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Review

Fermentation of micro- and macroalgae as a way to produce value-added products

Olga Babich [a], Svetlana Ivanova [b,c,*], Philippe Michaud [d], Ekaterina Budenkova [a], Egor Kashirskikh [a], Veronika Anokhova [a], Stanislav Sukhikh [a]

[a] SEC "Applied Biotechnologies", Immanuel Kant BFU, Kaliningrad, Russia
[b] Natural Nutraceutical Biotesting Laboratory, Kemerovo State University, Krasnaya Street 6, Kemerovo, 650043, Russia
[c] Department of TNSMD Theory and Methods, Kemerovo State University, Krasnaya Street, 6, Kemerovo 650043, Russia
[d] Institut Pascal, Université Clermont Auvergne, CNRS, Clermont Auvergne INP, F-63000 Clermont-Ferrand, France

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ABSTRACT

Fermentation of both microalgae and macroalgae is one of the most efficient methods of obtaining valuable value-added products due to the minimal environmental pollution and the availability of economic benefits, as algae do not require arable land and drift algae and algal bloom biomass are considered waste and must be recycled and their fermentation waste utilized. The compounds found in algae can be effectively used in the fuel, food, cosmetic, and pharmaceutical industries, depending on the type of fermentation used. Products such as methane and hydrogen can be produced by anaerobic digestion and dark fermentation of algae, and lactic acid and its polymers can be produced by lactic acid fermentation of algae. Article aims to provide an overview of the different types potential of micro- and macroalgae fermentation, the advantages and disadvantages of each type considered, and the economic feasibility of algal fermentation for the production of various value-added products.

1. Introduction

Algae are part of a heterogeneous group of photosynthetic organisms. This group includes both multicellular organisms, macroalgae or seaweeds, reaching sizes up to 60 m in length, and unicellular organisms, also known as microalgae, ranging in size from less than 2 μm to a few cm [1].

Macroalgae, also known as seaweeds, are macroscopic marine algae that can grow to be several meters long. Macroalgae are classified into three main groups based on the presence of pigments: brown algae (Phaeophyceae), red algae (Rhodophyceae), and green algae (Chlorophyceae). A separate group is represented by flowering plants (Magnoliophyceae) living in aquatic environments. The main pigment of brown algae is fucoxanthin; phycoerythrin and phycocyanin cause pigmentation in red algae; and chlorophyll is predominant in green algae [2].

Microalgae are microscopic organisms found in both seawater and freshwater. They can be classified as eukaryotic microorganisms or prokaryotic cyanobacteria (blue-green algae), with more than 25,000 species already isolated and identified [3].

Macroalgae drift, which includes rhodophytes (red algae), chlorophytes (green algae), and ochrophytes (brown algae), is formed mainly by the separation of conglomerates of typically ephemeral filamentous or leafy macroalgae, which facilitates their dispersal and sometimes reproduction [4]. Recently, eutrophication-induced micro- and macroalgae blooms and temperature increases accompanying climate change have become a serious threat to benthic organisms, leading to coastal hypoxia [5]. Harmful macroalgae blooms have increased along the coasts of China, Mexico, Thailand, Vietnam, and Japan, causing significant social impacts and economic losses [6,7]. Blooms of some microalgae species are particularly dangerous, as they produce toxins with strong hepato- and nephrotoxic effects [7]. The economic losses caused by this phenomenon are $1 billion for European coastal waters and $2.4 billion for U.S. freshwater bodies [8]. Control of algal blooms includes physical, chemical, and biological methods. Physical methods are not harmful to the environment, but they have high costs and low efficiency. Chemical methods have the necessary effect but carry secondary contamination. Biological methods are the most appealing because they

Abbreviation: s: AD, Anaerobic digestion; DF, Dark fermentation; DPPH, 2,2-diphenyl-1-picrylhydrazyl.

* Corresponding author.
E-mail address: pavvm2000@mail.ru (S. Ivanova).

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have minimal secondary contamination and are cost-effective [9].

Not only does the processing of drifting macroalgae into value-added products solve the climatic and environmental problems of coastal zone cleaning, but it also has a significant economic impact, including a multiplicative nature, at least by increasing its tourist attractiveness [10]. The concept of "zero-waste production" is a key concept in today's biofuel industry. The use of algae for biofuels and other important products is justified under this idea because drift algae and algal bloom biomass can be considered waste. Because of their high carbohydrate content, rapid growth rate, and low environmental requirements, micro- and macroalgae have the potential to be used as a valuable source of feedstock in the biofuel, pharmaceutical, and food industries [11]. Furthermore, algae are characterized by low lignin content, thus ensuring the efficient use of biomass in the biotechnology industry since the indestructible structure of this biopolymer is a significant barrier to bioconversion [12].

Algae fermentation, unlike landfilling or incineration, is economically viable and low-waste method [12]. Incorporating algal biomass into the production of biofuels and bioactive compounds (a variety of beneficial compounds such as polyphenols and polyunsaturated fatty acids) provides a sustainable way to mitigate blooms while producing value-added products [13–15]. Algae are considered a source of biogas and biomethane (which can be produced by anaerobic digestion or ethanol from alcoholic fermentation), biodiesel (synthesized from lipids during anaerobic digestion), and biohydrogen (produced by fermentation with anaerobic methanogens) [16]. For example, lactic acid fermentation of algae biomass allows the production of food products, including functional and dietary purposes [17]. Algae extracts have antimicrobial, antioxidant, anti-inflammatory, and anti-cancer activities [18]. Also, algae can remove or neutralize heavy metals from water and/or soil [19]. Significant progress has been made in the development of technologies for the extraction and purification of valuable products from algae biomass in recent years [20].

