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Review Paper

The diversity of Cyanoprokaryota from freshwater and terrestrial habitats in the Eurasian Arctic and Hypoarctic

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Abstract The diversity and geographical distribution of cyanoprokaryotes in the Eurasian Arctic and Hypoarctic were investigated. We combined information from the literature and data from our own research in various parts of high-latitude regions. We collected and studied more than 1000 samples from terrestrial and freshwater habitats. The published data on cyanoprokaryotes include records from about 1500 locations. Both original and published data on biodiversity were used for the analysis. The data were submitted to the CYANOpro database (http://kpabg.ru/cyanopro/). A total of 603 species were recorded. In the Arctic zone, 482 species were found. The Eurasian Hypoarctic flora includes 428 species. The Murmansk region (359 species), Spitsbergen archipelago (314), and Bolshezemelskaya tundra (191) have the highest number of species among the studied territories. The flora is unevenly studied in different areas of the Arctic, and therefore, it is too early to suggest any significant specificity of the algal flora to particular areas.

Keywords Cyanobacteria · Distribution · Flora · Ecology

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Introduction

Cyanoprokaryota (Cyanobacteria) are widespread and ecologically important organisms of aquatic and terrestrial ecosystems of the Arctic. Their unique abilities to photosynthesize and fix molecular nitrogen make them a special group in production of organic matter in the water bodies and soils of high latitudes.

In Arctic water bodies, cyanoprokaryotes form dominant communities in phytoplankton and benthos. In southern parts of the Arctic, some species can cause «blooming» of the water bodies. In terrestrial habitats of high latitudes, cyanoprokaryotes can form visible growths on the surface of and in the soil. Reduced competition from higher plants allows cyanobacterial mats and films to occupy considerable areas. Cyanoprokaryotes occur on soil surfaces lacking vegetation, and on the surface of, and within cracks penetrating rocky substrata. Growth in cracks in rocks and internally amongst rock crystals provides protection against temperature changes, dehydration, and external physical influences (e.g., destruction by the wind). Cyanoprokaryotes are often the first organisms to inhabit glaciers and moraines (Kaštovská et al., 2005, 2007; Turicchia et al., 2005; Davydov, 2011). Their high abundance is seen in bryophyte communities of moist habitats along the shores of lakes, streams, pools, and the splash zone of waterfalls.

The current state of Cyanoprokaryota biodiversity has not been analyzed in the massive area (58.7 million km^2) occupied by the Eurasian Arctic and Hypoarctic (Fig. 1). The studies of cyanoprokaryotes in high latitudes are problematic due to much of the region being remote. The aim of this study was to combine all available published data and results of our own research on diversity of Cyanoprokaryota in the Eurasian sector of the Arctic and Hypoarctic.

Within Eurasia, the Arctic territories usually include continental margins and the entire Arctic Ocean with its archipelagos and islands. Recognition of zones within northern high-latitude regions varies among authors (Polunin, 1951; Aleksandrova, 1980; Bliss, 1981; Elvebakk, 1985; Matveyeva, 1998). The division of the Arctic into High Arctic and Low Arctic is commonly accepted (Bliss, 1975). In Russian research practice, two zones are usually distinguished in the Arctic: polar deserts and tundras which divide into Arctic tundra and Subarctic tundra (Aleksandrova, 1980, 1988). The High Arctic subzone includes polar deserts and Arctic tundras, and the Low Arctic subzone comprises Subarctic tundras.

Here, we assume that the southern boundary of the Arctic corresponds to the southern boundary of the tundra zone (Aleksandrova, 1980; Walker et al., 2005) and the Arctic includes the polar deserts zone and tundra zone. The transition zone from tundra to the forest is considered Subarctic or Hypoarctic (Yurtsev, 1994). According to B.A. Yurtsev (1994), it includes typical and southern tundras, forest tundra, and the northern edge of the boreal forest. Here, we place only transitional ecotone communities of forest tundra and northern taiga in the Hypoarctic. Consequently, we accept the boundary between the northern and middle taiga as the southern border of the Hypoarctic (Yurtsev, 1994).

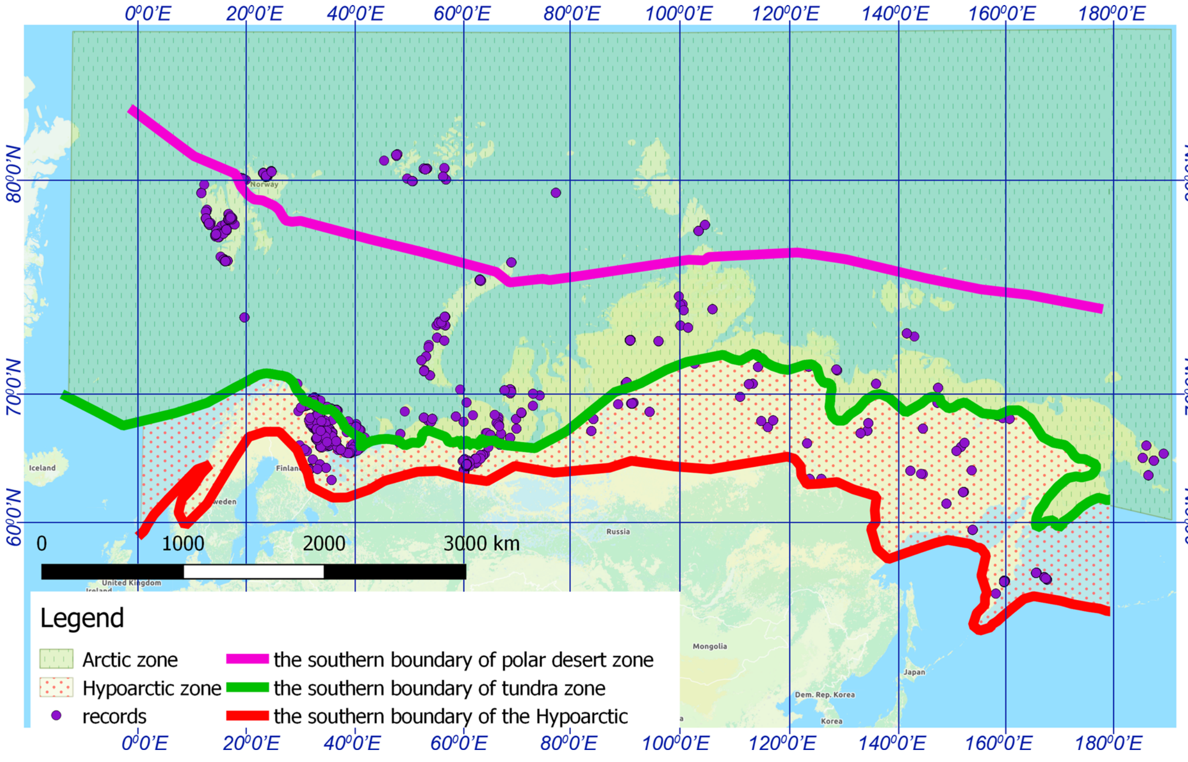

Fig. 1 The map of cyanoprokaryotes distribution in the Arctic and Hypoarctic. Color code: violet—the southern boundary of polar desert zone, green—the southern boundary of tundra zone, red—the southern boundary of the Hypoarctic, blue dots are all locations of cyanoprokaryota records

Historical review of studies on Cyanoprokaryota biodiversity in the Eurasian Arctic and Hypoarctic regions

The location of all regions is shown in Fig. 2. Spitsbergen (Svalbard) archipelago has the longest history of study of Cyanoprokaryota in the European sector of the Arctic. The first records were made in the late nineteenth and early twentieth centuries (Table 1). Spitsbergen archipelago has also been a focus for their role in colonization processes following glacial retreat (Kaštovská et al., 2005, 2007; Turicchia et al., 2005; Stibal et al., 2006; Kvíderová et al., 2011) including nitrogen fixation (Liengen & Olsen, 1997; Solheim et al., 2002; Zielke et al., 2002, 2005). Several species from Spitsbergen archipelago were the subject of taxonomic and biogeographic studies (Komárek et al., 2006; Strunecky et al., 2012; Richter & Matuła, 2013).

