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Prospects for the Use of Algae and Cyanobacteria from Extreme Habitats of Kamchatka in Biotechnology

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Abstract—Kamchatka is a unique natural laboratory, where the substrate is constantly refreshing under active volcanic conditions. It is believed that the first settlers of the lifeless volcanic deposits are microscopic algae and cyanobacteria, which are able to survive at high and low temperatures, low concentrations of nutrients, sharp fluctuations in the aggregate state of water, and other extreme environmental factors. The main ways photoautotrophs adapt to live in these environments by controlling the structure of the plasma membrane, making protective compounds like polyols, sugars, secondary carotenoids, vitamins, and more, and living with fungi and bacteria in biological crusts. This review indicates the possibility to use the widespread species, which were found on the peninsula: *Chlorella vulgaris*, *Tetradesmus obliquus*, *Chromochloris zofingiensis*, *Bracteacoccus minor*, *B. bullatus*, and *Chlorogloeopsis fritschii*, in biotechnological research. The detailed analysis of the environment and consideration of species-specific demands allow to select suitable strain and an increase in valuable component yield.

Keywords: adaptation, extremophiles, volcanic habitats, biota, microorganisms, thermostable enzymes

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INTRODUCTION

The Kamchatka Peninsula is a unique region that is part of the Pacific Ring of Fire, located in the Russian Far East. Volcanic activity influences the climate, natural environment, and fauna of the peninsula, contributing to the formation of extreme habitats. Volcanic biotopes characterized by high (in the case of hot springs or thermal fields) or low (snowfields) temperatures of the substrate, low acidity, increased ultraviolet radiation (UVR; volcanic deserts), sharp fluctuations in aggregate state of water (seasonal melting of permafrost and of snowfields on the slopes of volcanoes), and a deficiency of nutrients in the initial stages of succession of the lifeless substrate. It is believed that the first settlers of volcanic deserts were algae and cyanobacteria characterized by small sizes (within few microns) which permitted them to move easily via air masses [1–3]. Under unfavorable environmental conditions, algae change characteristics of the life cycle, the rate of physiological and biochemical processes, the structural composition of membranes, and the production of special protective substances [4, 5] (Fig. 1). The wide adaptive capabilities of algae and cyanobacteria from extreme biotopes can become a potential object and basis for biotechnological research (Table 1). This review includes an analysis of the climatic conditions of the peninsula, which form the unique microbial communities of terrestrial microalgae and cyanobacteria. The biotechnological potential of these microorganisms as producers of valuable compounds is important for biotechnology.

BRIEF DESCRIPTION OF THE KAMCHATKA PENINSULA'S CLIMATE

The climate of Kamchaka is cold and excessively humid. The humidity coefficient exceeds 1.3. The average annual precipitation is from 350 to 1000 mm. Prevalence of summer precipitation is observed. The snow cover thickness exceeds 50 cm, and in some areas reaches 100 cm. The average temperature in July does not exceed 15°C, in February—from –10 to –20°C [6]. Volcanic activity in Kamchatka contributes to an increase in soil temperature with depth and the absence of continuous permafrost, which is found in the goltsy and subgoltsy belts. Despite the relatively warm soils, due to the harsh climate, the vegetation period in Kamchatka is quite short (on average 100 days), the last frosts are observed in June—early July, the first—from mid-August [6].

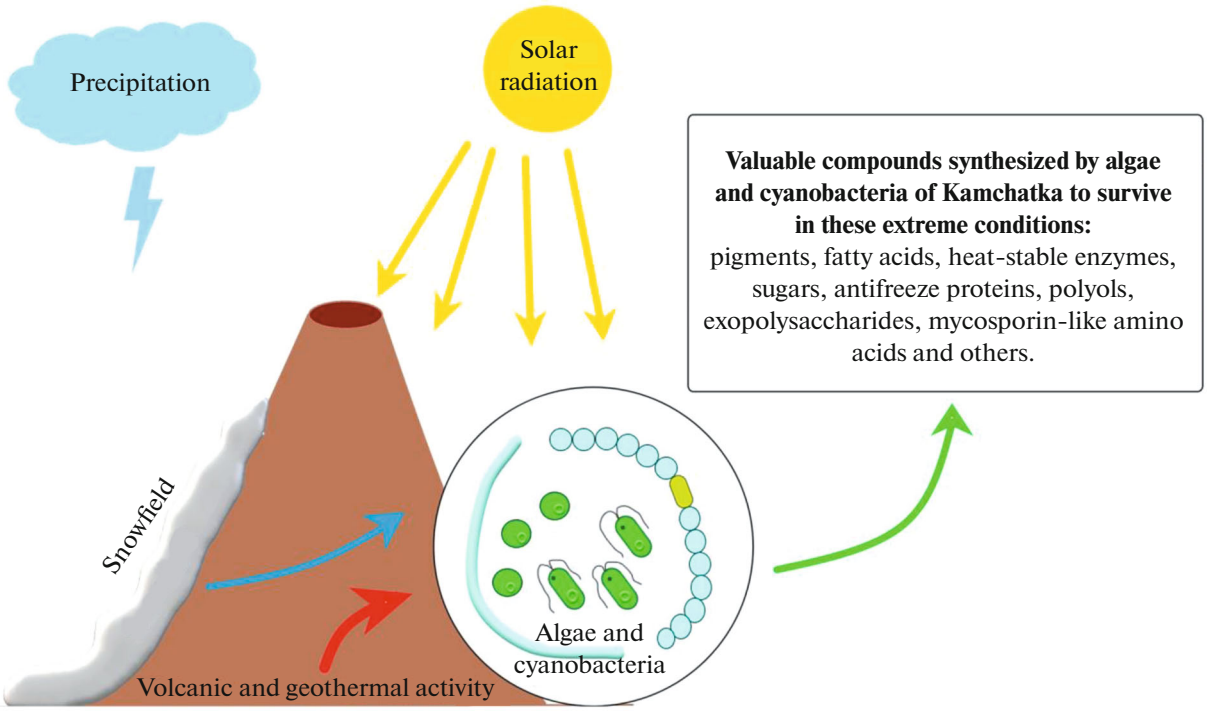

Fig. 1. The influence of environmental factors on algae and cyanobacteria of Kamchatka.