This review aims to investigate the different types of micro- and macroalgae fermentations, their conditions, and the microorganisms used. Furthermore, algal fermentation products, applications, and the economic justification for a specific fermentation method will be discussed.

2. Methane fermentation

Anaerobic digestion (AD) is a method of decomposing organic compounds to produce methane. The AD process can be divided into 4 stages: hydrolysis, acidogenesis, acetogenesis, and methanogenesis. The progression of each stage is controlled by specific microorganisms [21]. The use of AD allows for the utilization of various organic wastes, resulting in the production of biomethane and the use of the remaining solid sludge as fertilizer [22]. The following are some of the most commonly used microorganisms in AD: *Methanobacterium, Methanobrevibacter, Methanoculleus, Methanospirillum* and *Methanothermobacter, Methanosaeta*, and *Methanosarcina* [23]. The AD process of microalgae has been studied since the 1950s. The first study was published in 1957 [24].

In the context of algae methane fermentation, anaerobic digestion, which is defined as the fermentation of organic waste in the absence of oxygen, resulting in the conversion of complex compounds to methane and carbon dioxide, should be mentioned. AD culminating in methane fermentation improves the economic efficiency of microalgae-derived liquid biofuel production and opens the door to electricity generation from wastewater-derived microalgae [25]. Table 1 summarizes the main types of microorganisms and algae used for methane production. Thus, biomass from green algae, cyanobacteria (primarily Microcystis), and green microalgae is used to produce methane via anaerobic digestion [25]. The data reveals that the duration of anaerobic digestion, combined with the need to maintain temperature, renders the process unprofitable. Therefore, more research is required to improve the efficiency and speed of this process.

Methanosaeta and *Methanobacterium* are the most productive species in terms of methane biosynthesis under AD [30,33]. At the same time, the AD process should be conducted at 35–38 °C for 14 days (for *Methanobacterium*) and 80 days (for *Methanosaeta*).

The use of AD for algae processing has the advantage of eliminating the need for preliminary drying of biomass, which significantly reduces the cost of the process [34]. Also, the AD process does not require high temperatures and pressures [35]. The disadvantages of AD include difficulty in operating the equipment, maintaining a certain temperature, the need for additional treatment of organic sludge (in case the sludge will be used as fertilizer), the sensitivity of methanogenic bacteria to various compounds (in particular, antibiotics contained in wastewater), their low growth rate, as well as an unpleasant odor due to sulfur compounds. Furthermore, methane loss, process duration, and instability make AD technology economically unattractive [35]. The AD utilizes different types of algae (micro- and macroalgae) as well as different microbial communities (Table 1). Biogas produced from marine algae AD typically contains 50–70 % methane, 30–45 % carbon dioxide, <2 % hydrogen, and <3.5 % hydrogen sulfide [34].

3. Hydrogen fermentation

Currently, large-scale hydrogen production is performed using methods such as water electrolysis and coal gasification, which are somewhat destructive and harmful to the environment; therefore, alternative methods, i.e., using microorganisms, are being considered to improve the energy efficiency of hydrogen production [36].

Biohydrogen is an alternative source of energy that is promising because of its relative safety for the environment [18]. Algae can be a

Table 1
Microorganisms and algae used in methane fermentation.

Microorganisms	Algae	Algae type	Product	Fermentation conditions	References
Methanosarcina, Methanothrix	*Microcystis wesenbergii, Microcystis aeruginosaare*	Cyanobacteria	Methane	Anaerobic digestion in liquid phase at pH 8, 35.0 °C, 25 days	[26,27]
Firmicutes, Proteobacteria	*Microcystis* sp.		Methane	Anaerobic digestion in liquid phase, 60 days	[28]
Microbiota of activated sludge sediment from wastewater treatment plants	*Microcystis* sp.		Methane	Anaerobic digestion in liquid phase at 37 °C, 57 days	[29]
Methanosarcinaceae, Methanosaeta	*Chlorella* sp., *Scenedesmus* sp.	Green microalgae	Methane, biogas	Anaerobic digestion in liquid phase at 38 °C, 80 days	[30]
Methanosarcina sp., *Methanoregula* sp., *Methanospirillum* sp., *Methanoculleus* sp.	*Chlorella* sp.		Methane	Anaerobic digestion in liquid phase at 35 °C	[31]
Thermotogaceae, Cenarchaeum	*Enteromorpha prolifera*	Green microalgae	Methane	Anaerobic digestion in liquid phase at 55 °C, 16 days	[32]
Bacteroidetes, Firmicutes, Actinobacteriota, Chloroflexi, Rikenellaceae, Exiguobacterium, Petrimonas, Bacteroidia, Georgenia, Proteiniclasticum, Methanobacterium	Biomass of lake algal blooms	No data	Methane	Anaerobic digestion in liquid phase at 35 °C, 14 days	[33]

stable source of biohydrogen. The production of biohydrogen from algae is appealing and promising due to its low cost, high rate of algal biomass renewal, and ease of scaling up the process. Hydrogen is produced from algal biomass using dark fermentation (DF). DF is a light-independent process that involves the anaerobic conversion of a complex substrate into a simpler product through the use of facultative and obligate anaerobe fermentation. Microorganisms of the genus *Clostridium* are primarily used in the dark fermentation of algae to produce hydrogen [11,26,27,37,38,39,40,41,42]. Table 2 shows that microorganisms from the genera *Enterobacteriaceae, Acinetobacter, Terrisporobacter, Paraclostridium, Anaerostipes,* and *Caproiciproducens* also participate in hydrogen fermentation of algae [12]. In terms of algae types, both micro- and macroalgae are used for DF, with brown and red macroalgae predominating, as well as cyanobacteria and diatoms [26]. DF of hydrogen production has a shorter process time than AD and the algae used for DF develop at a lower temperature. Therefore, it can be said that compared to AD, hydrogen fermentation is a more cost-effective and simpler process.

