phase cultivation can be best interpreted as a hybrid treatment–valorization step, whose performance is intrinsically linked to upstream hydrothermal conditions and downstream integration requirements.

Biochemical and physiological characteristics of microalgae cultivated in hydrothermal aqueous phase

Cultivation in hydrothermal aqueous phase induces measurable biochemical and physiological responses compared with conventional growth media, primarily driven by nutrient availability, organic loading, and residual inhibitory compounds. These responses are strongly dependent on dilution strategy and strain-specific tolerance, indicating that biochemical outcomes are conditional rather than intrinsic to hydrothermal aqueous phase exposure.

Enhanced lipid accumulation is frequently reported under optimized dilution conditions. Lipid content increases of approximately 20–70% have been observed across studies, often associated with elevated carbon-to-nitrogen (C/N) ratios (>20–30) and partial nitrogen limitation rather than direct effects of inhibitory compounds (Tsarpali et al. 2021). These conditions promote carbon partitioning toward storage lipids, a response that is not unique to hydrothermal aqueous phase systems but reflects general metabolic adaptation in microalgae. However, not all hydrothermal aqueous phase conditions promote lipid accumulation. In many cases, inhibitory effects suppress both growth and lipid biosynthesis. For example, the presence of HTL-derived aqueous phase has been shown to slow lipid accumulation kinetics and reduce overall biomass energy content, despite supporting biomass production in the range of approximately 2.95–4.27 g L^{-1} (Ramírez-Romero et al. 2025). Lipid contents under these conditions typically ranged from 16 to 36%, remaining below values achieved in AP-free systems. These findings indicate that aqueous-phase toxicity can interfere with metabolic regulation and delay the onset of lipid accumulation.

This interpretation is further supported by studies demonstrating minimal changes in biochemical composition under low loading conditions. For instance, *Chlorella sorokiniana* cultivated in highly diluted HTC aqueous phases (0.25–2%) exhibited no statistically significant differences in lipid (~12.7–14.3%), carbohydrate (~32–35%), or protein (~35–41%) content compared with standard media, despite reduced growth rates (Koçer et al. 2023). Similarly, HTC-based systems have shown that aqueous phase composition affects biomass productivity more strongly than biochemical composition (Zora Tarhan et al. 2021). Collectively, these findings indicate that while growth rates may decrease by approximately 30–50%, biochemical composition often remains within comparable ranges.

Hydrothermal aqueous phase derived from algal biomass is often nutrient-rich, with nitrogen and phosphorus concentrations reported in the gram-per-liter range (Edmundson et al. 2017). Under controlled dilution, this nutrient availability can support growth while promoting lipid accumulation, often associated with partial nitrogen limitation or altered carbon-to-nitrogen (C/N) ratios that redirect carbon flux toward storage compounds. However, it should be noted that enhanced lipid accumulation is not necessarily a direct response to inhibitory compounds present in the aqueous phase. In many cases, such increases are driven by nutrient imbalances, particularly elevated C/N ratios or nitrogen limitation, which are well-established triggers for lipid accumulation in microalgae. Moreover, these responses may be strain-specific, as variations in metabolic pathways, stress tolerance, and nutrient assimilation capacity can lead to significantly different biochemical outcomes under similar conditions (Abdelkarim et al. 2025; Galieva et al. 2026). Furthermore, similar increases in lipid accumulation may also be observed under balanced nutrient control systems with adjusted C/N ratios, indicating that these responses are not exclusively linked to hydrothermal aqueous phase exposure but represent general metabolic adaptations in microalgae (Pereira et al. 2024; Yang et al. 2025b). Therefore, distinguishing between toxicity-induced stress responses and nutrient-driven metabolic shifts remains essential for accurately interpreting biochemical changes observed in hydrothermal aqueous phase cultivation systems. In addition, shifts in fatty-acid profiles toward higher proportions of saturated and monounsaturated chains have been reported, improving suitability for biodiesel production (Khoo et al. 2020).

Hydrothermal aqueous phase can also influence pigment content and macromolecular partitioning. Moderate organic loading has been associated with enhanced chlorophyll and carotenoid synthesis, suggesting that low to intermediate aqueous phase fractions can support photosynthetic capacity rather than suppress it (Belete et al. 2019). However, similar pigment responses may also arise from changes in nutrient availability or light utilization efficiency, rather than solely from the presence of inhibitory compounds. Carbohydrate accumulation is more variable, with reductions often observed under nutrient-replete conditions and increases reported under nitrogen limitation or stress, consistent with flexible metabolic adjustment (Yao et al. 2016). Protein content is frequently stable across a range of diluted hydrothermal aqueous phase conditions, indicating that appropriate dilution may preserve nitrogen assimilation and protein synthesis. For example, a 2023 study reported no statistically significant differences in lipid, carbohydrate, or protein fractions for *C. sorokiniana* cultivated in 0.25–2% HTC water derived from orange and olive pomace compared with BG-11 controls, supporting the view that biochemical shifts

depend on loading and stress intensity rather than hydrothermal aqueous phase presence alone (Koçer et al. 2023).