ECOLOGICAL FACTORS AND ADAPTIVE MECHANISMS OF PHOTOTROPHS

Low temperature. Temperature is one of the most important environmental factors of biotopes influencing metabolism and growth rates of microorganisms. The optimum growth temperature for mesophilic algae (temperate climate) is usually 20–30°C. An organism that can live at temperatures below 15°C but whose growth optimum is above this value is considered "psychrotolerant". According to Morgan-Kiss et al. [7], microorganisms whose growth optimum is below 15°C are considered "psychrophiles" (cold-loving). Photoautotrophs, living under low-temperature conditions, primarily aim to reduce the intensity of absorbed light to preserve the integrity of their light-harvesting complex components. This is because exposure to low temperatures can cause an excessive increase in the flux of absorbed light, surpassing the permissible norm. Thus, in *Chlamydomonas nivalis* (Bauer) Wille from polar latitudes, the light-harvesting capacity of photosystems decreasing due to an increased chlorophyll a/b ratio. These processes caused by a change in the ratio of the central protein of photosystem II (PSII) and peripheral light-harvesting proteins. Decrease in the expression of genes associated with light harvesting also negatively influences on photosynthesis [8]. A similar result was detected for *Chlorella vulgaris* Beijerinck in a study of intense light and low temperatures (5°C) effect on algal growth [9]. Under these conditions, a decrease in the content of chlorophyll and polypeptides of light-harvesting complex II was observed, which likely contributed to the decrease in the probability of light absorption. A similar acclimatization response to low temperature as in *C. vulgaris* was found in the mat-forming antarctic cyanobacterium *Phormidium murrayi* (West et West) Anagnostidis et Komárek (synonym *Wilmottia murrayi* (West et West) Strunecký, Elster et Komárek) [10]. It was found that the culture responded to stress factors by reducing the functional size of PSII due to a significant increase in the ratio of carotenoids to chlorophyll a. This is evidence that photoautotrophs adapted to low temperatures sense and respond to excitation pressure like mesophilic organisms [10].

In cases of excess light energy, algae cells have the ability to dissipate excess light as heat and reduce the light-harvesting capacity of PSII to maintain optimal levels of photosynthesis. Thus, in *C. vulgaris* cells, the increase of xanthophylls content and photosynthetic capacity at 5°C was observed. These changes caused by a concomitant increase in the electron flow through PSII reduced the pressure on the photosystem [11]. In *Chlamydomonas nivalis*, a significant increase in the effective photochemical quantum yield of PSII, a decrease in the proportion of closed PSII reaction centers, and unregulated energy dissipation were also detected [8].

Increased levels of stress factors (including low temperatures) reduce the rate of photosynthesis, and excess electrons are transferred to molecular oxygen (O_2) with the formation of reactive oxygen species (ROS) [12]. ROS cause oxidative damage to proteins,

Table 1. Application of algae and cyanobacteria strains from extreme habitats in biotechnology

An environmental factor that causes the synthesis of biologically active compounds	Strain	Special protective substances	Application in biotechnology	References
Low temperature	*Bracteacoccus bullatus* CCALA 1120	Monounsaturated fatty acids	Production of vegetable oil with high unsaturated fatty acid content	[22]
High temperature	*Tetradesmus obliquus*	Saturated fatty acids	Biodiesel production	[32, 33]
	Thermosynechococcus elongatus	Thermostable pigment phycocyanin	Cytotoxic activity of C-phycocyanin to various types of cancer cells	[37, 38]
	Chlorogloeopsis fritschii	Thermostable enzyme cyanophycin synthetase	Catalyzes the formation of cyanophycin, a substitute for polyaspartic acid needed in the paper, oil and paint industries	[36]
UVR	*Chlorogloeopsis* sp.	Mycosporin-like amino acids	Pharmaceutical and cosmeceutical applications: sunscreen base	[56, 57]
	Bracteacoccus minor	Secondary carotenoids	Production of natural dyes and industrial algal oils	[71]
Moisture deficiency	*Neocystis mucosa*	Exopolysaccharides	Industrial wastewater treatment	[81–84]
Nitrogen deficiency	*Chromochloris zofingiensis*	Lipids	Biodiesel production	[94]

DNA, and lipids [13]. The ROS scavenging system includes antioxidant enzymes (superoxide dismutase, catalase, and peroxidase) and non-enzymatic scavengers (carotenoids, vitamin E, and vitamin C) [14]. Therefore, the increase in carotenoid content and antioxidant enzyme activity in *C. nivalis* at low temperatures is associated with ROS scavenging [8].

There are a number of strategies developed in algae and cyanobacteria cells to protect the photosynthetic apparatus. These are the synthesis of specialized substances (polyols, sugars, antifreeze proteins) and the ability to change the structure of the cell membrane by forming protective compounds and regulating the composition of fatty acids. The cell wall is the first barrier that maintains the integrity of the cell under stress conditions. Accordingly, its resistance to extreme conditions is critical for the survival of organisms. A number of studies have shown that algenan is a key compound that affects the strength and permeability of the cell wall [15]. Algenan, also known as sporopollenin, is a complex biopolymer with high acid-base stability. Its presence complicates the process of extracting valuable compounds from algae cells. Thus, the detection of sporopollenin in the cells of *Chlorella protothecoides* Krüger (synonym *Auxenochlorella protothecoides* (Krüger) Kalina et Puncochárová), a potential object for commercial biofuel production, led to increase the costs of oil extraction [16].

Gonzalez-Hourcade et al. [17] showed that cells of *Coelastrella* and *Scenedesmus* strains did not stain with crystal violet, indicating the presence of algenan in their cell walls. Dye treatment of growth cultures at low temperature was performed for visualization of changes in cell wall permeability. All *Scenedesmus* cells became stained after the treatment. Probably, the walls of young cells are immature and susceptible to lower temperatures. Thus, knowledge of the resistance of microalgae cell wall components to stress factors will permit the development of strategies for extracting valuable substances from algae biomass.

