



Diversity of cyanobacteria and microalgae in hydro-terrestrial habitats in Svalbard and its ecological evaluation

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Abstract: The aim of this research was to study the biodiversity of cyanobacteria and microalgae in hydro-terrestrial habitats from the area of Hornsund fjord (Svalbard archipelago). This research is particularly important, because hitherto no complex research (including all taxonomic groups) has previously been conducted on the cyanobacterial and microalgal flora in Arctic water ecosystems. The research was conducted during the summer seasons of 2011 and 2013. Shannon's diversity index was used to describe species diversity and evenness. Data on cyanobacteria and microalgae were analyzed using the MVSP and PCA. Additionally, a basic analysis of the physicochemical properties of water in the studied ecosystems was performed. A total of 506 taxa were noted in the studied hydro-terrestrial habitats. The most numerous group was cyanobacteria, constituting 35% of all recorded taxa. Ochrophyta and Chlorophyta were almost equally numerous (percentage again as for cyanobacteria). Nineteen types of assemblages were noted in all studied hydro-terrestrial habitats. The diversity of cyanobacteria and microalgae and the assemblages formed by them were used to determine the characteristics of the studied ecosystems. Each type of water ecosystem was represented by specific phycoflora and assemblages. Ecological parameters along with biological data (the diversity of cyanobacteria and microalgae) allowed us to sort the studied hydro-terrestrial habitats by similarity. Our analyses clearly distinguished water ecosystem groups differing in species composition determining their trophic status. The research shows the usefulness of cyanobacteria and microalgae diversity defined by the Shannon-Weaver index for characterizing bodies of water and determining the trophic status of these habitats.

Key words: Arctic, Svalbard, phycoflora, assemblages, ecological features, trophic status.

Introduction

Arctic and Antarctic tundras are unusually diverse in terms of their plant communities and microorganism assemblages. Due to the difficult conditions in the Arctic regions, the dominant species are spore organisms, cyanobacteria and micro-algae assemblages. In polar tundras there are vast surfaces covered with cyanobacterial crust or mats occurring individually or forming various mosaics with mosses and vascular plants. Often moss tundras are interspersed with smaller or bigger watercourses, which additionally enriches the species composition of these ecosystems (Borge 1911; Schell and Alexander 1973; Alexander 1974; Barsdate and Alexander 1975; Matuła 1982; Plichta and Luścińska 1988; Oleksowicz and Luścińska 1992; Elster *et al.* 1994; Skulberg 1996; Villeneuve *et al.* 2001; Elster 2002; Matuła *et al.* 2007; Komárek and Elster 2008; Richter *et al.* 2009; Komárek O. and Komárek J. 2010; Komárek *et al.* 2012; Davydov 2013; 2014; 2016; 2017; Richter *et al.* 2015; Skrzypek *et al.* 2015; Davydov and Patova 2017). In vast seaside terraces there are various hydro-terrestrial habitats of planktonic and benthic organisms (Thomasson 1958; 1961; Foged *et al.* 1964; Willen 1980; Fumanti *et al.* 1995; Bonaventura *et al.* 2006; Kim *et al.* 2008; 2011; Kopalova *et al.* 2013; Nedbalova *et al.* 2013; Skácelová and Barták 2014). Learning about these organisms is particularly important because both plankton and the species forming crusts or mats at the bottom of these reservoirs are the greatest source of biomass in the waters of Arctic ecosystems and play a significant role in biocoenosis. Hitherto, phycologists were mainly interested in soil, snow or ice surface ecosystems (Gerdel and Drouet 1960; Kol 1969; 1971; Elster *et al.* 1997; Müller *et al.* 1998; Kubečková *et al.* 2001; Sävström *et al.* 2002; Kaštovská *et al.* 2005; Turicchia *et al.* 2005; Stibal *et al.* 2006; Matuła *et al.* 2007; Elster *et al.* 2008; Kim *et al.* 2008; 2011; Richter *et al.* 2009; Kvíderová 2012; Pushkareva and Elster 2013; Wojtuń *et al.* 2013; Sehnal 2015; Lutz *et al.* 2016a; 2016b; Kaczmarek *et al.* 2016; Pietryka *et al.* 2016; Uetake *et al.* 2016; Vonnahme *et al.* 2016; Zawierucha *et al.* 2017), sporadically in watercourses, usually in humid moss tundras (Matuła 1982; Elster *et al.* 1994; Komárek *et al.* 2012; Davydov 2013; 2014; Komárek and Kovačik 2013; Richter *et al.* 2014b; Sheath and Müller 1997), or in moss samples from the bottoms of water ecosystems (Davydov 2016). Studies connected with larger water ecosystems are sporadic and incomplete (they focus on individual groups) or outdated (Stockmayer 1906; Thomasson 1958, 1961; Foged 1964; Willén 1980, Bonaventura *et al.* 2006, Kim *et al.* 2011; Davydov 2013, 2014; 2017). They also tend to focus on individual species and their properties (Strunecký *et al.* 2011; 2012; Pinseel *et al.* 2014; Richter *et al.* 2014a; Richter *et al.* 2016), and not the whole cyanobacterial and microalgal flora. The level of knowledge about aquatic ecosystems from this area is still not sufficient to evaluate their biological diversity and its relation to the landscape. It also needs mentioning that

the phycoflora of these water reservoirs is fascinating because it could be where rare species or interesting biocenotic structures occur. As it was mentioned before, cyanobacteria and microalgae play a significant role in all Arctic ecosystems. These organisms are the dominant element not only numerically, but also in terms of biomass (Villeneuve *et al.* 2001; Solheim and Zielke 2002; Elster and Benson 2004; Kaštovská *et al.* 2005; Matuła *et al.* 2007; Thomas *et al.* 2008; Zakhia *et al.* 2008; Richter *et al.* 2009; Komárek *et al.* 2012; Pushkareva and Elster 2013; Richter *et al.* 2015). The dominance usually results from the characteristics of Arctic tundra habitats, the changing climate, cyanobacteria properties absent in other organisms, a broad spectrum of ecological tolerance, and the ability to colonize even the most extreme environments (De Winder 1990; Vincent and Roy 1993; Kirst and Wincke 1995; Whitton and Potas 2000; Elster *et al.* 2002; Elster and Benson 2004; Elster *et al.* 2008; Zakhia *et al.* 2008). The dominant role of cyanobacteria and microalgae in forming polar ecosystems suggests they should be included in habitat descriptions of the region. That would allow us to characterize these habitats in more detail and track changes occurring in them.

Moreover, those unique habitats (lakes, ponds, streams and rivers) contain various cyanobacterial and microalgal assemblages which are among the Arctic's main producers. Due to their ability to fix atmospheric nitrogen, cyanobacteria are not limited in fixing CO₂ from the atmosphere and, consequently, in increased organic matter production (Plichta and Luścińska 1988; Oleksowicz and Luścińska 1992; Vincent 2000; Zielke *et al.* 2005; Skrzypek *et al.* 2015). As a result, cyanobacteria fixing nitrogen and carbon from the atmosphere influence the quality of the tundra and play a significant role in shaping the global balance of carbon based compounds, especially CO₂. Therefore, complex studies of hydro-terrestrial habitats will help us understand microorganisms which significantly influence nitrogen supply, particularly carbon and nitrogen (Elster 2002; Skrzypek *et al.* 2015). Another important property of cyanobacteria and microalgae assemblages is their reaction to climatic changes, which is much quicker than in mosses and vascular plants. As a result they are more sensitive indicators of climatic alterations (Crawford 2008). The knowledge of these organisms as basic components of Arctic tundras is thus very important in observing global climatic changes, which occur initially in polar regions. Following the changes in these microorganisms and their assemblages along with tracking the direction and intensity in cyanobacteria and microalgae biodiversity would allow us to monitor climatic changes.

Therefore, the aim of this research was: (1) to evaluate the taxonomic diversity of cyanobacteria and microalgae, and distinguishing assemblages formed by dominant species; (2) to determine the relationships between these organisms and their assemblages and the habitat conditions (water current, distance from the sea, depth, pH and conductivity, etc.); (3) to ascertain the influence of ecological parameters on the structure of phytoplankton hydro-terrestrial habitats;

(4) to compare the studied ecosystems with regard to species composition and to discover the common parameters for particular hydro-terrestrial type of habitats, and, consequently, to evaluate the suitability of biodiversity of cyanobacteria and microalgae defined by the Shannon-Weaver index for characterizing and differentiating the trophic status of hydro-terrestrial habitats.

