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PHYTOPLANKTON, PHYTOBENTHOS, PHYTOPERIPHYTON

Global Occurrence of Cyanobacteria: Causes and Effects (Review)

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Abstract—This review is devoted to analyzing the global occurrence of cyanobacteria in water ecosystems, the possible causes of this phenomenon, and its consequences. In recent decades, cyanobacteria have been rapidly expanding in waterbodies all over the world. This expansion is accompanied by water pollution with dangerous cyanotoxin metabolites that represents a significant threat to humans, animals, and the environment. Purifying water of cyanobacteria is a serious problem, because it is necessary to eliminate toxins and the unpleasant taste and odor of drinking water, as well as fight the biocorrosion caused by cyanobacterial fouling. Cyanobacterial blooms concern not only issues related to the water supply, but also to fishing, the recreational use of waterbodies, and tourism. Global warming and climate change, the increasing eutrophication of natural waters, and anthropogenic pollution, as well as the unique physiological characteristics of cyanobacteria and their ability to adapt to a variety of environmental conditions, including extreme environments, are among the main factors contributing to the expansion of cyanobacteria.

Keywords: cyanobacterial blooms, cyanotoxins, microcystins, odorants, geosmin, 2-methylisoborneol

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INTRODUCTION

Cyanobacteria (or blue-green algae) were one of the first photosynthetic organisms. The increased interest in this group of organisms in recent decades is due to their rapid spread throughout the world and the colonization of waterbodies of various climatic zones: from the tropics to the Antarctic belt.

Cyanobacteria occur in fresh, brackish, and salt waters; make up a significant proportion of plankton; form cyanobacterial mats on the bottom of lakes; and live in symbiosis with higher plants and fungi (Burford et al., 2018). Being prokaryotes, they are similar to higher eukaryotic algae, but differ significantly from them in the structure and physiological and biochemical properties.

Cyanobacteria produce toxins differing in the biological effects: hepatotoxins, neurotoxins, cytotoxins, and dermatotoxins. As a result of numerous studies, toxin-forming species of gg. such as *Microcystis*, *Cylindrospermopsis* (*Raphidiopsis*), *Dolichospermum, Aphanizomenon, Planktothrix, Nodularia*, etc., have been identified and studied, but a significant number of species have still been insufficiently studied (O'Niel et al., 2012; Burford et al., 2016; Harke et al., 2016; Kurmaer et al., 2016; Li et al., 2016).

The massive development of toxin-producing cyanobacteria negatively affects aquatic ecosystems and leads to a change in the trophic structure of the community, fish death, the depletion of oxygen in the water column, and a deterioration of its quality (Robarts et al., 2005; Briland et al., 2020). Cyanotoxins pose a real threat to the health of humans, animals, and many representatives of plankton; therefore, studies of the potential synergistic action of various biotic and abiotic factors that affect the spread of cyanobacteria, the formation of toxins, and the ratio of toxigenic and nontoxigenic species in freshwater plankton are of particular importance (Kaplan et al., 2012; Rastogi et al., 2015).

Serious economic and social problems are associated with cyanobacteria. The main economic losses from cyanobacterial "blooms" are determined by the costs of purifying water of toxins and eliminating the unpleasant taste and odor of drinking water (Dodds et al., 2008). Many authors note that these problems will intensify on a global scale over time (Wagner and Adrian, 2009; Carey et al., 2012).

Despite the complex nature of this phenomenon, it is being intensively studied all over the world. Some progress has already been achieved, but many issues that are important for effectively protecting against the negative consequences of the massive development of cyanobacteria have not yet been resolved (Scholz et al., 2017). The present review is devoted to issues related to the global spread of cyanobacteria in freshwater waterbodies, the possible causes of this phenomenon, and its consequences.

Properties of Cyanobacteria Contributing to Their Dominance in Waterbodies

Cyanobacteria are an important component of phytoplankton communities; however, their mass development leads to a decrease in species diversity and is accompanied by the dominance of only a small number of species (Molot et al., 2014; Sulis et al., 2014).

As a result of long-term evolution, cyanobacteria acquired the ability to adapt to the most extreme climatic and geochemical conditions (Hallock, 2005; Paul, 2008). Due to the presence of capsules, they are able to withstand high temperatures; cyanobacterial pigments have a photoprotective function, and gas vacuoles make cells buoyant, which allows them to move in the water layer and easily adapt to changes in light levels or nutrient concentrations (Reynolds, 2006). In unfavorable conditions, dormant cells of cyanobacteria, the akinets, sink to the bottom of the waterbody, where they winter, and in spring they germinate and float to the surface (Zilius et al., 2016).

