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REVIEW PAPER

Fatty acids of microalgae: diversity and applications

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Abstract The possibility of obtaining commercially valuable products from microalgae stimulates scientific research in this direction. The ability of microalgae to accumulate lipids is very promising from the point of view of practical application. The diversity of the composition of microalgae lipids makes it possible to study a wide range of their applications: biofuel production, food products, feed for farm animals and birds, for aquaculture, food additives, etc. Fatty acids (FAs) are involved in the metabolic pathways of formation and conversion of most lipid classes, and their composition largely determines their properties and practical use. As a result, much attention is paid to the study of the composition of fatty acids in microalgae (including cyanobacteria). This review summarizes information on the diversity of the fatty acid composition of microalgae and cyanobacteria, taking into account their rare and unusual categories. The total variety of FA profile of microalgae from different habitats is formed by 135 FAs. Taking into account the length of the hydrocarbon chain, its structure and the presence of substituents, they are distributed into several groups: with an even number of carbon atoms in the chain—81 (short-chain FAs—2, medium-chain FAs—14, long-chain FAs—28, very-long-chain FAs—37), with an odd number of carbon atoms—33, with a branched hydrocarbon chain and additional functional groups—21. Among FAs of microalgae there are both saturated and unsaturated FAs with different numbers of double bonds: saturated FAs—19, monounsaturated FAs—26, polyunsaturated FAs—68. The FA profile of microalgae is rich in omega-3 and omega-6 fatty acids. The review also considers the use of fatty acids as an industrial resource, as well as a biomarker.

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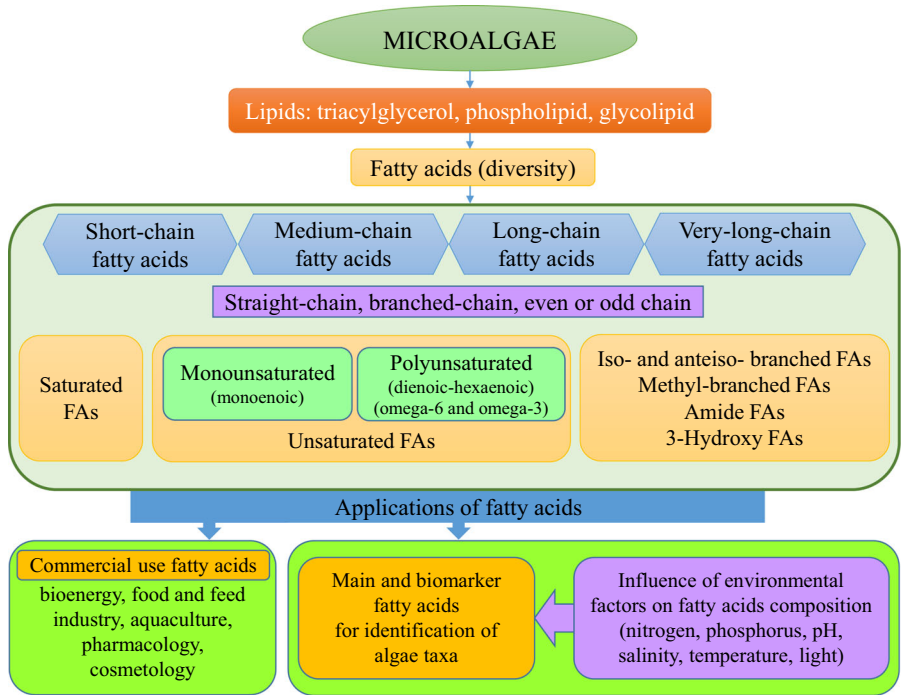
Graphic abstract



Keywords Microalgae · Cyanobacteria · Lipids · Fatty acids

1 Introduction

Natural resources are an integral part of economic production and meeting the needs of humanity. With the increase in the world population, the need for them is constantly growing. This makes the introduction of resource-saving technologies urgent, as well as the search for new sources of raw materials. This task is most acute in the direction of overcoming the shortage of energy and food resources.

According to researchers, algae can be used to replace traditional sources of biofuel, feed and a number of food products (see reviews: González-Fernández et al. 2012; Barkia et al. 2019; Figueroa-Torres et al. 2019; Sathasivam et al. 2019; Lever et al. 2020). Algae are a large group of photosynthetic organisms that live in a wide range of environmental conditions. They inhabit various aquatic and terrestrial ecosystems from the polar regions to the hot deserts of the tropics and account for more than half of the primary productivity of food chains (Guschina and Harwood 2009). Algae are represented by both macroscopic organisms, reaching a length of tens of meters, and microscopic, measured by several micrometers. Microscopic algae, along with eukaryotic representatives, include a diverse group of prokaryotes—cyanobacteria, which are one of the most ancient groups of photosynthetic organisms.

Microalgae are able to accumulate protein, carbohydrates, lipids and other biologically active compounds in significant amounts. In this regard, there is an increasing interest in microalgae (Milledge 2011; Chu 2012; Borowitzka 2013; Khan et al. 2018; Barkia et al. 2019; Sathasivam et al. 2019; Fabris et al. 2020). It has been established that the protein content in the biomass of some microalgae can reach 71% (Becker 2007; Plaza et al. 2009; Milovanovic et al. 2012), total lipids—75%, which exceeds many indicators among higher plants (for example, in soybeans—15–25% of lipids, 30–50% of protein) (Moraes et al. 2006; Chisti 2007; Mata et al. 2010). Polyunsaturated fatty acids (PUFAs): arachidonic acid (ARA), γ-linolenic acid (GLA), eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA) and other compounds (Carotenoids, Peptides, Phenolics, Phycocyanin, etc.)

accumulated by microalgae are also highly valuable for various activities (Pulz and Gross 2004; Spolaore et al. 2006; Borowitzka 2013; Barkia et al. 2019; Sathasivam et al. 2019; Chalima et al. 2019, 2020; Peltomaa and Taipale 2020; Levasseur et al. 2020). Currently, primarily species from the genera *Aphanizomenon*, *Botryococcus*, *Chaetoceros*, *Chlorella*, *Cylindrotheca*, *Crypthecodinium*, *Isochrysis*, *Haematococcus*, *Dunaliella*, *Neochloris*, *Nostoc*, *Nannochloropsis*, *Pavlova*, *Phaeodactina*, *Porphyridium*, *Arthrospira*, *Schizochytrium*, *Thalassiosira* are used for the production of commercial products (Pulz and Gross 2004; Safafar et al. 2016; Sathasivam et al. 2019; Xu et al. 2020). However, the entire potential of microalgae is not confined to this, and the search for highly productive species or strains that can be used to obtain valuable biological products continues.

The biotechnological value of microalgae is due to the wide range of compounds they synthesize, the rapidity of growth, the ability to increase the synthesis of target bioproducts changing the cultivation conditions (Sun et al. 2018; Li-Beissona et al. 2019; Levasseur et al. 2020). An important aspect is also the ability to grow them industrially in bioreactors, photobioreactors or in open tanks and stalls, which can be placed in desert, technogenic, saline and other territories not suitable for growing basic industrial and food crops. In addition, the amount of production from one unit of area that can be obtained by growing microalgae is significantly higher in comparison with higher plants (Hu et al. 2008). For example, microalgae containing 20–50% lipids in dry biomass can yield up to 14 thousand liters of oil per year from one hectare, while corn—172 L, soy—636 L, canola (rapeseed)—974 L, sunflower—1070 L (Wigmosta et al. 2011).

Now in the world there is a stable dynamics of increasing demand for biomass of microalgae. This is due to both the increase in the scale of traditional industries and the expansion of their range, the development of new products and applications from microalgae. According to various estimates, the annual production of *Arthrospira* and *Chlorella* alone is 6700–12,000 tons and 2000–5000 tons, respectively (Barkia et al. 2019; MU et al. 2019; Wang et al. 2020). Already in 2017, the global market of microalgae-based products was estimated at US $ 3.26×10^{10} and is projected to reach approximately US $ 5.343×10^{10} by 2026 (Rahman 2020).

Today, the deterrent of mass industrial cultivation of microalgae biomass is the higher costs of its production in comparison with raw materials of other origin. Reducing the cost and increasing the economic attractiveness of using microalgae biomass can be achieved in different ways. On the one hand, this is an increase in the efficiency of bioreactors (Guedes and Malcata 2011; Béchet et al. 2014; Huang et al. 2017), the use of cheap sources of nutrients, which can be represented by domestic and industrial wastewater (Pittman et al. 2011; Kamyab et al. 2016; Sharma et al. 2020), the most complete extraction of all valuable bioproducts (Bai et al. 2011; Santoro et al. 2019), including cascade bioprocessing of microalgal biomass (Bleakley and Hayes 2017). The use of environmentally friendly methods for extracting compounds from microalgal biomass is also of great importance. Ultrasound-assisted extraction, enzymatic, microwave, liquid extraction under pressure, supercritical fluid extraction, etc. are being studied (Abbas et al. 2008; Tuhy et al. 2012; Li et al. 2014; Michalak and Chojnacka 2014; Saravana et al. 2015; Mondal et al. 2017; Michalak et al. 2017; Santoro et al. 2019).

Another direction is the increase in productivity of already known strains of microalgae or isolation of new highly productive strains of microalgae, which will be characterized by better rates of biomass accumulation, a higher content of valuable bioproducts and their optimal proportions in comparison with those already known (Ng et al. 2020; Poole et al. 2020).When working with strains, the use of genetic engineering methods to increase the content of proteins, lipids and other valuable compounds in microalgal cells, the use of various stress factors during the cultivation of microalgae are considered quite promising.

The ability of microalgae to store lipids is extremely valuable in meeting the growing demand for food and raw materials for biofuel production. According to the analysis of publications by Michalak with co-authors (2017), lipids are the most frequently extracted compounds from microalgae and have the greatest potential for commercialization. A wide variety of the composition of microalgal lipids, taking into account the species diversity of the microalgae themselves, is a natural resource that is unique in the composition of the lipid and fatty acid (FA) profile. Microalgae synthesizing lipids in large quantities are considered a promising natural raw material for the

production of third generation biofuels (Chisti 2007; Hu et al. 2008; Piligaev et al. 2013; Ruffing and Trahan 2014; Newby et al. 2016; Maltsev et al. 2017; Unkefer et al. 2017; Qadariyah et al. 2018; Shaikh et al. 2019; Tanushree et al. 2020), production of food and feed additives, baby food, feed for aquaculture, pharmaceuticals and cosmetics (Pulz and Gross 2004; Boeckaert et al. 2008; Christaki et al. 2012; Borowitzka 2013; Michalak et al. 2017; Barkia et al. 2019; Sathasivam et al. 2019; Chalima et al. 2020; Levasseur et al. 2020; Peltomaa and Taipale 2020). In many respects, the targeted using of lipids synthesized by microalgae is determined by the composition of the FAs that form them. Different groups of FAs have different properties. In the commercial using of FAs, particular importance is attached to the length of the hydrocarbon chain, the presence, number and position of double bonds, the ratio of various FAs in lipids, etc. The growing interest in this area of research is accompanied by the rapid growth of new information. According to Jónasdóttir (2019), studies on microalgal FA contain thousands of FA profiles. Analytical processing of the results obtained becomes the basis for a fairly wide range of review works that touch on various issues of studying FAs of microalgae (Galloway and Winder 2015; Strandberg et al. 2015; Cañavate 2018; Jónasdóttir 2019). These works are important stages of generalization and formation of new strategies for mastering the resource potential of this group of organisms.

In this work, we set the goal: (1) to collect data on the composition of FAs of microalgae and cyanobacteria, taking into account rare and unusual FAs, (2) to analyze the general variety of FAs, (3) to discuss the use of FAs for obtaining commercial products, 4) and as a biomarker.