Materials and methods

Study area. — The research was conducted in the area of raised marine terraces (Rålstranda, Fuglebergsletta and Revdalen valley) located in the Hornsund fjord, Spitsbergen (Svalbard), (Fig. 1), with a total of 20 hydro-terrestrial habitats (Table 1; Fig. 1). The research was carried out during the summer season of 2011 and 2013. The climate of the research area is determined by the influence of several ocean currents, main one being the Gulf Stream, carrying warm Atlantic water northwards along the coast of Norway. It divides into two main branches and continues northwards with one branch on either side of Svalbard. The climate of Svalbard is characterized by a short summer and vegetation period (lasting 1–3 months); average temperature in January is between -7.7°C and -16.2°C ; average temperature in July is between $+2.3^{\circ}\text{C}$ and $+6.5^{\circ}\text{C}$; average annual rainfall is between 203 and 469 mm. July is the warmest month with an average temperature of $+6.8^{\circ}\text{C}$ recorded in 2013 (Elverland 2009; Láska *et al.* 2013).

Sampling and analysis. — Twenty hydro-terrestrial habitats were selected for the studies and 5–10 representative samples were collected from each. A total of 228 samples were analyzed during two vegetation seasons.

Phytoplankton samples were collected using a 25 μm mesh plankton net. In order to prepare the samples for quantitative analyses, 5 l of water was poured through the net and then concentrated to 200 ml. In the case of small, shallow watercourses the samples were collected directly into containers and then condensed. The samples of periphyton were collected from a surface of 20 cm^2 . All samples were collected using the same method, which was necessary for the comparison of water environments.

Samples were gathered from plankton, on the bottom from shingles and fine stones, rocks, sand, gravel and from the muddy bottom. In the case of stems among clumps of moss, samples were also collected from water squeezed from mosses.

The quantitative composition of particular taxa was determined under the microscope using modified Starmach's 6-grade scale, where 1 means the individual occurrence of a given species; 2 means 1 to 6 units on a standard viewing surface; 3 means 7 to 20 units on a standard surface (subdominant); 4 means from 1 to 10 visible units (subdominant); 5 means 11 to 30 visible

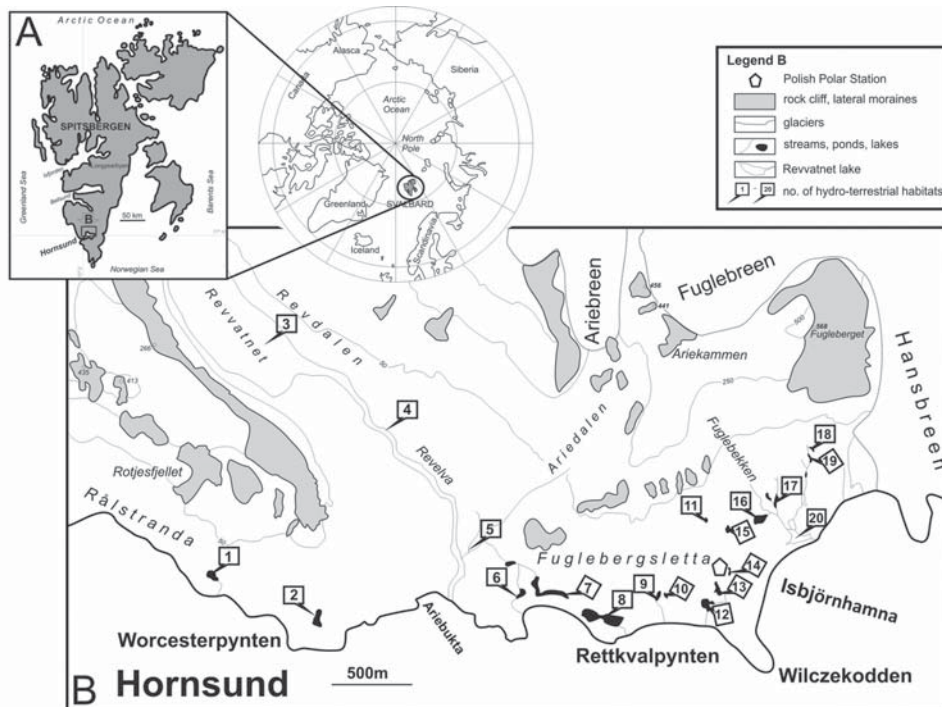


Fig. 1. Map of Spitsbergen Island – location of the Hornsund fjord (A), raised marine terraces Rålstranda and Fuglebergsletta, and Revdalen valley with sample plots (B). Description of 1–20 is in Table 1.

units (subdominant); 6 means water blooms or dominant species forming crusts or mats (over 30 units in every field). Species observation was conducted with a Nikon Eclipse TE2000-S digital microscope equipped with a Nikon DS-Fi1 camera. The identification was performed live and also on material preserved with “etaform” (3:1 alcohol, formalin). The taxonomy of cyanobacteria and microalgae is based on Ettl (1978), Starmach (1972, 1983), Komárek and Fott (1983), Krammer and Lange-Bertalot (1986, 1988, 1991a,b), Hoek *et al.* (1995), Komárek and Anagnostidis (1999, 2007), Coesel and Meesters (2007), Strunecký *et al.* (2013), Komárek (2013).

Physicochemical analyses. — Water pH and conductivity were measured using the multipurpose equipment Elmetron CX-601. For the purpose of statistical analysis for characteristics of hydro-terrestrial habitats numbers were attributed to unmeasurable properties (type of hydro-terrestrial habitats, influence of sea spray, influence of bird colonies, desiccation, water current), (explanation in Table 1).

Table 1

Study area – the topography and characteristics of the hydro-terrestrial habitats.

No. of samples	Locality coordinates	Location	Characteristics of water reservoirs							Physicochemical parameters		
			Type of hydro-terrestrial habitats ¹	Influence		Desiccation ⁴	Water current ⁵	Depth (m)	Distance (m)		Reaction (pH)	Conductivity (µS/m)
			A ²	B ³				C	D			
1	77°01'33" N, 15°59'50" E 015°22'48" N, 15°36'00" E	Marine terraces										
2		Rålstranda	lake	yes	–	0	1	up to 1.00	150	3750	8.10	82.10
3		Rålstranda	lake	yes	no	0	1	up to 1.00	350	3000	8.20	96.70
4		–	Revvatnet lake	no	yes	0	1	up to 40	1875	3250	7.08	52.60
5		Fuglebergsletta	Revelva river	no	yes	0	3	up to 0.50	1125	2125	7.10	59.50
6		Rålstranda\Fuglebergsletta	Revelva's backwaters	yes	yes	1	3	up to 0.15	500	1625	7.50	72.50
7		Fuglebergsletta	pond	yes	no	1	1	0.50	100	1375	7.85	179.30
8		Fuglebergsletta	lake	yes	no	0	1	0.30	75	1125	7.90	149.22
9		Fuglebergsletta	lake	yes	no	0	1	0.40	125	1000	7.35	102.82
10		Fuglebergsletta	shallow pond	no	no	1	1	0.15	175	750	7.60	135.50
11		Fuglebergsletta	shallow pond	no	no	1	1	0.15	200	750	7.60	140.90
12		Fuglebergsletta	pond	no	yes	1	1	0.40	875	250	7.70	145.90
13		Fuglebergsletta	pond	yes	no	0	1	0.30	100	825	7.80	117.20
		Fuglebergsletta	yes	no	0	1	0.30	250	750	6.83	187.20	

14	Fuglebergsletta	shallow pond	no	yes	1	1	0.20	350	625	9.06	157.50
15	Fuglebergsletta	pond	no	yes	0	1	up to 1.00	750	375	9.45	132.00
16	Fuglebergsletta	small lake and stream	no	yes	0	1 and 2	up to 0.50	325	500	8.90	175.00
17	Fuglebergsletta	stream	no	no	1	2	up to 0.30	350	500	7.50	138.20
18	Fuglebergsletta	shallow pond	no	no	1	1	0.20	400	625	7.09	79.50
19	Fuglebergsletta	shallow pond	no	no	1	1	0.20	375	625	7.15	77.10
20	Fuglebergsletta	stream	yes	yes	0	3	0.20	125	750	7.60	148.10

A of the sea spray

B of the bird colonies

C from the sea

D from the bird colonies, nesting on the Arietkammen slope

1 1 – pond, 2 – lake, 3 – river, 4 – backwater, 5 stream

2 1 – under the influence of sea sprays, 0 – without the impact of sea sprays

3 1 – under the influence of bird colonies, 0 – without the impact of bird colonies

4 1 – periodically drying out, 0 – not drying

5 1 – stagnant water, 2 – slowly flowing water, 3 – fast flowing water

Statistical analysis. — Shannon's diversity index (Shannon and Weaver 1949) was used to describe species diversity and evenness. In order to determine the correlation between the studied properties, diversity of cyanobacteria and microalgae defined by the Shannon-Weaver index (H'), evenness index (J') and number of taxa (S), for the phycoflora of hydro-terrestrial habitats, PCA was used. The statistical analyses were performed using the STATISTICA v. 12.5 package (StatSoft Inc. 2014). In order to create a model for data structuring and to determine the ordination technique detrended correspondence analysis (DCA) was conducted (Hill and Gauch 1980). After PCA and DCA, a Monte Carlo permutation test was performed (with 499 permutations, $p < 0.005$) to identify which of the factors significantly influenced the model. In order to determine the changeability of the studied hydro-terrestrial habitats and to determine the main environment gradients through cyanobacteria and microalgae species composition, detrended compatibility analysis PCA was used (CANOCO 4.5) and ordination diagrams were created using CanocoDraw software (ter Braak and Šmilauer 2002). In order to group the studied ecosystems by their similarity or dissimilarity to each other based on dominant species (Sorensen's similarity index) a classification analysis with the hierarchical method was performed. Data on cyanobacteria and algae were analyzed using the MVSP 3.1 software (Kovach 1985–1999).

