# DOI: 10.5586/asbp.3605

#### Publication history

Received: 2018-06-27 Accepted: 2018-12-02 Published: 2018-12-31

### Handling editor

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# Authors' contributions

DR, JM: conceived and designed the research; DR, JM, BW: performed the research; DR, JM, MP, BW, AZ, KZS, LS: analyzed the data; DR, JM, MP: wrote the paper

### Funding

The study was supported by grants from the Polish National Polar Project (2005–2007): "Biosphere – the structure, evolution and dynamic of the lithosphere, cryosphere and biosphere in the Arctic and Antarctic" (PBZ-KBN-108/ PO4/2004), TOPOCLIM No. 113/ IPY/2007/01/f, Polish Ministry of Science and Higher Education No. 81128, and Polish National Polar Project (No. N304 410139).

# **Competing interests**

BW served as guest editor of the issue; other authors: no competing interests have been declared

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# Citation

Richter D, Matuła J, Pietryka M, Wojtuń B, Zwolicki A, Zmudczyńska-Skarbek K, et al. Cyanobacterial and green algal assemblages in various tundra habitats in the high Arctic (West Spitsbergen, Norway). Acta Soc Bot Pol. 2018;87(4):3605. https:// doi.org/10.5586/asbp.3605

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# Cyanobacterial and green algal assemblages in various tundra habitats in the high Arctic (West Spitsbergen, Norway)

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# Abstract

The diversity of cyanobacteria and algae from various microhabitats in Spitsbergen is comparatively well known. However, the relationships between environmental factors and the structure of microflora communities remain largely unclear. This study was conducted in Hornsund Bay, which exhibits large variability in the physicochemical characteristics of habitats, particularly with regard to the availability of nitrogen and phosphorus. This variability, to a large degree, is caused by seabird colonies, which fertilize nutrient-poor terrestrial ecosystems near their nesting areas. The large variations in ecological conditions and vegetation types in the study area aid assessment of habitats representing different combinations of factors potentially influencing the formation of cyanobacterial and algal assemblages. The aim of this study was to examine the influence of physicochemical parameters on the taxonomic composition and diversity of green algae and cyanobacteria (particularly the coccoid, oscillatorialean, and heterocystous taxa). The study encompassed two groups of habitats - soil surface habitats and water-saturated habitats, both characterized by diverse influences of seabird colonies, vegetation cover, and moisture. Our results showed that taxonomic diversity and composition of cyanobacteria and algae were mainly influenced by P-PO<sub>4</sub><sup>3-</sup>, N-NH<sub>4</sub><sup>+</sup> and Ca<sup>2+</sup> (soil surface habitats), and NO<sub>3</sub><sup>-</sup>, as well as moisture (index of wetness) and pH (water-saturated habitats). The variability of these physicochemical properties was largely due to the variability of the seabird colony influence. Taken together, our findings aid in understanding the processes of formation of phycoflora assemblages in Arctic tundra.

# Keywords

cyanobacteria; green algae; physicochemical parameters; nutrient limitation; Arctic

# Introduction

The taxonomic diversity of cyanobacterial and algal assemblages in the high latitudes of the Arctic and Antarctic are well documented, particularly for the Antarctic [1–13]. Matuła [14,15], Oleksowicz and Luścińska [16], Oleksowicz et al. [17], Skulberg [18], Davydov [19–22], Stibal et al. [23], Matuła et al. [24], Kim et al. [25], Komárek et al. [26], Komárek and Kováčik [27], Pushkareva and Elster [28], and Raabová and Kováčik [29] provided similar information for the Svalbard archipelago in the European part of

the Arctic. These data suggest that cyanobacteria and algae are important phototrophic components of biocenoses in almost all polar habitats. However, there is limited information about how environmental factors influence the biodiversity of freshwater and terrestrial algal microflora in polar regions.

Although several studies have indicated the influence of physicochemical parameters of water and soil (especially the availability of nutrients) on the formation of cyanobacterial and algal assemblages [24,26,30–47], they do not address some important issues. In the majority of the publications, the relationships between cyanobacterial and algal assemblages and environmental factors are determined for specific ecosystems or habitats, e.g., lakes, rivers, streams, soil, snow, and glacier. However, few studies have compared different ecosystems, habitats, or microhabitats. There is also a lack of studies investigating the effects of interactions of various factors on phycoflora assemblages. The importance of small-scale habitat heterogeneity for cyanobacterial and algal biodiversity is not explored.