Cyanobacteria are involved in the creation of mutualistic and symbiotic associations with other microorganisms, plants, and animals, which also contributes to their survival in adverse conditions (Paerl, 2017). An example of such associations with fungi is lichens, which are widespread in nature (Tarasova et al., 2012).

These and other properties of cyanobacteria allow them to occupy extreme ecological niches such as ice lakes in Antarctica and hot springs and to dominate plankton and benthos in many regions of the Northern and Southern hemispheres (Carey et al., 2012; Lopes and Vasconcelos, 2011; Quiblier et al., 2013).

Benthic cyanobacteria form thick mats dominated by representatives of gg. *Oscillatoria* and *Phormidium* (Polyak and Sukharevich, 2019b; Heath et al., 2011). Cyanobacteria of gg. *Nostoc*, *Anabaena* (*Dolichospermum*), and *Scytonema* (Smith et al., 2011) are also typical representatives of benthos. In contrast to planktonic cyanobacteria, the mass development of which is characteristic mainly of meso- and eutrophic water bodies, the formation of cyanobacterial mats also occurs in oligotrophic waters (Scott and Marcarelli, 2012). Water in oligotrophic reservoirs is usually transparent; light reaches the bottom, which contributes to the development of benthic cyanobacteria.

The unique morphological, physiological, and biochemical properties of cyanobacteria listed above—their amazing ability to adapt to any environmental factors and survive in extreme conditions—is one of the reasons for their global spread, which, as a natural phenomenon, cannot be eliminated. Favorable environmental conditions, such as an increase in average annual temperatures, climate change, and anthropogenic factors, contribute to the manifestation of these properties of cyanobacteria and, as a consequence, their rapid worldwide expansion.

The Role of Global Warming and Climate Change in the Spread of Cyanobacteria

Cyanobacterial blooms occur mainly when the water temperature reaches 20–25°C, which exceeds the optimum for the development of other representatives of freshwater phytoplankton (Makhalanyane et al., 2015). However, some cyanobacterial species also reproduce in cold water, causing water blooms in lakes under ice in winter, and *Planktothrix agardhii* (Gomont) Anagnostidis & Komárek causes water bloom in water bodies all year round (Halstvedt et al., 2007).

A study of the processes occurring in 143 lakes in Europe and South America, located in different climatic zones, has revealed that, with an increase in water temperature, the occurrence frequency of cyanobacteria increases (Kosten et al., 2012). For example, the cyanobacterium *Cylindrospermopsis* (*Raphidiopsis*) *raciborskii* (Woloszynska) Seenaya & Sabbaraju, a typical inhabitant of subtropical regions, was detected in European lakes (Briand et al., 2004). The authors believe that the widespread occurrence of *C. raciborskii* in European lakes, observed since the end of the last century, is associated with global warming and climate change.

Global warming and associated hydrological changes significantly affect many physicochemical and biological processes, including the metabolism and reproduction of cyanobacteria. Warming can promote the growth of cyanobacteria, since the growth rate rises with increasing temperature (Paerl and Paul, 2012).

In addition, owing to the presence of photoprotective pigments (carotenoids) and ultraviolet absorbing components (mycosporin-like amino acids), cyanobacteria remain viable even at extremely high radiation levels (Paul, 2008; Carreto and Carignan, 2011). Under conditions of UV stress, other protective mechanisms are also activated, for example, the formation of antioxidant enzymes, superoxide dismutase, catalase, and glutathione peroxidase, along with antioxidant compounds, ascorbate, tocopherols, etc. (He and Häder, 2002; Xue et al., 2005).

As a result of global warming and associated climate fluctuations, the duration of rainy and drought seasons is increasing. Frequent severe droughts lead to an increase in water salinity in lakes, rivers, and estuarine zones. In such conditions, many species of cyanobacteria are able to persist for a long time in bottom sediments in the form of cysts (Potts, 1994). Some species of gg. *Anabaena, Anabaenopsis*, *Microcystis*, and *Nodularia* are tolerant to salinity (Tonk et al., 2007).

Since waterbodies differ in size, morphology, salinity, hydrological conditions, and other parameters, special systems are needed to control cyanobacteria, taking into account the complex of different impacts characteristic of each waterbody (Paerl and Paul, 2012).

