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Article

Typology of cyanoprokaryotes habitats in Arctic ecosystems based on the analysis of the Svalbard archipelago flora

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Abstract. This study proposes a framework for classifying the habitats of cyanoprokaryotes in Arctic regions, based on the European Nature Information System (EUNIS). Two major habitat groups are identified: freshwater and terrestrial. The latter is further subdivided into subaerophytic (those at the boundary between aquatic and aerophytic environments) and aerophytic (found on rocky substrates and soil surfaces). The variability of polar habitats can be represented along a moisture gradient, ranging from freshwater, through subaerophytic zones, to dry terrestrial environments. Differences in the frequency, amplitude, and regularity of habitat moisture levels lead to the differentiation of cyanoprokaryotes species composition. In the Svalbard Archipelago, four particular habitats support greater diversity and abundance of cyanoprokaryotes: 1) wet walls and rocks, 2) bare soils and biocrust communities, 3) warm, slow-flowing streams, and 4) specific over-moistened habitats – seepages.

Keywords: Cyanobacteria, ecology, functional groups, ecotopes, Arctic

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Научная статья

Типология местообитаний цианопрокариот арктических экосистем на примере анализа флоры архипелага Шпицберген

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Аннотация. В работе предложена основа классификации местообитаний цианопрокариот арктических территорий, построенная на Европейской информационной системе природы (EUNIS). Выделены две больших группы местообитаний: пресноводные и наземные. Последняя, в свою очередь, разделена на амфибиальную и типично наземную подгруппы. Вариабельность полярных местообитаний можно представить в виде градиента увлажнения, который проходит от пресноводных через субаэрофитные до сухих типично наземных. Различия периодичности, амплитуды и регулярности увлажнения местообитаний приводят к дифференцировке видового состава цианопрокариот. Наиболее благоприятными для них в условиях архипелага Шпицберген являются: 1) скальные сообщества с достаточным увлажнением, 2) оголенные грунты, на которых формируются биологические почвенные корочки, 3) медленные хорошо прогреваемые ручьи, 4) специфические переувлажненные местообитания – просачивания.

Ключевые слова: цианобактерии, экология, функциональные группы, экотопы, Арктика

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Introduction

The terrestrial Arctic spans approximately 11 million km², with about 7.2 million km² within the Russian sector. The extreme climatic conditions of Arctic ecosystems and the low availability of essential chemical elements, particularly bioavailable nitrogen, highlight the critical role of organisms like cyanoprokaryotes (cyanobacteria). In Arctic ecosystems, cyanobacteria predominate in most habitats, functioning as primary producers of organic matter (Elster, 2002; Gaysina et al., 2019; Zakhia et al., 2008).

In Arctic water bodies, cyanoprokaryotes form dominant communities in phytoplankton and benthos. In the southern parts of the Arctic, certain species can cause “blooming” in water bodies. In terrestrial high-latitude habitats, cyanoprokaryotes can form visible growths on surfaces and in soil, and they are typical of biological soil crusts.

The reduced competition from higher plants allows cyanobacterial mats to occupy significant areas on exposed substrates. Cyanoprokaryotes are also found within cracks and penetrate rocky ground. Growth within rock fissures provides protection against temperature fluctuations, dehydration, and external physical impacts. Cyanoprokaryotes are often the first organisms to colonize glaciers and moraines (Davyvov, 2011; Kaštovská et al., 2005, 2007; Turicchia et al., 2005). High abundances of cyanobacteria are observed in moss communities in moist habitats along lake shores, streams, and splash zones of waterfalls.

Despite the long history of studying cyanoprokaryotes in the Eurasian Arctic and Subarctic (Davydov and Patova, 2018), their current diversity in this region remains significantly underestimated. Efforts are needed to expand our knowledge of Arctic cyanobacteria.

An analysis of habitat types through long-term studies of cyanobacteria in various Arctic regions, including Svalbard (Davydov, 2013, 2014a, 2016, 2017, 2021a), the Polar Urals (Davydov, 2021b), Gydan peninsula, the Murmansk Region (Davydov, 2009a, b, 2010a, b, 2014b, 2018; Davydov and Redkina, 2021) and a compilation of available data for the entire Eurasian Arctic sector (Davydov, 2022; Davydov and Patova, 2018) has allowed us to identify habitat types specific to cyanobacteria. These have been correlated with the widely used habitat classification system within the European Nature Information System, EUNIS[1].

Materials and methods

Collection of Cyanoprokaryotes in the Svalbard Archipelago was conducted during the summer periods from 2004 to 2016 (excluding 2015) using the traditional route-reconnaissance method (single-day radial walking routes) based on an original methodology for studying microhabitats (Melekhin and Davydov, 2007, 2009).

The collection efforts on Svalbard covered several regions on the following islands: West Spitsbergen, Northeast Land, Prince Charles Land, and Barents Island (Fig. 1).

Species identification was performed based on anatomical and morphological characteristics using an AxioScope A1 light microscope (Zeiss, Germany), equipped with a differential interference contrast (DIC) system. For photo documentation, a ProgRes Speed XT core3 image capture system (Jenoptik, Germany) was used. In some cases, preliminary identification was carried out directly in the field using a Nikon Eclipse 80i microscope. These samples were subsequently re-identified under laboratory conditions. Identification guides and references were employed for the identification process (Komárek and Anagnostidis, 2008a, 2008b; Komárek, 2013).

In total, 753 samples were collected and identified from 290 locations. Detailed characteristics of the local conditions were provided in our previous work (Davydov, 2021a). Additionally, the entire dataset contained in literary sources was incorporated into the study. A total of 235 references from 157 locations are known from the previously published data. Information regarding all the locations from our own collections and the literary references was documented in a specially designed section of “L.” system[2] (Melekhin et al., 2013,2019).

[1] European Nature Information System. Copenhagen, Denmark. Web page. URL: http://eunis.eea.europa.eu (accessed: 10.02.2023).

[2] Cyanoprokaryota part of Information System L. RussiaWeb page. URL: https://isling.org/cyano (accessed: 10.02.2023).

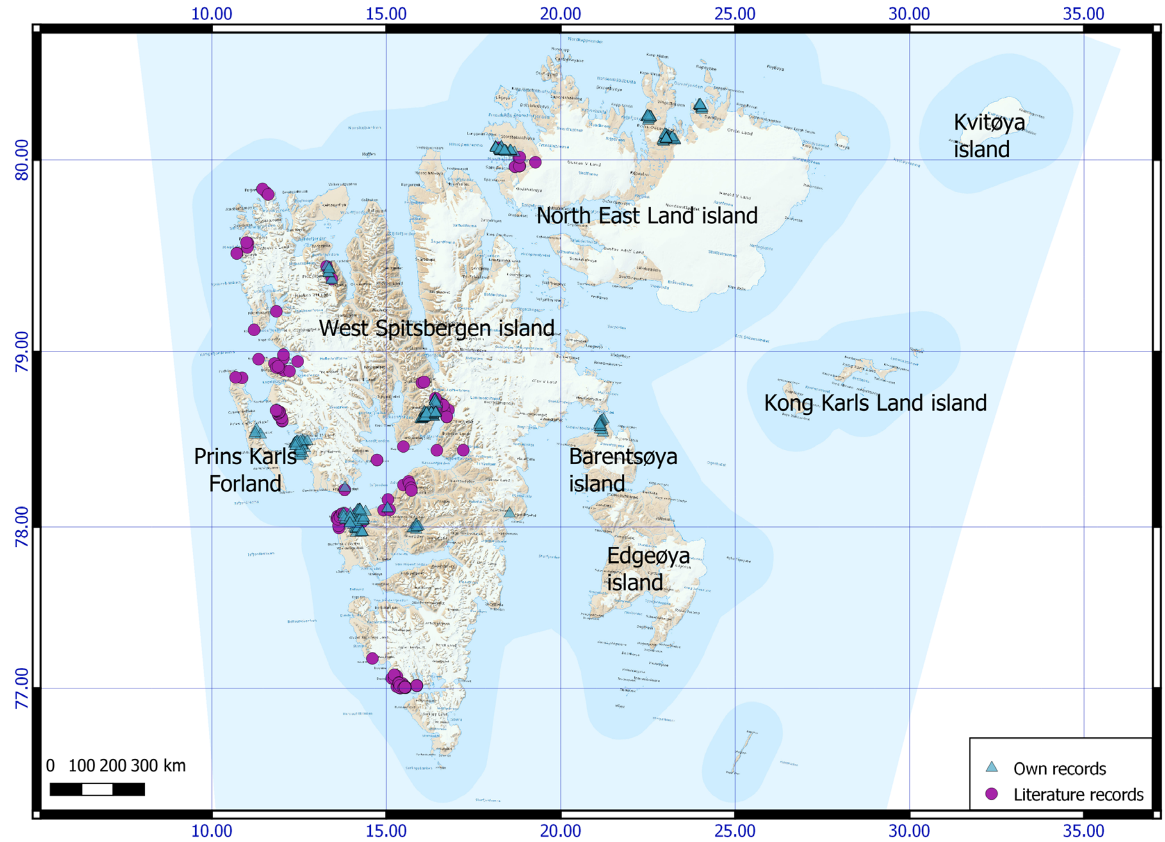

Fig. 1. Cyanoprokaryota sampling sites on the Svalbard Archipelago.