2 Data collection on fatty acids in microalgae

To establish the general diversity of FAs in microalgae and cyanobacteria, a search and subsequent analysis of publications containing information on the FA composition was performed. When selecting publications, priority was given to works covering a wide range of FAs of a complete lipid profile, unusual FAs or FAs of certain lipid classes. The analysis involved data on microalgae from different habitats (marine, freshwater, soil, snow) grown in different conditions and in different environments. In total, 55 articles were selected (Online Resource) and 2234 FA profiles for microalgae were analyzed, containing data on FA content as a percentage of the total FA content of all lipids (or a certain class of lipids). In the studies analysed, the main methods for determining the fatty acid content of the lipid fraction from microalgal extracts were gas chromatograph with flame ionisation detection (Lang et al. 2011; Contreras-Angulo et al. 2019) or with mass spectrometry (Ghazala and Shameel 2005; Gong and Miao 2019; Barone et al. 2020). Fatty acid methyl esters were obtained by transesterification of lipids.

3 Fatty acids in microalgae

3.1 Fatty acids classification

It is known that living organisms synthesize many different FAs. A good example of their diversity is the detection of 430 FAs in one milk fat sample (Schröder and Vetter 2013), more than 300 FAs in triacylglycerol (TAG) of seeds (Fatiha 2019). Harnessing the power of new sensitive analytical methods, such as gas–liquid chromatography flame ionisation detection or mass spectrometry, promotes the growth of information about FAs (Sud et al. 2007; de Carvalho and Caramujo 2018; Gong and Miao 2019; Barone et al. 2020).

The FAs molecule consists of a hydrocarbon chain, at one end of which there is a carboxyl group (COOH), and at the other end there is a methyl group (CH_3). FAs have nomenclature chemical names and may have their own names. In practice, short designations of FAs are often used. The designations consist of indicating the number of carbon atoms in the chain, the number and position of double bonds. When specifying the position of the double bond, the carbon atoms could be counted both from the side of the carboxyl group and from the side of the methyl group. For example, the designation C18:1n-9cis means that the FA has 18 carbon atoms, one double bond which begins at the ninth carbon atom when counting from the methyl group. This carbon atom is designated by the Latin letter n. The atom number could also be denoted by the Greek letter ω (omega) which is often used to distinguish the corresponding families of FAs. When specifying the position of several double bonds,

the position of only the first of them could be indicated. However, this is not always enough. FAs may differ from each other on this basis. In this case, it becomes necessary to list all carbon atoms that have a double bond. The most common approach in this case is the numbering of carbon atoms from the side of the carboxyl group. When counting from the side of the carboxyl group, the Greek letter Δ "delta" is used to represent the carbon atom.

An important characteristic of double bonds is the arrangement of substituents on one or opposite sides of the plane of the double bond. *Cis*-isomers have two substituents on one side of the double bond plane, and *trans*-isomers have two substituents on opposite sides of the double bond plane. FAs with the cis configuration are less densely packed and have a lower melting point. FAs with three or more double bonds are less stable and susceptible to rapid oxidation. By the location of the double bond with respect to the methyl group, various families of FAs are distinguished: omega-3, omega-5, omega-6, omega-7, omega- 9, etc. At the same time, these families do not include FAs, in which, while maintaining the position of the double bond closest to the methyl group, the remaining ones were displaced. Considering the exceptional importance of omega-3 and omega-6 of FAs for living organisms, and the associated interest in their industrial production, we have devoted a separate subsection to this group of FAs. Isomerism of the position of double bonds changes the properties of FAs. And FAs, which were characterized by high value, especially from omega-3 and omega-6, cease to be essential. Sometimes the carbon aliphatic chain of an FA can have branches and include additional functional groups and cycles. Methyl, hydroxyl, carbonyl and other groups, cyclopropane and cyclopentane rings can act as such substituents. Such FAs are often referred to as unusual.

The synthesis of FAs is carried out using a number of enzymes that are responsible for the lengthening of the hydrocarbon chain. Elongation predominantly occurs by two carbon atoms. Therefore, the most common are FAs with an even number of carbon atoms. The transformation of FA with the formation of double bonds occurs with the participation of other enzymes—desaturases. This is described in more detail, for example, by Los (2014) and other (Li-Beissona et al. 2019).

Thus, the variety of FAs in living organisms is primarily determined by differences in the length of the hydrocarbon chain: short-chain fatty acids (SCFAs), medium-chain fatty acids (MCFAs), long-chain fatty acids (LCFAs), very-long-chain fatty acids (VLCFAs), as well as by the presence, location and number of double bonds: monounsaturated fatty acids (MUFAs), PUFAs.

The ability to synthesize LCFAs and VLCFAs varies from organism to organism. Organisms also differ in their ability to synthesize PUFAs. Considering this, we structured the information on the FAs of microalgae taking into account the length of the hydrocarbon chain, and then, within the identified groups, we discussed saturated fatty acids (SFAs) and unsaturated fatty acids (UFAs).

3.2 Fatty acids in various lipids

The metabolism of FAs in microalgae and cyanobacteria has been studied in detail and discussed in a number of works (Sato et al. 2003; Riekhof et al. 2005; Hu et al. 2008; Los 2014; Petroutsos et al. 2014; Li-Beissona et al. 2019). In cells, FAs can be free or bound. FAs with the help of ether bonds are combined with glycerol and form glycerolipids. If all three carbon atoms of glycerol bind to FAs, then neutral fats are formed in the form of TAG. It is the main energetic substrate of cells and its amount in some microalgae can reach up to 80% of the total amount of lipids (Hu et al. 2008; Guschina and Harwood 2013). If, in addition to the FA at the first ($sn-1$) and second ($sn-1$) carbon atoms, the third ($sn-3$) atom combines with a carbohydrate fragment or with a phosphate group, then glycolipids or phospholipids are formed, respectively. These are polar lipids. Their polarity is ensured by the presence of hydrophilic carbohydrate groups (residues of glucose, mannose, etc.) or a phosphate group in the molecules. The content of glycolipids and phospholipids in lipids of some microalgae can be up to 93% (Williams and Laurens 2010).

Betaine lipids are another class of glycerolipids. Their polar head is a quaternary amino alcohol linked by an ether bond with a diacylglycerol fragment. Betaine lipids are widespread in microalgae and sometimes in significant amounts (Cañavate et al. 2016). The connection of FA not with glycerol, but due to the N-acyl-bond with sphingosine, represents a

special class of lipids—sphingolipids. In general, polar lipids in phytoplankton microalgae can account for 40–95% of the total lipids. However, they mainly include phospholipids and sphingolipids (Jónasdóttir 2019). Polar lipids are components of cell membranes and have a direct effect on its specific properties. In addition, it is believed that polar lipids can be precursors or intermediate compounds of cellular signaling systems that provide a response to changes in environmental conditions (Sharma et al. 2012). Another group of lipids, which include FAs, are waxes—esters of higher FAs and monohydric or dihydric alcohols with a long carbon chain. They are similar in structure and properties to neutral lipids (Guschina and Harwood 2009). For example, *Euglena gracilis*, under anaerobic conditions, forms waxesters from SFAs and alcohols with carbon chain lengths from 10 to 18, including odd chain lengths. The main constituents are myristic acid (C14:0) and myristyl alcohol (Tomiyama et al. 2019). In *Chroomonas salina*, SFAs were also present in the wax esters, and among them C13:0 was especially high (Henderson and Sargent 1989).

3.3 Diversity of fatty acids of microalgae

3.3.1 Total quantity of fatty acids

Now, as a result of numerous studies, there is a fairly rapid accumulation of data on the diversity of FAs in microalgae and cyanobacteria. Both individual species and strains and their various groups are studied (Volkman et al. 1989; Dunstan et al. 1993; Viso and Marty 1993; Zhukova and Aizdaicher 1995; Gugger et al. 2002; Taipale et al. 2013). The most extensive study of microalgal FAs was carried out by Lang with co-authors (2011). In total, they studied 2076 strains of microalgae from the Collection of the University of Göttingen (SAG) and identified 76 different FAs and 10 other lipophilic substances (Lang et al. 2011).

In order to study the FA composition, the entire lipid profile is most often covered (Gugger et al. 2002; Lang et al. 2011; Taipale et al. 2013) whether or not it is divided into separate classes of lipids. Less commonly, FAs of certain lipid classes are studied: phospholipids (Dijkman and Kromkamp 2006; Lu et al. 2013), glycerolipids (phospholipids and glycolipids) (Arisz et al. 2000), TAG (Yang et al. 2017), glycolipids (Xue et al. 2002), betaine lipids (Cañavate et al. 2016).

Analysis of the data on the collected FA profiles, taking into account all lipid classes, made it possible to identify 135 FAs in the lipids of microalgae and cyanobacteria. Taking into account the hydrocarbon chain, its structure, the presence of substituents, as well as the presence and amount of double bonds, FAs of microalgae were divided into corresponding groups and systematized in Table 1. The summarized information on the content of FAs in microalgae strains is presented in Online Resource.

3.3.2 Odd-chain fatty acids, branched chain fatty acids, etc

Odd-chain, branched chain, hydroxylated, methylated FAs, etc. (Bergé and Barnathan 2005; Moellering et al. 2016; Fatiha 2019) represent a relatively rare group and are rarely found in microalgae and cyanobacteria. This feature has already been emphasized earlier (Hu et al. 2008; Liu and Liu 2017).

The branched carboxylic acids of lipids are usually not classified as FAs proper, but are considered their methylated derivatives. Methylated at the penultimate carbon atom (*iso*-fatty acids) and at the third from the end of the chain (*anteiso*-fatty acids) are included as minor components in microalgal lipids. Odd-chain and branched chain FAs, for example, C15:0, C17:0, C18:1n-11cis are used as markers of bacterial contamination of microalgae and cyanobacteria cultures (Viso and Marty 1993). Nevertheless, the presence of such FAs was also established for microalgae. The most frequently noted area C14:0, anteiso C16:0, 10-Methyl C16:0, 10-Methyl 17:0, C15, C17 (Online Resource). As a rule, their content does not exceed 3–5% of all FAs. But sometimes it is quite significant. For example, C15 FAs accounted for 52.2% of all FAs in *Chlorococcum humicolum*, 31.92% in *Chaetophora elegans*, and C17 FAs—32.44% in *Zygnema stellinum* (Ghazala and Shameel 2005). The presence of FAs C27 and C29 was also noted in some microalgae. At the same time, FA C29:3 was found in an amount of up to 20% in *Chara contraria* and *Chaetophora elegans* (Ghazala and Shameel 2005).