Results

Diversity of cyanobacteria and microalgae in studied hydro-terrestrial habitats. — A total of 506 cyanobacterial and microalgal species belonging to 4 phyla were recorded in 20 hydro-terrestrial habitats from Hornsund fjord (Table 2, Figures 2–5, Appendix 1). The most numerous were Cyanobacteria (176 species, representing 35% of all the identified species) and Ochrophyta (174 species, 34.38%) represented mainly by the class Bacillariophyceae (163 species, 93.68% of Ochrophyta). Among cyanobacteria 68 species were represented by coccoid or colonial forms, 27 by filamentous forms with heterocytes and 82 by non-heterocytous filamentous species. Chlorophyta was also a large group (154 species, representing 30.43% of all identified species), including desmids (64 species), coccoid (60 species) and filamentous species (30 species). Euglenophyta were represented by only 2 species, constituting less than 0.4% of all the identified species.

The conducted PCA analysis aimed to comparing water bodies for biodiversity and evenness showed that the main changeability range was determined by the first two canonical axes, for which the values were, respectively, 2.528 and 0.449. The cumulated variance percentage for the aforementioned axes was, respectively, 84.292% and 14.967%. The first PCA axis was strongly correlated with H' , J' and S . The highest diversity was recorded in three water basins (no. 2, 8 and 14) and

Table 2

The number of the species of cyanobacteria and microalgae groups found in the researched hydro-terrestrial habitats. Description of hydro-terrestrial habitats (1–20) is in Table 1.

Name of taxonomic group	No. of hydro-terrestrial habitats																				Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Cyanobacteria (cyanobacteria)	6	31	28	7	7	20	30	45	19	16	18	21	11	49	22	16	20	16	21	15	176
cocoid and colonial cyanobacteria	1	16	15	3	3	9	12	22	10	6	7	9	3	17	5	3	9	4	7	4	68
filamentous heterocytous cyanobacteria	0	7	2	0	0	5	7	8	6	5	1	5	4	6	2	0	4	1	5	0	27
filamentous non heterocytous cyanobacteria	5	8	11	4	4	6	11	15	3	5	10	7	4	26	15	13	7	11	9	11	81
Chlorophyta (green algae)	13	24	7	6	13	8	6	33	6	2	6	9	15	17	16	17	2	14	6	13	154
cocoid green algae	12	11	3	1	1	1	0	11	2	0	4	1	3	5	6	8	0	2	0	2	60
filamentous green algae	0	4	3	3	3	2	2	4	1	2	0	4	4	5	4	6	0	6	1	4	30
desmids	1	9	1	2	9	5	4	18	3	0	2	4	8	7	6	3	2	6	5	7	64
Euglenophyta (euglenoids)	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2

Table 2 – cd.

Name of taxonomic group	No. of hydro-terrestrial habitats																				Total	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20		
Ochrophyta	7	22	8	9	15	16	15	25	10	7	10	20	24	14	8	11	17	16	8	24	174	
Chrysophyceae (chrysophytes)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
Xanthophyceae (xanthophytes)	2	2	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	0	0	0	2	10
Bacillariophyceae (diatoms)	5	20	8	9	14	15	15	24	10	6	9	19	24	13	8	10	17	16	8	22	163	
Total (S)	27	77	43	22	35	43	51	103	35	24	34	50	50	81	46	44	39	46	35	52	506	
Diversity Index (H')	3.17	4.193	3.576	2.927	3.351	3.602	3.806	4.478	3.392	2.983	3.321	3.744	3.755	4.335	3.748	3.639	3.525	3.753	3.452	3.844		
Evenness Index (J')	0.950	0.965	0.951	0.947	0.942	0.958	0.967	0.966	0.954	0.939	0.942	0.957	0.960	0.986	0.963	0.962	0.962	0.980	0.971	0.973		

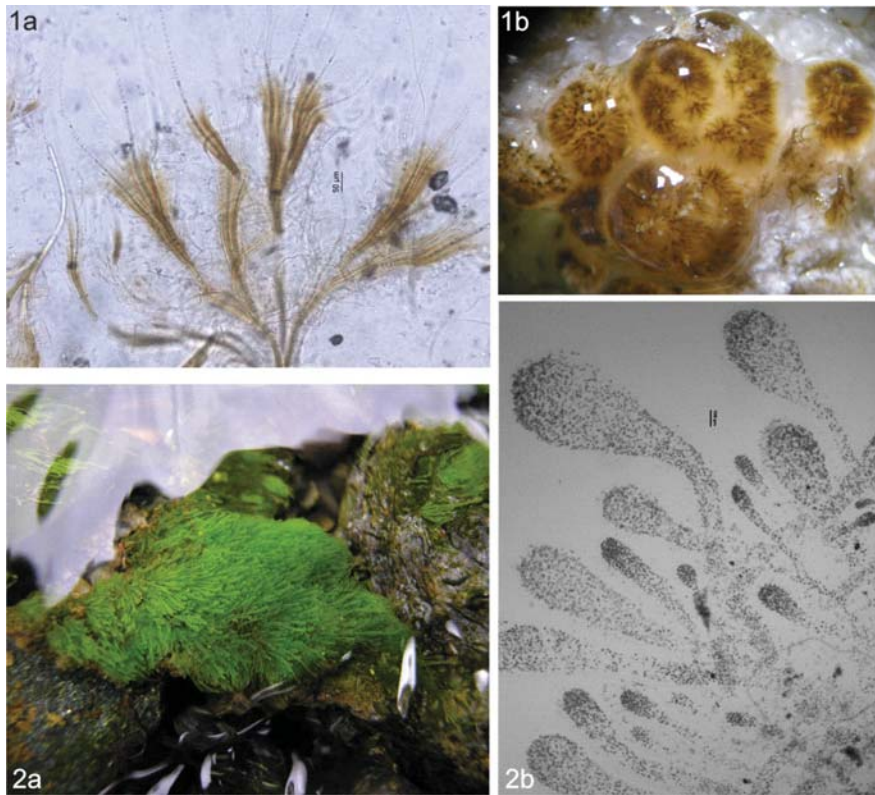


Fig. 2. 1. *Dichothrix gypsophila* (Kütz.) Bornet et Flah. microscopic view (a), macro-thalli (b); 2. *Tetraspora gelatinosa* (Vaucher) macro-thalli (a), Desvaux microscopic view (b).

was between 4.193 and 4.478. These ecosystems are distinguished by the highest identified number of cyanobacteria and microalgae (from 77 to 103 species). The lowest diversity (H') was recorded in hydro-terrestrial habitats 1, 4, 5, 10 and 11, where the H' value was, respectively, 3.165, 2.927, 3.351, 2.983 and 3.321. In the majority of the studied water ecosystems the study recorded species with the highest quantitative share in plankton or in cyanobacteria crusts or mats on rocks or reservoir bottoms. The evenness index (J') confirms this with values at a high level (lowest value 0.939) for individual hydro-terrestrial habitats. The lowest J' values were recorded in water reservoirs no. 1, 4, 5, 10 and 11, which suggests a diverse quantitative composition for particular species. The highest J' values were recorded in streams 18 and 19, pond 14 and stream 20. High values of this index indicate a balanced quantitative share of the majority of taxa in these habitats (an equal share of species). The J' index was around medium values for other ecosystems, where values did not exceed 0.9, which also suggests a significantly diverse quantitative composition of particular taxa (Table 2, Fig. 6).