The main concept in the typology of ecological analysis of individual species or the comparative analysis of local flora in different territories is the "habitat". It can be defined as a place where a living organism resides and is characterized by various physical properties, including topography, soil characteristics, climate, water quality, and the array of species that exist there (Davies et al., 2004). We define "microhabitat" as a spatio-temporal continuum limited by the continuity of environmental parameters within a specific habitat, within the amplitude of which the existence of a particular biological species is possible (Melekhin and Davydov, 2007).

Results

During the analysis of the species composition of cyanobacteria in Arctic ecosystems or the patterns of their distribution within landscapes, it becomes evident that certain groups of species are distinctly associated with specific habitat types (biotopes), and individual species are often specialized for particular microhabitats.

The key factor determining the development of cyanobacteria should indeed be considered as the level of moisture or water availability. In terrestrial polar ecosystems, many plants place a higher importance on moisture conditions than mineral nutrition or the cumulative effective temperature sum for their growth and survival (Bliss et al., 1994; Kennedy, 1993; Svoboda and Henry, 1987). This statement can also be applied to the algal flora (Elster, 2002). The distribution, abundance, and species richness of algae vary depending on the characteristics of their habitat (microenvironments). In places with a stable supply of moisture and nutrients, both the abundance and species diversity of cyanobacteria tend to be relatively high. However, as natural conditions deteriorate, primarily due to factors related to dehydration, both the abundance and species diversity decrease.

Habitat type classification

There are two ecological groups of species according to habitat type: aquatic and terrestrial (Elster, 2002; Metting, 1981) (Table 1). The latter can be sub-divided into subaerophytic (at the margins between aquatic and aerophytic habitats) and aerophytic (inhabitants of rocky substrates and soil surfaces). Subaerophytic habitats occupy an intermediate position between aquatic and typically terrestrial biotopes. The variability of polar habitats can indeed be conceptualized as a gradient of moisture, ranging from typically aquatic environments through amphibious habitats to dry terrestrial ones. These habitat groups differ in terms of periodicity, magnitude, and regularity of moisture availability (Kvíderová et al., 2019) (Table 2). The natural response to the differentiation of habitats is the development of various adaptive strategies by the species inhabiting them, which in turn shapes the composition of species within those habitats.

As with any classification of natural objects that exhibit a continuum, it is important to recognize that such classifications are inherently conditional. J. Elster (2002) inclusion of nearly all types of habitats in which liquid water is present for most of the summer period, in the transitional water-terrestrial group seems to be incorrect.

Based on our own experience and taking into account published data, we propose the following framework for the classification of cyanoprokaryote habitats in Arctic regions. This classification appears to align with the 2012 EUNIS. In essence, the EUNIS habitat typology resembles the approach of L.G. Ramensky (Golub, 2021), who argued that a combination of environmental conditions determines a habitat. According to Ramensky, a habitat represents a specific “potential set of conditions” that can give rise to various environments depending on the formed phytocoenosis (Ramensky, 1971).

It's understandable that comprehensive classification systems like EUNIS can include numerous fine-grained elements that may not be directly applicable to the analysis of Arctic regions, which often have distinct and unique ecological characteristics. Likewise, some elements in the cited classification may be absent due to the specific ecological conditions in Arctic environments.

Characteristics of the Cyanoprokaryote species composition in the conditions of Svalbard

Let's delve into greater detail regarding the species composition of cyanobacteria in different habitats in Svalbard, recognized as one of the most extensively studied regions within the entire Euro-Asian Arctic sector, based on the established classification.

A. FRESHWATER

A1. Inland surface waters

This group includes all water bodies located on the continent, excluding snowfields and glaciers.

A1-1. Surface standing waters

This group comprises stagnant or still water bodies. Based on the EUNIS classification, only two groups of these water bodies are identified on Svalbard: permanent oligotrophic water bodies and permanent lakes, the majority of which remain ice-covered for most of the summer.

Permanent oligotrophic lakes are widespread across the archipelago. However, research on the large lakes of Svalbard remains insufficient. Sampling has been conducted throughout the waters, but only Linnévatnet, Stemmeatnet, and Kongressatnet lakes have been studied in detail (Davydov et al., 2013). Lake Linnévatnet, in particular, merits attention due to its significant depth, reaching 35 m. This depth results in low temperatures (2.4 °C at a depth of 6 m and 2.6–2.9 °C at the surface during sampling on July 13, 2011) and limited cyanobacterial richness, with only isolated cells of *Leptolyngbya angustissima* (W. West et G.S. West) Anagn. et Komárek being observed. Several large lakes located in other areas were studied without the use of boats; plankton and benthos were collected from the coastal zone.

In contrast, numerous small water bodies are abundant on Svalbard. Typically, these have a depth of approximately 1.5 meters, allowing for relatively efficient heating and abundant growth of algal vegetation.

Permanent or almost permanent ice formations of lakes are a distinctive feature of the hydrological network in the archipelago due to its climatic characteristics and the widespread presence of glaciers.

In this study, we do not differentiate the species composition of lakes into subgroups. One reason for this is the need to account for published data, which may not always provide specific details about the type of surveyed water bodies. By consolidating all types of water bodies, we can collectively characterize benthic, planktonic, and tychoplanktonic communities.

Table 1. Types of cyanoprokaryotes habitats of Svalbard.

A. AQUATIC	**B. TERRESTRIAL**	
	Ba. Subaerophytic	**Bb. Aerophytic**
A1. Inland surface waters	***Ba1. Coastal habitats***	***Bb1. Tundra***
A1-1. Surface standing waters	Ba1-1. Coastal dunes and sandy shores	***Bb2. Grasslands***
A1-1.1. Plankton	Ba1-2. Coastal shingle	***Bb3. Enriched grassland under bird colonies***
A1-1.2. Benthos	Ba1-3. Rock cliffs, ledges and shores	***Bb4. Inland unvegetated or sparsely vegetated habitats***
A1-1.3. Tychoplankton	***Ba2. Temporary ponds and pools***	Bb4-1. Biological soil crusts
A1-2. Surface running waters	***Ba3. Littoral zone of inland surface waterbodies***	Bb4-2. Small caves
A1-2.1. Thermal springs	Ba3-1. Shingle and sandy shores of freshwater lakes	Bb4-3. Screes
A1-2.2. Permanent non-tidal, fast, turbulent watercourses	Ba3-2. Shingle and sandy shores of streams	Bb4-4. Rocky outcrops
A1-2.3. Permanent non-tidal, smooth-flowing watercourses	Ba3-3. Shingle and sandy shores of rivers	Bb4-5. Large boulders on a plain
A1-2.4. Rivers	***Ba4. Minerotrophic marshes/ wetlands***	***Bb5. Snow or ice-dominated habitats***
	Ba5. Seepages	Bb5-1. Glacial moraines and cryoconite
		Bb5-2. Cryogenic landforms

A1-1.1. Plankton

The planktonic communities exhibit relatively low species richness (27 species) despite being well-studied (with 82 recorded occurrences). Here, similar prevalence is observed among: *Aphanocapsa incerta* (Lemm.) G. Cronberg et Komárek, *Chroococcus minutus* (Kütz.) Näg., *Nostoc kihlmanii* Lemm., *Pseudanabaena catenata* Laut., *Woronichinia compacta* (Lemm.) Komárek et Hindák (Fig. 2).