From a downstream conversion perspective, biomass produced in hydrothermal aqueous phase can yield bio-oils comparable to those obtained from conventionally cultivated microalgae, with some reports indicating improved bio-oil composition (Almutairi 2022). However, prolonged exposure to recycled aqueous phases may affect biomass quality, including slower lipid accumulation kinetics or increased inorganic content, potentially influencing thermochemical conversion efficiency (Ramírez-Romero et al. 2025). Conditioning strategies such as dilution, selective supplementation, staged cultivation and co-cultivation may therefore be required to balance nutrient recycling with biochemical optimization (Chen et al. 2020; Ramírez-Romero et al. 2025).

Transformation of hydrothermal aqueous phase after cultivation

Microalgal cultivation in hydrothermal aqueous phase substantially improves effluent quality through nutrient assimilation and partial transformation of dissolved organic compounds. Across multiple studies, reductions in chemical oxygen demand (COD) and total nitrogen (TN) typically range from 60 to 95%, while total phosphorus (TP) removal frequently exceeds 90%, confirming the role of microalgae as effective biological polishing agents within integrated hydrothermal treatment systems (Fig. 2) (Belete et al. 2019). A 2021 study, for instance, reported approximately 80% total organic carbon reduction, 55% TN removal, and 90% TP removal following cultivation of *B. braunii* and *C. minutissima* in HTC-derived aqueous phase (Zora Tarhan et al. 2021).

Nitrogen removal is primarily achieved through assimilation of ammonium and nitrate into cellular biomass, while phosphorus is incorporated into intracellular pools and may also associate with extracellular polymeric substances. Removal efficiencies are strongly influenced by initial nutrient concentrations, inoculum density, cultivation duration, and CO_2 availability, with optimal performance commonly reported under moderate CO_2 supplementation (~5%), mixed-media strategies, and cultivation periods of approximately one week (Yetilmezsoy et al. 2020; Yuan et al. 2023). In parallel with nutrient uptake, partial detoxification occurs through biological transformation of organic constituents; aromatic and furanic compounds may be partially oxidized or incorporated into extracellular matrices, reducing overall toxicity (Nguyen et al. 2023). Medium pH often trends toward neutrality during cultivation due to CO_2 assimilation and ammonium uptake, further improving effluent characteristics.

Nevertheless, hydrothermal aqueous phase typically retains recalcitrant and potentially inhibitory constituents

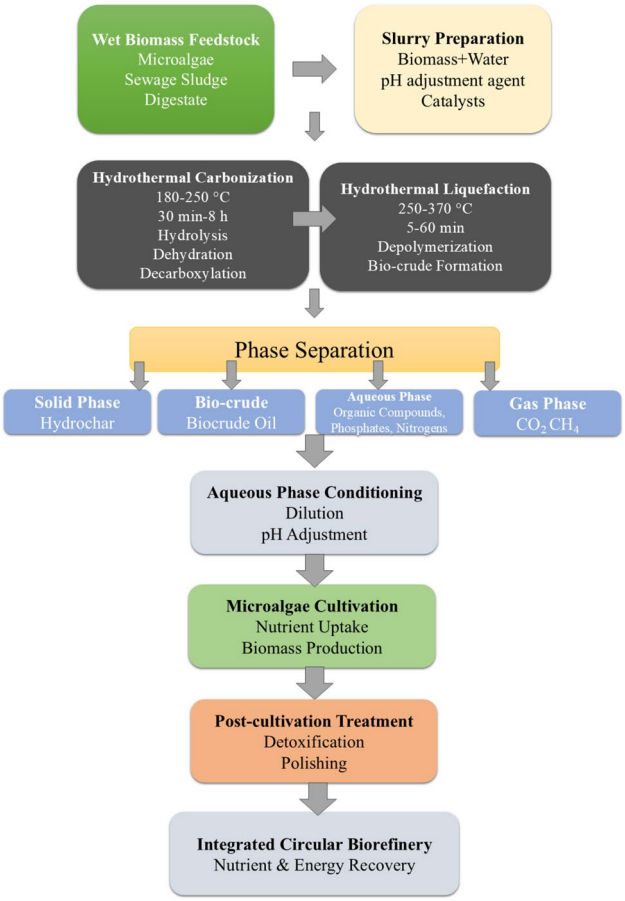


Fig. 2 Schematic representation of nutrient assimilation and organic-compound transformation in hydrothermal aqueous phase during microalgae cultivation

after cultivation, including phenolics, nitrogen-containing organics (amides, amines, heterocycles), and, in some cases, mobilized heavy metals such as arsenic, indicating that effective nutrient removal does not necessarily equate to complete detoxification (Bilgili et al. 2012; Li et al. 2021). Specific nitrogen-containing organics, including 2-pyrrolidinone and β-phenylethylamine, have been reported to inhibit microalgal growth at concentrations above approximately 75 mg L^{-1}, underscoring the continued relevance of dilution and conditioning for safe reuse (Bagnoud-Velásquez et al. 2018). Selection-based adaptive strategies can enhance tolerance and enable higher HT-AP reuse fractions; however, these approaches do not eliminate recalcitrant nitrogen-containing organics and therefore cannot fully substitute for physicochemical conditioning steps (Ramírez-Romero et al. 2025).