Nine different types of 3-OH FAs (3-hydroxy fatty acids) were found in 28 strains of cyanobacteria (Li et al. 1998). Their total content was small—2–5% of

Table 1 Overview of the fatty acids identified in microalgae

Fatty acids*	Short-chain	Medium-chain	Long-chain	Very-long-chain	Odd chain of different length
Iso- and anteiso branched FAs	–	Anteiso-12:0	Anteiso-16:0	–	Iso-15:0
		Anteiso-14:0	Iso-16:0		Iso/anteiso-17:1 (n.a.)
		Iso-14:0	Iso-18:0		
Methyl-branched FAs	–	–	10-Me 16:0	–	10-Me 17:0
					16/15-Me 17:0
3-Hydroxy FAs	–	3-OH 12:0	16:0 N alcohol	–	3-OH 15:0
Amide FAs		3-OH 14:0	3-OH 16:0		3-OH 15:1 (n.a.)
			3-OH 16:1 (n.a.)		
			3-OH 16:3 (n.a.)		
			3-OH 18:0		
			3-OH 18:1(n.a.)		
Saturated	6:0	10:0 (Capric)	16:0 (Palmitic)	20:0 (Arachidic)	11:0
	8:0	12:0 (Lauric)	18:0 (Stearic)	22:0 (Behenic)	13:0
		14:0 (Myristic)		24:0 (Lignoceric)	15:0
					17:0 (Heptadecanoic)
					19:0
					21:0
					23:0
					27:0
					29:0
Monounsaturated	–	10:1 (n.a.)	16:1n-11cis (cis-Δ5)	20:1n-9cis (cis-Δ11) (Gondoic)	13:1 (n.a.)
		12:1 (n.a.)	16:1n-13trans (trans-Δ3)	22:1n-9cis (cis-Δ13) (Erucic)	15:1n-5cis (cis-Δ10)
		14:1n-7cis (cis-Δ7)	16:1n-9cis (cis-Δ7) (Hypogenic)	24:1n-9cis (cis-Δ15) (Nervonic)	17:1n-8cis (cis-Δ9)
		14:1n-6cis (cis-Δ8)	16:1n-8cis (cis-Δ8)		17:1n-7cis (cis-Δ10)
		14:1n-5cis (cis-Δ9)	16:1n-7cis (cis-Δ9) (Palmitoleic)		19:1n-8cis (cis-Δ11)
			16:1n-5cis (cis-Δ11)		21:1 (n.a.)
			18:1n-12cis (cis-Δ6)		23:1 (n.a.)
			18:1n-9trans (trans-Δ9) (Elaidic)		
			18:1n-9cis (cis-Δ9) (Oleic)		
			18:1n-7cis (cis-Δ11) (Vaccenic)		
			18:1n-5cis (cis-Δ13)		
Polyunsaturated		12:2n-6cis (cis-Δ3,6)	16:2n-7cis (cis-Δ7,9)	18:2n-9cis (cis-Δ5,9)	5:2 (n.a.)
		12:2n-3cis (cis-Δ6,9)	16:2n-7cis (cis-Δ5,9)	18:2n-9cis (cis-Δ6,9)	11:2n-3cis (cis-Δ5,8)
		14:2n-6cis (cis-Δ5,8)	16:2n-6cis (cis-Δ7,10)	18:2cis (cis-Δ8,x)	13:2n-6cis (cis-Δ4,7)
		12:3n-3cis (cis-Δ3,6,9)	16:2n-4cis (cis-Δ9,12)	18:2n-6trans (trans-Δ9,12) (Linolelaidic)	15:2n-6cis (cis-Δ6,9)
			16:3n-6cis (cis-Δ4,7,10)	18:2n-6cis(cis-Δ9,12) (Lenoleic, LA)	17:2n-8cis (cis-Δ5,9)
			16:3n-4cis (cis-Δ6,9,12)	18:2n-4cis (cis-Δ9,14)	
			16:3n-3cis (cis-Δ7,10,13) (Hexadecatrienoic)		

Table 1 continued

Fatty acids*	Short-chain	Medium-chain	Long-chain	Very-long-chain	Odd chain of different length
		14:3n-3cis (cis-Δ5,8,11) 14:5 (n.a.)	16:3n-1cis (cis-Δ9,12,15 16:4n-3cis (cis-Δ4,7,10,13) 16:4n-1cis (cis-Δ6,9,12,15) 16:4n-4cis (cis-Δx,x,x,12) 18:4n-3cis (cis-Δ5,9,12,15) 18:4n-3cis (cis-Δ6,9,12,15) (Stearidonic, SDA) 18:4n-1cis (cis-Δ8,11,14,17) 18:5n-3cis (cis-Δ3,6,9,12,15)	18:2n-4cis (cis-Δ11,14) 18:2n-3cis (cis-Δ12,15) 20:2n-6cis (cis-Δ11,14) (Eicosadienoic) 22:2n-6cis (cis-Δ13,16) (Docosadienoic) 18:3n-6cis (cis-Δ5,9,12) (Calendic) 18:3n-6cis (cis-Δ6,9,12) (γ-Linolenic, GLA) 18:3n-4cis (cis-Δ8,11,14) 18:3n-3cis (cis-Δ9,12,15) (α-Linolenic, ALA) 18:3n-1cis (cis-Δ11,14,17) 20:3n-7s (cis-Δ7,10,13) 20:3n-6cis (cis-Δ8,11,14) (Dihomo-gamma-linolenic, DGLA) 20:3n-3cis (cis-Δ11,14,17) (Eicosatrienoic) 22:3(n.a.) 20:4n-6cis (cis-Δ5,8,11,14) (Arachidonic, ARA) 20:4n-5cis (cis-Δ6,9,12,15) 20:4n-3cis (cis-Δ8,11,14,17) (Eicosatetraenoic, ETA) 20:6(n.a.) 22:4n-6cis (cis-Δ7,10,13,16) (Adrenic) 20:5n-3cis (cis-Δ5,8,11,14,17) (Eicosapentaeonic, EPA) 22:5n-6cis (cis-Δ4,7,10,13,16) (Osbond) 22:5n-3cis (cis-Δ7,10,13,16,19) (Docosapentaenoic, DPA) 22:6n-3cis (cis-Δ4,7,10,13,16,19) (Docosahexaenoic, DHA) 22:6n-6cis (cis-Δx,x,x,x,13,16) 28:7n-6cis (cis-Δ4,7,10,13,16,19,22) 28:8n-3cis (cis-Δ4,7,10,13,16,19,22,25)	17:2n-8cis (cis-Δ6,9) 17:2n-5cis (cis-Δ9,12) 19:2n-7cis (cis-Δ9,12) 11:3 (n.a.) 13:3n-3cis (cis-Δ4,7,10) 15:3n-3cis (cis-Δ6,9,12) 17:3n-5cis (cis-Δ6,9,12) 17:3n-3cis (cis-Δ8,11,14) 17:3n-6cis (cis-Δx,x,11) 29:3 (n.a.) 15:4 (n.a.) 19:4 (n.a.)

FAs notation: the number of carbon atoms in the chain, the number of double bonds, relative stereochemical configuration of the double bond (*cis*—two substituents are on the same side of the double bond plane; *trans*—two substituents are located on opposite sides of the double bond plane), the position of double bonds from the methyl end of the molecule (n); prefixes iso, anteiso—iso-fatty and anteiso-fatty acids; Me—the position of the methyl group on carbon atoms from the carboxyl end of the molecule. In brackets—the numbers of carbon atoms in which the double bond is located when counting from the carboxyl end of the molecule (Δ), and the relative stereochemical configuration of the double bond are indicated: *cis*- or *trans*

*The designation of fatty acids is given in accordance with the IUPAC nomenclature

all FAs. The most common were 3-OH C14:0, 3-OH C16:0 and 3-OH C16:3.

3.3.3 Short-chain and medium-chain fatty acids in microalgae

SCFAs and MCFAs are rare in microalgae and cyanobacteria. Sometimes their detection can be associated with the presence of other microscopic organisms in the culture of microalgae. Therefore, when establishing the origin of such FAs, the possibility of the influence of bacterial contamination on the FA profile of microalgal culture is analyzed.

Information on the presence of FAs with a C6–C8 chain length in microalgae is sparse. For example, FA C6:0 in the amount of 1.48–3.93% of all FAs was observed in *Nannochloropsis* sp. (Melanie and Fithriani 2020). In *Arthrospira platensis* and *Galderia sulphuraria* (ACUF 064), FA C8:0 was found in an amount of 0.04% and 0.06%, respectively (Barone et al. 2020). At the same time, in *Galderia sulphuraria*, FA C8:0 was observed only during cultivation under autotrophic conditions and was absent under heterotrophic conditions.

FAs with an average chain length (C10–C14) are quite often noted by researchers in the composition of lipids of microalgae, but in insignificant amounts—less than 1% of all FAs or a little more (Online Resource). The ability to produce MCFAs in significant quantities is rare. As the analysis of the table data shows (Online Resource), MUFAs with a C12–C14 chain length are observed in 25–33% of strains producing SFAs with the same chain length.

The maximum amount (up to 79.2%) of FA C14:0 in the total FA composition was noted for individual *Euglena gracilis* strains. Moreover, in 21 out of 26 *Euglena gracilis* strains from the SAG collection, its content did not exceed 5% (additional file 1 in Lang et al. 2011). The white mutant strain 1224–5/1f, which has no stigma and lacks a paraxonemal body, is especially productive (Lebert and Hader 1997). Another similar mutant (strain 1224–5/9f) produced only 13.6% of this FA. Among other Euglenophyceae, a high content of FA C14:0 was found in *Astasia longa*—28.1% (Lang et al. 2011).

According to Lee and Loeblich (1971), *Prymnesium parvum*, which according to modern views is classified as Haptophyta (Frey 2015) and living in a fairly wide range of water salinity (0.5–30 psu), accumulates FA C14:0 to 68.9%. *Emiliania huxleyi* forms up to 35.1% of FA C14:0 of all FAs. It is a representative of phytoplankton of almost all oceanic ecosystems with various trophic parameters and it often forms water bloom (Volkman et al. 1981; Tyrrell and Merico 2004).

Among diatoms, *Biddulphia aurica* is often indicated as an object illustrating the significant production capacity of lipids and directly FA C14:0 (Hu et al. 2008; Graham et al. 2012; Levitan et al. 2014; Akubude et al. 2019) based on Orcuut and Patterson's work (1975). Attention is drawn to its ability to accumulate up to 32.0% of FA C14:0. This data may be related to another organism, *Biddulphia aurita* (*Lyngbye*) Brebiccon 1838, and there was a misprint in Orcuut and Patterson (1975).

A fairly high content of FA C14:0 was also noted in a number of other diatom strains: *Nitzschia palea*—26.1% (Lang et al. 2011), *Chaetoceros* sp. (CS256)—23.6% (Renaud et al. 2002).

Up to 18% of FA C14:0 of all FAs was noted for the marine phytoplankton species *Rhodomonas lens* from Cryptophyta (Beach et al. 1970), 16.2%—for *Pyrenomonas salina* (Lang et al. 2011). Even less, in the range of 10–12% of all FAs, was FA C14:0 in *Gymnodinium splendens* from Dinophyta (Lee and Loeblich 1971).

Only a few species of green microalgae are able to synthesize FAs C10–C14 in an amount exceeding 5% of all FAs. As examples, strains of such representatives as *Chlamydomonas asymmetrica*, which synthesizes FA C14:0 in an amount of 14.2%, *Chlorella* sp.—10.9% (Lang et al. 2011), *Rhizoclonium riparium*—8.05% (Osuna-Ruiz et al. 2019), *Scenedesmus obliquus*—5.0% (Orazova et al. 2017) should be noted. An increase in the C14 FA content from 4.76 to 9.79% was established for *Dunaliella salina* when it was transferred from a 0.5 mol NaCl solution to a 3.5 mol NaCl solution. In addition, the production of FA C14:2 increased especially significantly, almost threefold (Azachi et al. 2002).

Among cyanobacteria, FA C14:0 in the amount of 27.05% was recorded for *Limnothrix redekei*, 25.9%—for *Scytonema bohneri*, 22.7%—for *Lyngbya maior*, 21.2%—for *Pseudanabaena catenata* (strain 254.80) (Lang et al. 2011). An interesting pattern was found by Gugger et al. (2002) in toxic and non-toxic strains of cyanobacteria. In non-toxic strains *Anabaena*, *Nostoc* C14:0 was absent, and in hepatotoxic

strains it was found in the amount of 5–7% and 3.1–4.0%. This gave them the opportunity to offer FA C14:0 as a taxonomic biomarker of the hepatotoxic strains *Anabaena* and *Nostoc*.