Acinetobacter and *Caproiciproducens* are the most productive in terms of hydrogen biosynthesis [11,27,39]. The process should be carried out for 48 days (for *Acinetobacter*) and 109 days (for *Caproiciproducens*) at 36 °C.

The DF process generates hydrogen due to the activity of the microbial hydrogenase enzyme [44]. Heterotrophic bacteria produce a variety of end products when producing hydrogen from organic compounds without light. They follow different biochemical pathways. The first pathway is the pyruvate ferredoxin oxidoreductase (PFOR) pathway, which is found in Clostridium and is used to oxidize pyruvate to acetyl-CoA. The second pathway operates in *Escherichia coli* and pyruvate is converted to acetyl-CoA and formated using the enzyme pyruvate formate-lyase [45].

One of the main limitations in using algae for hydrogen production by DF is their unyielding cell wall. The hydrogen yield without pretreatment of algae is 4.1–17.7 % of the stoichiometric yield [46]. Micronutrients, which play a key role in the activation of important microbial enzymes, are used to increase hydrogen yield from algal biomass. Iron is an important constituent of key proteins responsible for the formation of molecular hydrogen [11]. The positive effect of metal nanoparticles on hydrogen production by microorganisms from algae has been shown in many studies [11,42,47,48,49,50]. Furthermore, subsequent AD can improve the efficiency of DF because, in addition to hydrogen, a large amount of volatile fatty acids are produced during DF [26]. Co-fermentation of sewage treatment plant sludge and algae is an interesting and cost-effective way to improve hydrogen production [11].

4. Lactic acid fermentation

Lactic acid (CH3-CHOHCOOH), or 2-hydroxypropionic acid, is a chemical compound present in two enantiomeric forms, L (+) lactic acid and D (-) lactic acid. Lactic acid can be produced either by chemical synthesis from hydrocarbon-based sources or by microbial fermentation [51]. Lactic acid fermentation (LAF) is a microbial fermentation process that produces lactic acid. LAF is subdivided into homofermentative (the yield of lactic acid in this type of fermentation is up to 90 %), and heterofermentative (the yield of lactic acid in this type of fermentation is up to 50 %). LAF is carried out by a variety of microorganisms, including fungi and lactic acid bacteria. Lactic acid bacteria grow and develop in an acidic environment (pH 5.5–6.5). The most abundant genus of lactic acid bacteria, *Lactobacillus*, includes approximately 80 species [51]. The preferred substrate for lactic acid production by bacteria is simple sugars [52]. LAF of grains, vegetables, and seafood is an important technology that has provided suppression of the growth of harmful microorganisms in foods in regions where adequate preservation facilities are not available [53]. In addition, foods fermented in this way have positive health benefits, especially for those with food allergies. Lactic acid bacteria produce a wide range of compounds such as vitamins, organic acids, polysaccharides, antimicrobial compounds, etc. [54].

The production of lactic acid is in high demand due to its wide potential in the food, pharmaceutical, textile, cosmetic, and packaging industries [55]. For example, polylactic acid is an environmentally friendly alternative to petroleum-based polymers. Carbohydrate-rich algae can be converted to lactic acid through fermentation [56]. LAF is not only used for the production of lactic acid from algae, but also for the production of functional beverages and foods, organic acids, and phenols. Moreover, the silage of algae by lactic acid bacteria increases their shelf life while inducing the biological activity of the resulting product [57]. Both micro- and macroalgae and cyanobacteria are used for LAF. Microorganisms used for LAF include the genera *Lactobacillus, Lacticaseibacillus, Lactococcus, Tetragenococcus, Bacillus, Leuconostoc*, and *Weissella*. LAF is produced in both liquid and solid phases (Table 3).

Arthrospira, Dunaliella, and *Sargassum* are the most efficient sources of biofuel in lactic acid fermentation [58–61,63,67]. The process must be carried out for 72 h at 37 °C (for *Arthrospira* and *Dunaliella*) [61,63] and at 30 °C (for *Sargassum*) [67].

Table 2
Microorganisms and algae used in hydrogen fermentation.

Microorganisms	Algae	Algae type	Product	Fermentation conditions	References
Clostridium butyricum	*Microcystis wesenbergii, Microcystis aeruginosaare*	Cyanobacteria	Hydrogen	Dark fermentation in liquid phase at pH 6, 35 °C, 72 h	[26]
Clostridium pasteurianum (MTCC116)	*Lyngbya limnetica*		Hydrogen	Dark liquid fermentation at 35–42 °C and pH 6–8, 168 h	[42]
Microorganisms from biogas plant sludge	*Microcystis, Diatom*	Microalgae, diatoms	Hydrogen, methane	Dark liquid fermentation	[43]
Enterobacteriaceae, Acinetobacter, Acinetobacter towneri, Clostridium symbiosum, Clostridium tertium, Terrisporobacter, Clostridium sensu stricto 13, *Clostridium tetani* E88, *Clostridium tertium, Paraclostridium, Terrisporobacter*	*Laminaria japonica*	Brown algae	Hydrogen	Dark fermentation in liquid phase at pH 7, 36 °C, 48 h	[11,27]
Sludge from wastewater treatment plants (composition not specified)	*Laminaria japonica*		Hydrogen	Fermentation in liquid phase at 36 °C, 24 h	[37]
Clostridium butyricum DSM 10,702	*Gelidium amansii*	Red algae	Hydrogen	Fermentation in liquid phase at 37 °C, 30 h	[38]
Clostridium sp., *Anaerostipes* sp., *Caproiciproducens* sp.	*Echeuma spinosum*		Butyric acid and propionic acid, hydrogen	Fermentation in liquid phase at pH 5.5, 109 days	[39]
Clostridium beijerinckii Br21	*Kappaphycus alvarezii*		Hydrogen	Fermentation in liquid phase at 35 °C, 8 h	[40]
Clostridium butyricum	*Gelidium amansii*		Hydrogen	No data	[41]

Table 3
Microorganisms and algae used in LAF to produce lactic acid and other products.