There have been few psychological studies on Franz Josef Land archipelago and Novaya Zemlya archipelago (Table 1).

Murmansk region is well studied with 359 species described. This is one of the richest floras in Russia, possibly due to the long history of research in the region starting with Elfving (1895). The history of research and a combined list of species for the region are provided by Davydov (2010a).

Three hundred and twenty species have been recorded from Eastern European tundra. Several studies have examined the tundras of Bolshezemelskaya and Malozemelskaya and the Polar and Subpolar Urals (Table 1).

There have been several studies in the Asian sector of the Arctic. Soil communities in polar deserts have been studied by Patova & Belyakova (2006). At lower latitudes, soil and freshwater species are described for Taimyr Peninsula, Yamalo-Nenets Autonomous Okrug, and rivers of Yakutia. Few studies have been carried out in the Chukotka and in Magadan regions.

Literature survey and data analyses

We combined our new findings with records from our CYANOpro database (http://kpabg.ru/cyanopro/) (Melechin et al., 2013), obtained during an extensive literature analysis, in order to review Cyanoprokaryota

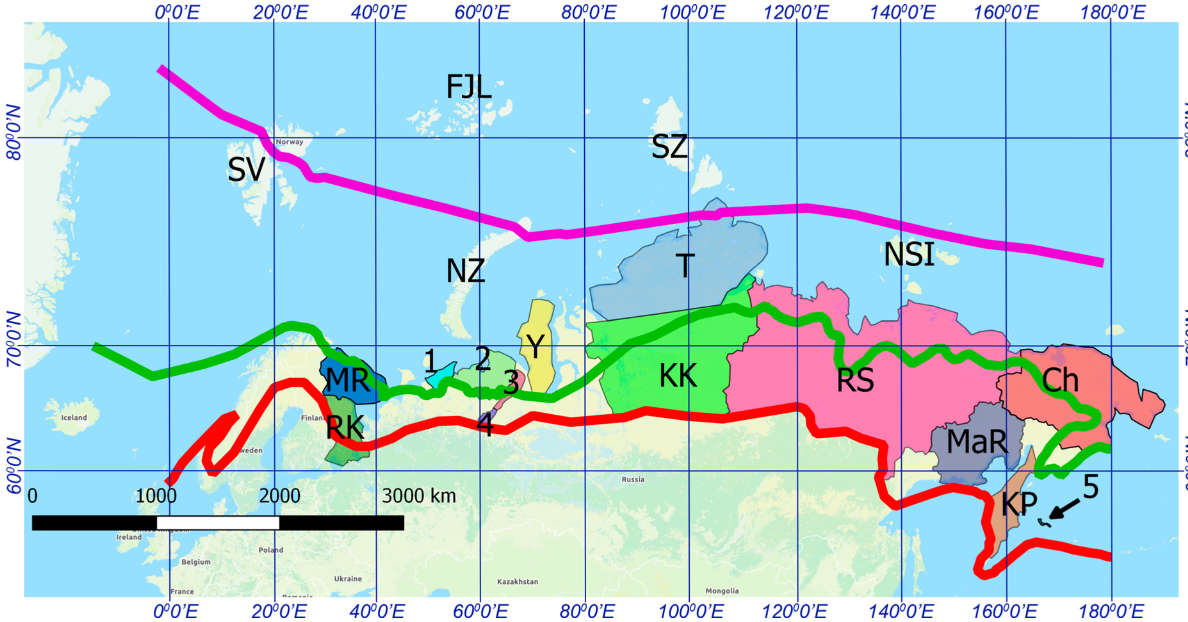

Fig. 2 The regions included in the research: *1* Malozemelskaya tundra, *2* Bolshezemelskaya tundra, *3* Polar Urals, *4* Subpolar Urals, *5* Commander Islands, *Ch* Chukotka peninsula, *FJL* Franz Josef Land archipelago, *KK* Krasnoyarsk kray, *KP* Kamchatka peninsula, *MaR* Magadan region, *MR* Murmansk region, *NSI* New Siberian Islands, *NZ* Novaya Zemlya archipelago, *RK* Karelia republic, *RS* Sakha (Yakutia) republic, *SZ* Severnaya Zemlya archipelago, *SV* Spitsbergen archipelago, *T* Taimyr peninsula, *Y* Yamalo-Nenets Autonomous Okrug

Table 1 Total numbers of Cyanoprokaryota species recorded from various regions of the Arctic and Hypoarctic

Region	Number of species	Published papers
Arctic regions		
Bolshezemelskaya tundra (BT)	191	Getsen et al. (1994), Patova (2004)
Chukotka peninsula (Ch)	84	Dorogostaiskaya (1959), Batov et al. (1978), Belyakova (2001)
Franz Josef Land archipelago (FJL)	68	Borge (1899), Kosinskaya (1933), Shirshov (1935), Novichkova-Ivanova (1963, 1972)
Malozemelskaya tundra (MT)	122	Patova (2001), Stenina & Patova (2007)
New Siberian Islands (NSI)	10	Zakharova et al. (2005)
Novaya Zemlya archipelago (NZ)	60	Wille (1879), Palibin (1903), Shirshov (1935)
Polar Urals (PU)	89	Voronikhin (1930), Patova & Demina (2008), Patova & Sterlyagova (2016)
Severnaya Zemlya archipelago (SZ)	41	Patova & Belyakova (2006)
Spitsbergen archipelago (SV)	314	Wittrock & Nordstedt (1882), Wittrock (1883), Lagerheim (1894), Stockmayer (1906), Borge (1911), Strøm (1921), Summerhayes & Elton (1923), Thomasson (1958, 1961), Willen (1980); Matuła (1982), Plichta & Luścińska (1988), Perminova (1990) (30), Oleksowicz & Luścińska (1992), Skulberg (1996) (87), Liengen & Olsen (1997), Solheim et al. (2002), Zielke et al. (2002, 2005), Davydov (2005, 2008, 2010b, 2011, 2013, 2014, 2016), Kaštovská et al. (2005, 2007), Turicchia et al. (2005), Komárek et al. (2006), Stibal et al. (2006), Matuła et al. (2007), Kim et al. (2008, 2011), Richter et al. (2009, 2015), Kvíderová et al. (2011), Komárek et al. (2012), Strunecky et al. (2012), Richter & Matuła (2013), Raabová et al. (2016)
Taimyr peninsula (T)	123	Kosheleva & Novichkova (1958), Yermolaev et al. (1971), Sdobnikova (1986)
Yamalo-Nenets Autonomous Okrug (Y)	62	Voronkov (1911), Perminova (1990), Naumenko & Semenova (1996), Bogdanov et al. (1991; 2004)
Hypoarctic regions		
Commander Islands (CI)	62	Perminova (1990)
Kamchatka peninsula (KP)	27	Perminova (1990)
Karelia republic (RK)	189	Komulainen et al. (2006)
Krasnoyarsk kray (KK)	66	Bondarenko & Schur (2007)
Magadan region (MaR)	63	Kuzmin (1986), Pivovarova (1987), Perminova (1990), Gabyshev (2015)
Murmansk region (MR)	359	Davydov (2010a)
Sakha (Yakutia) republic (RS)[a]	161	Vasilieva-Kralina et al. (2005), Gabyshev (2015)
Subpolar Urals (SPU)	150	Voronikhin (1930), Patova & Demina (2008), Patova & Sterlyagova (2016)

Europe SV, FJL, NZ, MR, RK, MT, BT, PU, SPU; *Asia* SZ, Y, T, KK, RS, NSI, Ch, KP, MaR, CI

[a]Most part of the Sakha (Yakutia) republic located in the Hypoarctic, but northern territories belong to Arctic

diversity in the Eurasian Arctic and Hypoarctic. The database has free and open access to Cyanoprokaryota biodiversity data, it is accessible through the Internet and only registration is needed. For species identification, recent monographs were used (Komárek & Anagnostidis, 1998, 2005; Komárek 2013). We studied 1500 database records of cyanoprokaryotes and our data (both new and published) obtained from 1000 samples collected in terrestrial and aquatic ecosystems. We used a special program code of CYANOpro database system to filter data and select data points for the polar deserts of the Arctic and Hypoarctic.