Unglaciated and periglacial areas of the Arctic and Antarctic are characterized by chronic deficiency of nutrients such as nitrogen, phosphorus, potassium, magnesium, and calcium. Over time, these extreme habitats undergo changes due to the input of nutrients from various sources, e.g., from the decomposition of accumulated organic matter from vegetation [48–52]. The intensity of these processes can vary considerably on a local scale, thus causing high heterogeneity of ecological conditions. The area of northern Hornsund Fjord, where the study was conducted, is a good example. It is characterized by a high diversity of physicochemical and hydrological properties, and vegetation types; the high variability in the concentration of nutrients (including nitrogen, phosphorus, potassium, and magnesium) has been reported previously [50–55]. Due to the substantial diversity of environmental conditions in this area, it is possible to investigate a wide spectrum of habitats and the associated assemblages of cyanobacteria and algae.

The aim of this study was to determine the taxonomic diversity and composition of phycoflora assemblages in relation to environmental variables. We mainly focused on the evaluation of the responses of cyanobacteria and algae (particularly green algae and coccoid, oscillatorialean, and heterocystous taxa of blue green algae) to nutrient enrichment caused by seabird colonies.

# Material and methods

### Study area

The study area is located on the plain of the raised marine terrace Fuglebergsletta and in the Fuglebekken catchment area on the northwest side of Hornsund Fjord, in the vicinity of the Polish Polar Station (Fig. 1). Part of this area is influenced by seabird breeding colonies situated on the slope of Ariekammen. Samples were collected during summer (July and August).

A total of 77 sites were selected (Fig. 1) to represent different habitats: crust and mats on soil surfaces, shallow and slow current streams, shallow lakes, and watersaturated sites with various types of Arctic vegetation. From each habitat, three to six samples were collected depending on the size of habitat. The sampled habitats differed considerably in terms of physicochemical properties, especially moisture and nutrient supply (mainly nitrogen and phosphorus supply from different sources). For example, habitats located outside the reach of seabird influence are usually very poor in nutrients [46,47,49–52], whereas soil surface habitats often suffer water shortages, because of typically long dry periods. On the basis of this differentiation, the studied habitats were classified as follows:

Group I – soil surface habitats (within this group, there is a considerable variation in the influence of seabird colonies and moisture):

Sites 1–6 – mountain slopes under the influence of seabird colonies with *Prasiola* crispa, *Plagiomnium ellipticum*, *Sanionia uncinata*, *Tetraplodon mnioides*, and *Dicranum* sp. (Sites 1–3) or with *P. crispa*, *Chrysosplenium tetrandum*, *Cochlearia* groenlandica, *Poa alpina* var. vivipara, Cerastium arcticum, Salix polaris, Plagiomnium





*elipticum, Sanionia uncinata, Tetraplodon mnioides, Dicranum* sp., and *Brachythecium turgidum* (Sites 4–6), very dry;

- Sites 31–36 patterned ground, 800–900 m distance from the base of Ariekammen slope, periodically dried out;
- Sites 37–39 the vicinity of the lateral moraine Hansbreen with initial stage of cyanobacteria-moss communities, moderately wet;
- Sites 46–48 snowbeds and small depressions in the ground with cyanobacteria crust, supplied with water from melting snow and rain, 850–900 m from the base of Ariekammen slope, moderately wet.

Group II – water-saturated habitats (habitats in this group also differ in the intensity of seabird colony influence):

• Sites 7–11, 23–27, 40–45, and 59–61 – moss-dominated vegetation areas: wet turf, shallow streams, and erosive hollows with slow current waters, permanently supplied with water;

# Tab. 1 Cyanobacteria and green algae composition in the studied habitats (Sites 1–77). Study sites are described in the text.