Maintaining cell membrane fluidity is another mechanism that permits microorganisms to adapt to the effects of low temperatures [18]. Changing the composition of fatty acids in the membrane (including polyunsaturated, short-chain, branched, or cyclic fatty acids) of psychrophiles allow them to regulate membrane fluidity [19]. In particular, the degree of unsaturation of fatty acids in membrane lipids plays an important role to prevent membrane rigidity under low-temperature conditions. Sato et al. [20] compared the fatty acid composition in cells of *Anabaena variabilis* Kützing ex Bornet et Flahault (synonym *Trichormus variabilis* (Kützing ex Bornet et Flahault) Komárek et Anagnostidis), grown isothermally at 38 and 22°C, and concluded that the cyanobacterium adapted to the lower temperature by fluidizing membrane lipids, increasing the unsaturation of C18:1

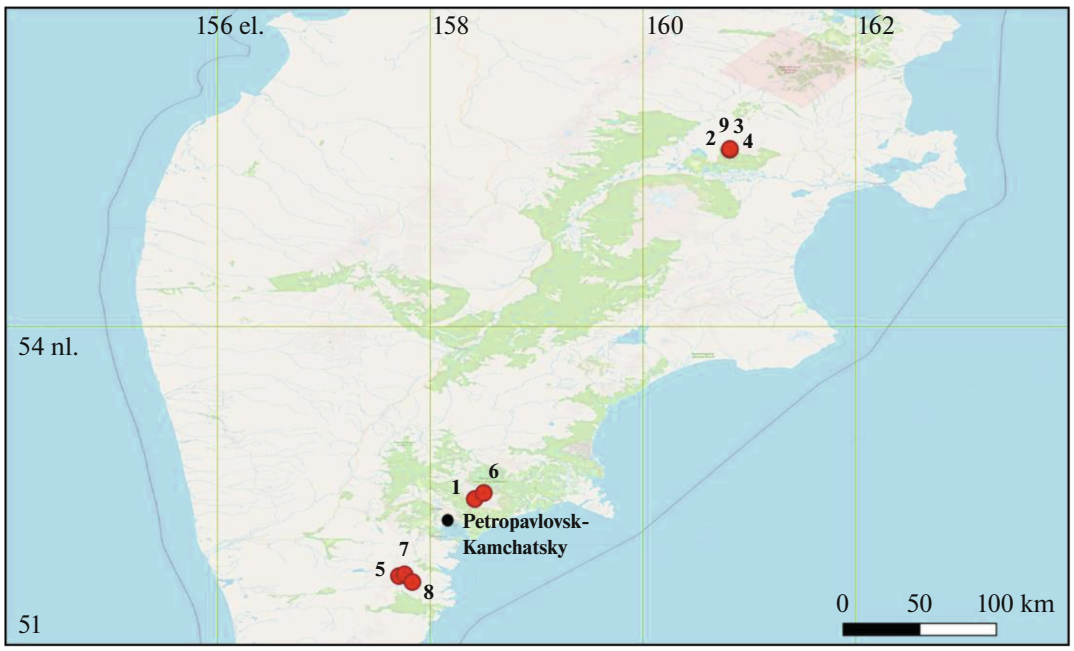

Fig. 2. Map of the study area with sampling locations, where strains were found: 1—*B. bullatus*, 2—*C. vulgaris*, 3—*T. obliquus*, 4—*C. fritschii*, 5—Community of *M. thermotolerans* and cyanobacteria of the genera *Microcoleus* and *Stenomitos*, 6—*C. zofingiensis*, 7—*B. minor*, 8—*N. mucosa*, 9—*M. inermum*.

acids. The ability of microalgae and cyanobacteria to accumulate C18:1 indicates the potential of these organisms as producers of high-quality biodiesel fuel.

During the study the algal and cyanobacterial diversity from volcanic habitats of Kamchatka, *Bracteacoccus bullatus* Fuciková, Flechtner et Lewis was detected [21] (Fig. 2). The strain was isolated from pyroclastic material beneath the mountain-tundra species *Arctous alpina* (L.) Niedenzu and *Ledum palustre* L. subsp. decumbens (Ait.) Hult. The sample was collected on Koryaksky Volcano (N 53°16.732′, E 158°44.496′). The *B. bullatus* CCALA 1120, isolated from a similar low-temperature habitat (mountain snow in Spain), contains a high proportion of fatty acids (15.3% of dry weight) [22]. Moreover, monounsaturated fatty acids make up about 30%, and the most noticeable compounds are oleic (18:1ω-9) and vaccenic acids (18:1ω-7). The ratio of polyunsaturated fatty acids (PUFA) ω-6/ω-3 was 1 : 1.16, i.e., close to the ideal ratio of 1 : 1 recommended by the World Health Organization. These results demonstrate the suitability of *B. bullatus* for the low- temperature production of vegetable oil with high unsaturated fatty acid content.

The next mechanism activated at sub-zero temperatures is the production of cryoprotectants by algae, which include polyols, sugars, and antifreeze proteins [23]. Sugars have been shown to promote freezing tolerance by acting as osmolytes, ROS scavengers, and signaling molecules, although this is species-dependent [24]. They typically interact with the lipid layer during the freezing phase, maintaining the integrity of the plasma membrane. Sucrose production is part of the cold adaptation strategy of *Klebsormidium flaccidum* (Kützing) Silva, Mattox et Blackwell [25] and the response to cold shock of *C. vulgaris* [26]. *C. vulgaris* was isolated from a tephra sample collected along the Baydarnaya river bed on the Shiveluch volcano (N 56°33.57′, E161°8.24′) [2] (Fig. 2). Possibly the ability to survive under low temperature conditions permits such coccoid algae to inhabit lifeless volcanic ecotopes.

The formation of symbiotic relationships by microalgae is another way of adaptation. Dickson [27] reported increased frost resistance of the species *Asterochloris excentrica* (Archibald) Skaloud et Peksa and *Trebouxia* sp. only in lichen-type communities [28]. Symbiotic algae are protected from harmful environmental influences due to the stable microclimate in the lichen thallus [29].

Thus, the main strategies of algae and cyanobacteria at low temperatures are regulation of cell membrane fluidity, synthesis of additional compounds to protect cell integrity, and response to excitation pressure by changing the ratio and composition of the components of the photosynthetic apparatus. The flexibility of the cell membrane composition permits psychrophiles to be sources of valuable fatty acids.