Floristic similarity was investigated using the Sørensen index (KS) (weighted pair-group method using arithmetic averaging) in the program module GRAPHS (Nowakowskiy, 2004): $KS = 2a/(a + b) + (a + c)$, where a is the number of species common to both sets; c is the number of species unique to the first set; and b is the number of species unique to the second set.

Estimate of the current cyanobacterial biodiversity in the Eurasian Arctic and Hypoarctic and perspectives of further studies

Comparative analysis of species composition along the latitudinal gradient from polar deserts to the Hypoarctic

Within the Eurasian sector of the Arctic and Hypoarctic, 603 species of cyanoprokaryotes were found of which 482 were in the Arctic zone. This diversity belongs to 113 genera, 38 families, and 8 orders.

In the Eurasian sector of polar deserts, 156 species of cyanoprokaryotes were noted. Most species (147) were found in the Barentz province of the polar desert zone which includes North-East Land Island in the Spitsbergen archipelago, Franz Josef Land archipelago, and the northern tip of Novaya Zemlya. Siberian province (Severnaya Zemlya archipelago, the northern tip of Taimyr) had only 45 species.

Flora of polar deserts in Spitsbergen archipelago is presently the best studied among high-latitude regions and had 118 species. Flora of Franz Josef Land, the whole territory of which is entirely within the polar desert zone, had 69 species. Species similarity between archipelagos is low (Sørensen index of 26%) with only 25 common species, most being typical hydrophytes. A more detailed study of Franz Josef Land could result in a lower floristic difference.

Franz Josef Land and Severnaya Zemlya floras are closer (Sørensen index of 33%); however, the number of common species is only 18.

As expected, the number of species increases in the less harsh conditions of the Arctic tundra. 456 species are recorded for the territories of which 129 are common to polar deserts and Arctic tundra (Sørensen index of 41%). 30 species of cyanoprokaryotes were found only in polar deserts but not in the tundra. Most of them were found in southern areas of the Hypoarctic, except for 11 species (*Chroococcus obliteratus* P. G. Richt., *Coleodesmium wrangelii* ([C. Ag.] Born. et Flah.) Borzì ex Geitl., *Gomphosphaeria cordiformis* (Wille) Hansg., *Leptolyngbya aeruginea* (Kütz. ex Hansg.) Komárek, *L. gelatinosa* (Voronich.) Anagn. et Komárek, *Merismopedia hyalina* (Ehrenb.) Kütz., *Microchaete calothrichoides* Hansg., *Phormidium lividum* Näg., *Symplocastrum aurantiacum* (Hansg. ex Hansg.) Anagn., *Trichocoleus tenerrimus* (Gom.) Anagn., *Xenococcus minimus* Geitl.) which were not found there. We do not consider these as typical species of polar deserts because they have a worldwide distribution.

Four hundred and twenty-eight species have been recorded from the Eurasian Hypoarctic. The floristic similarity between the tundra zone and Hypoarctic is high (Sørensen index of 65%). A high similarity is also noted between the flora of the polar deserts and the Hypoarctic (Sørensen index of 45%). 307 species are found in the Hypoarctic flora but not in the Arctic zone; a significant number (117) is found in polar deserts and probably will be discovered in the tundra zone. 190 species are found only in the Hypoarctic. Some can be described as boreal species, in particular the representatives of the genera *Anabaena* (*A. aequalis*, *Anabaena augstumalis*, *A. catenula* (Kütz.) Born. et Flah., *A. cylindrica* Lemm., *A. verrucosa* B.-Pet. et al.), *Dolichospermum* (*D. affinis*, *D. circinale*, *D. lemmermannii*), *Hapalosiphon* (*Hapalosiphon hibernicus* W. West et G. S. West, *H. intricatus*, *H. pumilus*), *Rivularia* (*R. aquatica* De-Wild., *R. beccariana* [De Not.] Born. et Flah., *R. borealis* P. G. Richt., *R. haematites*), as well as the species *Aulosira laxa* Kirchn. ex Born. et Flah., *Gloeotrichia echinulata*, *G. pisum* Thur. ex Born. et Flah., *Gomphosphaeria virieuxii* (Virieux) Komárek et Hind. and *Woronichinia karelica* Komárek et Kom.-Legn.

Comparative studies of territorial floras of the Arctic and Hypoarctic

Regions and territories within the Arctic and Eurasian Hypoarctic have received varying intensities of study. The highest number of species has been observed in the well-studied Murmansk region (408 taxa, 359 species). The high number of species is detected on Spitsbergen archipelago (314) and Bolshezemelskaya tundra (191), Karelia Republic. Taimyr peninsula (123), Malozemelskaya tundra (122), Polar Urals (89), Chukotka (84), Subpolar Urals (150), Franz Josef Land archipelago (68), Magadan region (63), Novaya Zemlya archipelago (60), Yamal peninsula (62) have been only partially studied and have lower numbers of species. The smallest number of species was found in Severnaya Zemlya archipelago (41).

The reason for the rich flora of the Murmansk region is the wide diversity of habitats and the long history of studies. Vegetation zones vary from the northern boreal forests to the southern tundra. The number of species that are similar to Spitsbergen flora is high, considering that a large part of Spitsbergen (60%) is covered by glaciers. The floristic diversity of the Spitsbergen archipelago is probably due to a wide range of environmental conditions from mountainous territories with a varied geology to large areas of lowland tundra with many small ponds. Despite the small area of Malozemelskaya tundra, there is a rich flora (122 species). Some parts of the Urals region have been well-studied. The north part (Polar Urals) has 89 species, and the southern part (Subpolar Urals) has 150 species. The species richness could be explained by diverse mountain conditions (considerable altitudinal range and diverse landscapes), and the relatively low latitude of the Urals regions. Taimyr has a large number of species but an increase in species richness would be expected after more detailed studies as in addition to the large area it has several vegetation zones.

Similarities of species composition between different regions are generally quite low (Fig. 3). A high similarity (Sørensen index of >50%) only occurs for relatively well-studied flora of the Murmansk region and Spitsbergen archipelago (54%), and for Franz Josef Land and Novaya Zemlya (51%). The similarities between floras of Polar Urals and Subpolar Urals (30%), Polar Urals and Bolshezemelskaya tundra (43%), and Bolshezemelskaya tundra and Taimyr (38%) may be due to their similar geology.

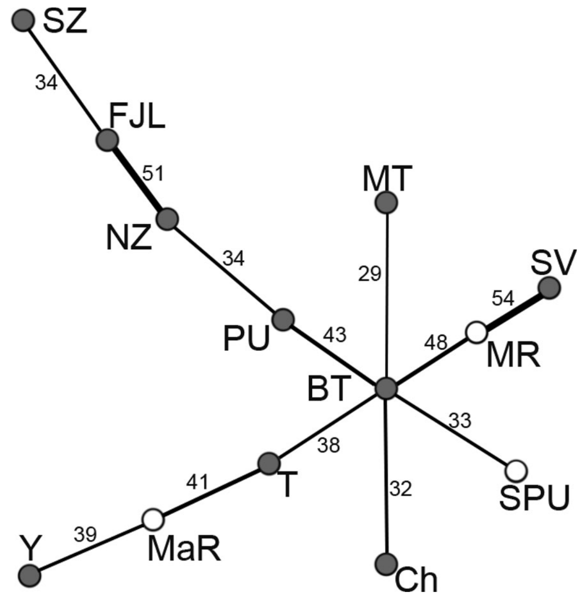

Fig. 3 A complete graph of similarity between Cyanoprokaryota floras in studied areas of the Arctic (gray circle) and Hypoarctic (white circle) (Sørensen index). For clustering, the mean distance between elements of each cluster was used with weighted pair-group method using arithmetic averaging, numbers on the ridges are similarity index shown in percentages where *BT* Bolshezemelskaya tundra, *Ch* Chukotka, *FJL* Franz Josef Land archipelago, *MaR* Magadan region, *MR* Murmansk region, *MT* Malozemelskaya tundra, *NZ* Novaya Zemlya archipelago, *PU* Polar Urals, *SPU* Subpolar Ural, *SV* Spitsbergen archipelago, *SZ* Severnaya Zemlya archipelago, *T* Taimyr peninsula, *Y* Yamal peninsula

The distribution of species amongst habitats

There are two ecological groups of species according to habitat type: aquatic and terrestrial. 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).