A1-1.2. Benthos

For the benthic communities in the lakes of Svalbard, it is characteristic to have relatively few findings of cyanobacteria (57 in total). A total of 32 species have been recorded in these communities. Among them, *Nostoc commune* Vauch. ex Born. et Flah. (7 occurrences). Additionally, *Calothrix parietina* Thur. ex Born. et Flah. (5), *Leptolyngbya gracillima* (Hansg.) Anagn. et Komárek (4), *Phormidesmis nigrescens* (Komárek) Raabová et al. (Davydov and Vilnet, 2022) (4), *Aphanocapsa grevillei* (Berkeley) Rabenh. (3), *Oscillatoria tenuis* C. Ag. ex Gom. (3), and *Phormidium uncinatum* Gom. ex Gom. (3) were also not uncommon. Based on the species composition, it is evident that benthic communities are not highly specific habitats for cyanobacteria in Svalbard, as the dominant species here are the most adaptable. Some species are associated with lake shores but can also be found in the benthos (such as *Chamaesiphon polonicus* (Rost.) Hansg., *Chroococcus cohaerens* (Bréb.) Näg., *Gloeocapsa kuetzingiana* Näg., *Oscillatoria tenuis*, *Pseudanabaena frigida* (Fritsch) Anagn., among others). Additionally, specific inhabitants that are found exclusively in this habitat have been identified in the lake benthos, including *Geitleribactron periphyticum* Komárek, *Leibleinia epiphytica* (Hieron.) Compère, *Nostoc pruniforme* (L.) C. Ag. ex Born. et Flah., and *Rivularia* cf. *dura* Roth ex Born. et Flah.

In the conditions of Svalbard, within the benthic assemblages formed by mats of *Leptolyngbya* spp., several planktonic species are also present. These include *Snowella lacustris* (Chodat) Komárek et Hindák and *Woronichinia karelica* Komárek et Komárk.-Legn.

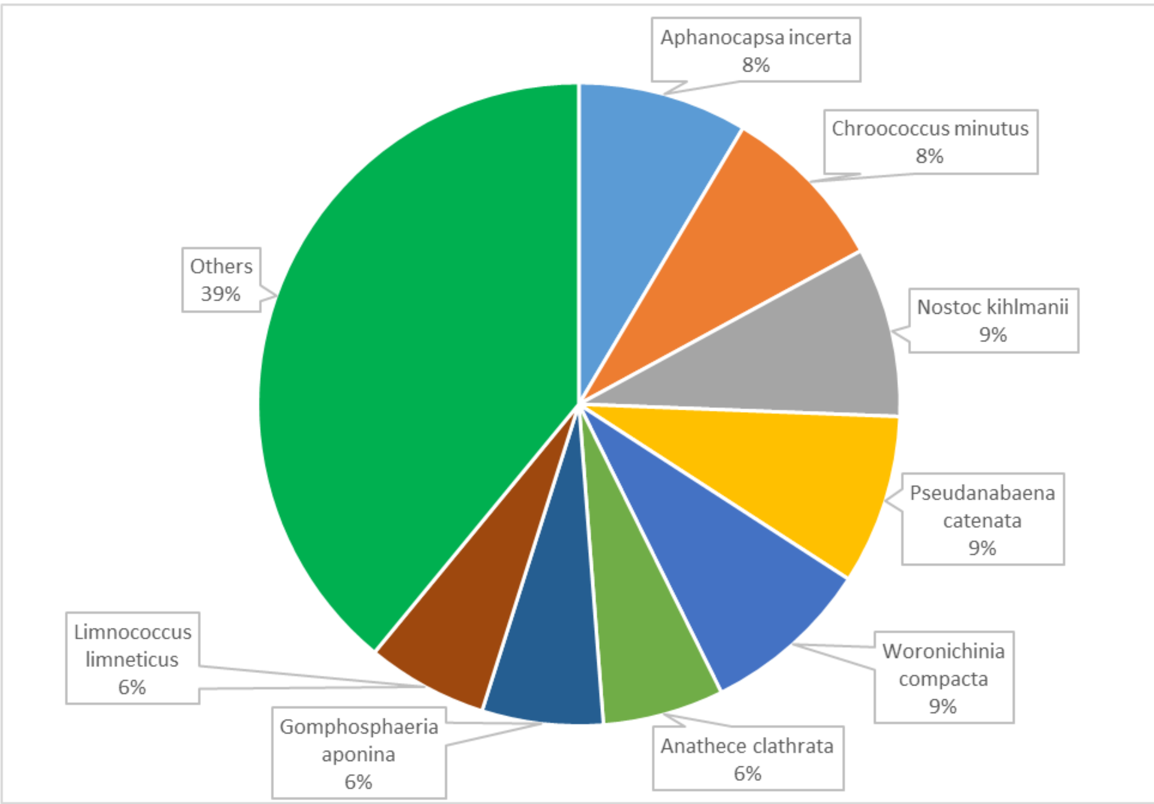

Fig. 2. Occurrences of cyanoprokaryota in plankton communities of oligotrophic lakes.

Table. 2. Ecological characteristics of habitats of cyanoprokaryotes of Svalbard. T – temperature level, V – factor variability, PAR – illumination level; [1] – excluding drying out, [2] – physiological drought at low temperatures.

Habitats	Temperature		Freezing	illumination		Water availability	Desiccation
	T	V		PAR	V		
			Aquatic habitats				
Standing waters	low	low	seasonal	low	low	permanent	no[1]
Running waters							
Thermal springs	high	low	no	high	high	permanent	no
Permanent fast, turbulent watercourses	low	low	seasonal	high	high	permanent	no
Permanent smooth-flowing watercourses	medium / high	high	seasonal	high	high	permanent / occasional	occasional
Rivers	low / medium	low	seasonal	low	low	permanent	no
			Subaerophytic				
Coastal habitats							
Temporary ponds and pools	medium / high	high	seasonal	high	high	occasional	occasional
Littoral zone of inland surface waterbodies	low / high	high	seasonal	high	high	occasional	occasional
Minerotrophic marshes	medium / high	high	seasonal	high	high	permanent / occasional	sparse

Habitats	Temperature		Freezing	illumination		Water availability	Desiccation
	T	V		PAR	V		
Seepages	medium / high	high	seasonal	high	high	occasional	occasional / seasonal
Aerophytic							
Tundra	medium / high	high	seasonal	high	high	occasional	occasional
Grasslands	medium / high	high	seasonal	high	high	low	permanent
Enriched grassland under bird colonies	medium / high	high	seasonal	high	high	low	occasional
Inland unvegetated or sparsely vegetated habitats							
Biological soil crusts	medium / high	high	occasional / seasonal	high	high	low	occasional
Small caves	medium / low	high / medium	occasional / seasonal	medium / low	low	low	occasional
Screes	medium / high	high	occasional / seasonal	high	high	low	permanent
Rocky outcrops	medium / high	high	occasional / seasonal	high / medium	high	occasional	occasional
Large boulders on a plain	medium / high	high	occasional / seasonal	high	high	low	permanent
Snow or ice-dominated habitats	low	low	permanent	high	high	occasional	no[2]

A1-1.3. Tychoplankton

These are algal assemblages formed on the bottom of water bodies but transitioning into plankton. This situation is characteristic of both large and small lakes. In Svalbard, 17 species have been recorded in such habitats: *Anathece clathrata* (W. West et G.S. West) Komárek et al., *Calothrix parietina*, *Chroococcus minutus*, *Jaaginema profundum* (Schröt. et Kirchn.) Anagn. et Komárek, *J. subtilissimum* (Kütz. ex Forti) Anagn. et Komárek, *Kamptonema chlorinum* (Kütz. ex Gom.) Strunecký et al., *Leptolyngbya angustissima*, *Leptolyngbya* sp., *Limnothrix mirabilis* (Böcher) Anagn., *Nostoc* sp., *Oscillatoria anguina* Bory ex Gom., *O. lutea* Ag. ex Gom., *O. tenuis*, *Phormidium uncinatum*, *Stigonema hormoides* (Kütz.) Born. et Flah., *Synechocystis aquatilis* Sauv., and *Synechocystis* sp. All species are found one time.

A1-2. Surface running waters

The group of running water basins includes fast turbulent streams, slow streams, thermal springs, and rivers.

A1-2.1. Thermal springs

The flora of cyanobacteria on the Sverrefjellet Mountain in the Bockfjorden region, which is the only area on the archipelago where it has been studied, is associated with residual volcanism. Two thermal springs are located in this area, and the cyanobacterial flora in both springs is similar, comprising seven species: *Chamaesiphon confervicolus* A. Braun, *Chroococcus minor* (Kütz.) Näg., *Kamptonema formosum* (Bory ex Gom.) Strunecký et al., *Leptolyngbya laminose* (Gom.) Anagn. et Komárek, *Microcoleus autumnalis* (Trev. ex Gom.) Strunecky et al., *Phormidium aerugineo-caeruleum* (Gom.) Anagn. et Komárek, and *P. ambiguum* Gom. The two species, *Chamaesiphon confervicolus,* and *Leptolyngbya laminosa* are unique to this habitat.