Microorganisms	Algae	Algae type	Product	Fermentation conditions	References
Lactiplantibacillus plantarum ATCC 8014	*Arthrospira platensis* F&M-C256	Cyanobacteria	Lactic acid, functional beverages	Fermentation in liquid phase at 37 °C, 72 h	[58,59]
Lactobacillus acidophilus ATCC 43,121	*Arthrospira platensis*		Lactic acid	Fermentation in liquid phase at 37 °C, 24 h	[60]
Lacticaseibacillus casei 2240, *Lacticaseibacillus rhamnosus* GG	*Arthrospira platensis*		Fermented lyophilized spirulina powder	Solid phase fermentation	[61]
Lactobacillus plantarum AN7, *Lactococcus lactis* subsp. *lactis* Kushiro-L2	*Aphanizomenon flos-aquae*		Fermented cyanobacteria with immunomodulatory antioxidant properties	Fermentation in liquid phase at pH 7, 7 days	[62]
Lactococcus lactis subsp. lactis Uruma-SU1, *Lactobacillus plantarum* Uruma-SU4	*Dunaliella tertiolecta, Pleurochrysis carterae, Nostoc commune, Euglena* sp.	Green microalgae, haptophytes, cyanobacteria	Phenols with antioxidant activity	Fermentation in liquid phase at pH 7, 37 °C, 72 h	[63]
Lactobacillus buchneri B-1837, *Tetragenococcus halophilus* B-4244	*Nannochloropsis gaditana*	Green microalgae	Organic acids (lactic acid, isovaleric acid, propionic acid, acetic acid, butyric acid)	Silage at room temperature for 30 and 180 days	[57]
L. acidophilus BCRC 10,695	*Gracilaria*	Red algae	Lactic acid	Repeated fermentation (48-hour cycle) at 30 °C	[64]
Bacillus coagulans	*Eucheuma cottonii*		L-lactic acid	Fermentation in liquid phase at pH 4.8, 37 °C, 25 h	[65]
Lactobacillus plantarum KP3, *Lactobacillus plantarum* KP4, *Leuconostoc mesenteroides* K8, *Lactobacillus paracasei* subsp. *paracasei* DP2	*Porphyra*		Phenyllactic acid	Fermentation in liquid phase at 37 °C, 120 h	[66]
Lactobacillus plantarum, Lactobacillus sakei, Lactobacillus rhamnosus, Weissella cibaria, Weissella sp., *Weissella paramesenteroides*	*Ulva* sp., *Gracilaria* sp., *Sargassum cristaefolium*	Green, brown, red algae.	Lactic acid	Fermentation in liquid phase at pH 5.5, 30 ℃	[67]

Algae extracts have a number of biological activities such as, antioxidant [68–73], antimicrobial [73–77], anticancer [78–82], antidiabetic [72,83,84,85], antihypertensive [86,87], and others. The presence of polysaccharides, polypeptides, phenols, and pigments in algae results in biological activities, many of which have health benefits (such as antioxidant, anti-inflammatory, antimicrobial, and anticoagulant properties). Fermentation of both micro- and macroalgae promotes the yield of bioactive compounds and, in some cases, leads to their synthesis [15]. For example, the anti-glycation activity of the brown macroalgae *Sargassum horneri, Undaria pinnatifida*, and *Gelidium elegans* was increased by fermentation with the lactic acid bacterium *Lactobacillus plantarum* Miura-SU1 [88].

Algal polysaccharides regulate the composition of the intestinal microflora (by increasing microorganisms of the genera *Bacteroides, Akkermansia, Bifidobacterium*, and *Lactobacillus* while reducing the number of *Firmicutes*), reduce the risk of cardiovascular disease, stimulate immunity, and induce apoptosis [13]. Polysaccharides applied to nanoparticles reduce the side effects of anticancer chemotherapy [79]. This is due to the ability of sulfated polysaccharides to act on therapeutic targets such as anti-inflammatory cytokines, adhesion molecules, nuclear factor NF-kB, reactive oxygen and nitrogen species [89]. The fact that algal polysaccharides are not destroyed by human digestive enzymes facilitates their delivery to the intestine, where they boost the production of important metabolites by intestinal microflora [90]. Alginate, fucoidan, and laminaran repair damage to the intestines [91]. Fermentation is used to isolate polysaccharides [18]. Fermentation with lactic acid bacteria enhanced polysaccharide-driven biological activities in the macroalgae *Sargassum* sp. [92]. Algal polysaccharides have proven anti-cancer activity [92]. They improve the efficacy of conventional chemotherapeutic drugs with relatively low toxicity to normal human cells [78]. Fucoidan, a brown algae polysaccharide, was produced by fermenting a yeast and L. *plantarum* mixed culture. The resulting polysaccharide exhibited cytotoxicity in cancer cells [93].

Algae fermentation helps increase antioxidant content [94]. Fermentation by lactic acid microorganisms L. *plantarum* and L. *acidophilus* increased the phenolic content of red algae *Gelidium* sp. and rhodophytic algae of the genus *Eucheumacottonii*, and decreased the pH of the samples [94]. Thus, Eom et al. [95] selected the most effective strain of microorganisms isolated from traditional Korean fermented food products for fermentation of brown algae from the kelp family *Eisenia bicyclis* (sea oak) in their study. *Candida utilis* fermentation increased its biological activity by increasing the biomass content of total phenolics in the extracts as well as antioxidant activity. Sakulpong et al. investigated the ability of lactic acid microorganisms to ferment the freshwater algae *Spirogyra* spp., *Cladophora*, and *Microspora*. Among these algae, *Spirogyra* sp. extracts fermented with lactic acid bacteria showed the highest flavonoid content, antioxidant capacity, and DPPH free radical scavenging activity [96].