Accordingly, post-cultivation hydrothermal aqueous phase often requires complementary conditioning prior to reuse or discharge. Reported strategies include overliming, air stripping, adsorption, partial oxidation, and solvent extraction, which can reduce inhibitory organic loads and improve downstream biological processing, particularly

anaerobic digestion (Zhou et al. 2024). Integration with anaerobic digestion enables additional resource recovery as methane, although inhibition by residual organics may necessitate prior detoxification (He et al. 2022). More advanced pathways such as catalytic supercritical water gasification have also been demonstrated to achieve high removal efficiencies for dissolved organics and nitrogen-containing compounds while producing hydrogen-rich gas streams, albeit with increased energy demand and process complexity (Xu et al. 2019). Overall, microalgal cultivation functions most effectively as an intermediate treatment step within integrated hydrothermal biorefineries, enabling substantial nutrient recovery and partial detoxification, while robust reuse typically requires sequential polishing to address residual toxicity, colour, and ionic strength (Yuan et al. 2023).

Challenges and future perspective

Despite significant progress in the reuse of hydrothermal aqueous phases for microalgae cultivation, several challenges must be addressed to enable reliable scale-up and industrial integration. Foremost among these is the inherent variability of aqueous-phase composition, driven by feedstock heterogeneity and hydrothermal operating severity, which complicates standardization of cultivation conditions and performance prediction (Tsarpali et al. 2021). Future research should therefore prioritize robust characterization frameworks linking hydrothermal process parameters to aqueous-phase chemistry and biological response, enabling predictive design rather than empirical optimization (López Barreiro et al. 2015).

Strain selection and development remain critical. While dilution and conditioning strategies mitigate toxicity, long-term cultivation stability will likely depend on microalgae with enhanced tolerance to phenolics, nitrogen-containing organics, and elevated ionic strength (Bagnoud-Velásquez et al. 2018). Adaptive laboratory evolution has emerged as a promising approach to improve tolerance to hydrothermal aqueous phases, enabling sustained growth and nutrient recovery at higher aqueous-phase loadings. This approach relies on selection-driven adaptation under defined environmental pressures, allowing microalgal populations to develop enhanced tolerance without direct genetic engineering (Ramírez-Romero et al. 2025). In parallel, co-cultivation strategies involving bacteria or fungi have demonstrated potential to alleviate toxicity through adsorption and enzymatic transformation of inhibitory compounds (Chen et al. 2020).

From a process design perspective, reactor concepts that decouple detoxification from biomass production, such as staged or hybrid cultivation systems, may allow higher aqueous-phase utilization while preserving biomass quality (Yuan et al. 2023). Hydrothermal aqueous phases should therefore be regarded as multifunctional process streams rather than direct culture media, with optimal use involving sequential nutrient recovery, biological upgrading, and physicochemical polishing. Integration with nutrient recovery technologies, including struvite precipitation and membrane-based concentration, may further reduce inhibitory pressure and improve overall process efficiency (Zhou et al. 2024).

In addition to these biological and process-related challenges, several engineering and economic considerations must also be addressed to enable large-scale implementation. Hydrothermal aqueous phases frequently require dilution to mitigate toxicity from phenolics, furans, and nitrogen-containing heterocycles, which are known to inhibit microalgal growth and metabolic activity (Zuccaro et al. 2021). This requirement increases water demand and reactor volume, thereby affecting process scalability and operational costs. In addition, the dark coloration and elevated turbidity of these streams can significantly reduce light penetration in photobioreactors, limiting photosynthetic efficiency and biomass productivity due to light attenuation within dense or optically complex media (Bernard and Lu 2022). Variability in aqueous-phase composition resulting from differences in feedstock and hydrothermal operating severity may further complicate process control and stability in continuous systems.

Biomass harvesting remains a major economic bottleneck in microalgal systems, with downstream processing costs reported to account for up to ~20–30% of total production expenses (Okoro et al. 2019). This highlights the need for efficient and scalable separation strategies such as bio-flocculation, immobilized cultivation, or microbial consortia, which can reduce energy demand and improve overall process economics (Novoveská et al. 2023). Consequently, the successful integration of microalgae cultivation into hydrothermal biorefineries will depend on process designs that combine aqueous-phase conditioning, optimized photobioreactor configurations, and efficient downstream biomass valorisation, ultimately enabling both environmental and techno-economic sustainability within circular biorefinery systems (Zhang et al. 2026). In addition to these engineering and economic considerations, physical and ecological challenges also play a critical role in large-scale implementation. From a physical perspective, limitations related to mixing efficiency, mass transfer, and CO_2 availability can significantly affect photosynthetic performance and biomass productivity, particularly in dense or optically complex aqueous-phase systems. These constraints are strongly influenced by reactor design and hydrodynamic conditions at scale (Huang et al. 2017). From an ecological standpoint, large-scale

microalgae cultivation systems are inherently susceptible to contamination, competition with other microorganisms, and predation, especially in open or semi-open systems (Deruyck et al. 2019). Maintaining stable and productive cultures under such conditions remains a major challenge and may require controlled environments, selective cultivation strategies, or the development of robust and resilient strains. Addressing these physical and ecological constraints is essential for translating laboratory-scale results into reliable industrial-scale processes (Ahamefule et al. 2025).