Aquatic habitats

A reduction of species diversity in freshwater waterbodies Cyanoprokaryota from south to north is one of the main environmental features of high latitudes. This happens since the majority of water bodies in the polar desert zone of the Arctic are oligotrophic and also ultra-oligotrophic as they have a glacial origin and low temperature in the summer and the short vegetation period. Under such conditions, the species diversity and biomass of cyanoprokaryotes in plankton and benthos is low. The most common planktonic species are shown in Table 2.

Table 2 The typical species of aquatic habitats in various regions of Arctic and Hypoarctic

Species	Ecology	Distributions	
		Arctic	Hypoarctic
Ammatoidea normannii W. West et G. S. West	Epilithon (slow streams)	SV	MR
Anabaena aequalis Borge	Plankton	SV, BT	MR, RS
Anabaena augstumalis Schmidle	Plankton	MT, BT	MR, KK
***Anabaena cylindrica* Lemm.	Plankton in rivers	MT, BT, PU, T	MR, KK, RS
Anabaena echinospora Skuja	Plankton (only in Hypoarctic lakes)		MR
Anabaena elliptica Lemm.	Plankton (only in Hypoarctic lakes)		MR
Anabaena laxa (Rabench.) A. Braun ex Born. et Flah.	Plankton (in rivers)	FJL, BT, SZ	MR, RS
***Anabaena minutissima* Lemm.	Plankton (only in Hypoarctic lakes)	MT, PU	SPU
***Anabaena oscillatorioides* Bory ex Born. et Flah.	Plankton (only in Hypoarctic lakes)	MT, T, Ch	MR, SPU, RS, MaR
Anabaena sedovii Kossinsk.	Plankton (only in Hypoarctic lakes)	FJL	KK, MaR
***Anabaena sphaerica* Born. et Flah.	Plankton	BT, MT	SPU, RS, KP
Anabaena verrucosa Boye-Petersen	Plankton (in Arctic and Hypoarctic lakes)	MT, BT, PU	RS
Anathece bachmannii (Kom.-Legn. et G. Cronb.) Komárek et al.	Plankton (lakes, rivers and estuary)	BT	RK
Anathece clathrata (W. West et G. S. West) Komárek et al.	Plankton (lakes and rivers)	SV, BT, MT, PU, T	MR, SPU, KK, RS
***Aphanizomenon flos-aquae* Ralfs ex Born. et Flah.	Plankton (in Arctic, Hypoarctic lakes, rivers and estuary)	MT, BT, PU, Y, T	MR, RK, KK, RS
Aphanocapsa conferta (W. West et G. S. West) Kom.-Legn. et G. Cronb.	Plankton	FJL, Y, Ch	MR, SPU
Aphanocapsa delicatissima W. West et G. S. West	Plankton	SV, MT, Y	MR
Aphanocapsa elachista W. West et G. S. West.	Plankton	SV, FJL, NZ, PU	MR
Aphanocapsa grevillei (Berk.) Rabenh.	Epilithon (slow streams)	SV, MT, BT, NZ, PU, T	MR, RK, SPU, KK, RS
Aphanocapsa holsatica (Lemm.) G. Cronb. et Komárek	Plankton	T, PU	MR, RS
Aphanocapsa hyalina Hansg.	Epilithon (slow streams)	SV, BT	MR
Aphanocapsa incerta (Lemm.) G. Cronb. et Komárek	Plankton	SV, FJL, BT, MT, PU, SZ, T, Ch	MR, RS
Aphanocapsa rivularis (Carm.) Rabenh.	Epilithon (slow streams)	SV	MR, RS
Calothrix braunii Born. et Flah.	Epilithon (slow streams)	BT, PU	MR, RK, SPU
Calothrix clavata G. S. West	Epilithon (slow streams)	MT, BT, PU	SPU, KK, RS
Calothrix parietina Thur. ex Born. et Flah.	Epilithon (slow streams)	SV, BT, MT, PU, SZ	MR, SPU, KP
Chamaesiphon confervicolus A. Braun.	Epilithon (mountain lakes; rivers high rocky banks)	MT, NZ, BT, PU, SPU	MR, RK, RS
Chamaesiphon incrustans Grun.	Epilithon and benthos (mountain lakes)	SV, MT	MR, SPU
Chamaesiphon polonicus (Rost.) Hansg.	Epilithon and benthos (Arctic and mountain fast streams)	SV	MR
Chamaesiphon rostafinskii Hansg.	Periphyton and benthos (mountain lakes); epilithon (rivers high rocky banks)	SV, NZ	RK, SPU, RS

Table 2 continued

Species	Ecology	Distributions	
		Arctic	Hypoarctic
Coelospherium kuetzingianum Näg.	Epilithon (rivers high rocky banks)	SV, FJL, NZ, BT, Y, Ch	MR, RK, SPU, RS
**Dichothrix gypsophila* (Kütz.) Born. et Flah.	Epilithon (slow streams)	SV, MT, BT, PU, SZ, Ch	MR, RK, SPU
Dolichospermum affinis (Lemm.) Wacklin et al.	Plankton (only in Hypoarctic lakes)	MT	MR, KK, RS
Dolichospermum circinale (Rabenh. ex Born. et Flah.) Wacklin et al.	Plankton (only in Hypoarctic lakes)		MR, KK, RS
Dolichospermum flos-aquae ([Lyngb.] Bréb. ex Born. et Flah.) Wacklin et al.	Plankton (in arctic and Hypoarctic lakes)	MT, BT, PU, Y, T	MR, SPU, KK, RS
Dolichospermum lemmermannii (P. G. Richt.) Wacklin et al.	Plankton (in arctic and Hypoarctic lakes)	MT, BT, PU, Y, T	MR, RK, SPU, KK, RS
Dolichospermum solitarium (Kleb.) Wacklin et al.	Plankton (in arctic and Hypoarctic lakes)	MT, BT, T	SPU, RS
Gloeotrichia echinulata [J. E. Smith et Sowerby] P. G. Richt.	Plankton (in arctic and Hypoarctic lakes)	MT, BT, PU	MR, RK, RS
Gloeotrichia pisum Thur. ex Born. et Flah.	Epilithon (slow streams)	MT, BT	MR, RK
Gomphosphaeria aponina Kütz.	Plankton (in Arctic and Hypoarctic lakes)	SV, FJL, MT, BT, NZ	MR, RK, RS
Hapalosiphon intricatus W. West et G. S. West	Periphyton and benthos (in Arctic and Hypoarctic lakes)	MT	MR, SPU
Hapalosiphon pumilus Kirchn. ex Born. et Flah.	Periphyton and benthos (in south Arctic and Hypoarctic lakes)	MT, Ch	MR, SPU
Hydrocoryne spongiosa Schwabe ex Born. et Flah.	Periphyton and benthos (in Hypoarctic lakes and rivers)		MR, KK
Leptolyngbya aeruginea (Kütz. ex Hansg.) Komárek	Epilithon in slow stream	SV	
Leptolyngbya compacta (Hansg. ex Hansg.) Komárek	Epilithon in slow stream	SV	MR
Leptolyngbya valderiana (Gom.) Anagn. et Komárek	Epilithon (rivers and slow stream)	SV, BT, PU, Y, T, Ch	MR, KK, CI
Limnothrix guttulata (Van Goor) Umezaki et M. Watanabe	Plankton (in Arctic lakes)	SV	
Limnothrix mirabilis (Böcher) Anagn.	Plankton (in Arctic lakes)	SV	RK, RS
Limnothrix planctonica (Wolosz.) Meff.	Plankton	MT, BT, Y	MR, RK, KK, RS, MaR
Merismopedia elegans A. Br.	Plankton	SV, MT, BT, NZ, PU, Y, Ch	MR, RK, RS
Merismopedia glauca (Ehr.) Kütz.	Plankton	SV, MT, BT, FJL, NZ, Y, T, NSI	MR, RK, RS
Merismopedia minima Beck	Plankton	SV	RK, RS
Merismopedia punctata Meyen	Plankton	SV, FJL, NZ, MT, BT, PU, Ch, NSI	MR, RK, KK
**Microcoleus autumnalis* (Trev. ex Gom.) Strunecky et al.	Benthos (in slow streams)	SV, FJL, NZ, BT, PU, T, Ch, NSI	MR, KK, RS, MaR, CI
Microcystis aeruginosa (Kütz.) Kütz.	Plankton	MT, BT, PU, Y, T	MR, RK, SPU, KK, RS