There is evidence that under conditions of nitrogen deficiency, *Synechococcus* sp. accumulates a total of about 23.8% of caprylic acid (C10:0) and myristic acid (C14:0) (Karatay and Dönmez 2011). Similar data (up to 19.6–22.5% C14:0) were obtained for the strains of *Synechococcus* sp. from the SAG collection (Lang et al. 2011). At the same time, there are species of this genus that do not form these FAs or form them in insignificant amounts. According to Gong and Miao (2019) for the studied strains of *Synechococcus* sp. an increase in the production of FAs C12 + C14 from 2.44% in general to 2.44% and 2.84%, respectively, of the total amount of FAs was noted when using cerulenin at a concentration of 7.5 g L^{-1} (cerulenin has a specific inhibition of KAS I (FabB) and KAS II (FabF), which are responsible for carbon chain lengthening) (Gong and Miao 2019). Among filamentous cyanobacteria, for *Trichodesmium erythraeum*, the ability to synthesize 27–50% of C10 FA of the total amount of FAs was noted (Parker et al. 1967).

Unsaturated, including polyunsaturated short- and medium-FAs, were found in a wide variety in the snow alga *Chloromonas brevispina* (Řezanka et al. 2008). For example, C14:3 accounted for 4.63%, various C16:3 in total—15.56%, C16:4—9.56%. A wide variety of unusual SCFAs and MCFAs were noted in some freshwater green microalgae from Pakistan (Ghazala and Shameel 2005). Some of them reached a significant number. For example, C14:1 accounted for 40.58% of all FAs in *Zygnema stellinum*.

3.3.4 Long-chain fatty acids in microalgae

The FA profiles of microalgae are usually based on a group within the C16–C18 chain length. The most common FAs are Palmitic (C16:0), Stearic (C18:0), Palmitoleic (C16:1), Oleic (C18:1), Linoleic (C18:2), and Linolenic (C18:3) acids (Liu and Liu 2017).

Saturated C16 and C18 are the main FAs synthesized in the plastids of eukaryotic microalgae or on the thylakoids of cyanobacteria undergoing further various modifications (Los 2014). In this case, the ratio between FAs C16 and C18 can be different. Some microalgae have a preferential accumulation of FA C16 in comparison with C18. Thus, in *Synechococcus* sp. PCC 7942, their content is 63.49% and 18.44%, respectively (Gong and Miao 2019), 55.2% and 5.0% is in *Chaetoceros* sp. (Renaud et al. 2002), 47.3% and 10.1% is in *Nannochloropsis* sp. (Sukenik 1999). On the contrary, the prevalence of C18 in comparison with C16 was established for *Dunaliella tertiolecta* (Nielsen et al. 2019)—77.93% and 17.53%, respectively, for *Scrippsiella* sp.—62.6% and 10.1% (Mansour et al. 1999), for *Rhodomonas salina*—55, 81% and 11, 87% (Nielsen et al. 2019), for *Rhodomonas lens*—53.5% and 24.2% (Beach et al. 1970), for *Scenedesmus obliquus*—50.31% and 29.8% (Orazova et al. 2017). Sometimes their content is quite close. For example, in *Gymnodinium sanguineum* (Mansour et al. 1999), C16 FAs and C18 account for 27.4% and 24.3%, respectively.

In this group of FAs, the most common is palmitic acid (C16:0). One of the leaders in its content are the *Chlamydomonas* strains: *Ch. applanata* (SAG 11-36a)—88.57%, *Ch. media* (SAG 10.87)—88.12%. More than 50% C16:0 from all FAs accumulate: *Ch. callosa* (SAG 9.72)—54.0%, *Ch. monadina* (SAG 8.87)—57.36%, *Ch. maxima* (SAG 31–1)—57.49%, *Ch. proteus* (SAG 2.85)—59.36% (Lang et al. 2011). *Nannochloropsis* sp. contains Palmitic acid in significant amounts—61.06% (Melanie and Fithriani 2020). Some cyanobacteria are also capable of synthesizing C16:0 FA in large amounts: 48.4% in *Calothrix* (Gugger et al. 2002), 47.93% in *Synechococcus* sp. PCC 7942 (Gong and Miao 2019), *Scytonema lyngbyoides* (SAG 40.90)—54.63%, *S. mirabile* (SAG 83.79)—69.52%, *Spirulina labyrinthiformis* (SAG 59.90)—58.7% (Lang et al. 2011).

FA C18:0 in FAs composition of microalgae is on average 2–3% (Online Resource). However, there are strains that accumulate Stearic acid in significant amounts: *Parachlorella kessleri* (SAG 17.80)—71.5%, *Tetracystis texensis* (SAG 99.80)—65.79% (Lang et al. 2011). Strains capable of synthesizing more than 50% of Stearic acid from all FAs are widely represented among Chlorophyta, especially Chlorophyceae and Trebouxiophyceae (*Chlorosarcinopsis negevensis* (SAG 68.80), *Desmatractum bipyramidatum* (SAG 3.97), etc.), and are practically absent in the composition of other divisions of eukaryotic microalgae. The amount of Stearic acid in cyanobacteria rarely exceeds 1–2% (Gugger et al. 2002). Only in an insignificant part of the strains, the Stearic acid content is higher than 20%, and in *Westiellopsis prolifica*

(SAG 23.96) it reaches a maximum value of 44.95% (Lang et al. 2011).

Among MUFAs, C16:1 and C18:1 are widespread in microalgae and cyanobacteria and can be formed in significant quantities. For example, the cyanobacterium *Synechococcus* sp. PCC 7942 synthesizes C16:1 and C18:1—up to 38.2% and 15.84% of the total of FAs, respectively (Gong and Miao 2019). Slightly less C16:1 was found in *Planktothrix* and *Nostoc*—25.4% and 29.3%, respectively (Gugger et al. 2002). In the diatom *Chaetoceros* sp. C16:1 was 36.5% (Renaud et al. 2002). Quite often, C16:1 is noted in Eustigmatophyceae in an amount exceeding 20%.

For example, in *Nannochloropsis* sp. C16:1—up to 23.5–27.4% (Sukenik 1999; Melanie and Fithriani 2020), in *Monodus subterraneus* (Cohen 1999)—up to 26.9%. FA C18:1 in an amount of up to 21.91% was noted in *Isochrysis galbana* (Nielsen et al. 2019), up to 20.02% in *Chlorella vulgaris* SDEC-3M (Qi et al. 2019). A high amount of C18:1 was noted for *Tribonema aequale* (Lee and Loeblich 1971)—73.1%. Detailing the location of the double bond in the hydrocarbon chain, geometric (*cis*- and *trans*-) isomerism, allows one to obtain additional information about the peculiarities of the distribution of these FAs (Online Resource). The most frequently noted FAs are C16:1n-7cis, C18:1n-7cis, C18:1n-9cis.

Polyunsaturated C18 FAs, which belong to the omega-6 and omega-3 families, are discussed below.

3.3.5 Very-long-chain fatty acids in microalgae

FAs with a long hydrocarbon chain (C20–C22 and more) are not very typical of cyanobacteria and are formed in insignificant amounts. For example, for *Synechococcus* sp. PCC 7942 FAs C20–C22 in total did not exceed 0.46% of the total amount of FAs on the 20th day of cultivation (Gong and Miao 2019). In eukaryotic microalgae, FAs C20–C22 are more diverse and can accumulate in significant amounts.

FAs with a chain length exceeding C22 are rare in microalgae. The C24:0 content is generally limited to 1%, but sometimes it is more. So, it is noted in the amount of 5.82% in *Zygnema stellinum* (Ghazala and Shameel 2005), 4.0% in *Rhodomonas baltica* (Patil et al. 2007). And its maximum content of 21.31% was recorded in *Lagerheimia hindakii* (Lang et al. 2011). The presence of FAs with an even longer carbon chain (C28) was noted in some marine and freshwater microalgae. C28:8 in an amount of 1.7–2.2% was found in *Prorocentrum mexicanum*, *Scrippsiella* sp., *Gymnodinium* sp., *Fragilidium* sp. C28:7 was in an amount of 0.7–0.8% in *Prorocentrum micans*, *Symbiodinium microadriaticum* (Mansour et al. 1999).

3.3.6 Omega-6 and omega-3 fatty acids

Omega-6 and omega-3 FAs are of great interest among FAs. They have a wide range of applications in various spheres of human economic activity, which will be shown in detail below. Microalgae have different capacities to produce these FAs.

In the omega-6 FA family, the most important are linoleic (LA) and GLA acids, dihomo-gamma-linolenic acid (DGLA), ARA; in the omega-3 FA family, the most important are α-linolenic (ALA), stearidonic acid (SDA), EPA, docosapentaenoic acid (DPA), DHA acids. Of these, LA and ALA constitute a special category of the so-called essential FAs, which take a significant part in the metabolism of humans and animals, but cannot be synthesized by them (Cunnane 2003; Harwood 2019). Conditionally essential acids, the synthesis of which depends on the presence of LA and ALA, include ARA, DHA, EPA acids. As a rule, these acids can be synthesized in animal organisms, not being essential in the strict sense, but they are conventionally referred to as essential FAs, since they are able to eliminate the symptoms of deficiency of LA and ALA (while ARA is 10 times more active than LA in normalizing the resulting disorders) (Berezhnoi and Korneva 2016).

The content of LA in microalgae is highly variable. For example, its content in *Heterococcus endolithicus* (SAG 63.90) is 53.37% (Lang et al. 2011), in *Trebouxia simplex* is 45.9% (Lang et al. 2011), in *Bracteacoccus bullatus* (strain MZ–Ch32) is 23.8% (Maltsev et al. 2020) and *Bracteacoccus bullatus* (strain MZ–Ch11) is 13.9% (Mamaeva et al. 2018), in *Chlorella sorokiniana* is 36.0% (Patterson 1970). Among cyanobacteria, many accumulate up to 10% and a little more (for example, up to 20.8%—*Nostoc* (Gugger et al. 2002), up to 17.6%—*Arthrospira platensis* (Xue et al. 2002), up to 15.2%—*Cylindrospermum* (Gugger et al. 2002), up to 13.8%—*Planktothrix* (Gugger et al. 2002)). However, there are strains producing LA in significant quantities: 54.75% is in *Chamaesiphon polonicus* (SAG 32.87), 46.78% is

in *Pseudanabaena galeata* (SAG 13.83), 41.10% is in *Phormidium autumnale* (SAG 78.79) (Lang et al. 2011). There are species among diatoms that synthesize LA in significant amounts, for example, *Cystoseira sauvageauana* (15.35% LA) (Kord et al. 2019).

GLA acid is formed mainly in an amount of up to 1%, rarely more. These are separate representatives of the divisions of eukaryotic microalgae. For example, in *Chlorococcum* sp. (strain 2076) its content is 28.7%, in *Chlamydomonas zebra* (strain 25.86) is 18.3%, in *Cryptomonas* sp. (strain 20.88) is 17.7% (Lang et al. 2011), in *Isochrysis galbana* (Volkman et al. 1981) is 7.0%, in *Scrippsiella* sp. (Mansour et al. 1999) is 5.2%. It is found in significant quantities in some cyanobacteria: in *Microcystis aeruginosa*—22.0–33.3% (Piorreck et al. 1984; Lang et al. 2011), in *Arthrospira maxima* (strain 84.79)—24.8% (Lang et al. 2011), in *Arthrospira platensis*—up to 20.3% (Xue et al. 2002).