A1-2.2. Permanent fast turbulent watercourses and waterfalls

Permanent fast streams are typically glacier outflows characterized by their high flow velocity, temperatures slightly above freezing, and turbid water. Algal vegetation in these watercourses consists of epiliths that form slimy growths on the surfaces of large boulders. These are typically low-diversity communities. In fast streams of Svalbard, you can frequently encounter species such as *Microcoleus autumnalis*, *Chamaesiphon polonicus*, *Trichocoleus delicatulus* (W. West et G.S. West) Anagn., *Schizothrix facilis* (Skuja) Anagn. and less frequently *Phormidium uncinatum*.

This category also includes cyanobacteria from waterfalls. In cases of small drops and low water flow, waterfalls exhibit rich vegetation, though specific species are absent. Alongside the aforementioned species characteristic of fast streams, one can also discover benthic inhabitants of slow streams and lakes, such as *Leptolyngbya compacta* (Hansg. ex Hansg.) Komárek, *Phormidium interruptum* Kütz. ex Gom., and *Cyanothece aeruginosa* (Näg.) Komárek.

In total, 42 species of cyanobacteria have been recorded in this group, 27 of which were also found in slow streams. However, the frequency of findings of these species in calmer and warmer water flows is significantly higher. For example, *Microcoleus autumnalis* has been indicated 13 times in fast streams and 42 times in slow streams, *Phormidium uncinatum* – 5 times in fast streams and 36 times in slow streams, *Chamaesiphon polonicus* – 6 times in fast streams and 20 times in slow streams, and so forth.

Eight species were exclusively found in this type of habitat, among which *Chamaesiphon rostafinskii* Hansg., and *Schizothrix facilis* stand out in terms of frequency of occurrence.

A1-2.3. Permanent smooth-flowing watercourses

Slow streams are characterized by low flow velocities, shallow depths, and high water transparency. These streams warm up more easily compared to fast streams, with 105 species recorded in this habitat. The total number of occurrences is also high, making slow streams the second-largest group after rocky habitats, accounting for 13% of all records. The most common species are *Microcoleus autumnalis* (11.6% of all records in this habitat), *Phormidium uncinatum* (9.9%), and *Chamaesiphon polonicus* (5.5%). The first two species form benthic mats that may contain other species, while *Chamaesiphon polonicus* grows as an epilithon but can also be part of the mats. *Microcoleus autumnalis* is more frequently found in very small streams. The rocky substrates along the streams can also be covered by other cyanobacterial species, such as *Ammatoidea normanii* W. West et G.S. West, *Aphanocapsa grevillei*, *A. muscicola* (Menegh.) Wille, *A. rivularis* (Carm.) Rabenh., *Tolypothrix distorta* Kütz. ex Born. et Flah., and *T. tenuis* Kütz. ex Born. et Flah.

In the upper reaches of slow streams, often originating from snow patches, *Phormidium uncinatum* is the "pioneer" species. Further downstream, it is joined by *Leptolyngbya aeruginea*, (Kütz. ex Hansg.) Komárek, *L. compacta*, and *L. valderiana* (Gom.) Anagn. et Komárek. The small pebbles on the streambed are a characteristic habitat for *Dichothrix gypsophila* (Kütz.) Born. et Flah., which is also common in ephemeral waters, small lakes, and can occasionally be found on rocks.

In addition to the similarity in species composition with fast-flowing streams, there is also an affinity in the flora of slow streams and the littoral zones of lakes (33 shared species), the benthos of lakes (22), and especially the flora of streams and puddles (45).

A1-2.4. Rivers

In Svalbard, rivers are typically multi-channel, meandering, and not very deep. They are located in mountain valleys and usually occupy a significant portion of the valley's width, sometimes creating stagnant waterlogged mossy swamps or areas of mobile viscous alluvium. These rivers are primarily fed by glacier and snowmelt. The glacier-fed runoff in the upper reaches of the rivers forms turbulent flows of cloudy cold water, differing from fast streams only in higher flow rates. This has an adverse effect on the species richness of cyanobacteria. In the lower reaches, the flow rate slows down, but water transparency and temperature often remain low.

In total, seven species have been recorded in the rivers (*Chroococcus minutus*, *C. montanus* Hansg., *Gloeocapsa compacta* Kütz., *Leptolyngbya tenuis* (Gom.) Anagn. et Komárek, *Merismopedia minima* Beck, and *Microcoleus autumnalis*, *M. favosus* (Gom.) Strunecky et al.), each of which was collected only once. The species composition of cyanobacteria in the middle and lower reaches of rivers is similar to that in smaller watercourses, such as streams.

B. TERRESTRIAL

Ba. Subaerophytic

In terms of frequency of occurrence, subaerial habitats are the most common in high latitudes; in these habitats, cyanobacterial species richness is the highest.

Ba1. Coastal habitats

These are those located above the tidal level but directly along the coast, experiencing marine influence in the form of splashes and aerosols. In group Ba1, three subgroups are distinguished.

Ba1-1. Coastal dunes and sandy shores.

This subgroup has relatively sparse vegetation, often dominated by communities of *Puccinellia phryganodes* (Trin.) Scribn. et Merr., and *Stellaria humifusa* Rottb. Cyanobacteria are relatively common in such habitats, with a total of 84 records comprising 28 species. Small growths may occur within the sand, at a depth of about 1 cm or on its surface. Noticeable mats are formed by *Oscillatoria tenuis*, and *Pseudanabaena frigida*. There are occasional colonies of *Nostoc commune,* the most common species in these habitats, sometimes -*Anabaena inaequalis* (Kütz.) Born. et Flah., *Aphanocapsa grevillei*, *A. muscicola*, and *Gloeocapsa violascea* (Corda) Rabenh. (Fig. 3).

Ba1-2. Coastal shingle habitats in Svalbard are often devoid of cyanobacteria. In such habitats, only the following cyanobacteria have been found: *Aphanocapsa grevillei, A. muscicola,* and *Calothrix parietina*.

Ba1-3. Rock cliffs, ledges and shores in Svalbard primarily consist of hard rock formations and are mainly covered with lichens of the genera *Caloplaca* spp. и *Verrucaria* spp. Among algae, *Prasiola* sp., and *Ulothrix flacca* (Dillw.) Thur. are occasionally found. Cyanobacteria are scarce in these environments, with only*Gloeocapsa atrata* Kütz.

Unvegetated rock cliffs, ledges, shores and islets may have algae in rocky crevices but do not harbor cyanobacteria.

Rock cliffs, ledges and shores with vegetation are more diverse in cyanobacterial species. Here, you can find species such as *Jaaginema kuetzingianum* (Näg. ex Gom.) Anagn. et Komárek, *Leptolyngbya gracillima*, *Nostoc commune*, *N. punctiforme* (Kütz. ex Hariot) Hariot, *Oscillatoria tenuis*, and *Phormidium kuetzingianum* (Kirchn. ex Gom.) Anagn. et Komárek. It appears that the presence of vegetation and the formation of primary soil enable the colonization of terrestrial cyanobacteria species of non-marine origin in these habitats.

For the subgroup a total of seven species have been recorded, with a relatively small overall number of findings, totaling 11. Among these, *Gloeocapsa atrata* (4) is the most frequently encountered, with four sightings.

Across the entire coastal habitats group, a total of 32 cyanobacterial species have been discoverd.

Ba2. Temporary ponds and pools

In addition to typical water bodies, the flora of small ephemeral water bodies and puddles deserves special attention. These water bodies often form over established vegetation and exhibit a complex composition of cyanobacterial flora. Cyanobacterial growths in puddles can take the form of mats, where