Table 2 continued

Species	Ecology	Distributions	
		Arctic	Hypoarctic
Nodularia harveyana Thur. ex Born. et Flah.	Plankton (in Arctic, Hypoarctic rivers and estuary)	MT, BT	MR, MaR, CI
Nostoc coeruleum Lyngb.	Epilithon (slow stream)	MT, BT, NZ, NSI	MR, RK, SPU, RS
Nostoc kihlmanii Lemm.	Plankton (in Arctic and Hypoarctic lakes)	SV, FJL, NZ, MT, BT, PU, NSI	MR, RK, RS, MaR
Nostoc linckia Born. ex Born. et Flah.	Plankton (in Arctic and Hypoarctic lakes); periphyton and benthos; epilithon (rivers high rocky banks)	SV, FJL, MT, PU, Y, SZ, T, Ch	MR, SPU, KK, MaR
Nostoc pruniforme C. Ag.	Periphyton and benthos	SV, MT, PU, T	MR, SPU
Oscillatoria limosa C. Ag. ex Gom.	Periphyton and benthos	SV, MT, BT, PU, T	MR, RK, SPU, KK, RS, MaR, CI
Oscillatoria limosa C. Ag. ex Gom.	Plankton (in lakes)	SV, MT, BT, PU, T	MR, RK, SPU, KK, RS, MaR, CI
Oscillatoria tenuis C. Ag. ex Gom.	Periphyton and benthos (in lakes)	SV, BT, NZ, Y, Ch	MR, KR, KK, RS
Oscillatoria tenuis f. *uralensis* (Voronich.) Elenk.	Periphyton and benthos	BT, PU	
Phormidesmis molle (Gom.) Turicchia et al.	Periphyton and benthos	MT, FJL, NZ, T	SPU, KK, RS, KP
Phormidium granulatum (N. L. Gardn.) Anagn.	Plankton (in rivers and estuary)	SV, MT, BT	RK, SPU, KK, RS, MaR
Phormidium uncinatum Gom. ex Gom.	Periphyton and benthos (in lakes and fast streams)	SV, FJL, NZ, PU, Y, SZ, T	KK
Planktolyngbya limnetica (Lemm.) Kom.-Legn. et G. Cronb.	Plankton (in lakes)	SV, BT, Ch	MR, RK, SPU, RS
Planktothrix agardhii (Gom.) Anagn. et Komárek	Plankton (only in Hypoarctic lakes)	MT, PU	MR, RK, KK, RS
Planktothrix isothrix (Skuja) Komárek et Komárková	Plankton (only in Hypoarctic lakes)	MT	MR, RK
Pulvinularia suecica Borzi	Periphyton and benthos		MR, SPU
Rivularia biasolettiana Menegh. ex Born. et Flah.	Epilithon (rivers high rocky banks)	SV, MT, BT	MR
Rivularia haematites [DC] C. Ag. ex Born. et Flah.	Epilithon (rivers high rocky banks; slow streams)	BT, NZ	MR, RK
Schizothrix facilis (Skuja) Anagn.	Epilithon (fast stream)	SV	MR
Scytonema crispum (C. Ag.) Born.	Periphyton and benthos (mountain lakes)	FJL, PU	RK, MaR
Stigonema mamillosum [Lyngb.] C. Ag. ex Born. et Flah.	Epilithon (rivers high rocky banks)	SV, MT, BT	MR, RK, SPU
Tolypothrix distorta Kütz. ex Born. et Flah.	Periphyton and benthos (in lakes); epilithon (rivers high rocky banks)	SV, BT, MT	RK, MR, SPU, RS
Tolypothrix tenuis Kütz. ex Born. et Flah.	Benthos (in lakes); epilithon (rivers high rocky banks)	SV, FJL, NZ, MT, BT, PU, Y, SZ, Ch	MR, RK, SPU, KK, RS

Table 2 continued

Species	Ecology	Distributions	
		Arctic	Hypoarctic
Trichocoleus delicatulus (W. West et G. S. West) Anagn.	Epilithon (fast stream)	SV	
Woronichinia compacta (Lemm.) Komárek et Hindák	Plankton (in lakes)	SV, FJL, BT, PU, Y, T, Ch	RK, SPU, RS
Woronichinia naegeliana (Under) Elenk.	Plankton (in lakes)	SV, MT, FJL, NZ	MR, SPU, RK, RS

Note for the Tables 2, 3, and 4: Distributions: *BT* Bolshezemelskaya tundra, *Ch* Chukotka Peninsula, *CI* Commander Islands, *FJL* Franz Josef Land archipelago, *KK* Krasnoyarsk Kray, *KP* Kamchatka Peninsula, *MaR* Magadan Regions, *MR* Murmansk Region, *MT* Malozemelskaya tundra, *NSI* New Siberian Islands, *NZ* Novaya Zemlya archipelago, *PU* Polar Urals, *RK* Karelia Republic, *RS* Sakha (Yakutia) Republic, *SPU* Subpolar Urals, *SV* Spitsbergen archipelago, *SZ* Severnaya Zemlya archipelago, *T* Taimyr Peninsula, *Y* Yamal Peninsula. For the references of Cyanoprokaryota species distributions, see Table 1. The most widespread species of the Arctic are indicated by "*" and of the Hypoarctic by "**"

There is low species diversity in typical planktonic genera (*Anabaena, Aphanizomenon, Dolichospermum*) in floras of high-latitude regions of Spitsbergen, Franz Josef Land and Novaya Zemlya archipelagos but their diversity increases markedly in the subarctic tundra. For example, a typical widespread species, *Aphanizomenon flos-aquae*, has not yet been found in any Arctic archipelagos (Spitsbergen, Franz Josef Land and Novaya Zemlya, Severnaya Zemlya) but it is frequently observed in the more southern tundra and Hypoarctic territories (e.g., Murmansk region, Malozemelskaya tundra and Bolshezemelskaya tundra, Taimyr) where it often colors water with its vigorous growths.

Plankton of large lakes of polar deserts usually includes tychoplanktonic species from *Pseudanabaena*, *Leptolyngbya*, *Jaaginema*, and *Oscillatoria*. Cyanoprokaryota of benthic habitats in Arctic and Hypoarctic lakes are more diverse and abundant. One of the most common benthic species in the lakes of high latitudes on Spitsbergen archipelago, and probably in other Arctic territories, is *Oscillatoria tenuis* (Table 2). Benthic mats formed by *Phormidium uncinatum* are also frequent.