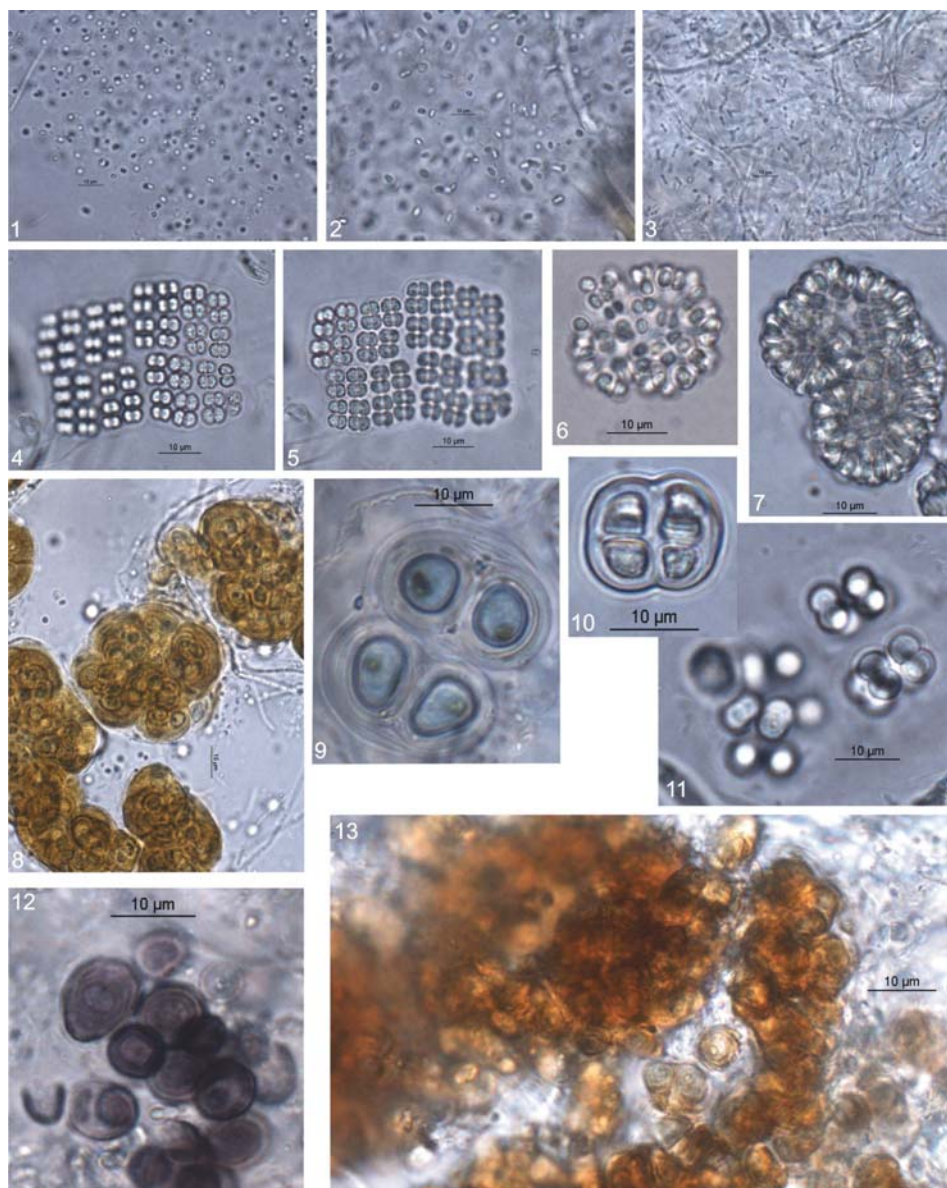


Fig. 3. 1. *Aphanocapsa planctonica*; 2. *Aphanothece clathrata*; 3. *Aphanothece caldariorum*; 4–5. *Merismopedia glauca*; 6. *Snowella lacustris*; 7. *Woronichinia compacta*; 8. *Gloeocapsa kuetzingiana*; 9. *Chroococcus* cf. *schizodermaticus*; 10–11. *Chroococcus minutus*; 12. *Gloeocapsa lignicola*; 13. *Gloeocapsa tornensis*.

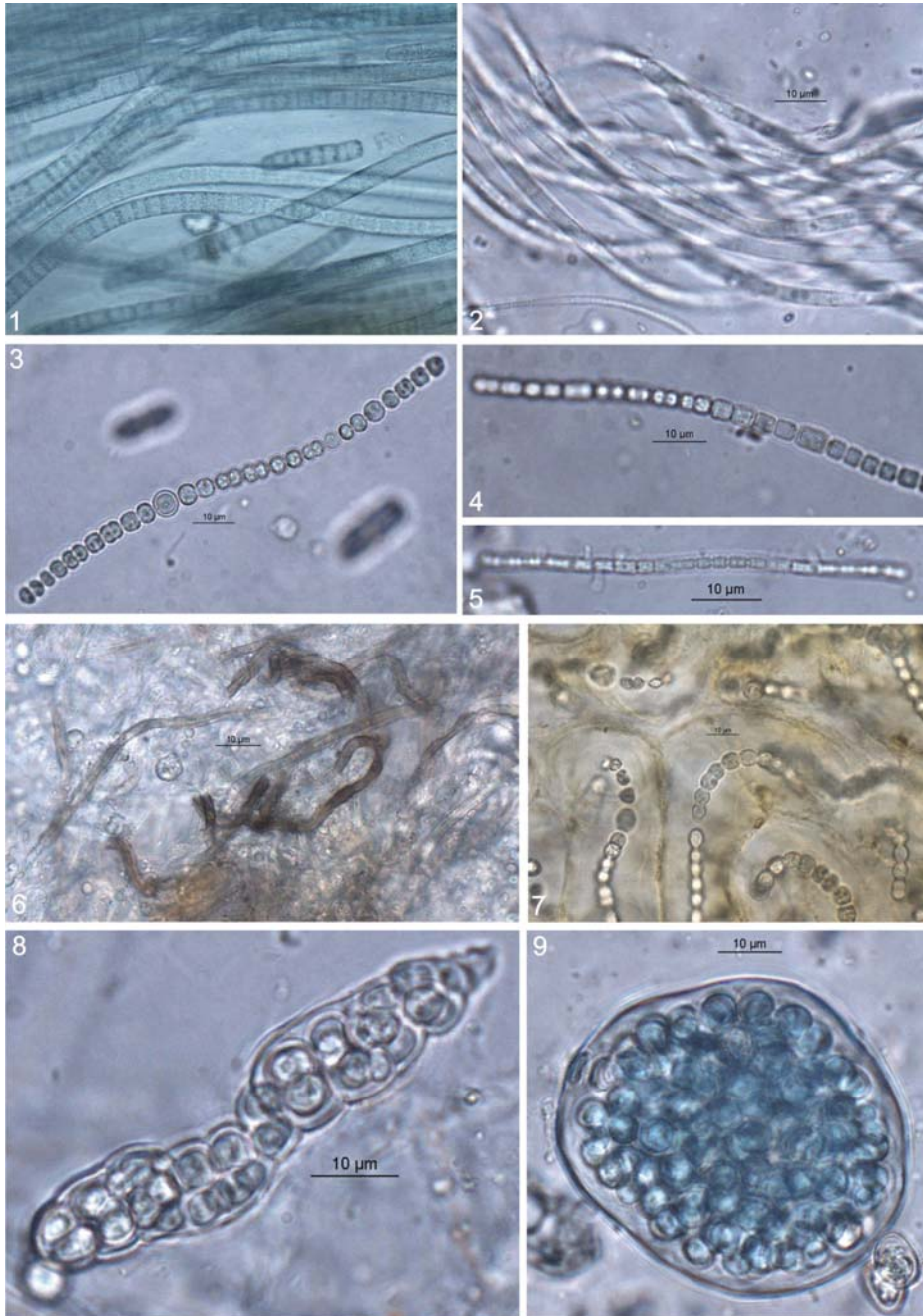


Fig. 4. **1.** *Microcoleus autumnalis*; **2.** *Microcoleus vaginatus* Gomont ex Gomont; **3.** *Dolichospermum* cf. *affine*; **4.** *Anabaena cylindrica*; **5.** *Pseudanabaena catenata*; **6.** *Leptolyngbya sieminskae*; **7.** *Nostoc commune*; **8.** *Nostoc punctiforme*; **9.** *Nostoc* cf. *kihlmani*.