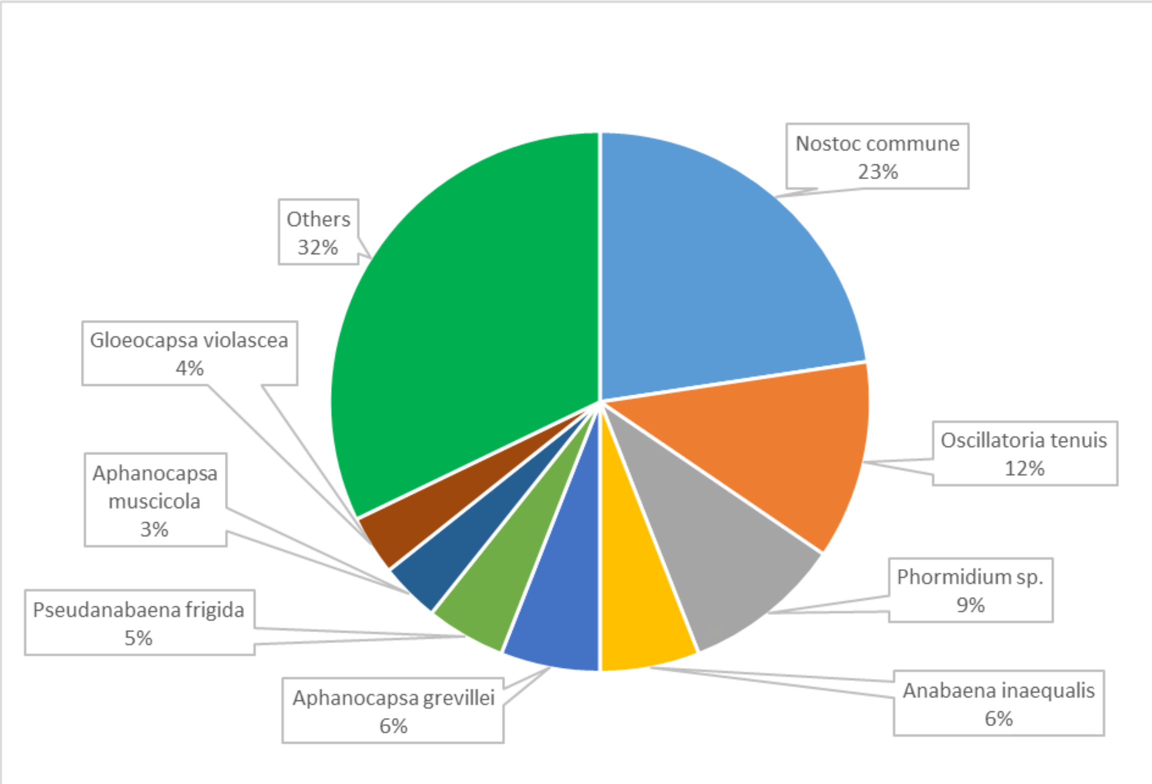

Fig. 3. Occurrences of cyanoprokaryota on sandy sea coasts and sea marshes.

the dominant species are similar to those found in the littoral zones of lakes. Alternatively, they can appear as individual colonies on pebbles or soil, primarily featuring species common in seepages, wet tundra, or bog environments. In puddles, 95 cyanobacterial species have been recorded (7.6% of all observations). The most common species is *Nostoc commune* (20 records), with characteristic species including *Chroococcus turgidus* (Kütz.) Näg., and *Microcoleus autumnalis* (Fig. 4).

Specific species (*Aphanocapsa delicatissima* W. West et G.S. West, *Aphanothece nebulosa* Skuja, *Calothrix fusca* Born. et Flah., *Clastidium cylindricum* Whelden, *Johanseninema constrictum* (Szafer) Hasler et al., *Komvophoron groenlandicum* Anagn. et Komárek, *Leptolyngbya margaretheana* (G. Schmid) Anagn. et Komárek, *Lyngbya aestuarii* Liebman ex Gom., *L. martensiana* Menegh. ex Gom., *Nostoc zetterstedtii* Aresch. ex Born. et Flah., *Oscillatoria simplicissima* Gom., and *Schizothrix borealis* P. Richt.) are mostly noted only once.

Ba3. Littoral zone of inland surface waterbodies

Ba3-1. Shingle and sandy shores of freshwater lakes

The littoral zone of lakes is not rich in species, with 59 cyanobacterial taxa found here (5.6% of all observations). The most frequently encountered species in this zone are *Nostoc commune*, *Calothrix parietina*, and *Dichothrix gypsophila*.

Small lakes on flat terraces gradually dry up, and cyanobacterial mats form on their shores. The most common species in such communities are *Phormidium uncinatum*, which occupies the upper layer of the mats, *Leptolyngbya* cf. *gracillima* and *Pseudanabaena* cf. *minima* (G.S. An) Anagnostidis, forming the lower layer. The areas covered by such growths usually amount to several square meters.

Mats involving representatives of the genus *Petalonema* (*Petalonema alatum* Berk. ex Kirchn., and *P. crustaceum* C. Ag. ex Kirchn.) are less common. As the shores of water bodies become overgrown, fungal and moss-like organisms actively infiltrate cyanobacterial communities.

Ba3-2. Shingle and sandy shores of streams

The shores of streams contain 47 species of cyanobacteria. The flora of this habitat has a transitional character with species typical of tundra, as well as benthic stream dwellers. In addition to the most common *Nostoc commune,* other species more frequently encountered include *Aphanocapsa gre-*

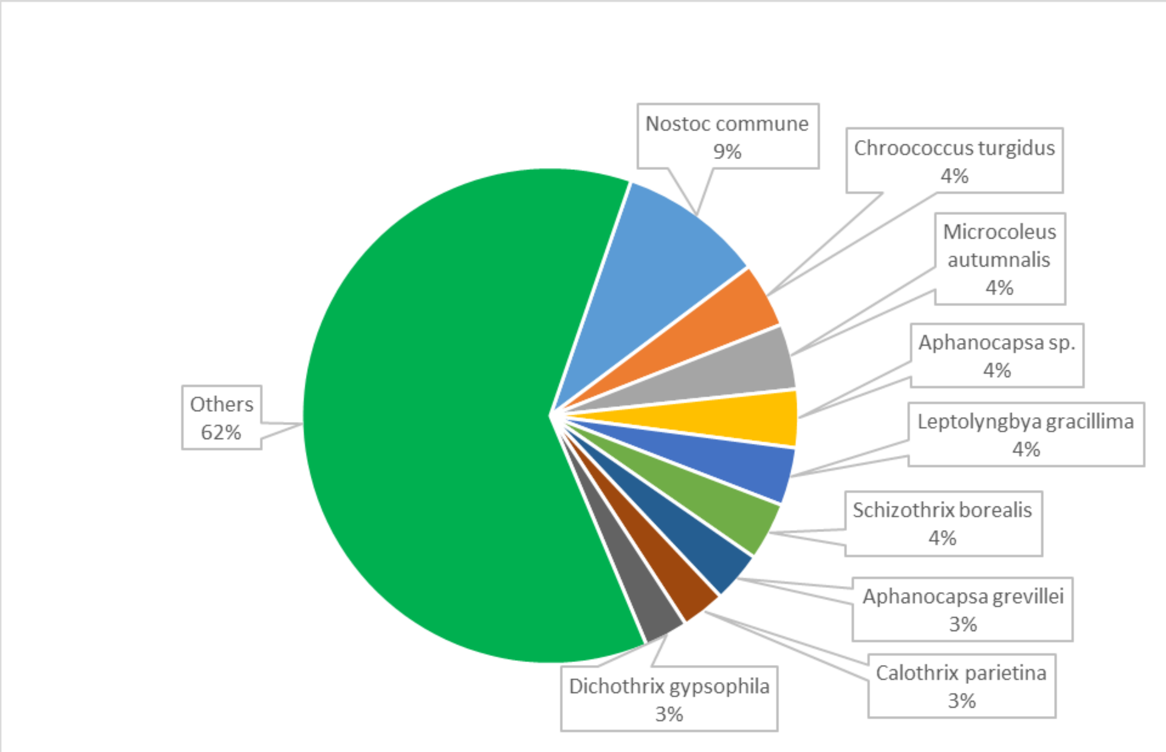

Fig. 4. Occurrences of cyanoprokaryota in ephemeral pools and dried-up ponds.

villei, *Tolypothrix distorta*, *Chroococcus pallidus* (Näg.) Näg., *Gloeocapsa violascea*, and *Petalonema incrustans* (Kütz.) Komárek.

The list of specific taxa is relatively small:*Anabaena catenula* (Kütz.) Born. et Flah., *Dichothrix gelatinosa* Böcher, *Phormidium terebriforme* (C. Ag. ex Gom.) Anagn. et Komárek, *Pseudanabaena biceps* Böcher, and *Rhabdoderma irregulare* (Naumann) Geitl.

Ba3-3. Shingle and sandy shores of rivers

Riverbanks become overgrown with cyanobacteria only when bare alluvial deposits are present. In this habitat, only seven species have been found: *Calothrix parietina*, *Gloeothece confluens* Näg., *Leptolyngbya gracillima*, *Nostoc commune*, *Phormidium* cf. *calcareum* Kütz. ex Gom., *Pseudanabaena frigida*, and *Trichocoleus sociatus* (W. West et G.S. West) Anagn.

Ba4. Minerotrophic marshes/wetlands

Wetlands in the tundra are formed in the valleys of large rivers, where mosses dominate, forming hummocks and peatlands (Koroleva, 2016). In such habitats, 24 species of cyanobacteria have been identified, with *Microcoleus favosus* being the most frequently encountered. Cyanobacteria in minerotrophic marshes grow both in peatlands, forming growths at the bottom, and as epiphytes on mosses. The species composition of bogs is most similar to the flora of coastal sandy marshes, with 11 species in common.