Aphanizomenon flos-aquae are brackish and freshwater species of cyanobacteria found throughout the world, including the Baltic Sea and the Great Lakes. Fermentation of these cyanobacteria biomass by microorganisms L. *plantarum* and *Lactococcus lactis* has been shown to increase DPPH and O^{2-} radical scavenging capacity and iron reducing capacity [62]. Marine lactic acid bacteria are effective in fermenting seaweed. The biomass of *Sargassum* sp. fermented by this group of microorganisms had high antioxidant activity. Further purification of bioactive molecules may facilitate the therapeutic application of these algae [92]. The biomass of the Gram-negative filamentous cyanobacterium *A. platensis* was subjected to lactic acid fermentation by L. *plantarum* microorganisms. This contributed to an increase in digestibility, phenolic content (by 79 %), and antioxidant activity of biomass (by 320 %) of fermented cyanobacteria [59]. The addition of carbohydrate sources during fermentation by a strain of lactic acid bacteria L. *acidophilus* of marine algae *Gelidium* sp. biomass increased the final product's antioxidant activity. The addition of another carbohydrate source increased the number of viable microorganisms and phenolics while decreasing the pH of the hydrolysate [97].

Lactic acid fermentation also contributes to the antihypertensive effect of algae. For example, the biomass of *Sargassum horneri* (a seaweed with antihypertensive properties) showed an enhancement of this biological activity after lactic acid fermentation by *Lactiplantibacillus pentosus* bacteria. It was found that glycerol was responsible for the antihypertensive action in this case [98].

In addition to producing biologically active compounds, lactic acid

fermentation produces polysaccharide fermentation end products that have potent probiotic activity [99]. Algae-based fermented foods include primarily dairy products: cheese, cream, dairy desserts, yogurt, cottage cheese, processed cheese, and lactose-free beverages. The combination of fermented products with a high content of lactic acid bacteria with algae containing biologically active metabolites of natural origin allows not only for high nutrient content products, but also for the creation of a fundamentally new segment of fermented foods [100]. Fig. 1 presents the benefits of the algae fermentation process and its effect on the nutritional and biological value of algae.

5. Alcoholic fermentation

The anaerobic conversion of sugars such as glucose and fructose into ethanol and carbon dioxide is commonly referred to as alcoholic fermentation [101]. Alcoholic fermentation is primarily carried out by the yeast *Saccharomyces cerevisiae* (the world's most common industrial microorganism [101]) and a few bacteria such as *Zymomonas mobilis* [101]. Acetoin, 2,3-butanediol, higher alcohols, glycerol, diacetyl, esters and succinic acid are among the by-products formed during alcoholic fermentation [102]. Yeast fermentation is one of the oldest human technologies and its origins date back to the Neolithic period. Nowadays, alcoholic fermentation is used to produce alcoholic beverages and ethanol. *S. cerevisiae* is unique in that it can convert sugars into ethanol under both oxygen and oxygen-free conditions [103]. Wild-type *S. cerevisiae* strains ferment glucose, mannose, and fructose via the Embden–Meyerhof glycolysis pathway, whereas galactose is fermented via the Leloir pathway [104]. Traditional crops used for alcoholic fermentation, such as cereals and legumes, corn, sugar beet, wheat, and barley [105], cannot meet the global demand for bioethanol production because they are valued primarily as a food source [106]. Algae, which contain high amounts of carbohydrates and are widely distributed in nature, can serve as an alternative to food crops as a substrate for alcoholic fermentation [106]. Microalgae with high starch content include the genera *Chlorella, Dunaliella, Chlamydomonas*, and *Scenedesmus* [105]. Macroalgae species with the highest polysaccharide content include *Ascophyllum* (42–70 %), *Palmaria* (38–74 %), and *Porphyra* (40–76 %). The carbohydrate content of macroalgae: green, red, and brown algae is 25–50 %, 30–60 % and 30–50 %, respectively [105]. Macroalgae also contain up to 11 % cellulose (depending on the species), which can be hydrolyzed to simple sugars [107]. However, there are technical and economic constraints that prevent commercialization of this technology. The cost of production can be minimized by recovering valuable secondary by-products [108]. Also, the efficiency of alcoholic fermentation may be due to prior chemical hydrolysis. The yield of ethanol from algae can be up to 75 % [109]. The main microorganisms used for alcoholic fermentation of both micro- and macroalgae are the yeast *S. cerevisiae*; but the microorganisms *Trichoderma harzianum, Z. mobilis,* and *E. coli* are also effective (Table 4). Both microalgae, including cyanobacteria, and green, red, and brown macroalgae can be fermented. The use of *S. cerevisiae* allows the process to proceed under both aerobic and anaerobic conditions, which greatly simplifies the technology.

Saccharomyces cerevisiae is the most productive in bioethanol production. The process should be carried out for 24–54 h at 25–35 °C [115, 116].