A number of green microalgae shows a high content of ALA. Some strains of *Chlamydomonas* contain it up to 62.3% (Lang et al. 2011), *Dunaliella tertiolecta*—60.2% (Nielsen et al. 2019), *Chaetopeltis orbicularis*—up to 57.5% (Lang et al. 2011), *Carteria*—up to 54.6% (Lang et al. 2011), *Scenedesmus obliquus*—41.17% (de Oliveira et al. 2020). Many cyanobacteria accumulate ALA from 20% and more (48.6%—in *Planktothrix*, 41.4%—in *Nostoc*, 38.8%—in *Aphanizomenon*, 38.1%—in *Anabaena* (Gugger et al. 2002), *Anabaena*—up to 54.6–64.0%, *Nostoc*—up to 54.4%, *Cylindrospermum*—up to 52.3%, *Calothrix*—up to 40.0%, etc. (Lang et al. 2011)). From Chrysophyceae, a fairly significant (39.5%) amount of ALA was noted in *Poterioochromonas malhamensis* (strain 933-1d) (Lang et al. 2011), from Eustigmatophyceae—in *Ellipsoidion parvum* (strain 40.86) (42.0%) (Lang et al. 2011), in *Nannochloropsis* sp. (35.7%) (Melanie and Fithriani 2020), from Xanthophyceae—in *Tribonema aequale* (strain 880-1) (25.3%) (Lang et al. 2011). Cryptophytes synthesize ALA often in an amount of more than 10%. Among them, for example, *Chilomonas* sp. (strain 977-2b) contains 28.9% ALA (Lang et al. 2011), *Rhodomonas salina*—21.14% (Nielsen et al. 2019), *Rh. lens*—16.0% (Beach et al. 1970).

Cryptophytic microalgae form SDA even more. For example, in the FA profile of *Hemiselmis brunescens*, the SDA is 30.0% (Chuecas and Riley 1969). Some green microalgae form SDA in amounts of 10% or more. For example, in *Tetraselmis suecica* (Nielsen et al. 2019) SDA—is 11.75%, in some *Ankistrodesmus strains* is up to 21.4%, in *Chlamydocapsa* is up to 27.2%, in *Chlamydomonas* is up to 52.3% (Lang et al. 2011). Quite often, this FA is found in noticeable amounts in cyanobacteria. For example, in *Stigonema* sp. (strain 49.90) its content is 30.3%, in *Anabaenopsis siamensis* is 29.5% (Lang et al. 2011), in *Microcystis* is up to 21.6% (Gugger et al. 2002), in *Arthrospira platensis* is 20.3% (Xue et al. 2002). Among cryptophytes, some *Cryptomonas* strains form SDA up to 27.0% (Lang et al. 2011). From dinophytes *Amphidinium carterae* (strain Amp) synthesizes SDA up to 33.0% (Lang et al. 2011). *Scrippsiella* sp. synthesizes SDA up to 10.6%, as well as rather rare SDA—up to 43.1% (Mansour et al. 1999).

FAs belonging to the omega-3 and omega-6 families and having a hydrocarbon chain length of C20 and more were noted in a small number of cyanobacterial strains and in an insignificant amount: EPA—4.4% in *Calothrix* sp. (strain 25.94), 11.3% in *Phormidium* sp. (strain 1463-1e) (Lang et al. 2011); DPA—1.0% in *Aphanocapsa* sp. (Kenyon et al. 1972), DGLA—0.6% in *Arthrospira platensis* (Xue et al. 2002), ARA—3.2% in *Calothrix desertica* (Lang et al. 2011).

Of the green EPA, up to 19.47%, is contained in the biomass of *Tetraselmis suecica* (Nielsen et al. 2019), up to 24.0%—in *Chlamydomonas allensworthii* (Lang et al. 2011). A similar EPA content was noted in some diatoms: 23.8% is in *Phaeodactylum tricornutum* (strain 1090-1b) (Lang et al. 2011), 26.0% is in *Biddulphia aurica* (Orcuut and Patterson 1975). Cryptophytes synthesize somewhat less EPA: 11.0%—*Hemiselmis brunescens* (Chuecas and Riley 1969), 13.0%—*Rhodomonas lens* (Beach et al. 1970), 15.22%—*Rhodomonas salina* (Nielsen et al. 2019). The leaders in the accumulation of EPA are a number of strains from eustigmatophytes (44.2%—*Nannochloropsis salina* (Safafar et al. 2016), 37.1%—*Monodus subterraneus* (Hu et al. 1997); 34.9%—*Nannochloropsis* sp. (Sukenik 1999)), dinophytes (41.1% is in *Pyrocystis lunula* (strain 2014) (Lang et al. 2011)).

The content of ARA in microalgae varies widely. A large amount of this FA was noted in some euglenids (34.3% is in *Khawkinea quartana* (strain 1204-9) (Lang et al. 2011), 41.3% is in *Rhabdomonas incurva*

(Lang et al. 2011)), Trebouxiophyceae (58.9% is in *Parietochloris incisa* (Khozin-Goldberg et al. 2002)).

FAs C22 are rare in microalgae. In this case, DHA is somewhat more frequent than DPA. The maximum DHA values are indicated for dinophytes: in *Crypthecodinium cohnii*, *Crypthecodinium* sp. and *Schizochytrium* sp.—up to 50–60% (Spolaore et al. 2006; Doughman et al. 2007; Ratledge and Cohen 2010); in *Ceratium horridum* (strain Cer)—29.3% (Lang et al. 2011); in *Gymnodinium sanguineum*—24.2% (Mansour et al. 1999). A significant DHA content is known for some haptophytes (28.37% in *Isochrysis galbana* (Nielsen et al. 2019)), green microalgae (26.13% in *Chlorella* sp.) (Sivaramakrishnan and Incharoensakdi 2020), Haptophyta (13.2%—*Pavlova* sp. (NIVA-4/92) (Patil et al. 2007)). The leaders in the amount of DPA are *Pyrocystis lunula* (SAG 2014) from dinophytes (41.08%), *Trachelomonas volvocina* (SAG 1283-4) from Euglenophyceae (23.66%) (Lang et al. 2011).

4 Fatty acids of microalgae as an industrial resource

4.1 Microalgae fatty acids market

A wide range of compounds synthesized by microalgae are very successfully used in various fields of human economic activity, which is discussed in a number of review works (González-Fernández et al. 2012; Barkia et al. 2019; Figueroa-Torres et al. 2019; Sathasivam et al. 2019; Lever et al. 2020). As a rule, such works are devoted either to a specific direction of use of microalgal compounds (bioenergy, food and feed industry, aquaculture, pharmacology, cosmetology) (Sathasivam et al. 2019; Levasseur et al. 2020) or their goal is to present the maximum variety of compounds and their application in various fields of activity (Pulz and Gross 2004; Chu 2012; Khan et al. 2018; Levasseur et al. 2020). The possibilities of the FAs market are limited by the rather high cost of obtaining and processing microalgal biomass (Hu et al. 2008; Bai et al. 2011; Li-Beissona et al. 2019). A comparative assessment of economic attractiveness and approaches to reducing costs in obtaining commercial FAs are discussed in detail in a number of works (Li et al. 2014; Michalak and Chojnacka 2014; Bleakley and Hayes 2017; Michalak et al. 2017; Mondal et al. 2017; Santoro et al. 2019; Sharma et al. 2020).

FAs are one of the main components of the biomass of microalgae and are present in cells mainly in the form of glycerolipids. In turn, glycerolipids are mainly composed of phospholipids, glycolipids and TAG. Their content in cells can be significant and be of interest for various industries. As part of this work, we set the task to analyze the commercial interest in various groups of FAs of microalgae.

4.2 Industrial interest in short-chain and medium-chain fatty acids

SCFAs are not very common for microalgae, and MCFAs are quite often observed in representatives of different divisions of eukaryotic microalgae, as well as in cyanobacteria. The content of some MCFAs can be significant (for example, C10 up to 27–50% of all FAs, C14—up to 79.2%). SCFAs and MCFAs play an important role both as nutrients and as regulators of metabolism. MCFAs constitute an important nutritional resource for patients with long-chain FA hydrolysis disorders. TAG containing MCFAs are rapidly absorbed when ingested with food or as a dietary supplement. At the same time, they have a low energy value, which is very important in some diets. A diet high in SCFAs and MCFAs increases energy expenditure and decreases body fat (Schönfeld and Wojtczak 2016). These features are important not only for the implementation of dietary nutrition, but also when assessing, for example, food chains in ecosystems (Iverson 2009; Taipale et al. 2009). Another important property of these FAs is their antibacterial action. When added to feed, they can represent an alternative to antimicrobial drugs (Rybin and Blinov 2001; Orazova et al. 2017). MCFAs are also valuable for the cosmetic industry, which is associated with their resistance to oxidation, easy absorption by the skin, and other valuable properties (Aripovsky and Titov 2013).

4.3 Industrial interest in long-chain and very-long-chain fatty acids, including omega-6 and omega-3 families

LCFAs represent a wide range of uses and are of greatest commercial interest. Saturated and unsaturated LCFAs of microalgae are valuable for producing

oils with different properties that are used in various industrial fields.

Biodiesel properties such as cetane number, kinematic viscosity, oxidative stability, etc., which are taken into account by international standards and specifications, depend on the profile of FAs used in the production process of microalgae (Biodiesel specifications) (Knothe 2009; Ma et al. 2016; Mondal et al. 2017; Xu et al. 2020). The composition of oils from microalgae can include PUFAs and FA methyl esters with 4 or more double bonds. Oxidizing during storage, they impair the suitability of such oils for biodiesel production (Chisti 2007; Ma et al. 2016; Mondal et al. 2017; Xu et al. 2020). It was found that a high content of esters of SFAs leads to an increase in the cetane number, and a sufficient amount of esters of MUFAs, for example, oleic acid ester, significantly improves the flow properties of biodiesel fuel at low temperatures (Knothe 2012). Thus, microalgae with a high content of SFAs and MUFAs in lipids are the most promising for the production of biodiesel fuel (Maltsev et al. 2021).

Microalgae containing large amounts of SFAs can become an alternative to the production of hydrogenated vegetable oils (Los 2014). Usually, to increase the content of SFAs, vegetable oils undergo catalytic hydrogenation. However, this process often leads to the appearance, in addition to *cis*-double bonds, also bonds in the transpositionin FAs. *Trans*-double bonds are not typical of most natural sources of unsaturated FAs, and regulation of the FA composition in food is currently considered an important task (Hodson et al. 2009).

The most developed direction is the search and use of microalgae strains synthesizing PUFAs in significant quantities. Special attention is paid to the ability of microalgae to accumulate PUFAs omega-6 and omega-3 (Harwood 2019; Sathasivam et al. 2019). As indicated above, ALA and LA acids are essential and are directly related to the formation of very long-chain PUFAs (VLCPUFA) C20–C22, which are therefore referred to as 'conditionally essential' (Cunnane 2003). These are primarily such VLCPUFAs: ARA, EPA and DHA acids. ARA, together with other FAs containing 20–22 carbon atoms (EPA, DHA, GLA), serves as a precursor for a large number of physiologically active substances—eicosanoids.

Intensification of food production of plant and animal origin, artificial breeding of fish changed the balance of the content of valuable PUFAs in the direction of oversaturation by omega-6 FAs and deficiency of omega-3 (Nazarov et al. 2009; Moellering et al. 2016; Harwood 2019; Poole et al. 2020). In the Western diet, the omega-6:3 ratio is (20–30):1, which adversely affects health indicators (Simopoulos 2016). It should be optimal from the point of view of ensuring a balanced diet from 1:1 to 4:1 (Berezhnoi and Korneva 2016; Peltomaa et al. 2019).

The lack of omega-3 can contribute to the development of various pathological processes. The enrichment of diets with these FAs has a positive effect on human health and is used in the prevention of a number of diseases. Much attention is paid to the analysis of these problems (Swanson et al. 2012; Haimeur et al. 2016; Calder 2018; Bhatt et al. 2019; Harwood 2019; Sathasivam et al. 2019).

Correction of the omega-6:3 balance in the human diet can be achieved both as a result of the use of food additives and by improving the quality and value of livestock, poultry and aquaculture products.