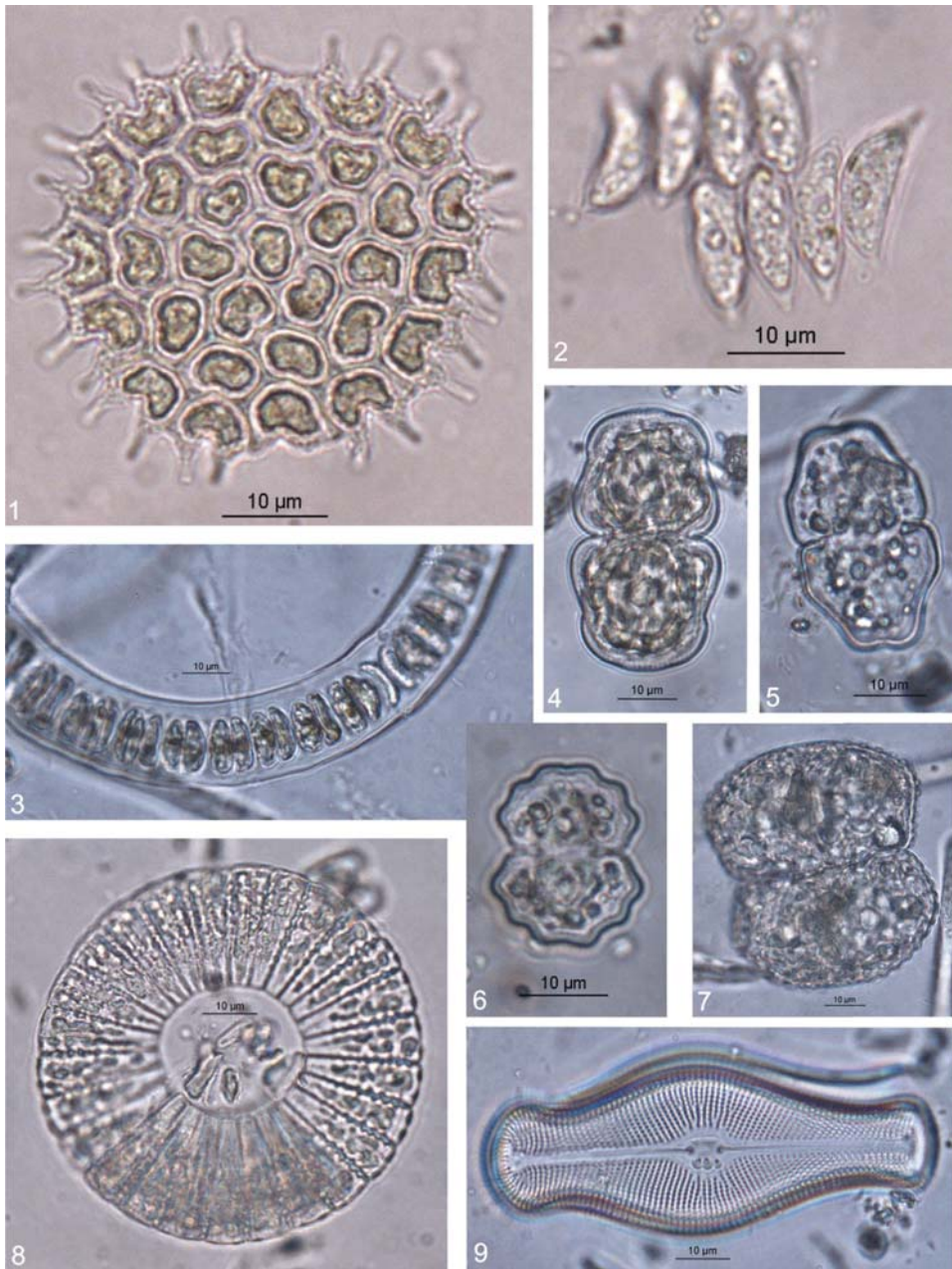


Fig. 5. 1. *Pediatrum boryanum*; 2. *Scenedesmus acutus*; 3. *Prasiola crispa* young filaments; 4. *Cosmarium holmiense*; 5. *Cosmarium pokoryanum*; 6. *Cosmarium meneghinii*; 7. *Cosmarium margaritatum*; 8. *Meridion circulare*; 9. *Didymosphenia geminata*.

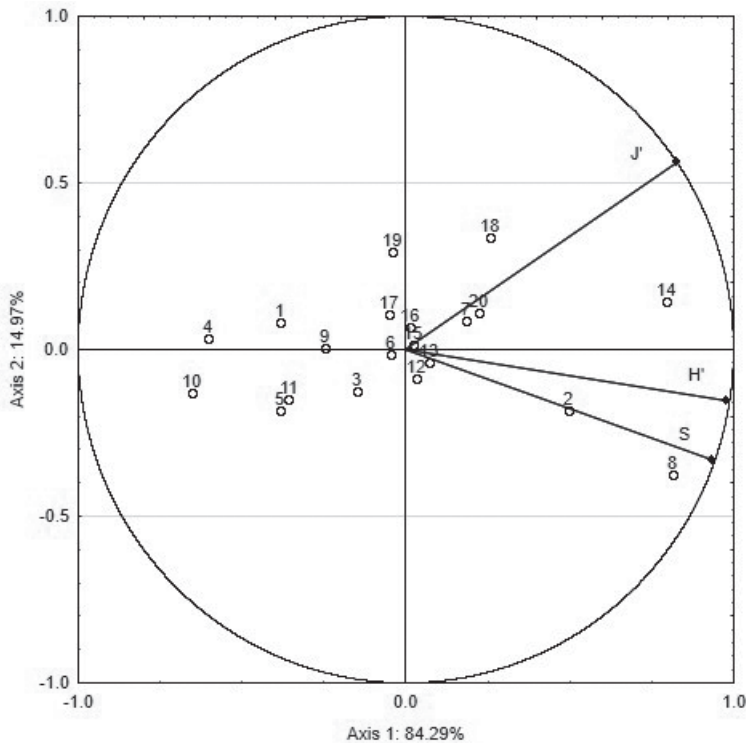


Fig. 6. The results of principal component analysis (PCA) in the first and second canonical axes. The analysis was prepared for diversity of cyanobacteria and microalgae defined by the Shannon-Weaver Index (H'), Evenness Index (J') and number of species (S).

Cyanobacterial and microalgal structure in relation to hydro-terrestrial habitats. — Each hydro-terrestrial habitat was represented by a particular phycoflora typical for itself with various composition of individual cyanobacteria and microalgae groups, represented by characteristic species (Table 2, Appendix 1). In individual hydro-terrestrial habitats cyanobacteria and microalgae also formed assemblages in plankton, on rocks and at the bottom (Fig. 7). It is clear that cyanobacterial and microalgal flora characterized by assemblages shows considerable similarities in qualitative composition between individual hydro-terrestrial habitats. A various degree of similarity determined by common dominant species was observed in the compared reservoirs. In particular hydro-terrestrial habitats there were also characteristic species, indicating their unique character (Fig. 7). The conducted analyses showed that one of the hydro-terrestrial habitats (lake no. 1) significantly differed from the others. Its uniqueness stems from the presence of amoeboid form species belonging to Xanthophyceae (absent in other hydro-terrestrial habitats), which, along with *Tribonema vulgare* and

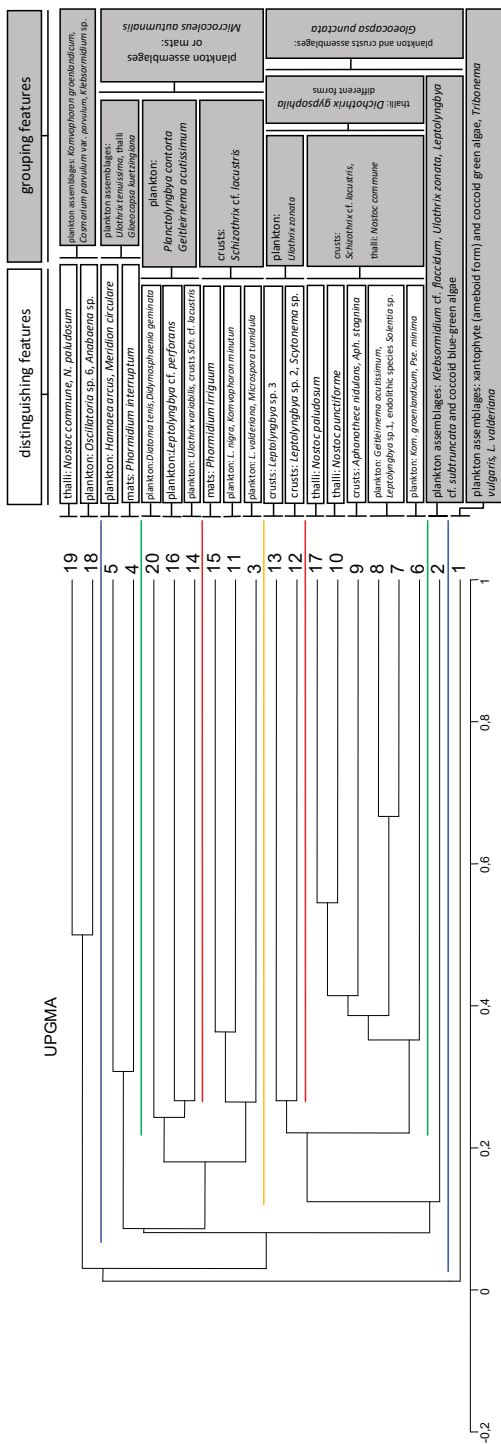


Fig. 7. Hierarchical cluster Sorensen's Coefficient analysis based on the similarity of dominant cyanobacteria and microalgae (assemblages) 1–20 – hydro-terrestrial habitats, description in Table 1. Colored lines separate groups, whose composition includes hydro-terrestrial habitats with various degrees in phycoflora similarity. Red lines separate hydro-terrestrial habitats with the highest similarity, whereas blue ones – the lowest similarity.

the coccoid form of green microalgae (*Trochiscia* sp., *Coenochloris* sp.) and *Chlamydomonas* sp., formed water bloom (plankton assemblages). In plankton, a filamentous form of cyanobacteria *Leptolyngbya valderiana* was also abundant. The water in the studied lake was emerald. The bottom was free from any cyanobacterial crusts. Two shallow ponds no. 18 and 19 situated at the side moraine of the glacier were significantly different from the others. They were connected by the presence of plankton assemblages formed of the same species occurring solely in their flora. In cyanobacteria and microgreen algae the study recorded mostly filamentous species.