Ba5. Seepages

The continFuous melting of snow during the summer period is accompanied by abundant runoff. In permafrost conditions, water percolating through the soil layer encounters an impediment and often resurfaces, leading to the over-hydration of the upper soil horizons.

In this type, 98 species are recorded (10.6% of all findings). On seepages, you can find common aerophytic species such as *Gloeocapsa kuetzingiana*, *G. sanguinea* (C. Ag.) Kütz., and *G. violascea*, as well as species more commonly found in ponds and streams: *Chroococcus turgidus*, *Microcoleus autumnalis*, *Oscillatoria tenuis*, *Phormidium kuetzingianum*, and *P. uncinatum*.

The most frequent species here are *Nostoc commune*, *Leptolyngbya gracillima*, *Microcoleus vaginatus* Gom. ex Gom., and *Dichothrix gypsophila* (Fig. 5).

Bb. Aerophytic

This group of cyanobacteria inhabits more dynamic environmental conditions than aquatic and subaerophytic forms. Here, there are greater fluctuations in factors, including potential moisture deficits and variations in air humidity. In Arctic conditions, excessive insolation can also be observed.

Bb1. Tundra

In Svalbard, the prevalent ground habitats are wet mossy tundras. There are a total of 66 species in this category (4.8% of all findings). Probably the most widespread and characteristic for any tundra habitat type, especially wet tundras, is *Nostoc commune* (35 records). Undoubtedly, this is the most typical species in Svalbard, found everywhere and able to thrive in various terrestrial habitats, from bare ground on glacier nunataks to rocky outcrops and the bottoms of small ponds. In wet mossy tundras, it can form extensive growths measuring tens of square meters. Nostoc colonies cover the surfaces of mosses, penetrate moss hummocks, and freely float in the water in small depressions. The other species are encountered much less frequently. Other typical species here include *Chroococcus cohaerens*, *Microcoleus vaginatus*, *Nostoc punctiforme*, and *Tolypothrix tenuis*. Dry tundra variants dominated by mosses, lichens, or variants of willow, Dryas, and Cassiope tundras are less suitable for cyanobacteria development. Two probable reasons underlie this: inability to compete with other groups and the significant moisture variations in the upper soil layer, as well as prolonged periods of moisture deficit. In less competitive conditions on bare soils, cyanobacteria can form cryptogamic crust communities (see Bb4-1).

Bb2. Grasslands

Communities dominated by grasses are not suitable for most cyanobacteria species due to low moisture levels. In such habitats, only six species have been found: *Anabaena inaequalis*, *Aphanocapsa parasitica* (Kütz.) Komárek et Anagn., *A. parietina* Näg., *Microcoleus autumnalis*, *Nostoc commune*, and *Pseudanabaena frigida*.

Bb3. Enriched grassland under bird colonies

The soil enriched with nitrogen compounds under bird colonies is densely covered with various grasses and mosses, and cyanobacteria are relatively rare in such conditions. However, more species

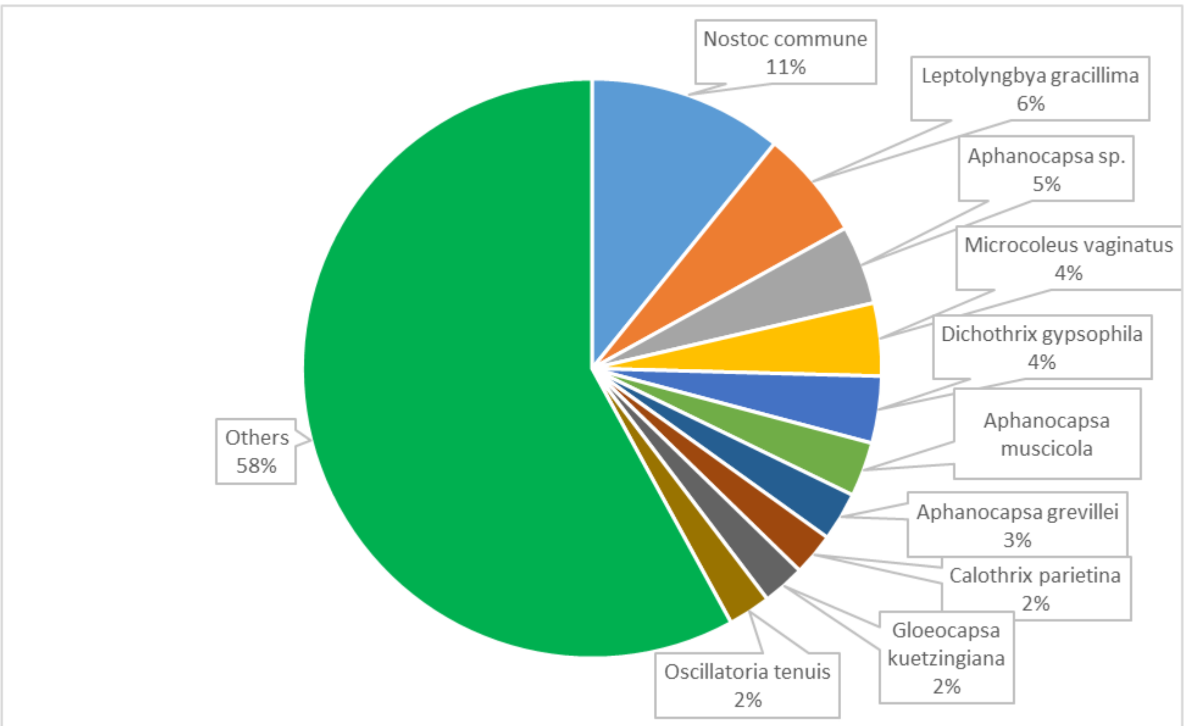

Fig. 5. Occurrences of cyanoprokaryota in seepages.

have been identified in these ecotopes than on meadows, totaling 20 species. The most common species is *Microcoleus autumnalis*. This is one of the most widespread taxa in Svalbard, with 80 known locations to date.

Bb4. Inland unvegetated or sparsely vegetated habitats

This group includes habitats that are either unsuitable for higher plants or are in the early stages of succession.

Bb4-1. Biological soil crusts

A distinctive group of habitats, formed with the participation of many species from different organism groups, is cryptogamic crusts (biocrusts). Open soil surfaces that develop biological soil crusts provide favorable habitats for cyanobacteria. These crusts act as protective matrices, facilitating cyanobacterial proliferation. Biocrusts are widespread across many natural zones (Belnap et al., 2003, 2016; Bowker et al., 2018; Dojani et al., 2014; Evans et al., 2003), but in the Arctic, they play a particularly important role in the formation of plant cover on bare areas (Pushkareva et al., 2016; Rippin et al., 2015).

Soil algae, which form growths on soil surfaces, can easily find suitable habitats due to the prevalence of bare areas. In this environment, 111 species have been identified, accounting for 11.5% of all records – making this the third most preferred habitat for cyanobacteria. There is a high number of unique species – 26 of which are found only in this habitat. The most frequently encountered species include *Nostoc commune*, *Gloeocapsa kuetzingiana*, *Calothrix parietina*, *Chroococcus turgidus* and others (Fig. 6).

Bb4-2. Small caves

Local shaded areas formed by the placement of rock slabs can significantly differ in microclimate and light conditions from similar rock walls. The illumination here can be almost zero for most of the day. In such habitats, only nine cyanobacterial taxa are found: *Aphanocapsa fonticola* Hansg., *Aphanocapsa* sp., *Calothrix* sp., *Chamaesiphon polonicus*, *Chroococcus* sp., *Desmonostoc muscorum* (C. Ag. ex Born. et Flah.) Hrouzek et Ventura, *Leptolyngbya antarctica* (W. West et G.S. West) Anagn. et Komárek, *Microcoleus vaginatus*, and *Oscillatoria tenuis*, most of which, apparently, are specific and require special systematic study.

Bb4-3. Screes

Mobile loose slopes consisting of boulders and scree are not suitable for cyanobacterial growth. Cyanobacteria are also poorly represented on large blocky scree slopes, probably, due to the arid nature of this habitat. Only five species have been identified here: *Aphanocapsa* sp., *Leptolyngbya foveolarum* (Rabench. ex Gom.) Anagn. et Komárek, *L. gracillima* (Rabench. ex Gom.) Anagn. et Komárek, *Nostoc commune*, and *Nostoc* sp.