The main dietary source of omega-3 PUFAs for humans is marine fish. Numerous evidences suggest that fish oil is actually enriched with omega-3 PUFAs through the marine food chain from zooplankton consuming microalgae containing omega-3 PUFAs or from microalgae directly. Thus, microalgae are one of the most important sources of valuable FAs (omega-3, omega-6) in aquaculture. In this regard, it is important both to maintain an optimal phytoplankton composition in aquaculture and to use microalgae-based supplements (Burns et al. 2011; Knutsen et al. 2019; Bruni et al. 2020).

Fortification of feed with PUFAs is a new strategy for the feed industry (Schmitt et al. 2018; Ma et al. 2019). The positive effect of the inclusion of PUFAs of microalgae in the diet was observed when growing various farm animals and birds (Lamminen et al. 2019; Moran et al. 2019b; Pajor et al. 2019; Petrolli et al. 2019). Fortification of the diet of chickens with microalgae-based supplements was accompanied by an increase in the content of omega-3 (DHA) in eggs, which increased their nutritional value (Moran et al. 2019a).

An important aspect of microalgae cultivation is the ability to simultaneously reduce environmental pollution. A positive experience was obtained with the cultivation of *Crypthecodinium cohnii* in environments with relatively high concentrations of acetic,

butyric or propionic acid as the main carbon source. As a result, the water was purified from the content of organic acids, and DHA accumulated in the biomass of the alga up to 29.8% (w w^{-1}) of the total amount of FAs (Chalima et al. 2019). It has been demonstrated by means of the example of other microalgae that the growth of microalgae depends on the pH of the medium and the presence of non-dissociated molecules of volatile FAs (Lacroux et al. 2020). The *Desmodesmus* sp. KNUA024 strain demonstrated a high level of PUFA accumulation (up to 54.83% of all FAs) with simultaneous purification of wastewater from ammonia and total nitrogen by 91–99% and total phosphorus by 95%. (Do et al. 2019).

5 Fatty acids are biomarkers

5.1 Main and specific fatty acids of microalgae

The search for biotechnologically valuable strains of microalgae is a rather urgent task. Important for its solution is the possibility of predicting the ability of microalgal species to accumulate lipids highly on the basis of clarification of their phylogeny (Fields and Kociolek 2015; Galloway and Winder 2015; Neofotis et al. 2016). As a number of studies show, for taxa of various ranks, a certain dependence can be traced at the level of predominance of certain groups of FAs in the profile (Bergé and Barnathan 2005; Petkov and Garcia 2007; Kelly and Scheibling 2012; Shukla et al. 2012; etc.). This gives the possibility of both a targeted search for new highly productive representatives of certain FAs among certain groups of microalgae, and the use of FA profile data for identifying taxa, determining the characteristics of food chains in ecosystems (Iverson 2009; Kühn et al. 2019; Taipale et al. 2009).

As a rule, when analyzing the FA composition, the main FAs are noted, which accumulate in the greatest amount, and specific ones, which can be used as a taxonomic biomarker (Tables 2, 3).

On the basis of numerous studies, conclusions were drawn about the FA profiles typical of various taxa of microalgae. This has been most successful for the division and class level (Lang et al. 2011; Taipale et al. 2013; Galloway and Winder 2015; Cañavate 2018). However, unambiguity in the composition of the FA profile at the level of species of the same genus, different strains of the same species has not yet been achieved (Lang et al. 2011; Procházková et al. 2019).

It is believed that prokaryotic organisms—cyanobacteria—synthesize significant amounts of FAs C16:0, C16:1, as well as PUFAs with 18 carbon atoms: C18:2n-6cis, C18:3n-3cis, C18:3n-6cis, C18:4n-3 (Gugger et al. 2002; Lang et al. 2011). According to the FA composition, cyanobacteria are divided into 4 groups (Kenyon et al. 1972; Li et al. 1998). The first group of cyanobacteria contains SFAs and MUFAs: C16:1n-7cis, C18:1n-9cis. A feature of the second group is the presence of ALA, the third—GLA, the fourth—SDA (Kenyon et al. 1972; Los 2014). There is a report on the isolation of the fifth group of cyanobacteria. It is described by Cohen et al. (1995) and is located according to the Kenyon-Murata classification system between groups 1 and 2. Strains in this group contain LA as the only C18 PUFA.

The specific group 3-OH FA (3-hydroxy fatty acid) found in cyanobacteria has also been considered as taxonomic biomarkers. The results of the studies showed that, in contrast to bacteria, in cyanobacteria, 3-OH FAs did not show any special taxonomic significance (Li et al. 1998).

In Chlorophyta, FAs are dominated by FAs with 16 and 18 carbon atoms. At the same time, different classes have their own characteristics in the FA profile, associated mainly with the composition of unsaturated and especially PUFAs. Jónasdóttir (2019), comparing the content of FAs C16, C18, and C20–22 (including C18:5n-3cis) in different classes of Chlorophyta, notes the predominance of FAs C16:2 and C16:3 in Trebouxiophyceae, Nephroselmidophyceae and C16:4 in Chlorophyceae, Chlorodendrophyceae, Pyramimonadophyceae, Mamiellophyceae; prevalence of C18:1n-7, SDA and EPA in Pyramimonadophyceae, Mamiellophyceae and C18:1n-9, C18:2n-6, C18:5n-3cis and C22:6n-3cis in Trebouxiophyceae, Nephroselmidophyceae, Chlorophyceae, Chlorodendrophyceae. A quite specific composition of FAs in relation to other classes of Chlorophyta is observed in Prasinophyceae (Dijkman and Kromkamp 2006).

In heteroconts (or stramenopiles), the value of C20 in the FA profile increases, and in Dinophyta, Haptophyta, Cryptophyta also the value of C22 increases (Dijkman and Kromkamp 2006; Taipale et al. 2013). Diatoms are characterized by a high content of C16 FAs, especially C16:1n-7cis. At the level of such classes as Cosciondiscophyceae and

Table 2 Main fatty acids for each algal class

Class (Order)	Main fatty acids		
	Cobelas and Lechado (1989)	Dijkman and Kromkamp (2006)	Taipale et al. (2013)
Cyanobacteria	16:0		–
	16:1		
	18:1		
Chlorophyceae	16:0	18:3n-3cis	18:3n-3cis
	18:1	16:4n-3cis	16:0
		16:0	18:1n-9cis18:2n-6cis
		18:1n-9cis	
Trebouxiophyceae	–	18:3n-3cis	18:3n-3cis
		16:3n-3cis	16:0
		16:0	18:1n-9cis
		18:2n-6cis	18:2n-6cis
Prasinophyceae	16:0	18:4n-3cis	–
	18:1	16:0	
		16:4n-3cis	
		18:3n-3cis	
Bacillariophyceae	16:0	20:5n-3cis	16:1n-7cis
	16:1	16:1n-7cis	20:5n-3cis
		16:0	16:0
		14:0	14:0
Eustigmatophyceae	16:0	–	–
	18:1		
Xanthophyceae	14:0	–	–
	16:0		
	16:1		
Chrysophyceae	16:0	–	–
	16:1		
	18:1		
Raphidophyceae	–	–	16:0
			20:5n-3cis
			18:4n-3cis
			18:3n-3cis
Synurophyceae	–	–	18:4n-3cis
			14:0
			18:3n-3cis
			16:0
Synurophyceae (Ocromonadales)	–	–	16:1n-7cis
			16:0
			18:2n-6cis
			18:1n-7cis
Euglenophyceae	16:0	–	16:0
	18:1		18:3n-3cis
			20:5n-3cis
			22:6n-3cis

Table 2 continued

Class (Order)	Main fatty acids		
	Cobelas and Lechado (1989)	Dijkman and Kromkamp (2006)	Taipale et al. (2013)
Dinophyceae	16:0	22:6n-3cis	–
		18:4n-3cis	
		16:0	
Prymnesiophyceae	16:0	22:6n-3cis (DHA)	–
	16:1	14:0	
	18:1	16:0	
		18:1n-9cis	
Cryptophyceae	16:0	18:4n-3cis	18:3n-3cis
	20:1	20:5n-3cis	16:0
		18:3n-3cis	18:4n-3cis
		16:0	
		22:6n-3cis	

Bacillariophyceae, the differences are in the content of PUFAs C16:3cis, where C16:3n-3cis and C16:3n-6cis are present in Cosciondiscophyceae, and not in Bacillariophyceae. Differences in the FA profile within Dinophyta mainly relate to the proportions in the content of DHA, OPA and EPA, and in Haptophyta differences in the FA profile mainly relate to the proportions in the content of FAs C16, C18, and > 20 PUFA (Jónasdóttir 2019). Euglenophyceae are distinguished by a high specificity of the composition of the main FAs (Taipale et al. 2013).

In the analysis of the FA profile, as mentioned above, FAs used as markers for certain groups of microalgae are often distinguished. It is believed that relatively rare FAs specific for a narrow group of organisms are good biomarkers (Kelly and Scheibling 2012; Galloway and Winder 2015). A certain ratio between FAs or the absence of a certain FA is also considered a marker. For example, when labeling marker FAs in Bacillariophyceae, it is noted that the amount of FA C18:1n-7cis is up to 10 times higher than the content of C18:1n-9cis, C16:3n-3cis and C16:3n-6cis are absent (de Carvalho and de Caramujo 2018; Jónasdóttir 2019). Summary information on FAs used as markers for various taxa of microalgae is presented in Table 3.

5.2 Fatty acids of freshwater and marine microalgae

The composition of both main FAs and FAs used as markers indicated in the works of various researchers is not always unambiguous (Tables 2, 3). A number of works are devoted to the analysis of the relationship between the composition of FAs and the ecological group of microalgae (marine, freshwater) (Galloway and Winder 2015; Cañavate 2018; Peltomaa et al. 2019). It was found that only 1–3% of the differences are associated with the marine or freshwater origin of the strains (Galloway and Winder 2015; Cañavate 2018). It was concluded that the main features of the FA profile are determined by phylogenesis (Galloway and Winder 2015; Cañavate 2018). In this case, the FA profile is determined at the early stage of phylogenesis, and the colonization of freshwater and saline ecotopes and adaptation to them does not cause significant changes in the FA composition. Based on the FA profile of marine microalgae, 14 classes from seven phyla and the phylum Bacillariophyceae were distinguished (Cañavate 2018). However, in some cases, a more pronounced difference in the FA composition is observed between marine and freshwater species. For example, in comparison with marine ones, freshwater Cyanobacteria had more C18:3n-6cis, and Bacillariophyceae had more 16:1n-7cis respectively. Within the classes Chlorophyceae and Trebouxiophyceae, the main differences in the FA

Table 3 Fatty acids—potential biomarkers for each algal class (phylum)

Class/phylum (order)	Fatty acids					
	Zhukova (2009)	Taipale et al. (2013)	de Carvalho and Caramujo (2014)	de Carvalho and Caramujo (2018)	Rozentsvet et al. (2019)	Jónasdóttir (2019)
Cyanobacteria	–	–	16:1n-7cis 18:1n-9cis 18:1n-7cis 18:2n-6cis (fr) 18:3n-6cis (fr) 18:3n-3cis	16:1n-7cis 17:1 18:1n-9cis 18:1n-7cis 18:2n-6cis (fr) 18:3n-6cis (fr) 18:3n-3cis 10-Me 18:0 10-Me 16:0	16:0 16:1n-7cis 16:4n-3cis 18:1n-9cis 18:0	–
Chlorophyta	–	–	16:2n-6cis 16:3n-3cis 16:4n-3cis 18:1n-9cis 18:2n-6cis 18:3n-3cis	–	16:1n-13trans 16:4n-3cis 18:1n-9cis 18:2n-6cis 18:3n-3cis	–
Chlorophyceae	16:2n-6cis 16:3n-3cis 16:4n-3cis 18:2n-6cis 18:3n-3cis 20:5n-3cis 22:6n-3cis—absent	16:2n-6cis 16:3n-3cis 16:4n-3cis	–	–	–	16:4 18:1n-9cis 18:2n-6cis 18:5n-3 22:6n-3cis
Trebouxiophyceae	–	16:2n-6cis 16:3n-3cis 16:4n-3cis	–	–	–	16:2 16:3 18:1n-9cis 18:2n-6cis 18:5n-3cis 22:6n-3cis
Nephroselmidophyceae	–	–	–	–	–	16:2 16:3 18:1n-9cis 18:2n-6cis 18:5n-3cis 22:6n-3cis
Chlorodendrophyceae	–	–	–	–	–	16:4 18:1n-9cis 18:2n-6cis 18:5n-3cis 22:6n-3cis