An additional consideration for circular biorefinery integration is the fate of heavy metals and trace elements present in the aqueous phase. Depending on the feedstock, hydrothermal processes may concentrate metals such as Fe, Cu, Zn, Ni, or Pb in the liquid fraction (de Castro e Silva et al. 2024). Microalgae are known to uptake and accumulate these elements, which may lead to elevated metal content in the resulting biomass. While this property can be advantageous for wastewater treatment and bioremediation, it raises important concerns regarding biomass utilization in feed or food applications (Zdziebłowska et al. 2024). In such cases, the presence of heavy metals may limit downstream valorization routes and compromise the circularity of the system. Therefore, careful monitoring of metal concentrations, selection of appropriate feedstocks, and implementation of pre-treatment or separation strategies may be required to ensure safe and sustainable biomass utilization (Yousefi et al. 2023).

Looking forward, future perspectives should focus on the development of integrated and adaptive biorefinery systems capable of handling the inherent variability of hydrothermal aqueous phases. Advanced monitoring and control strategies, coupled with data-driven and machine learning-based optimization approaches, may enable predictive management of aqueous-phase composition and biological performance (Butean et al. 2025; Malik et al. 2026). In addition, the design of robust microalgal strains and engineered microbial consortia, together with hybrid processing schemes combining biological and physicochemical treatments, will be essential to improve system resilience and efficiency (Semple and Pandhal 2025; Hasan et al. 2026). Techno-economic assessment and life cycle analysis should also be prioritized to evaluate the feasibility of large-scale implementation and guide process optimization toward commercially viable solutions (Watson et al. 2020; Illoussamen et al. 2026).

To provide clearer guidance for future research, it is essential to distinguish between the most critical fundamental scientific questions and the key applied engineering challenges that must be addressed to enable scale-up. From a scientific perspective, two primary questions emerge:

(i) How the complex and variable composition of hydrothermal aqueous phases influences microalgal metabolic pathways, toxicity thresholds, and product selectivity, and
(ii) How these interactions can be predicted and controlled based on hydrothermal process conditions and feedstock characteristics.

From an engineering standpoint, the most pressing challenges include (i) the development of scalable cultivation systems capable of handling high turbidity and compositional variability without compromising light utilization and productivity, and (ii) the design of cost-effective downstream processing and harvesting strategies suitable for low biomass concentrations. Addressing these challenges will be crucial for bridging the gap between laboratory-scale feasibility and industrial implementation.

Acknowledgments The author Hilal Kabakcı acknowledges financial support from the Council of Higher Education of Türkiye (YÖK) under the 100/2000 Doctoral Scholarship Program. The authors also acknowledge Yıldız Technical University for providing institutional support during the preparation of this review.

Author contributions **H.K.:** Investigation, data curation, writing—original draft preparation. **A.T.K.:** Conceptualization, investigation, methodology, writing-review and editing. **D.B**.: Supervision, writing-review and editing.

Funding Open access funding provided by the Scientific and Technological Research Council of Türkiye (TÜBİTAK).

Declarations

Conflict of 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.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Abdelkarim OH, Wijffels RH, Barbosa MJ (2025) Microalgal lipid production: a comparative analysis of *Nannochloropsis* and *Microchloropsis* strains. J Appl Phycol 37:15–34

Ahamefule CS, Osilo C, Idenyi JN, Ogbonna IO, Ogbonna JC (2025) Cultivation conditions and operating modes in large-scale microalgae processes. In: Severo IA, Ordóñez JC, Mariano AB, Vargas