A rise in average annual temperatures may not only promote the growth of cyanobacteria, but also affect the formation of toxins and the ratio of toxigenic and nontoxigenic species in plankton. It has been shown that species of cyanobacteria *Planktothrix* not forming toxins possess genes encoding the synthesis of a cyclic heptapeptide, microcystin, and it is able to start synthesis of toxins with an increase in temperature (Christiansen et al., 2008). Other authors (Dziallas and Grossart, 2011) also note that, with an increase in temperature, strains of *Microcystis aeruginosa* Kiitz. em. Elenk., which do not have toxic properties, begin to synthesize toxins, and the authors conclude that global warming contributes to an increase in the toxigenic potential of cyanobacteria. The combination of elevated temperature with other abiotic and biotic environmental factors may have a synergistic effect on the percentage of toxigenic species in phytoplankton (Rastogi et al., 2015).

Temperature also affects other features of metabolism in cyanobacteria, including the formation of various structural variants of microcystins. For instance, the synthesis of the highly toxic microcystin LR correlates with a temperature of 25°C, while the synthesis of the less toxic microcystin RR correlates with a higher temperature (Polyak and Sukharevich, 2017). In recent years, many authors (Paerl et al., 2016; Scholz et al., 2017) emphasized the significant effect of temperature on physical, chemical, and biological processes in waterbodies.

It is worth noting that, as a result of both regional and global warming, ice melting occurs earlier and water freezing is delayed (Hodgkins, 2013). This contributes to the high activity and growth of cyanobacteria (Kosten et al., 2012; Paerl and Paul, 2012).

The facts given above indicate that global warming may be considered the most important natural process contributing to the rapid spread and dominance of cyanobacteria in waterbodies. However, it should be noted that the assessment of the influence of this factor on the probability of the global spread of cyanobacteria has been made so far for only a small number of species (Scholz et al., 2017).

The Role of Anthropogenic Pollution of Waterbodies in the Expansion of Cyanobacteria

Over the past century, there has been a constant increase in the number of eutrophied waterbodies related to the intensive development of agricultural and industry, along with urban ones (Conley et al., 2009; Smith et al., 2015). Over the past decades, agricultural production has doubled and irrigated areas have grown, which, in addition, are fertilized with nutrients, nitrogen, and phosphorus (Novotny, 1999; Scholz et al., 2017). Nitrogen and phosphorus introduced into the soil easily penetrate into surface waters.

It is believed that wastewaters are the main source of nutrients (Paerl and Fulton, 2006). Population growth, economic development, urbanization, and imperfect water-treatment systems are causing an increase in the concentration of nitrogen and phosphorus in the waterbodies of many countries (Van Drecht, 2009). The problem of water pollution with nutrients is aggravated by the fact that they play a significant role in the development of mass species of cyanobacteria. The results of many studies confirm the important role of nitrogen and phosphorus in the processes of water blooming (Jiang et al., 2008; Moisander et al., 2009; Kahru et al., 2020).

Nitrogen is an essential nutrient for cyanobacteria, making up a significant portion of their biomass. Cyanobacteria need nitrogen not only for growth, but also for the synthesis of toxins. This primarily refers to cyanobacteria, which belong to not nitrogen-fixing species (Lehtimäki et al., 1997). For example, representatives of g. *Microcystis*, which do not possess a nitrogen fixation mechanism, are able to use organic sources of nitrogen and, first and foremost, free soluble amino acids such as alanine, arginine, leucine, and glutamic acid (Dai et al., 2009).

In addition to nitrogen, phosphorus is an essential element for the growth of cyanobacteria. This chemical element is a necessary component of cellular phospholipids, ATP, and nucleic acids. The data on the effect of phosphorus on the toxin formation of cyanobacteria are ambiguous. Some authors show that phosphorus significantly increases the synthesis of microcystin LR (Kotak et al., 1995); according to the results of others, it does not have a significant effect on the formation of microcystins (Polyak et al., 2013; Watanabe and Oishi, 1985). There is evidence that *Microcystis aeruginosa* forms the maximum amount of microcystin in the conditions of phosphorus limitation (Oh et al., 2000).

Alongside the nutrients themselves, their ratio is also an important factor influencing the dominance of cyanobacteria (Bulgakov and Levich, 1995). The massive development of cyanobacteria is associated with a relatively low ratio of nitrogen and phosphorus concentrations ($N : P < 25$). The concept of phosphorus as the main criterion for controlling cyanobacterial blooms probably requires revision (Rastogi et al., 2015).