High temperature. Thermophiles are microorganisms that can grow at high temperatures, exceeding the boiling point of water [30]. As with psychrophiles, changes in ambient temperature lead to changes in the

fatty acid composition of their membranes. Thus, in the thermophilic strain *Synechococcus elongatus* (Nägeli) Nägeli B-267, a decrease in temperature led to a two-fold decrease in the quantitative ratio of saturated and unsaturated fatty acids [31].

The green algae, *Tetradesmus obliquus* (Turpin) Wynne, was discovered in tephra samples along the left edge of the outcrop on the Shiveluch volcano (N 56°33.625′, E 161°8.398′) [2] (Fig. 2). The habitats were characterized by high temperatures of substrate (up to 90°C). Castro-Tapia et al. [32] showed that *Scenedesmus acutus* Meyen (synonym *T. obliquus*) accumulates more total lipids at 38°C than at 25 and 30°C. Palmitic and oleic acids predominated in the total amount of extracted lipids. Temperature changes during microalgae growth could be used to enhance lipid production and obtain fatty acids suitable for biodiesel production [32]. *Acutodesmus obliquus* (Turpin) Hegewald et Hanagata (synonym *T. obliquus*), isolated from a thermal reservoir ($t = 50$°C) in Lagoa Quente, was used in Brazil to produce biofuel [33]. The biodiesel productivity obtained on DAF medium was 25.6 t ha^{-1} $year^{-1}$, and on BBM medium, 32.9 t ha^{-1} $year^{-1}$, which was higher than that of soybeans, from which 0.542 t ha^{-1} $year^{-1}$ was obtained. Moreover, biodiesel production from *A. obliquus* requires 1.6–2.2% of the land and 5.5–7.2% of the water used for soybean biodiesel production.

In addition to the ability to regulate fatty acid composition, thermophilic microorganisms are characterized by the presence of thermostable enzymes, which provide a potential advantage over mesophylls, facilitating their survival at high temperatures [34]. Thermophilic cyanobacteria are the source of thermostable cyanophycin synthetase (CphA) encoded by the *cphA* gene and catalyzing the formation of cyanophycin. It is a substitute for polyaspartic acid, a biodegradable compound required for the synthesis of polyacrylate in the paper, oil, and the coatings industries [35]. Cyanophycin is also considered as a biodegradable substitute for the petrochemical industry and environmentally friendly plastics. A culture of the cyanobacterium *Chlorogloeopsis fritschii* (Mitra) Mitra et Pandey was isolated from a tephra sample collected from an outcrop (N 56°33.64′, E 161°8.40′) located near a dead forest area on the Shiveluch volcano [2] (Fig. 2). CphA of a thermophilic strain of *C. fritschii* isolated from the Gauri Kund hot spring in India was shown to be maximally active at 30 and 40°C, and was 66% stable when treated for 1 h at 45°C [36].

The thermostable pigment phycocyanin isolated from the thermophilic strain *Thermosynechococcus elongatus* Katoh, Itoh, Shen et Ikeuchi (synonym *Thermosynechococcus vestitus* (Copeland) Komárek et Strunecky) TA-1 showed stability in the range from 4 to 60°C, with an activity of 65.65% at 60°C [37]. Thermal stability is believed to be determined by the amino acid composition, ion pairs, hydrogen bonds, secondary structure, and surface polarity of the substance molecule [37]. C-phycocyanin (C-PC) of *T. elongatus* has been shown to exert cytotoxic effects on various types of cancer cells, including breast cancer cells [38]. The thermophilic *Chlorogleopsis* sp., collected in Yellowstone National Park (USA), has also been shown to produce C-PC. The maximum productivity of C-PC was achieved when treated with 20% CO_2 flow with a value of 0.09 ± 0.01 mg/mL day at CO_2 fixation rate of 0.17 ± 0.01 mg/mL day [39].

Jasser et al. [40] found a positive correlation between the thermotolerance of strains isolated from hot springs and the number of genes encoding heat shock proteins, which are known to help microorganisms adapt to stressful environments [41]. Three small heat shock protein genes, *hsp17.1*, *hsp17.8* and *HspA*, which protect PSII, maintain the integrity of thylakoid membranes and phycobilisomes aggregation under stress conditions [42], were found in thermophilic strains of cyanobacteria (*Calothrix thermalis* Hansgirg ex Bornet et Flahault, *Desertifilum tharense* Dadheech et Krienitz and *Hillbrichtia* sp.).

Thermotolerance also appears to be associated with the presence of genes encoding type I polyketide synthase (PKS) and nonribosomal peptide synthetase (NRPS). Both types of the studied genes were amplified in thermotolerant strains of *Trichormus variabilis* (Kützing ex Bornet et Flahault) Komárek et Anagnostidis, *C. thermalis*, *Hillbrichtia pamiria* Jasser, Panou, Sandzewicz, Gkelis et Kwiatowski, *Microcoleus anatoxicus* Stancheva et Conklin, *Thermoleptolyngbya hindakii* Panou, Kokocinski et Gkelis. *PKS* and *NRPS* genes are associated with nonribosomal synthesis of secondary metabolites in microorganisms living under unfavorable environmental conditions. The ecological role of metabolites encoded by *PKS*, *NRPS* or hybrids of these genes is not fully understood, but appears to be related to various types of stress, such as increased light and UVR intensity, as well as high temperature and increased adaptability of microorganisms in highly competitive environments [43].

The formation of giant cells in *Chlorella*-like algae is one of the adaptation mechanisms under stressful conditions (including the influence of supra-optimal temperatures) identified in laboratory [44]. Thus, two strains of *Micractinium* sp. TvB and SH were cultivated at supra-optimal temperature (45°C) and different salinity levels. It was shown that at 45°C and relatively high salinity, an initial increase in optical density was observed in the first two days, which occurred due to cell growth in volume with the formation of giant cells, without a simultaneous increase in cell density.

The ability of thermophilic strains to grow at higher temperatures permits to reduce the cost of cooling systems in closed reactors, where energy is spent on temperature stabilization [39, 45].

Thermophilic activity of photosynthetic microorganisms is supported by the ability to regulate mem-

brane fluidity, the presence of thermostable enzymes and a unique set of genes, the functional role of which is not fully understood. Thermostable compounds of these organisms may be useful in the field of pharmacology and for the production of biodiesel.