The next group comprises hydro-terrestrial habitats no. 2, 6–10, 12, 13 and 17. Significant similarities were found in water ecosystems no. 6–10 (located near the sea shore) and 17, then 12 and 13 due to the thalli of *Dichothrix gypsophila* and *Gloeocapsa punctata* recorded numerously on cyanobacteria crusts and subdominant crusts. Ecosystems no. 6–10 and 17 additionally show considerable similarities due to the dominant species in crusts – *Schizothrix* cf. *lacustris*. The study recorded the following crust-forming cyanobacterial species which were highly abundant: *Sch.* cf. *lacustris*, *Microcoleus vaginatus*, *Aphanothece clathrata*, *Aph. nidulans*, *Aph. stagnina*, *Aph. elabens*, *Aphanocapsa planctonica*, *Gloeocapsa kuetzingiana*, *G. punctata*, *Chroococcus obliterated*, and filamentous heterocytous species forming thalli on cyanobacteria crust: *Nostoc commune*, *N. punctiforme* (ponds no. 10, stream no. 17). Diatoms occurred usually individually in plankton, though the study recorded numerous filaments of *Komvophoron groenlandicum* and *Pseudanabaena minima*, *Geitlerinema acutissimum*, *Leptolyngbya* sp. 1, *Ulothrix zonata*, as well as coccoid species *Scenedesmus aculeolatus*, *Chroococcus minutus* and desmids. In lakes no. 7 and 8, the large quantity of endolithic species *Solentia* sp. is noteworthy. Ponds no. 12 and 13 distinguish themselves in this group due to dominant species forming cyanobacteria crusts – *Leptolyngbya* sp. 2 and *Leptolyngbya* sp. 3 and, additionally, crusts in pond no. 12 had filaments of *Scytonema* sp. forming mats. In the plankton there were filaments of *Ulothrix zonata* crossed with *Clastidium setigerum* and *Cosmarium norimbergense* var. *norimbergense*. In this group lake no. 2 distinguishes itself by exhibiting similarities to all other reservoirs in the group. In plankton filamentous species were more numerous: from cyanobacteria *Leptolyngbya* cf. *subtruncata*, from green algae *Ul. zonata* overgrown to a large extent by *Clastidium setigerum* and *Klebsormidium* cf. *flaccidum*. Among coccoid species the study recorded the following in higher quantities: *Aph. planctonica*, *Chroococcus minor*, *Gloeocapsa punctata* and the heterocytous blue green alga *N. paludosum*. As in the case of lake no. 1 no cyanobacteria crusts were found at the bottom. The final group was formed as a result of the similarity between hydro-terrestrial habitats no. 3–5, 11, 14–16 and 20, where the similarity was due to plankton assemblages formed by the nitrophilous *Microcoleus autumnalis*, occurring in plankton and forming mats. Three subgroups can be distinguished

here. The first one formed by the Revelva river (no. 4) and Revelva backwater (no. 5) with plankton with a high share of *Ulothrix tenuissima*. In both cases the most numerous group was Bacillariophyceae. On the rocks the study recorded irregular, mucilaginous, dirty brownish thalli of *Gloeocapsa kuetzingiana* and in the case of the river – *Phormidium interruptum* mats. Pond no. 14 and streams no. 16 and 20 are the second subgroup, where cyanobacteria and algae were represented by a similar number of species, and in stream no. 20 there was an additional presence of Bacillariophyta. In plankton, among cyanobacteria, the dominants were *Geitlernema accutissimum*, *Planktolyngbya contorta*, *Microcoleus autumnalis*, *Leptolyngbya valderiana*, *L. cf. perforans*, as well as numerous filamentous green algae *Ulothrix* spp. and *Binuclearia tectorum*. At the bottom of a small lake and stream (no. 16) there was also an epiphytic species, *Tetraspora gelatinosa* (Vaucher) Desvaux, which grew on rocks taking two forms (Richter *et al.* 2014a). In the flora of the third subgroup – Revvatnet lake (no. 3) and ponds no. 11 and 15 – the dominant group were cyanobacteria, which formed crusts at the bottom and on rocks. The main component of crusts were the filaments of *Schizothrix cf. lacustris* (apart from pond no. 15, where the species was noted with plankton) with accompanying *Microcoleus autumnalis* mats with *M. vaginatus* and *Gloeocapsa punctata*, *Aphanothece clatratha*, *Aph. elebens* and *Ph. irriguum* mats. In plankton, however, the study recorded the dominance of filaments of *Microspora tumidula* and *Leptolyngbya valderiana*, *Lynngbya cf. nigra* (recorded only in pond no. 11), *Komvophoron minutum* accompanied by equally numerous *Trochiscia granulata* and diatoms. In plankton the study recorded numerous *Microcoleus autumnalis* and the filamentous, young form of *Prasiola crispa*.

Cyanobacterial and microalgal assemblages in relation to hydro-terrestrial habitats. — The studied ecosystems are characterized by a rich and interesting phycoflora and numerous assemblages. Within the ecosystems we identified 12 plankton assemblages, 3 types of crusts and 4 types of mats (Fig. 7). Cyanobacterial crusts were, in majority of cases, formed by *Schizothrix cf. lacustris* (dirty greenish crusts), accompanied by coccoid (*Gloeocapsa* spp., *Aphanothece clatratha*, *Aph. elebens*, *Aph. nidulans*, *Aph. stagnina*, *Chroococcus obliteratus*) and filamentous cyanobacteria (*Microcoleus vaginatus*, *M. autumnalis*, *Leptolyngbya* sp. 1., *Leptolyngbya valderiana*, *Phormidium* sp. 4). Crusts were also formed by *Leptolyngbya* sp. 2 and *L. sp. 3* (pale green, grayish crust), accompanied in both cases by *Microcoleus vaginatus*. In plankton, the main component of the assemblages were amoeboid forms of xanthophyte with coccoid cyanobacteria and green algae or desmids and filamentous cyanobacteria and green microalgae. Diatoms often occurred in plankton in higher quantities (Fig. 7). Mats were formed by *Phormidium interruptum*, *Ph.*

irriguum, *Microcoleus autumnalis* and *Scytonema* sp. Cyanobacterial crusts and rocks often had expanded, leathery, olive to dark greenish and brownish thalli of *Nostoc commune* and nodular, brown and orange ones formed by various forms of *Dichothrix gypsophila* (Fig. 7).

Diversity of cyanobacteria and microalgae in hydro-terrestrial habitats and its relation to ecological parameters. — Depending on ecological parameters, each of the studied water reservoirs was represented by a particular cyanobacterial and microalgal flora. The biological variables used in the PCA analysis explained as much as 28.1% of the total reservoir differences, whereas the ecological conditions only explained 18.6%. Cumulative percentage variance of the species-environment relation was 46.7 for all axes. The eigenvalues for axes 1 and 2 were 0.752 and 0.619, respectively. Among ecological features the most important factors in grouping the studied ecosystems were as follows: distance to bird colonies, pH and conductivity and influence of bird colony. Distance to bird colonies should be regarded carefully as a factor, as it is not directly connected with the influence of bird colonies. This is due to the fact that distance from the colony is not the only bird colony related factor. In the case of biological parameters influencing the grouping of water reservoirs, both dominant and characteristic species were taken into account for particular water ecosystems.

Grouping water reservoirs by biological and ecological features (Fig. 8a, b) showed more similarities to the layout obtained on the basis of the dominant species (Sorensen's coefficient, Fig. 7). The analysis shows a greater influence of cyanobacterial and microalgal flora than ecological parameters on grouping the studied ecosystems. The first group consisted of oligo-mesotrophic and mesotrophic hydro-terrestrial habitats no. 4, 5, 15–16 and 20, the second – oligotrophic water ecosystems (no. 6–10, 12–13 and 17). Additionally, three water reservoirs (no. 3, 11 and 14) did not belong to the two groups as they had features characteristic of both of them. Another group consisted of two shallow ponds (no. 18 and 19) closest to the glacier moraine. Lakes no. 1 and 2 differed from other hydro-terrestrial habitats due to their location regarding bird colonies. In the case of lake no. 2 there was no influence of birds nesting on the Arieammen slope on their ecological parameters, whereas in lake no. 1 there was water bloom, which could suggest higher fertility of the water reservoir. In the case of lake no. 1 a bird colony nesting on the Rotesfjelle slope could have an influence on the phycoflora.