Bb4-4. Rocky Communities

One of the most typical habitats for cyanobacteria is rocky outcrops. Cyanobacteria thrive in rocky communities, especially under conditions of sufficient moisture, as these environments provide ideal conditions for their growth. On Svalbard, various types of rock formations are present, including granite, gneiss, quartzite, sandstone, basalt, bituminous shales, and others. The diverse range of rocks and the absence of competition from higher plants, and in perennially wet areas from lichens, positively affect the species richness of rock-dwelling cyanobacteria. The highest abundance is observed on wet rocks where runoff from snowbanks above flows down. In the presence of solid rocks, such runoff can be substantial over many meters in height on the slope. However, if the rocks are loose, they tend to drain easily, and such rocks are usually dry for most of the summer, hence not colonized by cyanobacteria.

In terms of the number of findings, this is the richest habitat (23.3%), with the presence of 105 species recorded. The following species are most commonly found on rocky outcrops: *Nostoc commune*, *Gloeocapsa violascea*, *Calothrix parietina*, *Leptolyngbya gracillima*, *Microcoleus autumnalis*, *Gloeocapsopsis magma* (Bréb.) Komárek et Anagn., and *Gloeocapsa kuetzingiana* (Fig. 7).

In Svalbard, unlike other mountainous regions, formations dominated by *Stigonema* are not as common. *Stigonema ocellatum* (Dillw.) Lyngb. ex Born. et Flah. (12 records), *S. minutum* (C. Ag.) Hass. ex Born. et Flah. (13), *S. informe* Kütz. ex Born. et Flah. (5) are the most frequently encountered among the Stigonema colonies. Often, among the *Stigonema* colonies, *Gloeocapsopsis magma*, *Gloeocapsa violascea*, can be found, forming low-species algal crusts.

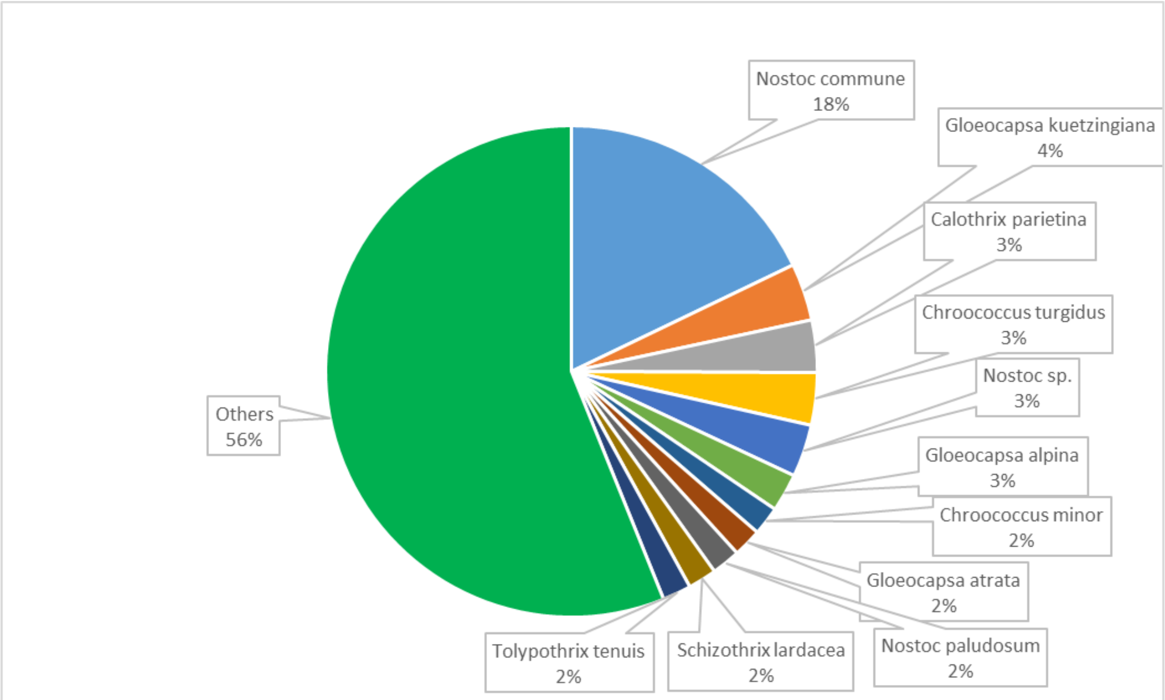

Fig. 6. Occurrences of cyanoprokaryota in bare soils.

Gloeocapsa-dominated rock formations are widespread, consisting of *Gloeocapsa kuetzingiana*, *G. compacta*, *G. atrata*, *G. alpina* (Näg.) Brand and some representatives of *Chroococcus*: *C. cohaerens*, *C. pallidus*, and *C. spelaeus* Erceg. Very typical for rocks are closely related morphologically *Gloeocapsa ralfsii* (Harv.) Kütz., and *G. sanguinea*.

Rock outcrops can be covered with crusts contest of *Phormidium uncinatum*, *Calothrix parietina*, *Phormidiochaete nordstedtii* (Born. et Flah. ex De Toni) Komárek, *Pseudanabaena frigida*, *Petalonema crustaceum*, *P incrustans*, *Cyanothece aeruginosa*, *Aphanocapsa grevillei*, *A. muscicola*, and *A. parietina*.

A relatively high number of specific species (20) are found exclusively in rocky outcrops, with *Dichothrix orsiniana* (Kütz.) Born. et Flah. being the most common. Endolithic forms can also be found among rocky outcrops and on individual stone substrates. The most prevalent of these are species from the *Chroococcidiopsis* genus, which are challenging to identify conclusively. The adaptability of endolithic cyanobacteria to extreme conditions allows them to survive even under simulated Martian environments (Billi et al., 2011; Onofri et al., 2012).

Bb4-5. Large boulders on a plain

Habitats on rocky walls of boulders and outcrops, located individually on the plateau, are quite specific. Here, 9 species of cyanobacteria have been discovered: *Aphanocapsa parietina*, *Aphanothece castagnei* (Bréb.) Rabenh., *A. saxicola* Näg., *Chroococcus pallidus*, *Chroococcus* sp., *Kamptonema formosum*, *Nostoc commune*, *Phormidium uncinatum*, and *Stigonema ocellatum*.

Bb5. Snow or ice-dominated habitats

These include snowfields, glaciers, and glacier plateaus. The melting of snow masses and the formation of liquid water combined with high insolation are often accompanied by the “blooming” of snow, which is the vigorous growth of algae. This is a well-known and widespread phenomenon that has attracted the attention of many researchers, including those in Svalbard (Kol and Eurola, 1974; Müller et al., 1998; Newton, 1982). G. Lagerheim (1984), in his article on algae inhabiting snow, describes *Aphanocapsa nivalis* Lagerh., and also mentions an atypical form of *Phormidium retzii* (C. Ag.) Gom. ex Gom. The samples of “blooming” snow collected by us on the archipelago usually contained representatives of *Chlamydomonas* spp., *Haematococcus* spp. but not cyanobacteria.

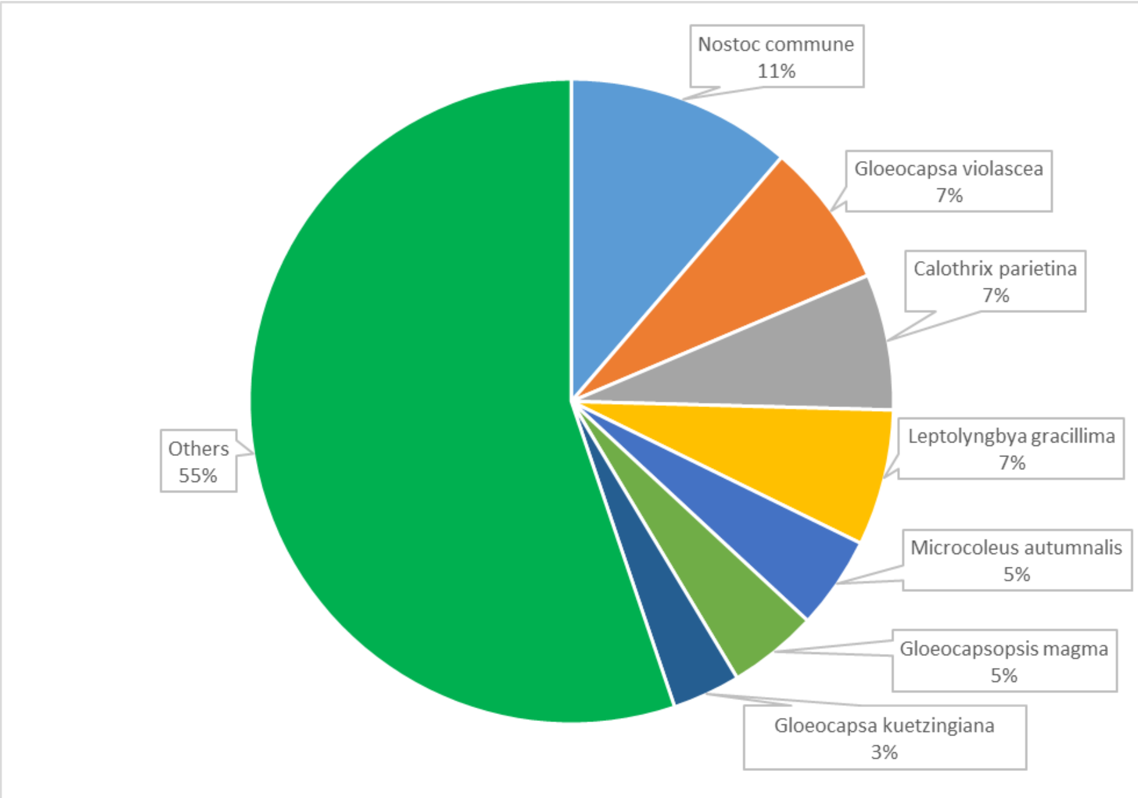

Fig. 7. Occurrences of cyanoprokaryota on rocks.