Cyanobacteria are photoautotrophic organisms, using the energy of light for their life. In addition, cyanobacteria are able to absorb organic carbon and use it as an energy source. At a low illumination level insufficient for photosynthesis, the heterotrophic utilization of organic substrates becomes an important component of the cyanobacterial survival strategy (Abdullin and Bagmet, 2016).

Some of the organic pollutants of aquatic ecosystems stimulate the growth and toxin production of cyanobacteria. For instance, the herbicide pentachlorophenol promotes the growth of *M. aeruginosa*; the antibiotic amoxylin stimulates the growth and formation of microcystin (De Morais et al., 2014; Liu et al., 2015). A significant increase in the synthesis of microcystin in *M. aeruginosa* was also noted in the presence of a nonionic surfactant, nonylphenol (Polyak and Sukharevich, 2016; Wang et al., 2007). Azole compounds inhibit the growth of cyanobacteria, but can contribute to the formation of more toxic structural variants of cyanotoxins (Polyak, 2015).

Anthropogenic substances entering waterbodies accumulate in bottom sediments and become a source of nutrients for benthic cyanobacteria (Paerl et al., 2016). With an increase in the concentration of nutrients, the turbidity of the water increases, limiting the photosynthetic activity of phytoplankton in the upper layers. Such conditions are favorable for buoyant cyanobacteria that are not nitrogen-fixing. Thus, representatives of the g. *Microcystis* often dominate in polluted lakes with increased turbidity (Paerl and Fulton, 2006).

In polluted waterbodies rich in nutrients, the dominance of cyanobacteria may also be associated with photosynthetic processes. The active photosynthesis upon the intensive reproduction of cyanobacteria is accompanied by a significant consumption of carbon dioxide and a sharp increase in pH (≥10). Such changes in hydrological conditions adversely affect other components of plankton (Paerl and Paul, 2012).

The majority of research on the influence of anthropogenic factors on the distribution of cyanobacteria concerns freshwater cyanobacteria, with marine cyanobacteria being studied to a much lesser extent. Nevertheless, the authors of these studies believe that the global distribution of cyanobacteria in the seas is also largely determined by an increase in the content of nutrients (Glibert and Burford, 2017). There is no doubt that global warming, climate change, and the enrichment of water bodies with nutrients and other pollutants of anthropogenic origin have a cumulative effect on the expansion of cyanobacteria.

Expansion of Toxigenic Cyanobacteria

The production of metabolites with increased toxicity, cyanotoxins, is the main negative and dangerous property of cyanobacteria. The global expansion of toxigenic cyanobacteria poses the most serious threat to the environment (Paerl, 2017). In fresh waters, up to 70% of cyanobacteria are toxigenic (Pham et al., 2015), and even species that do not produce toxins have genes encoding the synthesis of, e.g., microcystins (Christiansen, 2008).

According to their chemical structure, toxins are divided into three groups: peptides, alkaloids, and lipopolysaccharides. Toxins of the third group are a structural component of cell membranes (Voloshko and Pinevich, 2014). The role of toxins of the first two groups in the metabolism of cyanobacteria remains unclear. In cyanobacterial cells, they can perform various functions, including the function of siderophores; they can participate in the adaptation of cyanobacteria to changing environmental conditions (illumination, nutrient content), in the processes of quorum sensing regulation, and in allelopathic interactions (Omidi et al., 2018). Allelopathic interactions, as one of the forms of ecological competition between organisms, are widespread in nature, including aquatic biocenoses (Polyak and Sukharevich, 2019a). The accumulation of toxins in the food chain and a decrease in biodiversity are the ecological consequences of allelopathic effects and increased synthesis of cyanotoxins in the presence of other organisms (Pei et al., 2020)

Cyclic peptides (microcystins and nodularins) are water-soluble and easily penetrate the lipid membranes of all living beings (Table 1). Their high toxicity is determined by the presence of the unique Adda acid (3-amino-9-methoxy-2,6,8-thimethyl-10-phenyldeca-4,6-dienoic acid), which was detected only in cyanobacterial toxins (Harke et al., 2016), and a cyclic structure (Fig. 1). Linear peptides show almost no toxic properties; they are 100 times less toxic than their cyclic equivalents (Namikoshi and Rinehart, 1996)

Potent toxins include saxitoxin and its analogs, collectively known as paralytic shellfish toxins (PSTs). They are a diverse group of heterocyclic compounds (Carmichael, 1997). Anatoxins and PSTs have a pronounced neurotoxic effect (Table 1). Recently, there has been an increase in the number of reports on the release of saxitoxin-producing cyanobacteria from waterbodies not only in tropical and subtropical, but also temperate latitudes (Belykh et al., 2015).