JVC (eds) Microalgae Horizons. Grand Challenges in Biology and Biotechnology. Springer, pp 23–86
Ahn H, Kim D, Lee Y (2024) The effect of an acidic environment during the hydrothermal carbonization of sewage sludge on solid and liquid products: the fate of heavy metals, phosphorus and other compounds. J Environ Manage 365:121637
Almutairi AW (2022) Full utilization of marine microalgal hydrothermal liquefaction liquid products through a closed-loop route: towards enhanced bio-oil production and zero-waste approach. 3 Biotech 12:209
Bagnoud-Velásquez M, Damergi E, Peng G, Vogel F, Ludwig C (2018) Fate and reuse of nitrogen-containing organics from the hydrothermal conversion of algal biomass. Algal Res 32:241–249
Basar IA, Liu H, Eskicioglu C (2023) Incorporating hydrothermal liquefaction into wastewater treatment – Part III: aqueous phase characterization and evaluation of on-site treatment. Chem Eng J 467:143422
Belete YZ, Leu S, Boussiba S, Zorin B, Posten C, Thomsen L, Wang S, Gross A, Bernstein R (2019) Characterization and utilization of hydrothermal carbonization aqueous phase as nutrient source for microalgal growth. Bioresour Technol 290:121758
Bernard O, Lu LD (2022) Optimal optical conditions for microalgal production in photobioreactors. J Process Control 112:69–77
Bilgili MS, Varank G, Sekman E, Top S, Özçimen D, Yazıcı R (2012) Modeling 4-chlorophenol removal from aqueous solutions by granular activated carbon. Environ Model Assess 17:289–300
Butean A, Cutean I, Barbero R, Enriquez J, Matei A (2025) A review of artificial intelligence applications for biorefineries and bioprocessing: from data-driven processes to optimization strategies and real-time control. Processes 13:2544
Chen H, Hao S, Chen Z, O-Thong S, Fan J, Clark J, Luo G, Zhang S (2020) Mesophilic and thermophilic anaerobic digestion of aqueous phase generated from hydrothermal liquefaction of cornstalk: molecular and metabolic insights. Water Res 168:115199
Chen Z, Yang L, Wang Y, Wang H, Li T (2025) Synergistic hydrothermal treatment of incineration fly ash and sewage sludge: effect of hydrothermal solution circulation. ACS Omega 10:10506–10514
Chernova NI, Kiseleva SV, Vlaskin MS, Grigorenko AV, Rafikova YY (2019) Hydrothermal liquefaction of microalgae for biofuel production: the recycling of nutrients from an aqueous solution after HTL. IOP Conf Ser Mater Sci Eng 564:012112
Dahdouh A, Khay I, Bouizi Y, Kervern G, Steve P, El Maakoul A, Bakhouya M, Le Brech Y (2024) Hydrothermal carbonization of two-phase olive mill waste (Alperujo): effect of aqueous phase recycling. Biomass Bioenerg 184:107205
de Castro e Silva HL, Ghysels S, Robles-Aguilar AA, Akyol Ç, Ronsse F, Meers E (2024) Hydrothermal carbonisation of manure-derived digestates: chemical properties and heavy metals distribution in end-products. Chem Eng J 496:154110
Deruyck B, Nguyen KHT, Decaestecker E, Muylaert K (2019) Modeling the impact of rotifer contamination on microalgal production in open pond, photobioreactor and thin layer cultivation systems. Algal Res 38:101398
Dias RR, Deprá MC, de Menezes CR, Zepka LQ, Jacob-Lopes E (2025) Microalgae cultivation in wastewater: how realistic is this approach for value-added product production? Processes 13:2052
Durak H (2023) Comprehensive assessment of thermochemical processes for sustainable waste management and resource recovery. Processes 11:2092
Durak H, Genel S, Durak ED, Özçimen D, Koçer AT (2024) Hydrothermal liquefaction process of *Ammi visnaga* and a new approach for recycling of the waste process water: cultivation of algae and fungi. Biomass Conv Bioref 14:7149–7165
Edmundson S, Huesemann M, Rkruk R, Lemmon T, Billing J, Schmidt A, Anderson D (2017) Phosphorus and nitrogen recycle following algal bio-crude production via continuous hydrothermal liquefaction. Algal Res 26:415–421
Feng Y, Hu X, Xue Y, Tang X, Xu D, Zhang Y, Wu Y (2025) Hydrothermal carbonization of model compounds of municipal sludge: effects of reaction conditions and aqueous phase recirculation. J Environ Chem Eng 13:119889
Galieva G, El Rawas M, Khlebova D, Selivanovskaya S, Galitskaya P (2026) Temperature, nitrogen, and carbon constraints on growth and metabolism of regional microalgae strains. Environments 13:73
Garcia-Perez P, Cassani L, Garcia-Oliveira P, Xiao J, Simal-Gandara J, Prieto MA, Lucini L (2023) Algal nutraceuticals: a perspective on metabolic diversity, current food applications, and prospects in the field of metabolomics. Food Chem 409:135295
Ghaziaskar A, McRae GA, Mackintosh A, Lai EPC, Basu OD (2019) Production of organic compounds through catalyzed hydrothermal carbonization of woody biomass. Energy Fuels 33:9879–9885
Gupta R, Mishra N, Singh G, Mishra S, Lodhiyal N (2024) Microalgae cultivation and value-based products from wastewater: insights and applications. Blue Biotechnol 1:20
Hasan MA, Bakry AM, Safdar W (2026) Strain improvement for algae-based resource recovery and recycling. In: Mehmood MA, Malik S, Ralph PJ, Bose A, Betenbaugh MJ (eds) Algae biotechnology. Elsevier, Amsterdam, pp 97–133
He M, Cao Y, Xu Z, You S, Ruan R, Gao B, Wong KH, Tsang DCW (2022) Process water recirculation for catalytic hydrothermal carbonization of anaerobic digestate: water-energy-nutrient nexus. Bioresour Technol 361:127694
Hong C, Wang Z, Si Y, Li Z, Xing Y, Hu J, Li Y (2021) Effects of aqueous phase circulation and catalysts on hydrothermal liquefaction (HTL) of penicillin residue (PR): characteristics of the aqueous phase, solid residue and bio oil. Sci Total Environ 776:145596
Huang Q, Jiang F, Wang L, Yang C (2017) Design of photobioreactors for mass cultivation of photosynthetic organisms. Engineering 3:318–329
Illoussamen B, Dahdouh A, Khay I, Le brech Y, Bakhouya M, Mutelet F (2026) A review on hydrothermal biomass conversion: byproducts and valorization for a circular bioeconomy. Energy Fuels 40:105–132
Jagadale M, Jadhav M, Nagesh Kumar T, Shrivastava P, Kumar N (2024) Hydrothermal liquefaction as a sustainable strategy for integral valorization of agricultural waste. In: Mondal S, Kumar A, Pachauri RK, Mondal AK, Singh VK, Sharma AK (eds) Clean and Renewable Energy Production. Wiley, pp 175–200
Karacaoğlu B, Mercimek R, İnan B, Koçer AT, Bütün İ, Ghorbani M, Koşar A, Balkanlı D (2025) Comparison of microfluidic and traditional methods for separation of Antarctic microalgae cells and life cycle assessment. J Environ Chem Eng 13:120017
Khoo CG, Lam MK, Mohamed AR, Lee KT (2020) Hydrochar production from high-ash low-lipid microalgal biomass via hydrothermal carbonization: effects of operational parameters and products characterization. Environ Res 188:109828
Koçer AT, Mutlu B, Özçimen D (2020) Investigation of biochar production potential and pyrolysis kinetics characteristics of microalgal biomass. Biomass Conv Bioref 10:85–94
Koçer AT, İnan B, Özçimen D, Gökalp İ (2023) A study of microalgae cultivation in hydrothermal carbonization process water: nutrient recycling, characterization and process design. Environ Technol Innov 30:103048
Kulikova Y, Klementev S, Sirotkin A, Mokrushin I, Bassyouni M, Elhenawy Y, El-Hadek MA, Babich O (2023) Aqueous phase from hydrothermal liquefaction: composition and toxicity assessment. Water 15:1681
Kumar M, Oyedun AO, Kumar A (2018) A review on the current status of various hydrothermal technologies on biomass feedstock. Renew Sustain Energy Rev 81:1742–1770