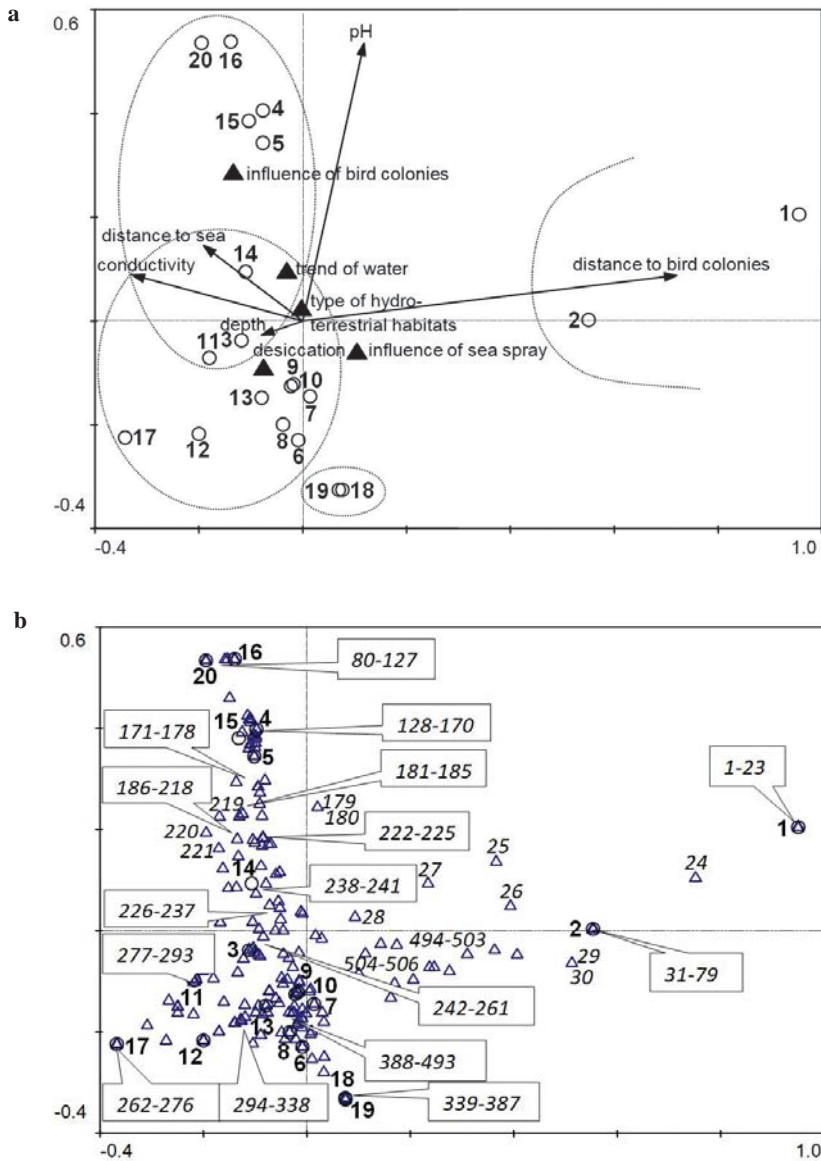


Fig. 8. The results of PCA analysis in the ordination space of the first and second PCA axis, PCA ordination showing the location of hydro-terrestrial habitats (no. 1–20) and their relation to the ecological properties (a) and cyanobacteria and microalgae (b), 1–509 number of taxa (description in Appendix 1).

Discussion

Studying the cyanobacterial and microalgal flora in Arctic hydro-terrestrial habitats is important because the knowledge of the diversity of microorganisms and their biocenotic and trophic relationships is much smaller than what for other habitats in the region (Matuła *et al.* 2007; Richter *et al.* 2009; Richter *et al.* 2014b; Pietryka *et al.* 2016; Davydov 2013; 2014; 2016; 2017). We can rarely find complete information about cyanobacterial and microalgal flora of Arctic hydro-terrestrial habitats, let alone assemblages, in the literature.

This paper contains research of Arctic hydro-terrestrial ecosystems which were, hitherto, neglected. The studied water reservoirs are characterized by an interesting phycoflora rich in quality. Individual cyanobacteria and microalgal assemblages, depending on their trophic conditions, have diverse taxonomic composition (they differ in species number, quantitative dependencies, the quantity of individual populations).

Cyanobacterial and microalgal structure in relation to level of trophic hydro-terrestrial habitats. — The study revealed three groups of hydro-terrestrial habitats differing in phycoflora characterized by various trophic levels. The first group is represented by mesotrophic and meso-eutrophic hydro-terrestrial habitats. The phycoflora of ecosystems no. 4, 5, 15–16 and 20 and their similarities were influenced by the filamentous green algae *Ulothrix* spp. and *Microspora tumidula* as well as the filamentous cyanobacterium *Microcoleus autumnalis*, a species recorded in mesotrophic and slightly polluted habitats (Komárek and Anagnostidis 2007). Additionally, numerous filamentous green algae according to Skowroński *et al.* (2002) indicate their eutrophic character. Some of the reservoirs also had nitrophilous *Prasiola crispa* (young filamentous form). This species occurs in habitats enriched with nitrogen (Hoek *et al.* 1995; Wojtuń *et al.* 2013; Richter *et al.* 2015). In the case of lake no. 1, the presence of Xanthophyceae species in higher quantities is noteworthy (ameboid form of xanthophyte and *Tribonema vulgare*) with a large share of coccoid green algae in the water bloom, which indicates a mesotrophic character of the hydro-terrestrial habitats. In plankton there was a large share of coccoid green algae characteristic of eutrophic water ecosystems (Burchardt *et al.* 2003). The same conclusion is suggested by the presence of Xanthophyceae species, *Tribonema* in particular (Round 1984; Richter and Matuła 2012). Another group consisted of hydro-terrestrial habitats no. 2, 6–10, 12–13 and 17–19, whose similarity was due to heterocytous species belonging to *Nostoc* spp., *Scytonema* sp., *Rivularia* sp., *Tolipothrix tenuis*, *Dolichospermum* cf. *affine*, *Calothrix fusca*, *Dolichospermum solitarius*, *Anabaena* sp. and *Dichothrix gypsophila* (various forms). In most cases the study recorded crusts

formed by *Schizothrix* cf. *lacustris* and *Microcoleus vaginatus* with large shares of *Gloeocapsa punctata*. Heterocytous species indicate the oligotrophic character of these water ecosystems. This fact is confirmed by nitrogen isotope analysis ($d^{15}N$) originating from N_2 bound in soil under cyanobacteria mats (Skrzypek *et al.* 2015). In studies conducted in polar ecosystems, in habitats where in cyanobacteria mats one component was *N. commune*, higher nitrogen concentration was also observed (Coufalík *et al.* 2016). It is caused by nitrogen fixation by heterocytous species (diazotrophs species), which compensate the lack of nitrogen in an oligotrophic habitat (Lee 1999; Graham and Wilcox 2000). Crusts formed by *Schizothrix* cf. *lacustris* are also characteristic of clear stagnant waters (Komárek and Anagnostidis 2007).

Hydro-terrestrial habitats no. 3, 11 and 14 had features of both aforementioned groups. Their flora had both *Microcoleus autumnalis* and heterocytous species, which suggests their oligo-mesotrophic character.

Cyanobacterial and microalgal flora of studied hydro-terrestrial habitats in relation to other Arctic ecosystems. — The studies conducted on cyanobacterial and microalgal flora of terrestrial and freshwater habitats (Kubečková *et al.* 2001; Kim *et al.* 2011) show that flora from other parts of Svalbard displays significant similarities to the flora of the studied area. Many common species were recorded in freshwater habitats, namely diatoms *Meridion circulare*, *Hannaea arcus*, *Achnanthes* cf. *minutissima*, *Didymosphenia geminate* and *Navicula rhynchocephala* and in the terrestrial habitat *Leptolyngbya foveolarum*, *Microcoleus vaginatus* and *Cosmarium subundulatum*. Additionally, studies of polar deserts (Davydov 2013; 2016), small water ecosystems and terrestrial habitats (Davydov 2014; 2017) showed that in the flora of the studied hydro-terrestrial habitats there are many cosmopolitan species also encountered as the main components of cyanobacterial flora in other parts of the Arctic, namely the heterocytous species *Nostoc commune*, *Dichothrix gypsophila*, *Calothrix parietina* and *Tolipothrix tenuis*, recorded in many types of humid habitats. Both in the present study and in the above-mentioned studies by Davydov, humid habitats from wet soils through wet moss tundra to plankton were rich in filamentous non-heterocytous species of the genus *Microcoleus* (*M. vaginatus*, *M. autumnalis* and *M. amoenus*) as well as *Phormidium interruptum* or *Pseudanabaena frigida*. Among coccoid species common ones were also recorded: *Aphanothece caldariorum*, *Chroococcus minutus*, *Gloeocapsa kuetzingiana*, *G. punctata*. In the waters of the studied hydro-terrestrial habitats there were also the filamentous green alga *Microspora tumidula* and the heterocytous cyanobacterium *N. commune*, which were recorded as the most widespread species in tundra streams in the area of North America (Sheath 1997). The research by Komárek *et al.* 2012

conducted in central Spitsbergen also confirmed the cosmopolitan character of Arctic habitats of species such as *Microcoleus autumnalis*, *Nostoc commune* or *Tolipothrix tenuis*.