Light. Photosynthetically active radiation (PAR) is radiation in the range of 400–710 nm that is necessary for photosynthesis, but its quantity and quality can either promote this process or suppress it when prolonged and intense exposure [46]. Excessively bright light typically causes oxidative damage to PUFA. Numerous studies have shown that cellular lipid and PUFA content decrease with increasing light intensity [47].

Avoidance is one of the strategies to mitigate or even prevent the harmful effects of UVR and ensure long-term survival of algae in microbiotic crusts. Crustacean algae are usually found in a matrix of polymeric organic and inorganic substances together with other groups of microorganisms. In North American desert crusts, green algae occupy a microenvironment within the matrix where they are protected from damaging levels of radiation [48]. A similar pattern on Gorely volcano in Kamchatka was observed [3]. Community of coccoid algae *Micractinium thermotolerans* Krivina, Sinetova, Savchenko, Degtyarev, Tebina et Temraleeva and cyanobacteria of the genera *Microcoleus* and *Stenomitos* was discovered in a sample taken from at the outlet of thermal vapors along the edge of the caldera on the southern slope (N 52°33.306′, E 158°01.742′) (Fig. 2). These filamentous cyanobacteria formed a dense mat, inside which favorable conditions for the existence of algae were created. The substrate temperature was about 32°C.

Cells in the deeper layers of the soil crust, where photosensitive species are likely to be located, may be protected from radiation by shading by cells in the outer layers [49]. High levels of UV-screening pigments appear to screen out close to 100% of the short-wavelength radiation, thus, biota inhabiting the lower layers of the mat are exposed to wavelengths of limited intensity (2% of PAR) in the yellow-red waveband. Therefore, phototrophic microorganisms living in the lower layers of the mat are likely adapted to shaded conditions [7]. A probable example of such acclimatization and/or adaptation to lower light intensity and/or differences in its quality is the difference in autofluorescence of two populations of *Synechococcus* living on and beneath the surface of the mat, at a distance of ~400–700 μm. Ramsing et al. [50] identified the co-occurrence of two genetically distinct populations of *Synechococcus*. The ~60° mat region contained a more fluorescent and deeper population (16S rRNA genotype A) that exhibited a unique reorientation of cells during the brightest part of the light cycle, providing evidence consistent with the differential light adaptation hypothesis [51]. In turn, the *Synechococcus* B′ population inhabited in the upper photic zone and was able to withstand high light intensities. In addition, surface populations of *Synechococcus* appear to shut down oxygenic photosynthesis during the brightest part of the day [50].

The main strategy of algae and cyanobacteria to maintain life under conditions of high insolation is the synthesis of protective compounds, including pigments, and the adjustment of their composition [52]. Thus, cyanobacteria are capable of synthesizing intracellular [53] and extracellular [54] compounds that protect them from UVR. Garcia-Pichel et al. [54] demonstrated the photoprotective role of the extracellular pigment scytonemin, which absorbs UVA, in the terrestrial cyanobacterium strain *Chlorogloeopsis* sp. O-89-Cgs(1). An example of extracellular protective components are mycosporin-like amino acids (MAAs), the absorption spectrum of which is in the range from 310 to 360 nm. The main function of MAAs is believed to protect cells from UV damage by absorbing incoming UVR [55], i.e. they act as sunscreens. Two mycosporin-type compounds (mycosporin-glycine and shinorin) have been found in representatives of the genus *Chlorogloeopsis* [56]. It has been statistically confirmed that an increase in shinorine content is associated with an increase in the duration of UVB exposure [56]. Besides other pharmaceutical and cosmetic applications, MAAs are a potential source for the development of natural sunscreen [57].

Increasing light intensity above saturation limits causes photoinhibition [58], which is associated with the destruction of chloroplast plates and inactivation of enzymes involved in CO_2 fixation [59]. The effect of such exposure and the threshold differ among species [60]. Increasing the light intensity from 80 to 120 μmol/m^2 s resulted in an increase in the growth rate of pre-conditioned (6% CO_2 treatment) *C. vulgaris* culture. The maximum biomass growth rate (0.78 g/L day) was obtained at 245 μmol photons/m^2 s [61]. In all 14-day experiments, no mass death of microalgae was observed, and an increase in biomass was observed. Thus, photoinhibition of the strains was not detected.

Scenedesmus obliquus (Turpin) Kützing CNW-N (synonym *T. obliquus*) is one of the potential sources of carotenoids and chlorophylls [62]. The highest specific growth rate of *S. obliquus* CNW-N cultivated in modified DM medium at light intensities from 60 to 540 μmol photons/m^2 s was about 1.65–1.8/day. The maximum biomass productivity of 840.57 mg/L day was observed at a light intensity of 420 μmol photons/m^2 s [63]. The two examples shown above confirm the thesis about the species-specificity of photoinhibition. Light utilization efficiency can be optimized by extending the dark period under high light intensity conditions, allowing the photosynthetic machinery in the cell to fully utilize the captured photons and convert them into chemical energy, thus, avoiding the photoinhibition effect [64].

Some algae species can use secondary pigments as a form of photoprotection [65]. In contrast to primary ones, they are not used directly at the stage of photosynthesis to collect light, but perform a protective function [66]. Astaxanthin is a secondary carotenoid produced by many species of snow algae, such as *C. nivalis* [67]. The pigment surrounds and protects the chloroplasts from strong radiation by absorbing some of the incident light and dissipating it as heat. By diverting this energy away from chloroplasts, the risk of photoinhibition and associated photodamage can be reduced [68].

The green alga *Chromochloris zofingiensis* (Dönz) Fucíková et Lewis was identified in a sample of pyroclastic material under the *Salix arctica* Pall. clump (N 53°20.096′, E 158°49.554′), collected on the saddle between Avachinsky and Koryaksky volcanoes [21] (Fig. 2). This species, like *C. nivalis*, is capable of synthesizing astaxanthin, but unlike the former, it is less demanding laboratory cultivation conditions. Due to the ability to synthesize carotenoid pigments (lutein, canthaxanthin and astaxanthin), as well as lipids and starch, *C. zofingiensis* has high biotechnological potential. It is also capable of achieving high biomass density under phototrophic, heterotrophic and mixotrophic cultivation regimes [69, 70]. Another well-known producer of secondary carotenoids, including astaxanthin, is *Bracteacoccus minor* (Schmidle ex Chodat) Petrová. Strain of this species was isolated from a sample of pyroclastic material collected on the eastern slope of Gorely Volcano under *S. arctica* and *Oxytropis pumilio* (Pall.) Ledeb. (N 52°34.267′, E 158°04.929′) [3] (Fig. 2). Commercially significant yields of ketocarotenoids and lipids (1.3–1.4 and 187–202 mg/L day, respectively) per liter of feedstock culture were shown to provide a promising basis for further exploration of this microalgae as a source of natural dyes and industrial algal oils [71].