Bb5-1. Glacial moraines and cryoconite

Cyanobacteria often serve as pioneering organisms in glacial and moraine environments in Svalbard. They are among the first life forms to colonize these harsh and recently deglaciated landscapes. Cryokonite holes are indeed unique environments. Cryokonite refers to rock debris that is ejected onto the surface of ice. It absorbs radiation and melts the underlying ice, creating a hole or pool (Fogg, 1998). Cryokonite holes and ponds are occupied by algal communities (Vincent, 1988). There are indications of several taxa found in cryokonite (Stibal et al., 2006): *Leptolyngbya foveolarum*, *Leptolyngbya* cf. *notata* (Schmidle) Anagn. et Komárek, *Microcoleus vaginatus*, *Nostoc* sp., *Microcoleus amoenus* (Kütz. ex Gom.) Strunecky et al., and *Chlorogloea* sp.

Moraine material, on the other hand, is a mixture of ice and rocks that forms on the surface of a glacier, creating ridges or mounds. It contains buried ice, except in formed moraines where the ice is already absent. In this subgroup, a total of 16 species have been discovered, all with single records.

Bb5-2. Cryogenic landforms

These are various manifestations of bulging due to thawing and frost sorting processes, resulting in exposed soils. In such medallions, 26 species of cyanobacteria have been found. The most common species is *Nostoc commune*, along with it, *Gloeocapsa compacta*, *G. violascea*, *Chroococcus pallidus*, *Microcoleus favosus*, and *M. vaginatus* are also commonly found here.

Discussion

Most researchers of cryptogamic organisms in northern ecosystems, when differentiating habitats, primarily base their classification on phytocenoses (plant communities). Conducting ecological analysis and grouping cyanobacteria in Arctic ecosystems by habitat types rather than association with plant communities is determined by the same factors, as noted by V. Fedosov in his work on the analysis of the moss flora in the Hypoarctic region (2014). Distribution is primarily influenced by physical factors, with relationships between species (in our case, cyanobacteria, and in the cited study, mosses) and representatives of other groups being more correlative than functional. Using similar principles, V. Fedosov identified habitat types in his analysis of the moss flora of Taymyr (2014), which vary in specific substrates, moisture conditions, and other environmental factors.

The majority of habitat types used in this work are determined by abiotic factors. However, some types are named after characteristic biotic communities (plankton, benthos), which simplifies comprehension. It would be more accurate to describe these types as pelagic water masses and benthic (or bottom habitats). This would allow for a more consistent delineation of units and adhere to the principle of division based on a single criterion (Komulaynen, 2011).

Some other types cannot be formalized based solely on abiotic factors. For example, pelagic communities are a unique transitional type that arises due to disturbances in the benthic environment by winds and currents, as well as the filling of cyanobacterial mats with oxygen bubbles, giving them buoyancy. Thus, pelagic cyanobacteria are a part of the life cycle for some species.

It's quite evident that both species richness and the frequency of cyanobacteria occurrence vary significantly in different ecotopes (Table 3).

The largest number of species was found in soil crust communities (111), on rocks (105), in permanent slow streams (105), and in seepage areas (98). A similar distribution is observed when comparing the number of records, but with a clear dominance of rocky outcrops - they are the most "popular" type of habitats. On the one hand, this reflects the diversity and frequency of these habitats, while on the other hand, it highlights the ecological preferences of cyanobacteria species in the flora of Svalbard and likely across the entire "high" Arctic region. As we move southward, increased competition in the plakor terrestrial habitats brings moist rocks to the forefront among ecosystems that drive the richness of cyanobacterial species.

Cyanobacteria exhibit the greatest species diversity and play a significant role in shaping the vegetation cover in ecosystems that are "unattractive" to other organism groups. Large expanses of cyanobacterial growth are formed in wet rocky cliffs, bare soils saturated with water, and on the bottoms and shores of small well-heated slow streams.

In drier aerophytic habitats, cyanobacteria typically form communities of crusts alongside fungi, lichens, and mosses. Due to excessive moisture from abundant snowmelt on Svalbard, these communities often do not experience limitations related to moisture availability. Consequently, many species with subaerophytic preferences are found here. As you move south, crust communities are displaced by higher plants and may only persist on primary soils typical of high mountains, permafrost disturbances, and local topographic elevations. In all cases, there is a shift towards moisture conditions that are unfavorable for cyanobacteria. The persistent lack of moisture limits the development of most species, leaving only those highly resilient to desiccation *Nostoc commune, Microcoleus vaginatus,* and *Stigonema* spp.

A similar pattern is observed along the latitudinal gradient with seepage communities. They are extremely widespread on the archipelago and, to the same extent as crust communities, are displaced as one moves southward.

Conclusion

In summarizing the ecological characteristics of cyanobacteria, it should be emphasized that the proposed classification of habitats is applicable to other Arctic regions as well. All habitats are categorized into two major groups: aquatic and terrestrial. The terrestrial category, in turn, can be divided into two subgroups: subaerial (amphibious) and aerophytic habitats. Their variability can be represented as a moisture gradient ranging from typically aquatic through subaerial to dry terrestrial environments. Based on the frequency of findings and species richness, it can be concluded that the most favorable habitats for cyanobacteria in Svalbard and across the High Arctic include: a) rocky communities under sufficiently humid conditions; b) exposed soils where biological soil crusts form; c) slow well-heated streams; d) specific over-moistened habitats, such as seepages.

As one moves southward, significant transformations occur in most of these habitats. Competition from higher plants intensifies, leading to reduced species richness and abundance of cyanobacteria in the majority of the aforementioned ecotopes. However, cyanobacteria continue to exhibit high species richness and play a noticeable role in the composition of the vegetation cover, particularly on rocks and to some extent within soil crust communities.

In essence, the cyanobacterial species composition in Svalbard reflects a dynamic interplay between species diversity, habitat specificity, and adaptive strategies, all of which contribute to their successful survival and proliferation in the Arctic environment.

Table 3. Species richness and occurrence frequency of cyanoprokaryotes in specific habitats of the Svalbard Archipelago.

No	Habitat	Number of species	Number of records
A1-1.1	The planktonic communities of lakes	27	82
A1-1.2	The benthic communities of lakes	32	57
A1-1.3	Tychoplankton	13	14
A1-2.1	Thermal springs	7	17
A1-2.2	Permanent fast, turbulent watercourses	42	84
A1-2.3	Permanent smooth-flowing watercourses	105	362
A1-2.4	Rivers	7	7
Ba1-1	Coastal dunes and sandy shores	29	84
Ba1-2	Coastal shingle habitats	3	4
Ba1-3	Rock cliffs, ledges and shores	7	11
Ba2	Temporary ponds and pools	95	211
Ba3-1	Shingle and sandy shores of freshwater lakes	59	155
Ba3-2	Shingle and sandy shores of streams	47	114
Ba3-3	Shingle and sandy shores of rivers	7	9
Ba4	Minerotrophic marshes	24	31
Ba5	Seepages	98	295
Bb1	Tundra	66	134
Bb2	Grasslands	6	8
Bb3	Enriched grassland under bird colonies	19	53
Bb4-1	Biological soil crusts	111	319
Bb4-2	Small caves	9	10
Bb4-3	Screes	5	5
Bb4-4	Rocky outcrops	105	645
Bb4-5	Large boulders on a plain	9	10
Bb5-1	Glacial moraines and cryoconite	16	16
Bb5-2	Cryogenic landforms	26	39

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