Species	Symbol	Sites
(	CYANOBACTE	ERIA
Coccoid	l or colonial cy	anobacteria
Aphanocapsa sp. 1 / densely distributed cells	Aph.sp1	1–3, 8, 11, 42
Aphanocapsa sp. 2 / loosely distributed cells	Aph.sp2	49, 50, 55
Aphanocapsa sp. 3 / round cells	Aph.sp3	7, 59, 68–70, 72, 75
Aphanothece caldariorum Richter	Aph.cal	4, 6, 43, 45, 49–51, 53, 55, 76, 77
Aphanothece cf. minutissima (W. West) KomLegn. et Cronberg	Aph.min	71–73
Aphanothece clathrata W. et G. S. West	Aph.cla	43-45, 65-67
Aphanothece microscopica Näg.	Aph.mic	53–55
Aphanothece sp.	Aph.sp	68–70
Aphanocapsa saxicola Näg.	Aph.sax	37–39
Aphanothece stagnina (Sprengel) A. Braun in Rabenh.	Aph.sta	20, 21, 59, 60–62, 65–70, 75
Chlorogloea purpurea Geitler	Chl.pur	43–45
Chroococcus helveticus Näg.	Chr.hel	4-6, 37-39, 74
Chroococcus minor (Kütz.) Näg.	Chr.min	50
Chroococcus minutus (Kütz.) Näg.	Chr.mi2	21, 23, 28–30, 33, 34, 40, 49, 50, 52–55, 59, 65, 66, 68–70, 74
Chroococcus sp.	Chr.sp	19, 43–45
Chroococcus turgidus (Kütz.) Näg.	Chr.tur	43-47, 54, 55, 68-70, 74, 79
Chroococcus varius A. Braun in Rabenh.	Chr.var	71–73
Clastidium setigerum Kirchner	Cla.set	62, 65
Gloeocapsa alpina (Näg.) Brand	Glo.alp	49, 53–55
Gloeocapsa biformis Ercegović	Glo.bif	33-35, 37-40, 43-45, 48, 55, 73
Gloeocapsa compacta Kütz.	Glo.com	44, 45, 49, 51–55, 59, 68, 69, 77
Gloeocapsa kuetzingiana Näg.	Glo.kue	28, 33–36, 40, 46, 47, 49, 51–55, 62–64, 74, 75
Gloeocapsa punctata Näg.	Glo.pun	21, 28–36, 40–48, 55–57, 59, 62–67, 69–71, 74, 77
Gloeocapsa sanguinea (Agardh) Kütz.	Glo.san	74, 77
Gloeocapsa tornensis Skuja	Glo.tor	22-28, 31-34, 36-39, 63
Gloeocapsa sp.	Glo.sp	38-42, 74
<i>Gloeocapsopsis</i> cf. <i>pleurocapsoides</i> (Nováček) Kom. et Anag.	Glo.ple	68–70
Gloeothece cf. palea (Kütz.) Rabenh.	Glo.pal	74, 77
Gloeothece sp. 1	Gle.sp1	4–6
Merismopedia sp.	Mer.sp	1–6
Merismopedia cf. marssoni Lemm.	Mer.mar	9, 11–16
Woronchinia sp. 1 / small cells	Wor.sp1	52, 54, 59
Woronchinia sp. 2 / with aerotopes	Wor.sp2	40, 55, 60, 61
Woronichinia compacta (Lemm.) Kom. et Hindák	Wor.com	74
Heterocyto	us filamentous	cyanobacteria
Calothrix cf. parietana (Näg.) Thuret	Cal.par	33-35, 47, 51, 52, 54, 55, 57, 62-64, 68-70, 77
Calorhrix sp. 1 / spreading sheaths	Cal.sp1	43-45, 59