In benthos of more southern lakes of the tundra zone species of *Tolypothrix* and *Hapalosiphon* are most frequent, whilst in mountain lakes these are replaced by species of *Scytonema* and *Chamaesiphon*.

Rivers at high latitudes are fed by meltwater from glaciers and snow fields. Upper reaches of rivers are cold, fast, and have large amounts of suspended mineral particles. These are extremely unfavorable conditions for development of cyanoprokaryotes. Towards the lower reaches, river flow slows but transparency and temperature often remain low. Cyanoprokaryota communities in rivers have similar species composition to those in smaller streams (Table 2).

Watersheds of more southern rivers are located in waterlogged boggy areas, so the transparency of the water is low due to high concentrations of humic acids. Turbulent rapids are often common for Hypoarctic and Arctic rivers. High rocky banks are typical of rivers in the mountains. Epilithon in these diverse rivers comprises species of *Merismopedia*, *Microcystis*, *Coelospherium*, *Chamaesiphon*, *Stigonema, Tolypothrix*, and *Rivularia* (Table 2).

In large rivers, massive growth of cyanoprokaryotes is only observed in their estuaries where phytoplankton blooms are caused by species of *Aphanizomenon*, *Dolichospermum*, *Nodularia*, and *Phormidium*.

Arctic streams are divided into two types: fast and slow. Fast streams are fed by glaciers. These have water that is cloudy with suspended sediment and only a few degrees above freezing. Algal communities are restricted to epilithon that forms mucous films on the surface of large boulders. Diversity is low being from 1 to 8 species (Table 2).

A greater diversity is found in slow streams. *Phormidium uncinatum* is the first alga to appear in upper reaches of slow streams which usually begin

Table 3 The typical species of transitional habitats between aquatic and aerophytic environments in various regions of the Arctic and Hypoarctic

Species	Ecology	Distributions	
		Arctic	Hypoarctic
Anagnostidinema amphibium (C. Ag. ex Gom.) Strunecký et Komárek	Seepage	SV, MT, BT, PU, Y	MR, SPU, RS
Aphanocapsa fonticola Hansg.	Seepage; puddles and streams; waterlogged moss tundras	SV	MR
**Aphanocapsa muscicola* (Menegh.) Wille	Waterlogged moss tundras	SV, SZ, T, Ch, NSI	MR, SPU, RS
Aphanothece castagnei (Bréb.) Rabenh.	Seepage; puddles and streams; waterlogged moss tundras	SV, FJL, NZ, PU	MR, RK, RS
Aphanothece saxicola Näg.	Seepage; puddles and streams; waterlogged moss tundras	SV, NZ, Y, T, Ch	MR, SPU
**Chroococcus cohaerens* (Bréb.) Näg.	Seepage; puddles and streams; waterlogged moss tundras	SV, MT, BT, PU	MR, SPU
Chroococcus turgidus (Kütz.) Näg.	Seepage; puddles and streams; waterlogged moss tundras	SV, MT, BT, FJL, NZ, PU, T, SZ, Ch, NSI	MR, RK, SPU, KK, MaR
Fischerella muscicola (Thur.) Gom.	Waterlogged moss tundras	MT, BT, PU	MR
Gloeocapsa kuetzingiana Näg.	Seepage; puddles and streams	SV, Y	MR, RK, KK, MaR
Gloeocapsa sanguinea (C. Ag.) Kütz.	Seepage; puddles and streams	SV, FJL, NZ	MR
Gloeocapsa violascea (Corda) Rabenh.	Seepage; puddles and streams	SV	MR
Hapalosiphon pumilus Kirchner ex Bornet et Flahault	Waterlogged moss tundras	MT	MR, SPU
Leptolyngbya cf. *gracillima* (Zopf ex Hansg.) Anagn. et Komárek	Bottom of shallow ephemeral lakes	SV, MT, FJL, Y, T	MR, SPU
**Nostoc commune* Vauch. ex Born. et Flah.	Bottom of shallow ephemeral lakes; seepage; waterlogged moss tundras	SV, FJL, MT, BT, NZ, PU, Y, SZ, T, NSI	MR, RK, SPU, KK, RS, CI
Petalonema alatum Berk ex Kirchn	Bottom of shallow ephemeral lakes	SV, MT	SPU
**Petalonema crustaceum* C. Ag. ex Kirchn.	Bottom of shallow ephemeral lakes	SV, MT	MR, SPU, CI
Phormidium kuetzingianum (Kirchn.) Anagn. et Komárek	Seepage; puddles and streams	SV	MR
**Phormidium uncinatum* Gom. ex Gom.	Bottom of shallow ephemeral lakes; seepage; puddles and streams	SV, FJL, NZ, PU, Y, SZ, T	KK
Pseudanabaena cf. *minima* (G. S. An) Anagn.	Bottom of shallow ephemeral lakes	SV, MT	MR, SPU
Scytonema hofmannii C. Ag. ex Born. et Flah.	Waterlogged moss tundras	FJL, NZ, PU	RK, KK, RS, CI
Scytonema ocellatum [Dillw.] Lyngb. ex Born. et Flah.	Waterlogged moss tundras	SV, MT, SZ	MR, RK, MaR
Symplocastrum friesii [C. Ag.] ex Kirchn.	Waterlogged moss tundras	SV, MT, BT, FJL, NZ	MR, RK, SPU
Tolypothrix distorta Kützing ex Bornet et Flahault	Bottom of shallow ephemeral lakes; seepage; waterlogged moss tundras	SV, MT, BT, Ch	MR, SPU, RS
Tolypothrix saviczii Kossinsk.	Bottom of shallow ephemeral lakes; seepage; waterlogged moss tundras	SV, BT, NZ, PU	MR, RK
Trichocoleus sociatus (W. West et G. S. West) Anagn.	Bottom of shallow ephemeral lakes; seepage; waterlogged moss tundras	SV	MR, KK, MaR

Table 4 The typical species of aerophytic habitats in various regions of Arctic and Hypoarctic