Lachos-Perez D, Torres-Mayanga PC, Abaide ER, Zabot GL, De Castilhos F (2022) Hydrothermal carbonization and liquefaction: differences, progress, challenges, and opportunities. Bioresour Technol 343:126084

Leng L, Li J, Wen Z, Zhou W (2018) Use of microalgae to recycle nutrients in aqueous phase derived from hydrothermal liquefaction process. Bioresour Technol 256:529–542

Leng S, Jiao H, Liu T, Pan W, Chen J, Chen J, Huang H, Peng H, Wu Z, Leng L, Zhou W (2022) Co-liquefaction of *Chlorella* and soybean straw for production of bio-crude: effects of reusing aqueous phase as the reaction medium. Sci Total Environ 820:153348

Li H, Cao M, Zhang Y, Liu Z (2021) Hydrothermal liquefaction accelerates the toxicity and solubility of arsenic in biowaste. J Hazard Mater 418:126341

Liao Z, Wang C, Tang X, Wang Y, Lin Z, Ren P, Wang L, Xu H, Yang J, Cai J (2022) Product characterization of hydrothermal liquefaction and supercritical water gasification of water hyacinth. Environ Eng Sci 39:268–286

Libra JA, Ro KS, Kammann C, Funke A, Berge ND, Neubauer Y, Titirici MM, Fühner C, Bens O, Kern J, Emmerich KH (2011) Hydrothermal carbonization of biomass residuals: a comparative review of the chemistry, processes and applications of wet and dry pyrolysis. Biofuels 2:71–106

Liu T, Li Z, Kudo S, Gao X, Hayashi J (2024) Leaching char with acidic aqueous phase from biomass pyrolysis: valorization of the leachate via catalytic hydrothermal gasification. Fuel 373:132264

López Barreiro D, Riede S, Hornung U, Kruse A, Prins W (2015) Hydrothermal liquefaction of microalgae: effect on the product yields of the addition of an organic solvent to separate the aqueous phase and the biocrude oil. Algal Res 12:206–212

Malik HA, Shahid R, Rehman O, Su K, Fan Z, Usman M, Zhao A, Solovchenko AE, Shahid A, Xu J (2026) Development of algal industry 4.0 for efficient cultivation, resource recovery, and bioproducts production. In: Mehmood MA, Malik S, Ralph PJ, Bose A, Betenbaugh MJ (eds) Algae biotechnology. Elsevier, Amsterdam, pp 355–374

Mau V, Neumann J, Wehrli B, Gross A (2019) Nutrient behavior in hydrothermal carbonization aqueous phase following recirculation and reuse. Environ Sci Technol 53:10426–10434

McGaughy K, Reza MT (2018) Recovery of macro and micro-nutrients by hydrothermal carbonization of septage. J Agric Food Chem 66:1854–1862

Minhas AK, Gaur S, Sunny S, Paladugu C, Ravishankar GA, Pereira L, Ambati RR (2026) Microalgae-based wastewater treatment processes for the bioremediation and valorization of biomass: a review. Phycology 6:18

Nazari L, Wang H, Ray MB, Xu C (2025) Comparative studies of co-conversion of waste activated sludge and lignocellulosic wastes through hydrothermal liquefaction. Biomass Bioenergy 194:107671