6. Butyric acid and acetone-butanol fermentation

Butyric acid is a short-chain fatty acid with four carbons that is widely used in the chemical, food, and pharmaceutical industries. Butyric acid is typically produced through chemical synthesis from petroleum, but in some industries, butyric acid produced through microbial synthesis is highly valued [116]. Butyric acid fermentation was discovered in 1861 by scientist Louis Pasteur, who discovered bacilliform microorganisms that grow in the absence of air and are inhibited in its presence. The major microorganisms with the ability to produce butyric acid include microorganisms of the genera *Butyribacterium, Butyrvibrio, Clostridium, Eubacterium, Megasphera, Sarcina*, and *Fusobacterium* [117]. Simple carbohydrates, which are abundant in algae, serve as the substrate for butyric acid fermentation. For example, the yield of butyrate (butyric acid salts and esters) from *Laminaria japonica* is 11 % [118]. The use of the brown alga *Saccharina japonica* in conjunction with rice straw to produce butyric acid is also known. Rice straw in this case helped to overcome the limitations of the algal component, mannitol, which was inefficiently consumed by *Clostridium tyrobutyricum* microorganisms [119]. The red algae *Gelidium amansii* is an economically important algae species that is common in shallow coastal waters of many Asian countries. Also, this species is attractive because of its high content of galactose, which in turn can be hydrolyzed to butyric acid. However, levulinic acid and 5-hydroxymethylfurfural are formed during the hydrolysis of *G. amansii*. These substances inhibit the growth of microorganisms that consume galactose. Lee et al. isolated a strain of *Clostridium* sp. S1, which is resistant to these inhibitors and actively digests galactose to butyric acid [120]. Table 5 demonstrates examples of the use of microorganisms of the genus *Clostridium* for butyric acid fermentation of macroalgae.

Another type of algal fermentation that also utilizes microorganisms of the genus *Clostridium* is acetone-butanol fermentation. It is a chemical process in which acetone-butanol bacteria decompose carbohydrates anaerobically to produce acetone, butyl alcohol, acetic acid, butyric acid, hydrogen, and carbon dioxide. This type of fermentation was originally used to produce acetone, with butanol as a byproduct. However, acetone is not in high demand at the moment, and butanol has significant advantages over ethanol as a gasoline additive due to its higher calorific value, lower affinity for water, lower corrosivity, and lower vapor pressure [121]. Although the most preferred substrate for acetone-butanol fermentation is glucose from food starch, the search for new substrates from inexpensive raw materials is necessary [122]. A study by Efremenko et al. compared different microalgae species for

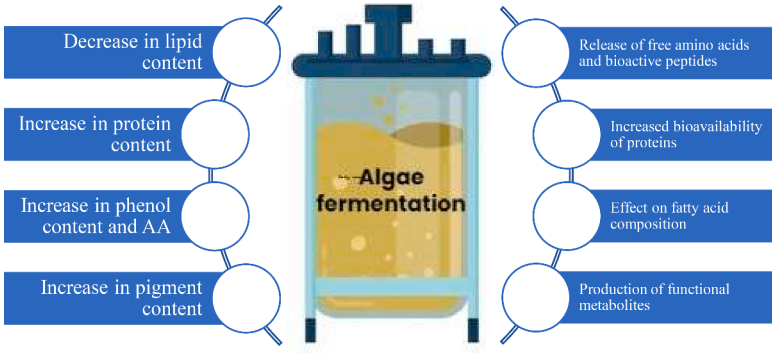

Fig. 1. Results of microbial fermentation on nutritional and biological value of algae.

Table 4
Microorganisms and algae used for alcoholic fermentation.

Microorganisms	Algae	Algae type	Product	Fermentation conditions	References
Saccharomyces cerevisiae LPB-287	*Arthrospira platensis*	Cyanobacteria	Bioethanol	Fermentation in liquid phase at 30 °C, 24 h	[60]
Saccharomyces cerevisiae	*Arthrospira platensis*	Cyanobacteria	Ethanol	Anaerobic fermentation at 38 °C, 72 h	[110]
Saccharomyces cerevisiae	*Spirulina platensis*	Cyanobacteria	Ethanol	No data	[111]
Trichoderma harzianum	*Chlamydomonas reinhardtii*	Green microalgae	Ethanol	Dark fermentation in liquid phase at 20 °C, 5 days	[112]
Saccharomyces cerevisiae	*Eucheuma cottonii*	Red algae	Bioethanol	Fermentation in liquid phase at pH 4.8, 43 °C, 48 h	[65]
Saccharomyces cerevisiae, Z. mobilis	*Padina tetrastromatica, Sargassum swartzii*	Brown algae	Bioethanol and biodiesel	No data	[113]
E. coli KO11	*Ulva lactuca, Gelidium amansii, Laminaria japonica, Sargassum fulvellum*	Green, red, brown algae.	Ethanol	Fermentation in liquid phase at pH 5.5 30 °C, 24 h	[114]
Sacharomyces cerevisiae	*Ulva lactuca* sp.	Green algae	Bioethanol	Fermentation in liquid phase at 25–35 °C, 24 h	[115]
Saccharomyces cerevisiae	*Rhizoclonium* sp.	Green algae	Ethanol	Fermentation in liquid phase at pH 5.5, 25 °C, 54 h	[116]

Table 5
Microorganisms and algae used for butyric acid fermentation.