The high toxicity of cyanotoxins is associated with an increased hazard when using water from the freshwater reservoirs and reservoirs in which cyanobacteria develop and for drinking and irrigation purposes, as well for recreational swimming and fishing in fresh and marine waters (Carmichael, 2001).

According to their functional properties, toxins are divided into five groups: hepatotoxins, neurotoxins, cytotoxins, dermatotoxins, and intracellular lipopolysaccharides (Rastogi et al., 2014). B-N-methylamino-L-alanine (BMAA) is also a neurotoxin. This latter nonprotein amino acid was discovered relatively recently, but has already been found in many countries of Africa, Asia, Europe, and America (Polyak and Sukharevich, 2017). VMAA, which is produced by almost all cyanobacteria, is highly toxic and can be the cause of serious diseases such as Alzheimer's and Parkinson's (Popova and Koksharova, 2016; Merel et al., 2013).

Table 1. Main groups of cyanobacterial toxins and their biological activity (according to Voloshko and Pinevich, 2014; Polyak and Sukharevich, 2017; Dittmann et al., 2013)

Toxins	Produces of toxins	Biological activity
	Peptides	
Microcystins	*Microcystis, Anabaena, Nostoc, Oscillatoria, Phormidium et al.*	Inhibit protein phosphatases, disrupt the cytoplasmic membrane, carcinogens
Nodularins	*Nodularia spumigena* Mertens ex Bornet et Flahault	
Cylindrospermopsins	*Anabaena, Aphanizomenon, Cylindrospermopsis, Umezakia*	Inhibit protein synthesis, cause necrotic damage to the liver, kidneys, spleen, lungs, and intestines
	Alcaloids	
Anatoxins	*Anabaena, Oscillatoria, Aphanizomenon, Phormidium*	Neurotoxins, inhibit acetylcholine esterase
Saxitoxin and its analogs	*Anabaena, Lyngbya, Planktothrix, Aphanizomenon, Cylindrospermopsis*	Neurotoxins, block sodium channels
	Lipopolysaccharides	
Lipopolysaccharides	Probably all cyanobacteria	Endotoxins, cause inflammation, irritate the gastrointestinal tract

In studies on toxigenic cyanobacteria, most attention is paid to planktic species; much less attention is paid to representatives of benthic communities of freshwater waterbodies. At the same time, it is known that benthic cyanobacteria produce many toxins, including toxic metabolites characteristic of planktonic forms (Quiblier et al., 2013). Toxin formation and the growth of benthic cyanobacteria, like planktonic bacteria, depend on many physicochemical, climatic, and anthropogenic factors.

In the course of intensive growth, benthic cyanobacteria form thick mats (up to 70 cm in thickness) (Dasey et al., 2005). When a certain thickness is reached, the mats can detach from the substrate and accumulate in the coastal zone. In this case, the risks to humans and animals increase.

Since cyanobacterial blooms are becoming a serious problem for many sectors of the economy, including water supply, fishing, recreational use of water bodies, and tourism (Carmichael, 2001; Paerl et al., 2018), cyanotoxins and their effects on humans are being actively studied. It has been revealed that cyanotoxins can cause various diseases, including fevers, nervous disorders, gastroenteritis, liver and kidney diseases, malignant tumors, and many others (Drobac et al., 2013; Kamal and Ahmad, 2014).

Cyanotoxins enter humans and animals with drinking water, food, and bathing in rivers and lakes, especially during water blooming. Numerous cases of human and animal diseases associated with cyanotoxins have been recorded in Europe, Asia, Africa, Australia, and America (Turner et al., 1990; Ueno et al., 1996; Jochimsen et al., 1998; Codd et al., 2005; Falconer, 2005).