Nguyen TAH, Bui TH, Guo WS, Ngo HH (2023) Valorization of the aqueous phase from hydrothermal carbonization of different feedstocks: challenges and perspectives. Chem Eng J 472:144802

Novoveská L, Nielsen SL, Eroldoğan OT, Haznedaroglu BZ, Rinkevich B, Fazi S, Robbens J, Vasquez M, Einarsson H (2023) Overview and challenges of large-scale cultivation of photosynthetic microalgae and cyanobacteria. Mar Drugs 21:445

Okoro V, Azimov U, Munoz J, Hernandez HH, Phan AN (2019) Microalgae cultivation and harvesting: growth performance and use of flocculants - a review. Renew Sustain Energy Rev 115:109364

Oliveira DT, Mescouto VA, Paiva RJ, Silva SRF, Santos LAB, Serra GM, Xavier LP, Noronha RCR, Nascimento LAS (2024) Use of residual lignocellulosic biomass and algal biomass to produce biofuels. Int J Mol Sci 25:8299

Olivito F, Manickam M, Ilham Z, Wan-Mohtar WAAQI, Nardi M, Procopio A (2026) Biomass conversion to second- and third-generation biofuels: recent developments. Biofuels Bioprod Bioref 20:987–1005

Onwudili JA, Lea-Langton AR, Ross AB, Williams PT (2013) Catalytic hydrothermal gasification of algae for hydrogen production: composition of reaction products and potential for nutrient recycling. Bioresour Technol 127:72–80

Özçimen D, İnan B, Koçer AT, Vehapi M (2018) Bioeconomic assessment of microalgal production. In: Jacob-Lopes E, Zepka LQ, Queiroz MI (eds) Microalgal Biotechnology. InTech, pp 195–213

Pereira ASADP, Magalhães IB, Silva TA, Reis AJD, Couto EA, Calijuri ML (2024) Municipal and industrial wastewater blending: effect of the carbon/nitrogen ratio on microalgae productivity and biocompound accumulation. J Environ Manage 370:122760

Qiu B, Tao X, Wang Y, Zhang D, Chu H (2025) Hydrothermal liquefaction for producing liquid fuels and chemicals from biomass-derived platform compounds: a review. Environ Chem Lett 23:81–115

Ramírez-Romero A, da Costa Magalhães B, Matricon L, Sassi JF, Steyer JP, Delrue F (2025) Aqueous phase recycling: impact on microalgal lipid accumulation and biomass quality. Environ Sci Pollut Res Int 32:16579–16593

Ruiz HA, Galbe M, Garrote G, Ramirez-Gutierrez DM, Ximenes E, Sun SN, Lachos-Perez D, Rodríguez-Jasso RM, Sun RC, Yang B, Ladisch MR (2021) Severity factor kinetic model as a strategic parameter of hydrothermal processing (steam explosion and liquid hot water) for biomass fractionation under biorefinery concept. Bioresour Technol 342:125961

Sarker TR, Meda V, Dalai AK (2022) Catalytic hydrothermal gasification of aqueous effluents obtained from microwave torrefaction of agricultural residue. J Environ Chem Eng 10:108835

Selvi Gökkaya D (2025) The potential of apricot tree resin as a viable feedstock for high-value chemicals via hydrothermal gasification. Catalysts 15:425

Semple A, Pandhal J (2025) Engineering the phycosphere: fundamental concepts and tools for the bottom-up design of microalgal-bacterial consortia. Appl Phycol 6:21–51

Şerbetçioğlu Sert B, İnan B, Özçimen D (2018) Effect of chemical pretreatments on bioethanol production from *Chlorella minutissima*. Acta Chim Slov 65:158–163

Shah AA, Toor SS, Seehar TH, Nielsen RS, Nielsen AH, Pedersen TH, Rosendahl LA (2020) Bio-crude production through aqueous phase recycling of hydrothermal liquefaction of sewage sludge. Energies 13:493

Shah AA, Khan MI, Noonari AA, Jatoi AS, Sandquist J (2026) Aqueous phase recirculation in hydrothermal liquefaction: a critical review. Biomass Bioenergy 207:108612

Sindhuwati C, Nahil MA, Williams PT (2026) Two-step hydrothermal liquefaction of waste biomass for increased bio-oil yield and enhanced bio-oil composition. Biomass Bioenergy 204:108456

Swaminaathan P, Saravanan A, Thamarai P (2024) Utilization of bioresources for high-value bioproducts production: sustainability and perspectives in circular bioeconomy. Sustain Energy Technol Assess 63:103672

Szkadłubowicz K, Mikusińska J, Pozarlik A, Wilk M (2025) Hydrothermal treatment of sewage sludge under different process conditions with a focus on energy properties and resource recovery. Energies 18:6071

Tsarpali M, Arora N, Kuhn JN, Philippidis GP (2021) Beneficial use of the aqueous phase generated during hydrothermal carbonization of algae as nutrient source for algae cultivation. Algal Res 60:102485

Wang X, Esakkimuthu S, Yuan C, Chen H, El-Mesery HS, Wang S, Hu X (2025) Two-stage cultivation using noodle soup waste water for the sustainable production of microalgal biomass and biodiesel. J Clean Prod 523:146438