Thus, the main adaptation strategies of photoautotrophs living under conditions of increased UVR include the synthesis of protective compounds – carotenoids and shading by more resistant microorganisms in biological crusts. The secondary pigments of these microorganisms are of special value.

Fluctuations in aggregate state of water. Moisture of soil has a decisive influence on the development of algae living in it [72]. Deficiency leads to serious functional changes in cells, which is associated with the suppression of photosynthesis, irreversible aggregation of macromolecules and the disintegration of organelles [49]. Soil algae are poikilohydric organisms and are able to tolerate moisture deficit for some time [73]. Different species and forms have various preferences, with diatoms being the most sensitive to water deficiency [28].

The cell wall, consisting mainly of carbohydrates (cellulose and hemicellulose), as well as some other compounds, plays an important role in water exchange with the environment, cell volume and turgor pressure. Desiccation can cause mechanical damage due to cell contraction as the water content and, hence its volume decreases. The flexibility of the cell wall permits it to fold, which is an adaptation to mechanical stress caused by desiccation [74]. The three-layer cell wall of some green algae contains sporopollenin [75]. As in the case of the influence of low temperatures and light radiation, sporopollenin permits to resist desiccation [76].

The biochemical defense strategy against desiccation involves the production of osmotically active carbohydrates such as polyols produced in particular by green algae of the class *Trebouxiophyceae* [77]. It appears that polyols synthesis in some green algae is a temporary response to water loss. Their role in protection against desiccation is due to the fact that they reduce intracellular water potential. Polyols such as glycerol, erythritol, arabitol, ribitol, mannitol, sorbitol and volemitol have been found in microalgae [76]. Polyols are of great interest to the food and pharmaceutical industries for the production of sugar-free products or for reducing the calorie content of products. Thus, sorbitol and erythritol are used as sugar substitutes for diabetics, and mannitol is used as a sweetener [78].

Another mechanism that permits microorganisms to survive under conditions of substrate desiccation is formation of mucous colonies. It has been shown that the soil crusts of the mountain tundra contain many species of green and charophyte algae capable of mucus formation. Algal mucus contains hydrophilic colloidal polysaccharides that protect the cells from sudden moisture fluctuations [79]. In a sample of pyroclastic deposits from the mountain tundra of the Mutnovsky volcano (N 52°29.952′, E 158°09.294′), *Neocystis mucosa* Krienitz, Bock, Nozaki et Wolf was discovered [3] (Fig. 2), which is characterized by the formation of abundant mucus containing extracellular polymeric substances. The monomeric composition of carbohydrates from the *N. mucosa* exopolysaccharides was analyzed using HPLC. Carbohydrates isolated using cation exchange resin, acidic, alkaline treatment and heating consisted of glucose, mannose, galactose and arabinose with a molecular ratio of 42 : 13 : 2 : 1 [80]. It has been noted that microalgae exopolysaccharides promote autoflocculation. Accordingly, these compounds can be used for industrial wastewater treatment [81–84].

The mucous secretions of algae promote the aggregation not only the cells of the algae themselves, but also soil particles, forming soil crusts. Such soil crusts may also be associated with cyanobacteria, bacteria, fungi, mosses and lichens. The mucus may store nutrients and protect the microorganisms within reducing the risk of desiccation and freezing [5].

Thus, a structured cell wall, the flexibility of which is regulated by the synthesis and inclusion of necessary

compounds, the production of mucus and osmotically active substances permit algae to live in a terrestrial-air environment and withstand sharp fluctuations in aggregate state of water in the soil.

Chemical composition of the substrate. Soil formation on the Kamchatka Peninsula occurs under conditions of active volcanism, where volcanic ash acts as the soil-forming rocks [85]. As a result of an explosive eruption acidic gases (CO_2, SO_2, H_2S, HCl, HF) are released, which are partially sorbed on the surface of ash particles. Then, the sorbed substances (Cl^-, F^-, SO_4^{2-}) enter the hydrosphere and soil as a result of being washed out by melt, rain and surface waters. In this case, leaching of petrogenic components (Mg, Ca, K, Na, Al, Fe, Si, as well as Cu, Mn, Sr, Ba, Zn and other microelements) from pyroclastic deposits occurs [86]. Thus, a water-soluble ash complex is formed on the surface of ash particles. It consists of ephemeral minerals (salts) formed as a result of chemical reactions of sorbed eruptive gases with petrogenic components extracted from the rock [87]. The chemical composition of fresh pyroclastic deposits is probably determined by the properties of the water-soluble ash complex.

The growth rate of algae depends on the rate of the most limiting nutrient uptake at optimum temperature and pH [88]. Long-term nutrient stress triggers adaptations that involve species-specific changes in metabolism [89].

One of the most important elements responsible for algae viability is nitrogen, which plays a major role in the synthesis of protein, DNA and chlorophyll. Nitrogen starvation affects growth, protein and carbohydrate synthesis, and in particular lipid accumulation [90–92]. Under nitrogen deficiency, a decrease in the content of thylakoid membranes, activation of acyl hydrolase and increased hydrolysis of phospholipids can be observed leading to an increase in the intracellular content of fatty acetyl coenzyme A [93]. Increasing the reserves of carbohydrates or lipids in algae cells during nitrogen starvation is actively used in biotechnology, especially in the production of biodiesel fuel. Thus, it was found that under nitrogen deficiency conditions in the cells of *Chlorella zonfingiensis* (synonym *Chromochloris zofingiensis*), the accumulation of lipids and carbohydrates increases, and the synthesis of carbohydrates occurs earlier than the synthesis of lipids [94]. Lipid accumulation under nitrogen-depleted conditions has also been shown for *Coccomyxa subellipsoidea* Acton [95], *S. acutus* (synonym *T. obliquus*) [96], *Lobosphaera incisa* (Reisigl) Karsten et al. [97] and many other species.