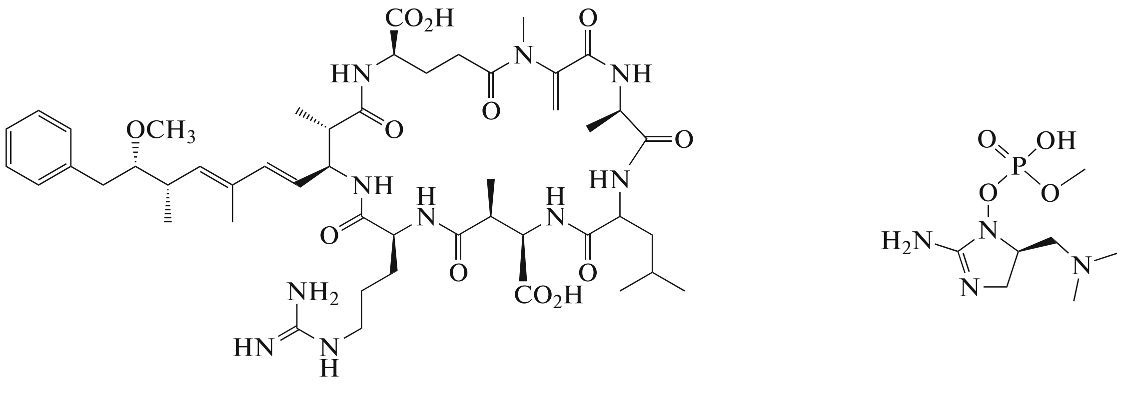
Monitoring and risk-management programs for toxic blooms are being adopted in many countries, but almost all of them concern planktonic cyanobacteria. Despite the fact that the producers of cyanotoxins found in drinking water in many cases are representatives of benthos (Izaguirre et al., 2007; Smith et al., 2012), guidelines for monitoring and managing risks associated with benthic cyanobacteria have been developed in only two countries, New Zealand and Cuba (Quiblier et al., 2013).

In Russia, despite the intensification of studies on the development of mass species of cyanobacteria, these studies are still few and far between as of recent years (Polyak et al., 2011; Rumyantsev et al., 2011; Voloshko and Pinevich, 2014; Polyak et al., 2014; Chernova et al., 2017; Belykh et al., 2020). There is no national program for monitoring toxic blooms and studying their pathogens in Russian Federation.

Cyanobacterial Odorants and Their Negative Effect on Water Quality

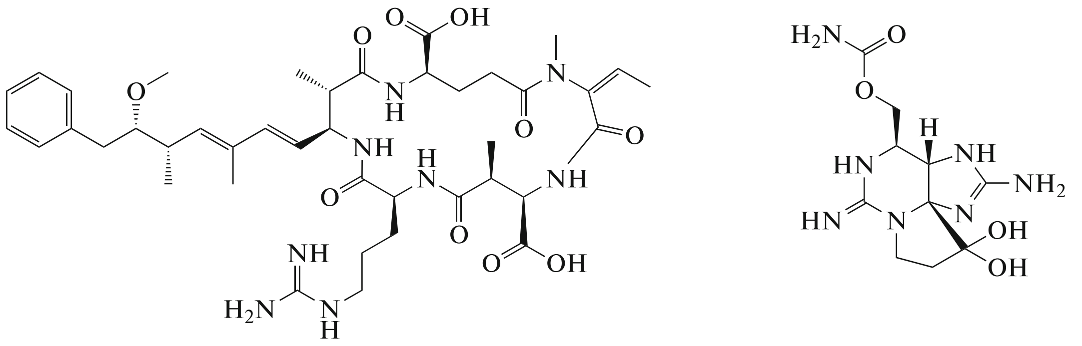
One more negative property of cyanobacteria should be noted, namely, the synthesis of metabolites that impair the organoleptic properties (taste and smell) of drinking water (Lee et al., 2017). The most famous and well-studied odorants are geosmin and 2-methylisoborneol (Fig. 2), each of which exists in the form of both (+) and (–) enantiomers. The presence of odor is mainly associated with (–) enantiomers (Watson et al., 2007).

Geosmin and 2-methylisoborneol occur naturally both simultaneously and separately; the concentration of each of them varies. These substances are nontoxic;



Microcystin

Anatoxin-a(s)



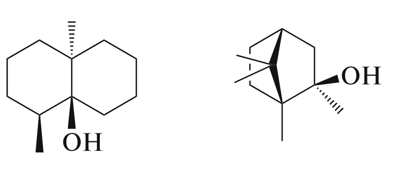
Nodularin

Saxitoxin

Fig. 1. Structures of microcystin, nodularin, anatoxin-a(s), and saxitoxin.

in addition, their formation is episodic, so, even with the annual blooming of the reservoir, the smell may not appear for years.