# Tab. 1 Continued

Species	Symbol	Sites
Calothrix sp. 2 / brown sheaths	Cal.sp2	50
Sacconema sp.	Sac.sp	33-36
Dichothrix gypsophila (Kütz.) Bornet & Flahault / sensu lato	Dic.gyp	40-42, 44, 45, 49, 55, 62-67
Dichothrix orsiniana (Kütz.) Bornet et Flah.	Dic.ors	40, 43–45, 74
Dichothrix sp.	Dic.sp	43, 44, 68, 69
Nodularia harveyana (Thwaites) Thuret	Nod.har	28, 45, 57, 70
Nostoc cf. paludosum Kütz.	Nos.pal	33-40, 48, 70
Nostoc cf. punctiforme (Kütz.) Hariot	Nos.pun	31, 32, 37
Nostoc commune 1 Vaucher / sensu lato	Nos.co1	28, 30, 33–39, 46, 47, 49–52, 55, 61, 63, 64, 66, 67
Nostoc commune 2 firn thalus	Nos.co2	40, 43-45, 49, 55-57, 68, 69
Nostoc commune 3 Vaucher / subaerophytic form	Nos.co3	71–73
Petelonema crustaceum Agardh ex Kirchner	Scy.cru	31-37, 46, 49, 51, 77
Tolypothrix sp. / brown sheaths	Tol.sp	50, 68–70
Tolypothrix tenuis Kütz.	Tol.ten	33–37, 51–53, 55, 62, 65–67, 74, 76, 77
Nonheterocyt	ous filamentous	cyanobacteria
Geitlerinema acutissimum (Kufferath) Anagnostidis	Gei.acu	4, 7, 8, 20, 21, 23, 55, 57, 59–61, 65–67, 69, 70
Glaucospira sp.	Gla.sp	57
Homeothrix cf. juliana (Bornet et Flahault) Kirchner	Hom.jul	62–64
Komvophoron minutum (Skuja) Anagn. et Kom.	Kom.min	8, 10, 13, 14, 21, 43, 44, 49, 68–70, 72–74, 76
Leiblenia epiphytica (Hieronymus) Compère	Lei.epi	69, 70
<i>Leptolyngbya foveolarum</i> (Raben. ex Gomont) Anagn. et Kom.	Lep.fov	4, 5, 8, 10, 27, 33, 34, 36–39, 76
Leptolyngbya sieminskae Richter & Matuła	Lep.sie	21, 31–36, 44–47, 49–55, 75, 76, 78
Leptolyngbya tenuis (Gom.) Anag. et Kom.	Lep.ten	17, 21, 28–30, 65, 67
<i>Leptolyngbya</i> sp. 1 / cells with grains	Lep.sp1	4, 6, 7, 9, 13, 18–21, 40–42, 52, 62–67, 73
<i>Leptolyngbya</i> sp. 2 / thin walls	Lep.sp2	7, 20–24, 33, 36
Leptolyngbya sp. 3	Lep.sp3	21, 22, 27–30, 62, 63, 65–67
Leptolyngbya sp. 4	Lep.sp4	1–3
Leptolyngbya valderiana (Voronchin) Anagn. et Kom.	Lep.val	7–12, 14, 15, 17–19, 22, 26, 27, 59–64, 68
Limnothrix vacuolifera (Skuja) Kom. et al.	Lim.vac	28-30
<i>Lyngbya aestuarii</i> Liebman ex Ganont	Lyn.aes	59–61, 69, 70
Lyngbya sp. 1	Lyn.sp1	16
<i>Lyngbya</i> sp. 2 / wide filaments	Lyn.sp2	44, 45
<i>Microcoleus autumnalis</i> Trevisan ex Gamout (Strunecky et al.)	Mic.aut	1–6, 8–26, 28–30, 56, 57
Microcoleus vaginatus Gomont ex Gomont	Mic.vag	28-30, 32, 40, 45-47, 53-57, 63-68, 70, 72, 74-76
Oscillatoria cf. ornata Kütz. et Gomont	Osc.orn	71, 73
<i>Oscillatoria fracta</i> Carlson	Osc.fra	4, 27
Oscillatoria rupicola Hansgirg	Osc.rup	4
Oscillatoria sancta Kütz. ex Gomont	Osc.san	44
Oscillatoria sp. 1 / thin walls	Osc.sp1	50