Species	Ecology	Distributions	
		Arctic	Hypoarctic
Aphanocapsa fusco-lutea Hansg.	Crusts on rocky outcrops; on wet soil; epiphytic on the mosses	SV, BT, T, Ch	MR, RS
Aphanocapsa grevillei (Berk.) Rabenh.	Crusts on rocky outcrops; wet rocks; crusts on bare spots; wet soil	SV, NZ, MT, BT, PU, T	MR, SPU, RS
Aphanocapsa muscicola (Menegh.) Wille	Crusts on rocky outcrops	SV, BT, SZ, T, Ch, NSI	MR, SPU, RS
Aphanocapsa parietina Näg.	Crusts on rocky outcrops	SV, BT, T	MR, SPU
Calothrix parietina Thur. ex Born. et Flah.	Crusts on rocky outcrops	SV, BT, MT, PU, SZ	MR, SPU, KP
Chroococcus cohaerens (Bréb.) Näg.	On wet rocks; on soil	SV, MT, BT, PU	MR, SPU
Chroococcus pallidus (Näg.) Näg.	On wet rocks	SV	MR
Chroococcus spelaeus Erceg.	On wet rocks; on soil	SV	MR
Cyanothece aeruginosa (Näg.) Komárek	Crusts on rocky outcrops; on soil	SV, FJL, NZ, BT, PU, Y, T, Ch	MR, RK, SPU, KK, CI
Desmonostoc muscorum (C. Ag. ex Born. et Flah.) Hrouzek et Ventura	On soil	PU, T	MR, SPU
**Gloeocapsa alpina* (Näg.) Brand	On wet rocks on which water from snow fields falls	SV, FJL, MT, BT, PU, SZ	MR, RK, SPU, RS, KP
Gloeocapsa atrata Kütz.	On wet rocks on which water from snow fields falls	SV, NZ	MR, RK,
Gloeocapsa compacta Kütz.	On wet rocks on which water from snow fields falls	SV, BT, Y, SZ, T	MR, SPU
Gloeocapsa kuetzingiana Näg.	On wet rocks on which water from snow fields falls	SV, Y, T	MR, MaR
Gloeocapsa ralfsii (Harvey) Kütz.	Wet rocks, on the soil	SV	
Gloeocapsa sanguinea (C. Ag.) Kütz.	Wet rocks, on the soil	SV, FJL, NZ	MR
Gloeocapsa violascea (Corda) Rabenh.	Wet rocks, on the soil	SV	MR
**Gloeocapsopsis magma* (Bréb.) Komárek et Anagn.	Wet rocks	SV, BT, PU, Y, SZ	MR, RK, SPU, KP, CI
Kamptonema animale (C. Ag. ex Gom.) Strunecký et al.	In soil	FJL, BT, Y, T	SPU, KK, RS, CI
Leptolyngbya boryana (Gom.) Anagn. et Komárek	Crusts on bare spots; in soil	SV, BT, PU, Y, T, SZ	MR, KK, RS, CI
Leptolyngbya foveolarum (Rabench. ex Gom.) Anagn. et Komárek	Crusts on bare spots; in soil	SV, FJL, BT, NZ, PU, Y, T, SZ	MR, SPU, KK, RS, Ch, KP, CI
Microcoleus autumnalis (Trev. ex Gom.) Strunecky et al.	Ornithogenic habitats, on soils	SV, FJL, NZ, BT, PU, T, Ch, NSI	MR, KK, RS, MaR, CI
**Microcoleus vaginatus* Gom. ex Gom.	Crusts on bare spots	SV, BT, SZ	MR, RK
Microcoleus favosus (Gomont) Strunecky et al.	Crusts on bare spots	SV, FJL, T	SPU, KK
Nostoc commune Vauch. ex Born. et Flah.	Crusts on bare spots, on soils, rocks, epiphytic on the mosses	SV, FJL, MT, BT, NZ, PU, Y, SZ, T, NSI	MR, RK, SPU, KK, RS, CI
Nostoc punctiforme (Kütz. ex Hariot) Hariot	In soil	SV, FJL, NZ, BT, MT, PU, T	MR, SPU
Nostoc microscopicum Carm. ex Born. et Flah.	Crusts on bare spots	SV, BT, PU, T	MR, SPU, RS, MaR

Table 4 continued

Species	Ecology	Distributions	
		Arctic	Hypoarctic
Petalonema incrustans [Kütz.] Komárek	Crusts on rocky outcrops	SV	
Phormidiochaete nordstedtii (Born. et Flah.) Komárek	Crusts on rocky outcrops	SV	MR
Phormidium ambiguum Gom.	In soil	SV, BT, PU, NZ, Y, SZ, T	MR, SPU, KK, MaR, CI
**Pseudanabaena frigida* (Fritsch) Anagn.	Crusts on rocky outcrops, on soils	SV, BT, FJL	MR, RK
**Scytonema ocellatum* [Dillw.] Lyngb. ex Born. et Flah.	Crusts on bare spots	SV, MT, BT, SZ	MR, RK, RS
Stigonema informe Kütz. ex Born. et Flah.	On wet rocks	SV, BT, PU	MR, RS
**Stigonema minutum* [C. Ag.] Hass. ex Born. et Flah.	On wet rocks; crusts on bare spots	SV, FJL, MT, BT, PU, SZ	MR, RK, SPU, KP, CI
**Stigonema ocellatum* [Dillw.] Thur. ex Born. et Flah.	On wet rocks; crusts on bare spots	SV, BT, PU, Y, T, SZ	MR, RK, SPU, RS, KP, CI
Tolypothrix tenuis Kütz. ex Born. et Flah.	On wet rocks; crusts on bare spots	SV, FJL, NZ, MT, BT, PU, Y, SZ, T, Ch	MR, RK, SPU, KK, RS

near snowfields. Further downstream species of *Leptolyngbya* appear. Small pebbles in the stream bed form a good habitat for *Dichothrix gypsophila.* This is also common in ephemeral ponds and small lakes.

Epilithon in streams also includes species of *Ammatoidea*, *Aphanocapsa*, *Chamaesiphon*, and *Tolypothrix* (Table 2). The bed of small streams is often covered by *Microcoleus autumnalis* which is one of the most common Arctic species.

Streams of southern Hypoarctic regions that are fed by ground springs have a high transparency. These are a good habitat for *Tolypothrix tenuis*, *T. distorta*, *Nostoc coeruleum*, *Calothrix braunii* Born. et Flah., *C. clavata*, *Calothrix parietina*, *Dichothrix gypsophila*, *Gloeotrichia pisum* and *Rivularia haematites*.

Terrestrial habitats

Terrestrial habitats support a greater diversity and abundance of cyanoprokaryotes with progression from South to North. A decrease in competition from higher plants and an increase in the range of ecological niches could explain this.

Subaerophytic habitats

These are transitional between aquatic and aerophytic habitats, typically being banks of water bodies, flooded areas of slopes and terraces and moss tundra wetlands. They are the most frequently occurring habitats in high latitudes and support the highest diversity of cyanoprokaryotes. Extensive mats (from 2 to 3 cm thick) are formed at the bottom of widespread, shallow, ephemeral lakes. These are dominated by *Phormidium uncinatum* which forms an upper layer and *Leptolyngbya* cf. *gracillima* and *Pseudanabaena* cf. *minima*, which form a bottom layer (Table 3). Mats dominated by *Petalonema* species (*P. alatum* and *P. crustaceum*) are less frequent.

Continuous snow melt during summer produces abundant runoff which results in waterlogging of upper soil horizons under permafrost conditions. Those habitats are called seepage (Komárek et al., 2012). Here, *Gloeocapsa kuetzingiana*, *G. sanguinea*, *G. violacea* and species that are often recorded in puddles and streams (*Chroococcus turgidus*, *Microcoleus autumnalis*, *Oscillatoria tenuis*, *Phormidium kuetzingianum*, *P. uncinatum)* are found.

Epiphytic on mosses in waterlogged moss tundra are *Chroococcus turgidus, Symplocastrum friesii*, *Hapalosiphon pumilus, Fischerella muscicola*, *Aphanocapsa muscicola*, *Scytonema ocellatum*, *S. hofmannii*, *Microcoleus vaginatus*, *Nostoc punctiforme*.

Nostoc commune is probably the most common species for all tundra habitats and especially in wet tundra. It is one of the most common species of the

Arctic which can be found everywhere due to its adaptability to a wide range of habitats from bare ground of glacier nunataks to the bottom of rocky outcrops and small ponds. In wet moss tundras, its colonies can form a continuous cover over several square meters. *Nostoc* colonies can cover moss surfaces as well as grow within moss cushions. They could also be found in small ponds and water filled depressions. The study on genetic variation using 16S rRNA sequencing and AFLP methods of different colonies in the studied regions confirmed that all the specimens belong to *Nostoc commune* (Patova et al., 2015).

Aerophytic habitats

Aerophytic cyanoprokaryotes are inhabitants of rocky substrates and soil surfaces. Elevated rocky surfaces of different origins and geology are widespread in the Arctic and Hypoarctic. Combined with a lack of competition from lichens and vascular plants, this stimulates species richness of cyanoprokaryotes. Greatest abundance is observed on wet rocks receiving water from snow fields. Loose rocks are easily drained and remain dry most of the summer which makes them a hostile environment which is not colonized by cyanoprokaryotes. Under typical Arctic conditions, the most common thin crusts on wet rocks are of species of *Gloeocapsa* and *Chroococcus* (Table 4). In Hypoarctic regions, the most frequent crusts are of *Stigonema ocellatum, S. minutum*, and *S. informe* with associated *Gloeocapsopsis magma* and *Gloeocapsa violascea*.