Table 3 continued

Class/phylum (order)	Fatty acids					
	Zhukova (2009)	Taipale et al. (2013)	de Carvalho and Caramujo (2014)	de Carvalho and Caramujo (2018)	Rozentsvet et al. (2019)	Jónasdóttir (2019)
Pyramimonadophyceae	–	–	–	–	–	16:4 18:1n-7cis 18:4n-3cis 20:5n-3cis
Mamiellophyceae	–	–	–	–	–	16:4 18:1n-7cis 18:4n-3cis 20:5n-3cis
Prasinophyceae	16:4n-3cis 18:3n-3cis 18:4n-3cis 20:5n-3cis	–	16:2n-4cis 16:4n-3cis 18:3n-3cis 22:5n-3cis	16:2n-4cis 16:4n-3cis 18:3n-3cis 22:5n-3cis	–	–
Bacillariophyceae	14:0 16:0 16:1n-7cis 16:2n-4cis 16:3n-4cis 16:4n-1cis 20:5n-3cis 22:6n-3cis	16:2n-7cis ** 16:2n-4cis 16:3n-4cis 16:4n-1** 18:4n-3**cis	16:1n-7cis 18:1n-7cis 16:2n-7cis 16:2n-4cis 16:3n-4cis 16:4n-1cis 20:4n-6cis 20:5n-3cis 22:5n-3cis 22:6n-3cis	16:1n-7cis 18:1n-7cis (up to tenfold more than 18:1n-9cis) 16:2n-7cis 16:2n-4cis 16:3n-4cis 16:4n-1cis 20:4n-6cis 20:5n-3cis 22:5n-3cis 22:6n-3cis	14:0 16:0 16:1n-3trans 16:1n-7cis 17:0 18:0 18:1n-9cis 18:2n-6cis 20:5n-3cis 22:6n-3cis	16:1n-7cis 16:3n-3cis—absent 16:3n-6cis—absent
Cosciondiscophyceae	–	–	–	–	–	16:1n-7cis 16:3n-3cis 16:3n-6cis
Synurophyceae (Synurales)	–	18:4n-3cis 22:5n-6cis	–	–	–	–
Synurophyceae (Ochromonadales)	–	16:3n-1cis 18:4n-3cis 22:5n-6cis	–	–	–	–
Raphidophyceae	–	16:2n-4cis 16:3n-4cis ** 16:3n-1cis 20:3n-3cis	–	–	–	–
Eustigmatophyceae	16:0 16:1n-7cis 20:5n-3cis	–	–	–	–	–

Table 3 continued

Class/phylum (order)	Fatty acids					
	Zhukova (2009)	Taipale et al. (2013)	de Carvalho and Caramujo (2014)	de Carvalho and Caramujo (2018)	Rozentsvet et al. (2019)	Jónasdóttir (2019)
Euglenophyceae	–	15:3n-3cis **	–	–	–	–
		15:3n-1cis				
		15:4n-3cis				
		17:2n-7/5cis **				
		17:3n-2cis **				
		20:2n-6cis				
		20:4n-3cis				
		20:3n-6cis				
		22:4n-6cis				
Dinophyceae	18:5n-3cis *	–	18:1n-9cis	18:1n-9cis	–	–
	22:6n-3cis		18:2n-6cis	18:2n-6cis		
			18:3n-3cis	18:3n-3cis		
			18:5n-3cis	18:5n-3cis		
			20:5n-3cis	20:5n-3cis		
			22:6n-3cis	22:6n-3cis		
Prymnesiophyceae	14:0	–	22:6n-3cis	22:6n-3cis	–	–
Pavlovophyceae	16:0					
	16:1n-7cis					
	18:4n-3cis					
	20:5n-3cis					
	22:6n-3cis					
Cryptophyceae	16:0	18:4n-3cis	18:1n-7cis	18:1n-7cis	–	–
	16PUFA	22:5n-6cis	18:3n-3cis	18:3n-3cis		
	18:0		20:5n-3cis	20:5n-3cis		
	18PUFA		22:5n-3cis	22:5n-3cis		
	20:5n-3cis		22:6n-3cis	22:6n-3cis		

Fr—freshwater

*the most indicative as a marker

**found only in phytoplankton

profile were associated with a higher content of C18:1n-9cis and 18:3n-3cis in freshwater representatives compared to marine ones (Cañavate 2018).

Recent studies of the profile (which denotes the amount of FAs in % of the total amount of FAs) and the content (as μg fatty acids per mg dry weight) of FAs of 10 diatoms and seven dinoflagellates originating from marine, brackish water and freshwater habitats showed that the phytoplankton group (46%) explained most of the differences in the fatty acid profile, and the habitat (31%) together with the phytoplankton group (24%) explained the differences in fatty acid content (Peltomaa et al. 2019). It was concluded that the FA profile can be genetically determined and the FA content varies depending on the environment.

5.3 Variability in fatty acids composition of various lipid classes

Fatty acid profiles are unique to specific lipid classes. SFAs and MUFAs are predominantly contained in TAG, PUFAs are in polar lipids (Harwood 2019; Xin et al. 2019). This pattern is inherent in many microalgae, including well-known producers of PUFAs such as EPA, DHA (*Nannochloropsis* sp., *Chroomonas sauna*, *Phaeodactylum tricornutum*, etc.). Based on the analysis of the FA composition and the amount of TAG, it was found that the content of FAs characteristic of taxa can be used to determine the TAG content in the composition of total lipids. The coefficients of correlation (r^2) of C16:0, C16:1 and EPA with TAG content were 0.96, 0.94, and 0.97, respectively, in the case of *Phaeodactylum tricornutum*. Given the inverse relationship between polar lipids and TAG, EPA was negatively correlated with TAG content (Shen et al. 2016). However, there are species capable of accumulating PUFAs in TAG. For example, in *Parietochloris incisa* in the stationary phase, the ARA content in TAG reaches 47% (Bigogno et al. 2002).

The FA composition also exhibits specificity at the glycolipid level. C16:0, C18:3n-6cis, and C18:2n-6cis were the main FAs in glycolipids of monogalactosyl diacylglycerol and digalactosyl diacylglycerol, while C16:0, and C18:2n-6cis were the main FAs in sulfoquinovosyl diacylglycerol (Xue et al. 2002).

The FA composition of betaine lipids differs significantly from the FA composition of total lipids (Armada et al. 2013; Cañavate et al. 2016). The differences are seen, first of all, in the ratio of SFAs and unsaturated FAs. The FA profile of betaine lipids has a greater amount of unsaturated FAs. It is assumed that the combined use of the composition of betaine lipids, the composition of FAs of betaine and total lipids can have a high chemotaxonomic potential.

Thus, the use of data on FAs of total lipids or a certain class of them also leads to differences in the FA spectrum of certain taxa. Changes can concern the sequence of the FAs in the spectra, and sometimes also its composition. This can be evidenced by data on the composition of the main FAs based on phospholipids (Dijkman and Kromkamp 2006) and total lipids (Taipale et al. 2013) (Table 2).

5.4 Influence of environmental factors on lipid profile and fatty acids composition

5.4.1 Change in lipid profile

The number and composition of lipids in different taxa of microalgae are different (Jónasdóttir 2019). This is used to determine the main profile of FAs and biomarker FAs. However, by changing the cultivation conditions, it is possible to achieve a change in the lipid composition and, accordingly, the FAs content. For example, the use of nitrogen and phosphorus starvation in some species of microalgae led to an increase in the synthesis of total lipids by 15–54%, temperature stress by 12–21.7% (Illman et al. 2000; Sharma et al. 2012). An almost threefold increase in lipid content in *Arthrospira* sp. was achieved with a decrease in temperature and nitrogen content in the cultivation medium (Macedo and Alegre 2001). Under conditions of moderate stress, when cells stop dividing but still photosynthesize, the lipid content can increase by two or three times, with up to 60–80% (DCW) of lipids recorded (Vince et al. 2012). The specific conditions of habitats can also influence the formation of biochemical phenotypes of microalgae. This has been demonstrated for a number of desmid strains (Stamenković et al. 2020).

Thus, the stimulation of lipid production and changes in their composition also entails changes in the profile of the FAs of microalgae. The sensitivity of the FA profile of microalgae species to changes in the ecological conditions of the habitat is well known and is used to change the FA content during cultivation. At the same time, the effectiveness of a wide variety of abiotic stresses is tested (restriction of nutrients, changes in heat, light, salt, etc. modes).

5.4.2 Fatty acid composition with nitrogen and phosphorus deficiency

The general trend in the change in the composition of FAs when using nitrogen and phosphorus starvation is a decrease in the content of PUFAs and an increase in MUFAs and SFAs. In this case, the lipid content itself increases, and the rate of microalgal biomass formation slows down. The severity of these changes is not the same for different taxa of microalgae. For example, the use of phosphoric and nitrogen starvation during the cultivation of *Coccomyxa elongata*

(Maltsev et al. 2019a) led to an increase in the content of palmitic to 24.7–25.6%, C16:1n-9cis to 14.8% and ALA to 9.1–10.1% acids in comparison with the control sample with such corresponding concentrations as 21.9%, 12.1% and below detection limits for ALA. The absence of nitrogen and both nitrogen and phosphorus led to a threefold increase in total FA in comparison with the control in the study of the strain *Parietochloris grandis* sp. nov. is described from forest soil (Maltsev et al. 2018). In *Parachlorella kessleri*, nitrogen starvation led to a decrease in PUFAs content from 57.7 to 50.8% and an increase in MUFAs from 2.4 to 8.2% and in SFAs from 28.1 to 33.1% (Gao et al. 2019). With nitrogen limitation during the cultivation of *Botryococcus braunii*, a decrease in the amount of trienoic FAs (from 52.8–57.2 to 19.5–24.7% of total FAs) and an increase in the content of oleic (C18:1n-9cis) (from 1.1–1.2 to 17.1–24.4%) and saturated (from 23.7–26.0 to 32.9–46.1%) acids in TAG and an increase in SFAs to 76.8% and a decrease in PUFAs to 6.8% in FAs of polar lipids (Zhila et al. 2005). The amount of SFAs, monoenoic and dienoic FAs increases, while the amount of PUFAs significantly decreases in *Chlamydomonas reinhardtii* under conditions of phosphorus restriction in the culture medium (Qari and Oves 2020).

5.4.3 *Influence of the environment and time of cultivation of microalgae*

An analysis of the influence of the composition of culture media, which may differ in nutrient content, as well as the duration of the cultivation period of strains in collections, is important in establishing the specificity of the FA profile and FAs used as markers for certain taxa of microalgae. For example, the *Pseudomuriella engadinensis* MZ–Ch33 strain cultivated on BBM medium differed from the *P. engadinensis* SAG 221-3 and SAG 221-4 strains grown on ESP Ag medium, almost twice as high in palmitic (C16:0) FA (20.1% and respectively 11.3% (SAG 221-3) and 10.1% (SAG 221-4)). An increased amount of LA (Δ9.12–18:2) was also noted—17.7% in MZ–Ch33, while 11.6 and 12.0% in SAG 221-3 and SAG 221-4, respectively (Maltsev et al. 2019b). In desmid strains (Stamenković et al. 2020) cultivated for more than 35 years the role of SDA increased in the FA profile.