Cyanobacteria and microalgae from the Arctic in morphological and molecular studies. — Also worth noting is the fact that certain species of polar ecosystems from the Arctic and the Antarctic were subjected to molecular analyses. Molecular research based on genes 18S rRNA and rbcL indicated a very close relation between all specimens of *Prasiola crispa* collected in the Hornsund fjord area (Spitsbergen). Moreover, the *P. crispa* from Spitsbergen is in the same clade as specimens from other regions of the world, including distant places, e.g. the Antarctic, forming one clade with high statistical support. This may mean that *P. crispa* is widespread across the world and that there is little variance within the species. In the majority of cases *P. crispa* reached mature thalli occupying large surfaces. Particular populations showed differences in the macroscopic structure of the thalli, which is connected with the areas where they occur and the intensity of nesting birds' activity in their vicinity (Richter *et al.* 2016). Strains of filamentous cyanobacteria of *Phormidium* (*Microcoleus*) type isolated from two polar regions (Arctic and Antarctic) were also selected for analyses. Although genotypes generally correspond to observed morphotypes, the genetic analyses revealed a high degree of biodiversity that could not be uncovered using solely morphological evaluations. According to the phylogenetic analysis, the three clones were divided into two major clades indicating that the phylogenetic distance between the separate clades was so large and they belonged to different genera. The polyphyletic position of strains of the genus *Phormidium* (*Microcoleus*) was confirmed by this research, attesting to the need to entirely revise the classification in this taxon in the future (Comte *et al.* 2007; Strunecký *et al.* 2011). Moreover, according to the molecular research by Strunecký *et al.* (2012; 2013) on *Microcoleus vaginatus* and *Phormidium autumnale*, it is necessary to revise *Microcoleus* to include *P. autumnale*.

Hydro-terrestrial habitats from the Arctic also deserve our attention due to the presence of interesting species occurring in their waters, e.g. growing on rocks at the bottom of water ecosystems – *Solentia* species (epilithic, endolithic/euendolithic species) occur in marine and tropical regions (Hoffmann 1999; Komárek and Anagnostidis 2007), though the one noted in Arctic ecosystems requires further research aimed at explaining its adaptation to extreme Arctic conditions. The studies conducted in Svalbard also recorded species new to science (among others Komárek and Kovačik 2013; Richter and Matuła 2013) which are endemic to the given area, suggesting that these ecosystems still offer much to discover.

Conclusions

This paper is the first to describe in detail the phycoflora of hydro-terrestrial ecosystems from the Arctic.

The MVSP analysis allowed us to group the studied hydro-terrestrial habitats in accordance with the similarities of their assemblages. As a result, the paper shows that the dominant taxa are relevant in forming assemblages which can be used to characterize water ecosystems.

Cyanobacteria and algae biodiversity defined by the Shannon-Weaver index may be used to group water reservoirs by their trophic status. It is clear that the studied hydro-terrestrial habitats have different trophic status, as indicated by their phycoflora. The fact is also confirmed by the PCA analysis, which suggests that biological factors are more relevant than ecological parameters.

It needs to be mentioned that due to the great species richness, the phycoflora of water ecosystems is a significant element characterizing Arctic hydro-terrestrial habitats. As a result, the research will broaden our understanding of cyanobacteria and microalgae diversity in aquatic ecosystems based on the example of the Hornsund fjord area. It will also show how important these organisms are in aquatic ecosystems forming diverse assemblages both in plankton and at the bottom or on rocks. The study also confirms the usefulness of cyanobacteria and microalgae biodiversity in evaluating trophic levels.

Furthermore, the paper shows how important these organisms are for characterizing the flora of Arctic areas with regard to species richness in these unique hydro-terrestrial habitats.

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Appendix 1

The list of cyanobacteria and microalgae in the studied hydro-terrestrial ecosystems with habitats of their occurrence. Habitats:

e – epiphytic, ec – epipelic, ed – edaphic, en – endolithic (euendolithic), ep – epilithic, m – metaphytic, p – planktonic, pe – periphytic. * *Solentia* sp. – a species still morphologically studied.

** *Scytonema* sp. – a species still morphologically studied and prepared for molecular research.

Species	No. of species in PCA analysis	Habitat	No. of hydro-terrestrial habitats																			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
coccoid and colonial cyanobacteria																						
<i>Aphanocapsa</i> cf. <i>elachista</i> W. et G.S. West	79	p	2																			
<i>Aphanocapsa delicatissima</i> W. West et G.S. West	492	p		1					1													
<i>Aphanocapsa holsatica</i> (Lemm.) Cronberg et Kom.	215	p											1									
<i>Aphanocapsa incerta</i> (Lemm.) Cronberg et Kom.	259	p		1				1	1	1												
<i>Aphanocapsa nubitum</i> Kom. et Kling	78	p	1																			
<i>Aphanocapsa planctonica</i> (G.M. Smith) Kom. et Anag.	499	p	3						3				2									
<i>Aphanocapsa</i> sp. 1	13	p	2																			
<i>Aphanocapsa</i> sp. 2	77	p	1																			
<i>Aphanocapsa</i> sp. 3	169	pe						2														
<i>Aphanocapsa</i> sp. 4	491	p																1				
<i>Aphanothece caldariorum</i> Richter	480	ep							3	2	2									2	1	
<i>Aphanothece clathrata</i> W. et G.S. West	493	p, ep		3						3	2									1	1	

Appendix 1 – continued

Species	No. of species in PCA analysis	Habitat	No. of hydro-terrestrial habitats																				
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
<i>Phormidium</i> sp. 2	63	p	2																				
<i>Phormidium</i> sp. 3	62	p	1																				
<i>Phormidium</i> sp. 4	267	pe		3								1											
<i>Phormidium</i> sp. 5	419	p				1																	
<i>Phormidium</i> sp. 6	201	p										1											
<i>Phormidium</i> sp. 7	154	p												1									
<i>Phormidium</i> sp. 8	366	p																			1		
<i>Planctolyngbya</i> cf. <i>limnetica</i> (Lemm.) Kom.-Leg. et Cron.	224	p, m				1												2	1	2		2	
<i>Planctolyngbya contorta</i> (Lemm.) Anag. et Kom.	183	p, e																4		4		4	
<i>Planctolyngbya lacustris</i> (Lemmerman) Anag. et Kom.	483	p																					
<i>Pseudanabaena catenata</i> Lauterborn	239	p	1															2		1		1	
<i>Pseudanabaena</i> cf. <i>biceps</i> Böcher	365	p																				1	
<i>Pseudanabaena frigida</i> (Fritsch) Anag.	228	p, ep	1									1	2					1	1	1	2	1	2
<i>Pseudanabaena limnetica</i> (Lemm.) Kom.	153	p																			1		
<i>Pseudanabaena minima</i> (G.S. An) Anag.	462	p				1												1	3	1		1	

Appendix 1 – continued

Species	No. of species in PCA analysis	Habitat	No. of hydro-terrestrial habitats																			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Cyanobacteria																						
<i>Pinnularia viridiformis</i> Krammer	341	p																		2		
<i>Placoneis</i> sp.	338	p																				1
<i>Planothidium</i> sp.	271	p																	1			
<i>Stauroneis anceps</i> Ehrenberg	246	p																1		1		
<i>Tabellaria flocculosa</i> (Roth) Kützing	495	p, ec, m	3	1		3													1	1	1	2
<i>Tabellaria</i> sp.	377	p							1													
<i>Tabularia fasciculata</i> (C. Agardh) D.M. Williams	382	ec								2												
unidentified diatom 1	35	p	1																			
unidentified diatom 2	34	p	1																			
unidentified diatom 3	33	p	1																			
unidentified diatom 4	32	p	1																			
unidentified diatom 5	251	p			1																	
unidentified diatom 6	250	p			1																	
unidentified diatom 7	418	p							1													
unidentified diatom 8	385	p							1													
unidentified diatom 9	383	p								1	1											
unidentified diatom 10	432	p									1											
unidentified diatom 11	431	p																		1		
unidentified diatom 12	426	p																		1		