Odorizing substances are formed by many benthic and pelagic microorganisms, as well as some eukaryotes: fungi, amoeba, and bryophytes (Jüttner and Watson, 2007). They are especially actively synthesized by actinomycetes of g. *Streptomyces*. Nevertheless, cyanobacteria are considered the main source of odorants in nature (Lee et al., 2017).



(a) (b)

Fig. 2. Structures of geosmin (a) and 2-methylisoborneol (b).

Geosmin and 2-methylisoborneol are contained both inside the cells of cyanobacteria and being dissolved in water. The ratio of intra- and extracellular odorants varies depending on the species of cyanobacteria and their physiological state, growth phase, and environmental conditions (Watson et al., 2016). The main mechanism for the release of odorants into the environment is the destruction of cells as a result of various processes (Jüttner and Watson, 2007).

Chemically, geosmin and 2-methylisoborneol are relatively stable; in addition, they are resistant to biodegradation (Peter and von Gunten, 2007). In this regard, they can persist in water for a long time, which complicates water purification (Li et al., 2012). The smell of geosmin is felt at a concentration of 0.001–0.02 μg/L; that of 2-methylisoborneol at 0.002–0.04 μg/L (Butakova, 2013). Under the influence of stress (decrease in temperature, photooxidation, etc.), as well as in late summer and autumn, the number of odorants produced by cyanobacteria and released into the environment increases (Jüttner and Watson, 2007).

Cyanobacteria not only pose a threat to humans and animals, but also require significant costs to purify water from toxins and odorants to create conditions safe for tourism (Ibelings and Chorus, 2007; Dodds et al., 2009;). Global warming and climate change may cause these costs to rise significantly over time.

The fight against biocorrosion (pipelines, equipment for power plants, dams, etc.) caused by cyanobacterial fouling in the form of biofilms also involves significant costs (Rumyantsev et al., 2011). The damage caused by cyanobacteria, disruptions in economic activity, and negative impact on the environment and human health show the need for intensive research by scientists from different countries on the processes of the global spread of cyanobacteria.

CONCLUSIONS

Currently, the rapid spread of toxigenic cyanobacteria in freshwater waterbodies around the world poses a significant threat to humans, animals, and the environment in general. Studies carried out in recent decades have made it possible to achieve real progress in understanding this phenomenon and assessing the effect of various factors on the development and spread of cyanobacteria, but many questions have not yet been answered.

The studies indicate that this dangerous phenomenon is largely determined by the unique physiology of cyanobacteria and their unique ability to adapt to various environmental conditions, including extreme ones. These properties determine their dominance in a wide variety of waterbodies and climatic conditions.

The spread of cyanobacteria in freshwater and marine waterbodies is associated with the constantly increasing eutrophication of natural waters. Many authors believe that the intensification of urbanization processes and population growth in the future will lead to even more active reproduction and an increase in the occurrence frequency of cyanobacteria.

Another major reason for this natural phenomenon is climate change, especially in combination with the eutrophication of waterbodies and the physiological characteristics of cyanobacteria. Laboratory and field observations of the anthropogenic pollution of natural waters with elevated temperatures and an increase in the content of carbon dioxide in the atmosphere create very favorable conditions for the dominance of cyanobacteria in various ecosystems.

Recently, many methods and approaches differing in complexity and cost, both in regards to time and money, have been proposed to solve this problem. According to some authors, in order to control the situation, special systems are needed to reduce the rate and degree of warming and to globally curb the greenhouse effect (Paerl and Paul, 2012). Otherwise, global warming and changes in the physicochemical parameters of waterbodies will contribute to the accelerated spread of cyanobacteria.

The most important tasks include more extensive and in-depth studies of benthic forms on which the distribution and preservation of the viability of cyanobacteria largely depend (Burford et al., 2020; Quiblier et al., 2013).

To reduce the negative consequences of cyanobacterial blooms, the effective environmental monitoring of waterbodies is required, including control over the degree of their eutrophication, studying the qualitative and quantitative composition of phytoplankton, and determining the content of cyanotoxins. Limiting the further spread of toxigenic cyanobacteria can become one of the most difficult tasks of the modern world, which requires laboratory and field research and the combined efforts of biologists, chemists, ecologists, and other specialists from different countries.

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