5.4.4 *Dynamics of the composition of fatty acids with changes in pH*

A change in the pH of the medium affects the metabolism of microalgae and is reflected in the accumulation of lipids and the composition of FAs. The growth and biochemical reactions of microalgae have been tested over a wide range of pH changes. Some microalgae showed the ability to grow well at pH from 4 to 10 (*Coccomyxa melkonianii* grew at pH 4–8, *Dunaliella bardawil* grew at pH 4–8, *Chlorella ellipsoidea* grew at pH 4–10), others (*Pleurochrysis carterae*, *Emiliania huxleyi*) could not grow at pH below 7.5 (Khalil et al. 2010; Moheimani and Borowitzka 2011; Soru et al. 2019). This indicates that each species of microalgae has its own optimal pH range. Alkaline pH stress in *Chlorella* led to the accumulation of TAG and a decrease in the amount of glycolipids and phospholipids (Guckert and Cooksey 1990). The accumulation of neutral lipids and the highest levels of their content have been noted in other studies in *Tetraselmis suecica* at pH 9 (Almutairi and Toulibah 2017). In general, under the action of alkaline pH values, new UFAs can be found in the FAs profiles of microalgae, as well as a decrease in the proportion of SFAs and MUFAs and an increase in PUFAs can be found in them. For example, the spectrum of FAs *Tetraselmis suecica* in response to pH changes was supplemented with linolelaidic acid (C18:2n-6trans), which contains two double bonds (Almutairi and Toulibah 2017). An increase in PUFAs content (from 39.93 to 56.97%) and a decrease in SFAs and MUFAs (from 40.72 to 30.37% and from 16.51 to 10.22%, respectively) were observed in *Chlorella sorokiniana* with a change of pH from 6.5 to 8.5 (Qiu et al., 2017).

5.4.5 *Dynamics of the composition of fatty acids under salt stress*

Salt stress is accompanied by an increase in lipid production in microalgae (Takagi et al. 2006; Mohammady and Fakhry 2014) and a change in the proportions of the content of various groups of FAs. An increase in the number of FAs with a longer hydrocarbon chain and the proportion of UFAs was observed in *Dunaliella* salina in the composition of lipids of microsome membranes under the action of high concentrations of (3.5 mol) NaCl. When

Dunaliella salina was grown in a 3.5 mol NaCl solution, the C22 FAs content was 8.8% of the total FAs, and when cells were transferred to a 0.5 mol solution, their concentration decreased to 4.45% (Azachi et al. 2002). An increase in the content of C18:3 from 25.9 to 37.2% in the composition of total lipids of *Dunaliella salina* was observed in another experiment when the NaCl concentration changed from 2.5 to 20% (Al-Hasan et al. 1987). At the same time, as the concentration of NaCl increased from 0.85 to 3.4 mol in the composition of polar lipids of *Dunaliella salina*, a decrease in the content of C18:3 and an increase in C18:2 and C18:1 were observed (Peeler et al. 1989). A decrease in the content of C18:3 and C18:2 under salt stress was noted for *Nannochloropsis oculata* (Mohammady and Fakhry 2014). In addition, an increase in the amount of SFAs and a decrease in UFAs were observed (from 23.0 to 33.7% and from 77.0 to 66.3%, respectively) with an increase in the NaCl content from 0 to 40 g L^{-1}. In studies with *Tetraselmis tetrathele*, more than 90% of FAs accumulated under conditions of salt stress were saturated (El-Kassas and El-Sheekh 2016), while *Botryococcus braunii* showed a 1.7–2.25-fold increase in the relative proportion of palmitic acid (C16:0) and a twofold increase in oleic acid (C18:1n-9cis) (Rao et al. 2007). The observed variability in the proportions between SFAs and UFAs may depend on the characteristics of changes in the lipid composition of cells in response to salt stress in different species of microalgae. Regulatory mechanisms may be associated with TAG accumulation, biosynthesis of polar lipids of membranes containing SFAs and UFAs in proportions sufficient to resist osmotic shock, or other actions.

5.4.6 *Influence of temperature on the composition of fatty acids*

Changes in environment temperature are reflected in the composition of the FAs of microalgae. As the temperature rises, the relative content of UFAs usually decreases in the composition of microalgal FAs (Sushchik et al. 2003; Guschina and Harwood 2006). For example, a decrease from 53 to 37% in the proportion of n-3 PUFAs (in particular, ALA) and a concomitant increase in the amount of SFAs in Scenedesmus obliquus were noted with a decrease in temperature from 28 to 20 °C (Fuschino et al. 2011). A decrease in culture temperature from 25 to 10° C within 12 h was accompanied by an increase in the EPA content in *Phaeodactylum tricornutum* (Jiang and Gao 2004). A similar effect was achieved in *Pavlova lutheri* when grown at 15° C (Fork et al. 1979). There is an indication that a decrease in temperature and an increase in illumination intensity are accompanied by an increase in the content of unsaturated FAs in microalgae (Los 2014). At the same time, the established relationship between an increase in membrane plasticity and changes of the amount of SFAs and unsaturated FAs in the composition of its lipids, is considered among the mechanisms of organisms that adapt to changing conditions of their habitat, including low temperatures. However, in species living in Arctic conditions, a high content of PUFAs is not a stable feature (Los 2014).

The opposite phenomenon was noted for *Emiliania huxleyi* (Bi et al. 2018). An increase in temperature caused an increase in PUFAs by 13% and a decrease in MUFAs by 20%. A significant relationship was also found between temperatures, N:P intake ratio, CO_2 concentration, and FA composition.

The inconsistency of data on the nature of changes in the content of PUFAs and SFAs with changes in environment temperature requires further research in this direction and clarification of the reasons for such variability of responses in different taxa of microalgae. A deep understanding of these relationships will allow not only to regulate the cultivation conditions of certain types of microalgae, but also to increase the objectivity of forecasting, for example, the global production of PUFAs by phytoplankton. Based on the existing patterns, climate change modelers indicate that global EPA production will decrease by 8.2% and DHA production will decrease by 27.8% with 2.5 °C rise in temperature (Hixson and Arts 2016).

5.4.7 *Influence of light regime on fatty acid composition*

Chlorella zofingiensis accumulated large amounts of C18:1 upon exposure to bright light, and the level of PUFA C16:3 decreased by about 50% (Liu et al. 2012). A less pronounced decrease in the C16 content and an increase in C18 (by 2.87% and 11.99%, respectively) was noted for *Chlorella protothecoides* with an increase in light intensity from 130 µmol m^{-2} s^{-1} to 420 µmol m^{-2} s^{-1}

(Krzemińska et al. 2015). Changes in light intensity also affect the percentage of SFAs, MUFAs and PUFAs. In an experiment with *Botryococcus braunii*, it was recorded that with an increase in light intensity, the percentage of MUFAs increases significantly, while the percentage of SFAs and PUFAs decreases (Wang et al. 2018). A decrease in the content of total n-3 FAs from 29 to 8% of the total amount of FAs was observed in *Nannochloropsis* sp. with increasing illumination (Fabregas et al. 2004). In *Chlorella vulgaris*, an increase in light intensity from 37.5 μmol m^{-2} s^{-1} to 100 μmol m^{-2} s^{-1} was accompanied by an increase in the SFAs content by 16.43–28.88% and a decrease in MUFAs and PUFAs by 20.24–24.65% and 25.82–26.77%, respectively (Khoeyi et al. 2011). In *Chlorella protothecoides*, with an increase in light intensity from 35 μmol m^{-2} s^{-1} to 130 μmol m^{-2} s^{-1}, the SFAs content increased from 14.93% to 18.72%, MUFAs practically did not change (49.71% and 49.54%, respectively), and PUFAs decreased from 12.34 to 11.56% (Krzemińska et al. 2015). When the light intensity reached 420 μmol m^{-2} s^{-1}, the SFAs content decreased to 15.24%, the MUFAs amount sharply increased to 65.43%, and the PUFAs content decreased to 7.44%. The observed differences demonstrate the differences in the relationships between photosynthetic processes and biosynthesis of FAs in microalgal species (Klyachko-Gurvich et al. 1999; Nzayisenga et al. 2020). It can be assumed that PUFAs are important for the adaptation of microalgae to low light intensity, and the synthesis of SFAs and MUFAs is an important mechanism for counteracting excessive light.

5.5 Problems and prospects

It should be noted that the description of the taxonomic profiles of the FAs of microalgae is based mainly on the data obtained under standard conditions, without taking into account stress effects. On the one hand, this makes it possible to give the greatest weight to the taxonomic variability of the FA profile. On the other hand, it does not allow us to answer the question how wide is the range of variability of the FA profile of marine, freshwater, and terrestrial species under abiotic stress and whether it coincides. It is believed that phylogenetic differences in taxa determine 3–4 times more variations in the FA profile of microalgae than the conditions for their growth (Galloway and Winder 2015). However, it is the ability to change the production of target bioproducts and FAs in the result of changing the cultivation conditions, that is one of the advantages of using microalgae in biotechnological processes, as already mentioned above (Sun et al. 2018; Li-Beissona et al. 2019; Levasseur et al. 2020).

Thus, the assessment of the features of the FA profiles of microalgae as one of the markers of the range of possibilities of their metabolism, biotic bonds, and trophic value, most likely, should be carried out taking into account the phylogenetic, ecological, geographical, chorological aspects, as well as the taxonomic specificity of the lipid composition and its dynamics when changing environmental conditions, the uniqueness of the FA composition of different classes of lipids, the diversity of response to the impact of key abiotic factors.

6 Conclusion

The composition of FAs in microalgae is very diverse. This review systematized information about 135 fatty acids of microalgae from different habitats. Taking into account the length of the hydrocarbon chain, its structure and the presence of substituents, they are distributed into several groups: with an even number of carbon atoms in the chain—81 (SCFAs—2, MCFAs—14, LCFAs—28, VLCFAs—37), with an odd number of carbon atoms—33, with a branched hydrocarbon chain and additional functional groups—21. Among FAs of microalgae there are both saturated and unsaturated FAs with different numbers of double bonds: SFAs—19, MUFAs—26, PUFAs—68. The FA profile of microalgae is rich in omega-3 and omega-6 fatty acids.

The FAs of microalgae are of wide commercial interest for various spheres of human activity: bioenergy, food and feed industries, aquaculture, pharmacology, and cosmetology. Further research is needed both to increase the productivity of commercially valuable FAs and to reduce the cost of their production through the introduction of effective technologies and the use of highly productive strains.

The presence and combination of certain FAs show a certain specificity within the phylogenetically isolated taxonomic groups of microalgae. However, in some cases, especially at the level of taxa of the lowest rank, the variability of the composition of the

FA profile is quite high, which reduces the unambiguity of its use and requires further research. Also, the composition of FAs of microalgae is characterized by a variety of responses to the action of key abiotic factors. There is no unambiguous answer to how much the composition and number of FAs can change under various abiotic stresses and will the uniqueness and recognition of the taxonomic profiles remain or not under stress conditions. Understanding these patterns will make it possible to make significant progress in optimizing the conditions for cultivating microalgae, selecting strains with maximum productivity of commercially interesting FAs, modeling and predicting various processes both within the framework of production and at the level of natural ecosystems of various scales.

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Declaration

Conflict of interest None of the authors have any potential financial or other interests that could be perceived to influence the outcomes of the research.

Appendix

Online Resource. FAME database established of all reviewed microalgal strains. The database contains information about phylum, class, genus and species identification (1st to 4th column) and strain number (5th column) and the amount of the different substances given as relative proportion (following columns). The second sheet of the table contains references used to construct the initial matrix of fatty acid profiles in marine and freshwater microalgae.

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