Cyanoprokaryota crusts on soil surfaces vary in composition and can occupy large areas due to the high occurrence of bare spots in the Arctic regions. Those habitats are from 1 to 10 m^2 or 20–90% of the area in the communities. Typical species of wet soils are *Aphanocapsa grevillei*, *Leptolyngbya boryana*, *Microcoleus favosus*, *M. vaginatus*, *Nostoc commune*, *N. punctiforme*, *Petalonema crustaceum, Stigonema ocellatum*, *S. minutum*, *Scytonema ocellatum, Tolypothrix tenuis*, and *T. distorta*.

Species often found at relatively high abundance in soils are *Chroococcus cohaerens*, *Cyanothece aeruginosa*, *Desmonostoc muscorum*, *Kamptonema animale*, *Leptolyngbya boryana*, *Leptolyngbya foveolarum*, *Phormidium ambiguum*, *Nostoc punctiforme*, *N. linckia*, and *N. microscopicum*. In ornithogenic habitats, such as downslope from bird colonies, species-richness is 4–5 species, but *Microcoleus autumnalis* is always found.

The presently known diversity of cyanoprokaryotes in the Eurasian Arctic and Hypoarctic comprises 603 species (Table 5). The Arctic has 80% of this total. In the Hypoarctic, 71% are observed. This could be attributed to the smaller area and the reduced range of environmental conditions (Fig. 2).

89% of species in the Arctic are found in the tundra zone while polar deserts have only 32%. The diversity of polar deserts in comparison with the total Arctic and Hypoarctic species is only 26%.

The harsh environment of polar deserts supports fewer species than Arctic tundra in which 456 species have been observed. This increased diversity can be attributed to the wider range of habitats that are favorable for cyanoprokaryotes.

The species richness within subclasses is similar in all zones. Oscillatoriophycidae (40%) is dominant in the total species list whilst Synechococcophycideae (32%) and Nostocophycideae (27%) are similar. The proportion of Nostocophycideae species increases in Hypoarctic. In the tundra zone and the Hypoarctic, species richness within orders is greatest in the Synechococcales and Nostocales. In polar deserts, there is an increase in the proportion of Chroococcales

Table 5 The numbers of Cyanoprokaryota species in different zones

Zone	Number of species	% of total number of species
Polar deserts zone	156	25.9
Tundra zone	456	75.6
Arctic	482	80
Hypoarctic	428	71
Total	603	100

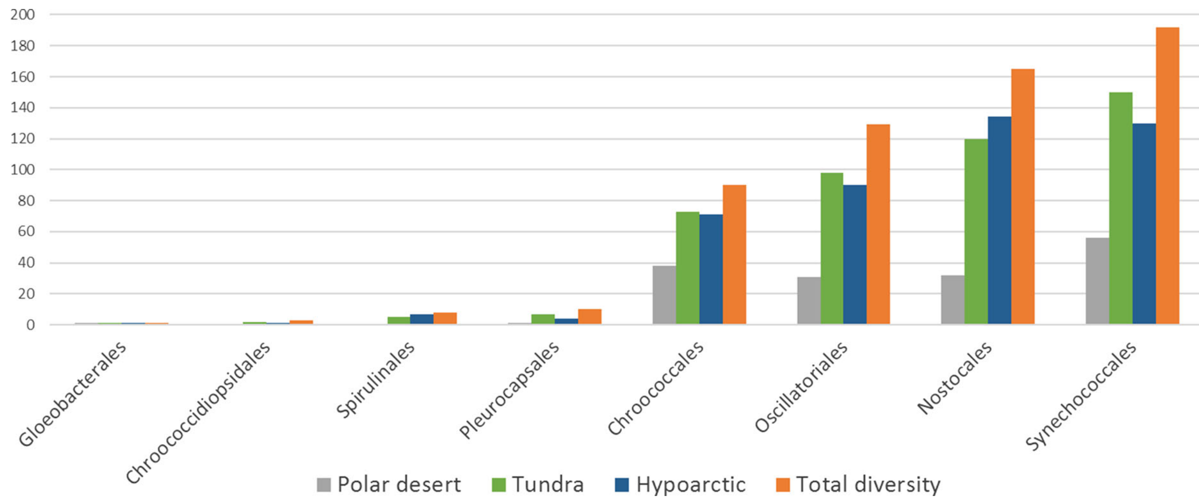

Fig. 4 Comparison of species richness within each order of cyanobacteria in the two Arctic zones and the Hypoarctic

and a decrease in the proportion of Nostocales (Fig. 4). This is due to the low diversity of *Anabaena* and *Dolichospermum* and the increase in diversity of *Gloeocapsa* and *Chroococcus* species.

Undoubtedly, Cyanoprokaryota floras of the Arctic and Hypoarctic are still unevenly and incompletely studied. Murmansk region (359 species) and Spitsbergen archipelago (314 species) are the most fully studied. They also have the greatest similarity of species composition (Sørensen index of >50%). Relatively well-studied floras of other regions have 100–300 species as well as high similarity in species composition. It can be predicted that important additions to knowledge of species occurrence for all studied regions will result from an expansion of research to new areas. A significant increase in the knowledge of diversity of Arctic Cyanoprokaryota would also result from the application of the techniques of molecular genetics to investigate morphologically similar species and others which are difficult to place within the current taxonomic system. Some researchers discuss a possible endemism of Arctic and bipolar species (e.g., Komárek et al., 2012).

Subaerophytic cyanoprokaryotes had the highest species diversity (300 species) of all ecological groups. Cyanoprokaryota diversity changes differently for aquatic and terrestrial environments in a latitudinal gradient from polar deserts to Hypoarctic tundra. One of the main observed environmental patterns is a notable reduction in diversity of typical aquatic species from south to north, and in contrast, an increase in diversity of subaerophytic and aerophytic species in the north. An increasing area of the terrestrial ecosystem is occupied by cyanoprokaryotes with progression from the Hypoarctic to polar deserts. The main reason appears to be the reduced competition from higher plants.

The most widespread species of the Arctic and Hypoarctic are indicated in the species lists given in Tables 2, 3, and 4.

Spitsbergen and Franz Josef Land archipelagos and Polar and Subpolar Urals are typical mountain areas of the Arctic. Cyanoprokaryota floras of these regions are characterized by epilithic species of *Gloeocapsa* and *Chroococcus* as well as by the same species composition of subaerophytic cyanoprokaryotes and the high number of species growing on primitive soils (species of *Leptolyngbya* spp., *Pseudanabaena* spp., *Microcoleus* spp.).

Perspectives and future directions

The diversity of Cyanoprokaryotes in the Eurasian part of the Arctic and Hypoarctic is similar to that of the Antarctic and sub-Antarctic islands (537 species) (https://data.aad.gov.au), of Sweden (558) and of the Czech Republic (505), all being regions where detailed studies have been made (Willen, 2001; Kaštovský et al., 2009). However, these regions all have less environmental diversity than the studied regions of the Arctic and Hypoarctic. We suggest that further research on Cyanoprokaryota in the Arctic and Hypoarctic, including modern molecular studies, would significantly increase the known species and indicate which of these are endemic.

This review has indicated the high diversity of Cyanoprokaryota in the Arctic and Hypoarctic and that species occupy a wide range of aquatic and terrestrial habitats where they form dominant communities. To the south, the pattern is reversed and aquatic cyanoprokaryotes grow in abundance and cause blooms but in terrestrial habitats cyanoprokaryotes are of greatly reduced importance.

A special feature of the Eurasian Arctic and Hypoarctic is the limited number of dominant species. However, these are not special species for high-latitude regions as they are also found in the southern boreal zone.

Further study is required of the ecological preferences of individual species and their role in the formation of microbial communities in aquatic and terrestrial ecosystems of high latitudes. An integrated study of Cyanoprokaryota biodiversity, ecology, and geography in the Arctic and Hypoarctic will enlarge knowledge of the structural and functional diversity of ecosystems and history of biota in the Eurasian region.

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