# Tab. 1 Continued

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Species	Symbol	Sites
Oscillatoria sp. 2 / long cels	Osc.sp2	76
Oscillatoria sp. 3	Osc.sp3	21
Oscillatoria sp. 4	Osc.sp4	37-39
Oscillaroria subbrevis Schmidle	Osc.sub	4
Oscillatoria tenuis Agardh ex Gomont	Osc.ten	28-30
<i>Phormidium amoenum</i> Kützing ex Anagnostidis et Komárek	Pho.amo	28–30, 37, 39
Phormidium sp. 1	Pho.sp1	37
Phormidium sp. 2	Pho.sp2	4
<i>Phormidium foveolarum</i> (Rabenh. ex Gomont) Anagn. et Kom.	Pho.fov	27
<i>Phormidium irriguum</i> (Kütz. ex Gomont) Anag. et Kom.	Pho.irr	28–30, 56
<i>Planctolyngbya</i> cf. <i>limnetica</i> (Lemm.) KomLeg. et Cronberg	Pla.lim	5, 6, 57, 62, 65
Planctolyngbya contorta (Lemm.) Anag. et Kom.	Pla.con	56, 57, 62–65
Pseudanabaena catenata Lauterborn	Pse.cat	8, 11, 19, 26, 27, 53, 55–57, 65–67, 71–73
Pseudanabaena cf. minima (G. S. an) Anag.	Pse.min	76
Pseudanabaena frigida (Fritsch) Anagn.	Pse.fri	7, 9, 14, 15, 37–40, 44, 45
Pseudanabaena limnetica (Lemm.) Kom.	Pse.lim	5, 6, 29, 30
Pseudanabaena sp.	Pse.sp	5
Schizothrix cf. calcicola Gomont / aerophytic form	Sch.ca1	20, 21
Schizothrix cf. calcicola Gomont/thin cells	Sch.ca2	62–64, 68–70
<i>Schizothrix</i> cf. <i>lacustris</i> A. Braun ex Gomont / subaero- phytic form	Sch.la1	5, 40, 42, 43, 45, 49, 51
<i>Schizothrix</i> cf. <i>lacustris</i> A. Braun ex Gomont / aero- phytic form	Sch.la2	33–39, 46–48, 74–77
<i>Schizothrix</i> cf. <i>lacustris</i> A. Braun ex Gomont / plankton form	Sch.la3	41, 42, 53–55
Schizothrix sp.	Sch.sp	3-6
Stigonema cf. mamillosum (Lyngbya) Agardh	Sti.mam	33, 36
Symplocastrum sp. 1 / thin filaments	Sym.sp1	6, 40–45
Symplocastrum sp. 2 / short cells	Sym.sp2	20, 21
Synechocystis sallensis Skuja	Syn.sal	52
(	CHLOROPHYTA	
	Desmids	
Actinotenium sp.	Act.sp	37
Cosmarium biretum var. biretum West & West	Cos.bir	29, 30, 56, 57
Cosmarium botrytis Ralfs var. botrytis West & West	Cos.bot	59–61
Cosmarium costatum var. costatum Nordst.	Cos.cos	20-22, 59-62, 68-73
Cosmarium formosulum Hoff	Cos.for	62–67
Cosmarium granatum Bréb.	Cos.gra	71–76
Cosmarium holmiense P. Lundell	Cos.hol	20, 22, 49, 50, 52, 59–61, 68–74, 76, 77