Phosphorus is another important compound responsible for the production of cellular components and metabolic pathways that include energy transfer and nucleic acid synthesis [98]. Approximately 0.03–0.06% phosphorus in the medium is required to support algal growth [99–101]. Phosphorus deficiency is also believed to lead to lipid accumulation. Thus, Xin et al. [102] observed an increase in the total lipid content from 23 to 53% in *Scenedesmus* sp. with a decrease in the initial concentration of total phosphorus (as phosphate) from 2.0 to 0.1 mg/L. In turn, Chu et al. [93] showed that the lipid yield of *C. vulgaris* grown for biodiesel production under phosphate-sufficient conditions was 58.39 mg/L day and was relatively higher than that under phosphate-deficient conditions. It is likely the phosphorus requirement is species-specific.

The above examples showing the effect of nitrogen or phosphorus deficiency on algal metabolism confirm that nitrogen and phosphorus starvation shifts the lipid metabolism from membrane lipid synthesis to neutral lipid storage. This, in turn, increases the total lipid content of green algae [103]. It is equally important to investigate the combined effect of these biogens on lipid synthesis. Thus, in *Parietochloris incisa* (synonym *Lobosphaera incisa*), it was shown that combined nitrogen and phosphorus limitation seemed to enhance arachidonic acid productivity better than nitrogen deprivation alone [104]. The better performance of N-P-deficient BBM medium may be due to the synergistic effect of combined nutrient stress. It was later shown that arachidonic acid may be an important factor in the adaptation of *L. incisa* to low temperatures, as it can help maintain the fluidity of chloroplast membranes [105].

Polyphosphate of microalgae is a form of cellular protection against metal toxicity because it is able to bind with metals into a detoxifying complex. *Chlamydomonas reinhardtii* Dangeard accumulated copper and cadmium and withstood metal toxicity in a polyphosphate-rich environment [100]. Mulbry et al. [106] have shown a significant capacity of algae to take up inorganic phosphate from wastewater due to adsorption ranging from 70 to 90% of the optimum level required for growth [107]. Microalgae growth and phosphate uptake were found to be linearly proportional to biomass yield.

Inorganic carbon is a necessary component of photosynthesis and, therefore, is important for the growth and reproduction of algae. A decrease of carbon fixation rate means a decrease of the growth rate. Carbon can be used for autotrophic growth in the form of CO_2, bicarbonate, and in the form of acetate or glucose in the heterotrophic mode of cultivation. Under increased CO_2 conditions, the growth rate decreases to varying degrees depending on tested species until it reaches a concentration that completely inhibits growth [108]. Microalgae adapt to these conditions, which may cause secondary inhibitory effects due to the degradation of proteins specialized for response to low CO_2 levels and a decrease affinity for CO_2 [109]. This acclimation consists of the carbonic anhydrase activity decrease and the ability to accumulate inorganic carbon [110].

Micractinium inermum Hoshina et Fujiwara was isolated from a sample taken along the Baydarnaya river bed of Shiveluch volcano (N 56°33.98′, E 161°8.41′) [111] (Fig. 2). This species has attracted the attention of researchers due to its rapid growth rate in a short period of time [112]. Dickinson et al. [113] found the highest growth and CO_2 fixation rates, and biomass yield of *M. inermum* cultures exposed to 1% CO_2 air flow. A further growth rates decrease with CO_2 concentration increasing from 5 to 10% is explained by the lack of acclimatization of the culture to the CO_2 concentration before the experiments [114, 115].

Trace metals are in algae cells in extremely small quantities, but play a significant role in their physiology. Iron (Fe), manganese (Mn), cobalt (Co), zinc (Zn), copper (Cu) and nickel (Ni) are the six major trace elements required by microorganisms for various metabolic functions [116]. Its deficiency limits growth, while excess or high concentrations (above the toxicity threshold) suppress it, disrupt photosynthesis, deplete antioxidant reserves and damage the cell membrane [117].

Iron is responsible for the growth and functioning photosynthesis and respiration of algae, as it serves as a redox catalyst in photosynthesis and nitrogen assimilation, and mediates electron transfer reactions [118]. Iron deficiency contributes to chlorophyll concentration decrease [119] and carotenoid composition reduction [120, 121]. High iron concentration resulted in increased lipid content in *C. vulgaris* culture [122].

Excess of some elements (e.g. Zn and Cu) can cause toxicity [123]. There are a number of functional groups that have a high affinity for metal ions and carry combined negative charge, mainly due to the presence of carboxyl, sulfhydryl and phosphate groups on the cell surface of algae [124]. These groups are binding sites that transport metal ions into the cell across the membrane. Carvalhido et al. [125] proposed to use a soil strain *M. inermum* to assess the toxic effects of copper and glyphosphate (the main component of the RoundUp ULTRA Max® herbicide) by measuring growth inhibition and calculating EC50 values. *M. inermum* growth was completely inhibited at the highest tested copper concentration (0.3 mg/L), resulting in complete cell death, while growth was stimulated at the lowest concentration of 0.03 mg/L.

Deficiency of macro- and microelements leads to viability of algae and cyanobacteria decrease, since it plays an important role in many vital processes. However, knowledge of the species- and strain-specific demands of microorganisms will make it possible to use this information in obtaining valuable compounds from the biomass of these microorganisms.

pH. The concentration of hydrogen ions determines the solubility and availability of CO_2 and essential nutrients, and pH can have a significant impact on algal metabolism [126, 127]. Alteration of soil pH can affect the development and distribution of soil algal communities through inhibition of photosynthesis and enzyme activity [128, 129]. It is believed that cyanobacteria prefer alkaline (pH > 7.0), diatoms—neutral soils (pH 7.0), and some charophytes and green algae are able to live in acidic soils (pH < 6.0) [29]. According to Litvinenko and Zakharikhina [85], "all volcanic soils of Kamchatka are acidic or weakly acidic and contain low concentrations of bases." The soils of alder elfin woodlands typically have the lowest pH of the soil water extract (no higher than 4.22) and the lowest for volcanic rocks contents of bases (1.7–5.9%). The soils of mountainous tundra are characterized by higher pH values (4.8–5.0) and are slightly richer in bases (15–18%).