Microorganisms	Algae	Algae type	Product	Fermentation conditions	References
Clostridium tyrobutyricum ATCC 25,755	*Laminaria japonica, Undaria pinnatifida*	Brown algae	Butyric acid	Fermentation in liquid phase at 37 °C, 120 days	[118]
Clostridium tyrobutyricum	*Saccharina japonica*	Brown algae	Butyric acid	Fermentation in liquid phase at 37 °C, 16 days	[119]
Clostridium sp. S1	*Gelidium amansii*	Red algae	Butyric acid	Fermentation in liquid phase at 37 °C, 50 h	[120]
Clostridium acetobutylicum	*Chlorella sorokiniana CY1*	Green microalgae	Butanol	Anaerobic digestion at 37 °C, pH 6, 7 days	[121]
Clostridium acetobutylicum	*Synechococcus elongates* PCC7942	Cyanobacteria	Butanol	Periodic fermentation in liquid phase at 37 °C 30–40 h	[125]
Clostridium acetobutylicum B-1787	*Arthrospira platensis, Nannochloropsis* sp., *Dunaliella tertiolecta, Dunaliella salina, Galdieria partita, Chlorella vulgaris, Cosmarium* sp. *Nostoc* sp.	Microalgae	Butanol, hydrogen, ethanol	Anaerobic digestion at 37 °C	[123]
Clostridium acetobutylicum. ATCC824	*Chlorella vulgaris* JSC-6	Green microalgae	Butanol	Anaerobic digestion at 37 °C, 24 h	[126]
Clostridium butyricum CGS5	*Chlorella vulgaris ESP6*	Green microalgae	Hydrogen	Fermentation in liquid phase at 37 °C, pH 7	[127]
Clostridium butyricum	*Scenedesmus obliquus*	Green microalgae	Hydrogen	Fermentation in liquid phase at 37 or 58 °C 144 h	[128]
Enterobacter aerogenes, Clostridium butyricum	*Scenedesmus obliquus*	Green microalgae	Hydrogen	Periodic fermentation in liquid phase at 37 °C 48 h	[129]
Clostridium acetobutylicum	*Chlamydomonas mexicana*	Green microalgae	Hydrogen, acetone, butanol, and ethanol	Periodic fermentation in liquid phase at 37 °C 24 days	[130]
Clostridium butyricum	*Spirogyra*	Green macroalgae	Hydrogen	Fermentation in liquid phase 36 h	[124]
Clostridium phytofermentans DSM1183	*Chlamydomonas dorsoventralis, Graesiella emersonii, Coelastrum proboscideum, Scenedesmus obliquus, Micractinium* sp., *Desmodesmus* sp. and *Chlorella* sp.	Microalgae from wastewater	Ethanol	Fermentation in liquid phase at 30 °C 120 h	[131]

butanol, hydrogen and ethanol production through fermentation by *Clostridium acetobutylicum* microorganisms. Among microalgae species *A. platensis, Nannochloropsis* sp., *Dunaliella tertiolecta, Dunaliella salina, Galdieria partita, Chlorella vulgaris, Nostoc* sp., and *Cosmarium* sp., the species *A. platensis* has the highest butanol and ethanol productivity [123]. In addition to butanol production, this type of fermentation is used to produce hydrogen from algae, particularly microalgae. The green filamentous *Spirogyra* macroalgae is found throughout Lake Baikal, forming large cotton-like clusters in some places on the shores. Being an atypical representative of Baikal's algoflora, the active spread of spirogyra contributes to the disturbance of the unique endemic flora and fauna and also reduces water quality. Ortigueira et al. proposed a method to process *Spirogyra* biomass to produce biohydrogen by fermentation with *C. butyricum* [124]. Examples of microbial production of hydrogen, butanol, ethanol, and acetone from algae are summarized in Table 5.

Clostridium phytofermentans is the most productive for bioethanol production via acetone-butyl fermentation, while *Clostridium acetobutylicum* is the most productive for biobutanol production via AD [128, 131]. Meanwhile, for hydrogen production, the green microalgae *Scenedesmus obliquus* is recommended to be treated with *C. phytofermentans* at 37 or 58 °C for 144 h [128]. In order to produce biobutanol from microalgae, the AD process is recommended to be carried out at a temperature of 30 °C for 120 h.

7. Existing obstacles in algae fermentation technology

The transition from laboratory-scale production of gaseous biofuels

to sustainable industrial production is fraught with challenges such as low yields compared to the theoretical maximum and the need to remove by-products [132]. Unfortunately, the majority of research has been done in laboratory settings, and rarely on a fractional-technical scale. This significantly limits the possibility of obtaining reliable data for a comprehensive assessment of technological, environmental, and economic efficiency of these technological solutions [16]. It is important to note that this area of research (obtaining useful compounds) is still new and more research is needed to understand the feasibility of using algal fermentation for food [15]. Also, the production of some algal products can be limited by the selection of suitable algae and its cultivation system, selection of microorganisms and fermentation technology [133]. Most authors have focused on brown algae, while red and green algae (especially the latter) have not been studied so much. Although brown algae are the most studied algae, their phenolic content does not always allow fermentation because polyphenols may have bactericidal properties [15].

To solve the problems associated with inefficient fermentation of algae, physical and chemical pretreatment methods [133]. However, obstacles related to the economic and environmental impacts of these methods need to be overcome [134]. Therefore, there is a need to find cheap and safe methods for pretreatment of algal biomass. Wang et al. proposed a method to increase the production of short-chain fatty acids by anaerobic fermentation of algae using coconut shell ash. This helped to increase the pH of the obtained hydrolysate, thereby reducing the use of alkaline reagents and increasing its stability in an acidic environment. The resulting waste containing inorganic compounds can be used as biofertilizer in agriculture [134]. Acid and alkaline catalysts are also used to increase the efficiency of the process. Chen et al. [43] used the biomass of freshwater algae harvested during their blooms to produce biohydane (this type of fuel is a hydrogen-methane mixture with a hydrogen concentration of 10 to 30 % by volume) through fermentation. Pretreatment with catalysts allowed more macromolecular substances to be hydrolyzed [43]. Also, to improve the energy conversion efficiency, algal biomass was subjected to vapor acid treatment before dark fermentation [26]. However, such treatment can negatively affect the yield of liquid and gaseous fuels because the excess sodium ions introduced to neutralize the acid inhibit the viability of methanogenic microorganisms [27]. Low-temperature (less than 100 °C) pretreatment has advantages such as low cost, simplicity, and energy conservation, which simplifies the use of technical means to improve biogas production. However, unlike high-temperature pretreatment (above 150 °C), which can break down complex polymerized substances in biomass, the action mechanism of biomass heat treatment is unknown [135].