Wang P, Diao Y, Gong X, Xu D, Liu T, Jiang G (2026) Microalgae-assisted regulation of hydrothermal liquefaction aqueous phase for pollutant removal and sustainable recycling. Biochem Eng J 230:110135

Watson J, Si B, Li H, Liu Z, Zhang Y (2017) Influence of catalysts on hydrogen production from wastewater generated from the HTL of human feces via catalytic hydrothermal gasification. Int J Hydrogen Energy 42:20503–20511

Watson J, Wang T, Si B, Chen WT, Aierzhati A, Zhang Y (2020) Valorization of hydrothermal liquefaction aqueous phase: pathways towards commercial viability. Prog Energy Combust Sci 77:100819

Wei X, Wang T, Jin S, Ma Z, Li Y, Yu Y, Wu S (2025) Effect of aqueous phase recirculation on product characteristics from hydrothermal carbonation of kitchen waste and the migration of O. J Environ Chem Eng 13:115958

Xu D, Liu L, Wei N, Guo Y, Wang S, Wu Z, Duan P (2019) Catalytic supercritical water gasification of aqueous phase directly derived from microalgae hydrothermal liquefaction. Int J Hydrogen Energy 44:26181–26192

Xu Y, Wang Y, Lu J, Yuan C, Zhang L, Liu Z (2022) Understand the antibacterial behavior and mechanism of hydrothermal wastewater. Water Res 226:119318

Xu S, Jiang Y, Liu Y, Esakkimuthu S, Chen H, Wang S (2024) Impact of constant magnetic field on enhancing the microalgal biomass and biomolecules accumulations and life cycle assessment of the approach. Algal Res 80:103563

Yabalak E, Akay S, Kayan B, Gizir AM, Yang Y (2023) Solubility and decomposition of organic compounds in subcritical water. Molecules 28:1000

Yang K, Wang J, Zheng J, Cai W (2025a) Microalgae-based wastewater treatment: advances and challenges in membrane harvesting technologies. Sep Purif Technol 360:130805

Yang L, Duan B, Lu Q (2025b) A review of marine microalgae-based lipids production: biosynthesis, technological advancements, and practical applications. Front Nutr 12:1664674

Yao C, Pan Y, Lu H, Wu P, Meng Y, Cao X, Xue S (2016) Utilization of recovered nitrogen from hydrothermal carbonization process by *Arthrospira platensis*. Bioresour Technol 212:26–34

Yetilmezsoy K, Özçimen D, Koçer AT, Bahramian M, Kıyan E, Akbin HM, Goncaloğlu Bİ (2020) Removal of anthraquinone dye via struvite: equilibria, kinetics, thermodynamics, fuzzy logic modeling. Int J Environ Res 14:541–566

Yousefi Y, Hanachi P, Samadi M, Khoshnamvand M (2023) Heavy metals (copper and iron) and nutrients (nitrate and phosphate) removal from aqueous medium by microalgae *Chlorella vulgaris* and *Scenedesmus obliquus*, and their biofilms. Mar Environ Res 188:105989

Yuan C, Zhao S, Ni J, He Y, Cao B, Hu Y, Wang S, Qian L, Abomohra A (2023) Integrated route of fast hydrothermal liquefaction of microalgae and sludge by recycling the waste aqueous phase for microalgal growth. Fuel 334:126488

Zdziebłowska S, Czarnecki M, Ciosek-Skibińska P, Ruzik L (2024) The microalgae's ability to accumulate selected trace elements studied by ICP-MS/MS and chemometric methods. J Trace Elem Med Biol 81:127351

Zhang B, Biswal BK, Zhang J, Balasubramanian R (2023) Hydrothermal treatment of biomass feedstocks for sustainable production of chemicals, fuels, and materials: progress and perspectives. Chem Rev 123:7193–7294

Zhang J, Ren K, He J, Xia A, Huang Y, Zhou M, Zhu X, Zhu X, Liao Q (2026) Energy, environmental, and techno-economic assessments of a renewable energy-driven light-guiding microalgae cultivation system. Algal Res 95:104661

Zhong J, Zhu W, Sun J, Mu B, Wang X, Xue Z, Cao J (2024) Hydrothermal carbonization of coking sludge: formation mechanism and fuel characteristic of hydrochar. Chemosphere 346:140504

Zhou S, Lin M, Zhang X, Zhan L, Li R, Wu Y (2024) Study of life cycle assessment: transforming microalgae to biofuel through hydrothermal liquefaction and upgrading in organic or aqueous medium. J Clean Prod 444:140942

Zora Tarhan S, Koçer AT, Özçimen D, Gökalp İ (2021) Cultivation of green microalgae by recovering aqueous nutrients in hydrothermal carbonization process water of biomass wastes. J Water Process Eng 40:101783

Zuccaro G, del Mondo A, Pinto G, Pollio A, De Natale A (2021) Biorefinery-based approach to exploit mixed cultures of *Lipomyces starkeyi* and *Chloroidium saccharophilum* for single cell oil production. Energies 14:1340

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.