In algal cultures, pH can increase significantly due to CO_2 uptake [130]. Maximum algae growth occurs at a neutral pH, although the optimum pH is the initial value at which the algae are adapted to grow. Physiological mechanisms through which algae survive at low pH include maintaining a positive membrane potential [131], reducing the permeability of the plasma membrane to protons, and maintaining proton pump activity to keep a neutral cytosol [132–134]. A stable plasma membrane also contributes to the resistance of acidophilic and acidotolerant algae to heavy metals and toxic anions and prevents their penetration into cells [132, 133, 135].

Algae that are tolerant of low external pH values likely have the ability to regulate internal pH in response to external fluctuations. In *Chlorella saccharophila* (Krüger) Migula (synonym *Chloroidium saccharophilum* (Krüger) Darienko et al.), an internal pH of 7.3 was maintained at an external pH of 5.0–7.5; however, a further decrease in pH to 3.0 caused a decrease in cellular pH to 6.4 [136]. The energy required to maintain the internal pH of acid-tolerant algae is conserved as the internal pH decreases. This mechanism for maintaining cellular metabolism gives them an energetic advantage over acidity-intolerant species at low external pH values [117].

Algae strains that are resistant to extreme pH levels have great potential for use in biotechnology. Pollutants in biogas die and resistant algae strains survive at pH > 9.0 [137–139]. The use of carbonate alkaline nutrient media in algal-bacterial photobioreactors promotes long-term efficient biogas production [140].

The main role in the adaptation of photoautotrophs to changes in the acidity of the environment is played by the plasma membrane, the composition and integrity of which determines the acid-alkaline balance of the cell. Algae strains that are resistant to extreme pH levels have great potential for use in biotechnology.

CONCLUSION: FROM ECOLOGY TO BIOTECHNOLOGY

To obtain valuable substances from microalgae and cyanobacteria, it is necessary to take into account the conditions of the natural habitat for initial selection the optimal conditions for their growth. After that, it is possible to identify more suitable parameters to promote the accumulation of biomass and the synthesis of compounds. It is absolutely essential to take into account that microorganisms are influenced by several factors in one moment: high radiation and low pH, high temperature and low pH, or a combination of all three in the case of microorganisms, isolated from hot springs. High insolation, moisture deficiency, low substrate temperatures allow to inhabit volcanic deserts.

During the study of the influence of environmental factors on soil algae of various types of mountain tundra and sparse forests of the Northern Urals, Ellenberg's ecological scales were used [141]. According to the obtained results, nitrogen content ($r = 0.58$; $P = 0.102$) and soil moisture ($r = 0.60$; $P = 0.088$) had the greatest impact on soil algal diversity. Accordingly, the selection of an optimal nutrient medium with the addition of nitrogen (nitrates, ammonium) will permit to maintain the cultures of cyanobacteria and algae isolated during this study.

Probably, multivariate analysis permits to expand the possibilities of laboratory experiments, taking into account the influence of natural ecological factors on microorganisms. Thus, to assess the impact of light intensity, temperature, and their interaction on the density of cultures, the content of chlorophyll a and carotenoids, and the maximum quantum efficiency of PSII of cyanobacteria and microalgae – aerophytes from the southern part of the Baltic Sea, a two-way ANOVA was used [142]. Irradiation and temperature, as well as their interaction, were found to significantly affect the chlorophyll a content in cyanobacteria (*Nostoc* sp., *Synechococcus* sp., and *Aphanothece* sp.; ANOVA, $p < 0.001$, for all) and in the tested green algae strains (*Oocystis* sp., *Coccomyxa* sp., *Kirchneriella* sp.; ANOVA, $p < 0.001$, for all).

To examine the effects of light quality and culture temperature on the growth kinetics and lipid production of *C. reinhardtii,* a two-way ANOVA using regression was applied [143]. It was found that in the late exponential phase, during a sufficient nutrient supply in the medium, the effect of light quality on the lipid synthesis and accumulation is weakly interactive ($P = 0.07$) with the temperature. In the late stationary phase, an increase in the interaction of these factors was observed ($P = 0.02$). Statistical analysis allows to prove the reliability of the obtained results and determine the environmental parameters affecting the productivity of strains.

Protective compounds (pigments, polyols, cryoprotectors, exopolysaccharides, fatty acids, etc.), synthesized by algae and cyanobacteria, promote their survival in the natural environment. Biotechnological research uses these metabolites as highly valuable raw materials to solve various problems. Cultivation of such organisms, taking into account species-specific demands and natural habitat characteristics, will permit choosing a more suitable strain and increasing the yield of valuable components. For example, when choosing a better astaxanthin producer, *C. zofingiensis* will have an advantage over the cryotolerant *C. nivalis* since the former is unpretentious to cultivation conditions.

An important aspect of working with microorganisms that have high production characteristics is maintaining their stability and safety. Probably, maintaining collections of algae and cyanobacteria cultures by routine serial sub-culture cannot guarantee the preservation of valuable production properties [144]. The exact events which cause the loss of these characteristics are most often not obvious. As a solution to this problem, a cryopreservation method has been proposed that ensures the stability of various characteristics that may be unstable when using a conventional maintenance regime [145]. Since this approach also has its drawbacks (the presence of a rigid, sometimes impermeable, cell wall in algae and complex cell structures—vacuoles, flagella insertion points, etc., which hinder the penetration of cryoprotectants), the issue of preserving and maintaining the production characteristics of photosynthetic microorganism strains remains open.

A complex of environmental factors (high temperatures, extreme pH values, high content of toxic elements in the volcanic substrate, low nutrient content, sharp fluctuations in aggregate state of water) determines the structure and uniqueness of the extreme habitats of the Kamchatka Peninsula. To survive under hard conditions, algae and cyanobacteria must have adaptive mechanisms that involve the production of biologically active compounds, which, in turn, are valuable to human. Consequently, the strains of phototrophic microorganisms from Kamchatka soils could considered promising objects for biotechnological production, and the extreme habitats of the peninsula can be considered a favorable environment for conducting large-scale research aimed at finding producers of biologically active compounds.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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