8. Economic analysis

Ecological and economic analysis as well as technological considerations indicate that methane fermentation in combination with bio-oil production is one of the most justified directions of energy utilization of microalgae biomass for energy purposes [136]. The use of wastewater, other liquid wastes or flue gases can reduce the cost of biofuel production while having a measurable impact on the environment [136]. According to Ansari et al., the payback period for using algae for fish feed is 7.5 years, and the payback period for biodiesel production (biomass waste can also be used for fish feed) is 6.8 years [136]. Table 6 shows that the annual biomass production of microalgae is higher than that from macroalgae, but cultivation of the latter requires less economic costs. At the same time, methane production in both microalgae and macroalgae is almost at the same level. However, the insufficient methane productivity of algae does not allow for economic benefits in the production of this type of fuel via microbial fermentation. Therefore, approaches to reduce the cost and complexity of algae cultivation are required, as are methods to increase methane production from biomass by AD. For example, the cost of biodiesel production from microalgae can be reduced to 0.73 kg^{-1} of dry weight when grown in wastewater or 0.54 L^{-1} when co-produced with sewage sludge [137].

Table 6
Comparison of economic characteristics of micro- and macroalgae in methane production.

Economic parameters	Microalgae	Microalgae	References
Biomass productivity (tons of dry matter/ha/year)	20–75	11–45	[138]
Methane production, L CH_4 g^{-1} $VS_{alg\text{-}t0}$	0.12–0.34	0.11–0.48	[138]
Cost of algal biomass (USD/kg)	2.14	0.1	[137,139]
Methane market price (USD/cubic meter)	0.1–0.5		

The main method of industrial hydrogen production is steam reforming [137]. This method of hydrogen production involves the reaction of hydrocarbons with water. The feedstock is usually natural gas. The cost of hydrogen produced in this way is US$2–7 per kg. However, such production results in the emission of large amounts of carbon dioxide. Ways to reduce carbon dioxide emissions make the process 30–40 % more expensive [140]. The cost of hydrogen produced by electrolyzing renewable energy sources is $6.47, while the cost of hydrogen produced from waste is $4.56. The cost of producing biohydrogen from algae is still quite high - $39.83 per liter (the cost of investment in an algae processing plant is estimated to be between $215 and 280 million [141]), but the advancement of research on this topic provides hope for the early cheapening of the technology through the development of biomass pretreatment methods [142]. As a result, algae is not currently processed for energy. It is also noteworthy that in Europe, for the first time in history, the cost of biohydrogen has become cheaper than fossil fuels, which gives a boost to the development of waste-to-biohydrogen technologies [142].

Bioethanol production from food resources is not in line with sustainable development strategies. Therefore, algae are regarded as a low-cost substitute for feedstock in ethanol production. The high cost of constructing and maintaining plants and equipment to convert algae into ethanol is an obstacle [108]. The calculated theoretical yield of conversion of digestible algal sugars into bioethanol is 61 % (additionally, 18.6 % of lipids can be obtained from the same biomass) [107]. Capital and operating costs for liquefaction, saccharification, fermentation, and distillation of marine algae are assumed to be equal to the cost of producing ethanol from dry corn. However, the cost of ethanol produced from corn is $0.83 per liter, whereas the cost of ethanol produced from algae is estimated to be $1.5 [143]. Currently, the marketing price of gasoline in the United States is 0.93 ($/L) [20]. To achieve this price level from marine algae, the annual production of marine algae would have to be 5.7 million tons (dry) [144]. Ethanol production from marine algae is recognized as economically unprofitable, but profitable production is only possible by lowering production costs and expanding cultivation areas [144].

Using computer modeling, the profit from processing fungi and algae into lactic acid was presented. Processing 1 ton of biomass per day, the annual net profit from the sale of lactic acid could be $422,699, with a payback period of 7.5 years. The productivity of lactic acid from algal biomass can be as high as 1.67 g of lactic acid/g of biomass [145].

9. Conclusion

Algae are appealing due to their fast growth rate, lack of arable land requirements, low lignin content, and high carbohydrate, protein, and fat content. In addition to producing valuable products, algae absorb significant amounts of biogens from water bodies or wastewater, thus solving the problem of eutrophication. Micro- and macroalgae are considered a new source of valuable bioactive compounds such as polysaccharides and polypeptides, many of which have health benefits (such as antioxidant, anti-inflammatory, antimicrobial, and anticoagulant properties). Six main types of micro- and macroalgae fermentation (methane, hydrogen, lactic acid, alcohol, butyric acid, and acetone-

butanol) were considered. It was found that the most productive methods are methane, hydrogen, and lactic acid fermentation. Economic analysis has shown that fermentation of algae as waste is currently not cost-effective because expensive pretreatment is required, and the low cost of methane, hydrogen, and lactic acid makes marketing algae fermentation products difficult. However, the economic crisis and the global unsustainable state of the fuel and energy industry require research aimed at optimizing and improving the efficiency of the enzymatic processing of algae. To increase the profitability of algae biofuel production, research must be organized on increasing the durability and stability of biomass catalysts in the raw material processing process, as well as reducing the polluting effect of solvents used in oil extraction.

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CRediT authorship contribution statement

Olga Babich: Conceptualization, Formal analysis, Project administration, Writing – original draft. **Svetlana Ivanova:** Formal analysis, Writing – review & editing. **Philippe Michaud:** Formal analysis, Methodology. **Ekaterina Budenkova:** Formal analysis, Methodology. **Egor Kashirskikh:** Formal analysis, Methodology. **Veronika Anokhova:** Formal analysis, Methodology. **Stanislav Sukhikh:** Conceptualization, Formal analysis, Methodology, Writing – original draft.

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

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

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