# Tab. 1 Continued

Species	Symbol	Sites
Cosmarium hornavaense Gutw.	Cos.hor	23–25, 27, 69, 70
Cosmarium laeve Rabenh.	Cos.lae	62–67
Cosmarium norimbergense Reinsch	Cos.nor	62–67
Cosmarium parvulum Bréb.	Cos.par	37–39
Cosmarium pokornyanum (Grunow) W. et G. S. West	Cos.pok	37–39
Cosmarium sp.	Cos.sp	74, 76, 77
Cosmarium speciosum P. Lundell	Cos.spe	12, 14–16, 18, 19, 23, 24, 26–30, 40–45, 52, 56, 57, 68–70, 72, 73
Cosmarium subcostatum Nordst.	Cos.sub	37–39
Cosmarium undulatum Ralfs	Cos.und	8, 11–17, 19, 59–61, 68, 69, 71–73, 77
Euastrum sp.	Eua.sp	37, 39
Mesotaenium sp.	Mes.sp	4
Staurastrum brebissonii Gutw.	Sta.bre	24–27
Staurastrum cf. borgeanum Schmidle	Sta.bor	68–70
Staurastrum sp. 1	Sta.sp1	40-42
Staurastrum sp. 2	Sta.sp2	8, 10, 11
Staurastrum sp. 3	Sta.sp3	68–70
Fil	amentous gree	n algae
Klebsermidium cf. montanum (Hansg.) S. Watanabe	Kle.mon	4, 5
Klebsormidium sp.	Kle.sp	4, 5
Microspora pachyderma (Wille) Legerheim	Mic.pac	7, 9, 11, 12, 17, 18, 21–23, 25
Microspora tumidula Hazen	Mic.tum	9, 13, 17, 19–21, 28, 56, 71, 72
Prasiola crispa (Lightf.) Meneghini	Pra.cri	1–10, 12–15, 17–22, 28
Ulothrix aequalis Kütz.	Ulo.aeq	25, 26
Ulothrix cf. oscillarina Kütz.	Ulo.osc	26, 44
Ulothrix subtilis Kütz.	Ulo.sub	9, 16, 19, 20, 21, 24–28, 56, 72
Ulothrix sp.	Ulo.sp	5, 6
(	Coccoid green a	algae
Not identified coccoid green algae	coc.gre	4–6
Gleocystis sp. 2	Gle.sp2	4–6
Monoraphidium cf. griffithi Kom. Legh.	Mon.gri	8, 10, 11
<i>Scotiella antarctica</i> Fritsch f. <i>svalbardensis</i> E. Kol et S. Eurola	Sco.anf	7, 8, 10–14, 17–19, 28
Scotiella antarctica Fritsch	Sco.ant	7, 9–11, 23, 24, 26, 27, 29–30, 74, 75, 77
Scotiella nivalis (Shuttlew) Fritsch	Sco.niv	7–9, 11, 12, 14–16, 18, 74, 76, 77
Scotiella tuberculata Bourr.	Sco.tub	7–10, 12–14, 17–19
Scotiellopsis terestris (Reisigl) Punčoch. & Kalina	Sco.ter	7–10, 12, 14, 18, 19
Scotiella oocystiformis (Lund) Punčoch. & Kalina	Sco.ooc	4, 5
Tetracystis sp.	<i>Tet</i> .sp	4, 6
Trochiscia granulata (Reinsch) Hansg.	Tro.gra	5, 6

7 of 21

- Sites 16–19, 68–70, and 71–73 puddles between mosses, permanently supplied with water;
- Sites 12–15 and 20–22 wet turf, permanently supplied with water;
- Sites 49–52 and 74–77 moist areas with *Saxifraga* spp. community, permanently supplied with water;
- Sites 53–55 surface of coarse rocks and stones with cyanobacteria crust and Sanionia uncinata, permanently supplied with water;
- Sites 28–30, 56–58, and 62–67 ponds and lakes.

#### Microscopic analysis

Phytoplankton samples were collected using a 25-µm mesh plankton net. For quantitative analysis, 5 L of water was poured through the net. Periphyton samples were collected from 20-cm<sup>2</sup> areas. All samples (plankton and periphyton) were collected using the same sampling methods, for effective comparison of water environments. Species were identified under a digital microscope (Nikon Eclipse TE 2000-S, Nikon, the Netherlands). The abundance of particular taxa was determined under the microscope using a modified Starmach's 6-point scale. Cyanobacteria and green algae were identified according to the available literature [56–62].

# Water and soil physicochemical analyses

Water and soil samples were collected in the summer (July and August). Surface water samples were collected in acid-washed 500-mL polyethylene bottles. Before collection, the bottles were rinsed with sampled water. Soil samples were collected in polyethylene bags. After collection, both water and soil samples were transferred to a dark and cold place as soon as possible. Electrical conductivity and pH of water samples (CPC-401 Elmetron, Poland) were measured in the laboratory shortly after sampling. Before the next analyzes, water samples were filtered through nitrocellulose filters (0.45  $\mu$ m; Millipore; Merck, Poland). Water samples were analyzed in the Polish Polar Station's laboratory. NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup> PO<sub>4</sub><sup>2-</sup>, S-SO<sub>4</sub><sup>3-</sup>, K<sup>+</sup>, Ca<sup>2+</sup>, Mg<sup>2+</sup>, and F concentrations were determined by high performance liquid chromatography (HPLC) with a two separated Metrohm Compact IC 761 System (Metrohm, Hensau, Switzerland). An analysis with a suppressor was performed only for anions.

Soil pH and concentration of inorganic N forms were determined on fresh samples. pH was measured at a soil:water ratio of 1:5 (w/v) (CPC-401 Elmetron). N-NH<sub>4</sub><sup>+</sup> and N-NO<sub>3</sub><sup>-</sup> were extracted by shaking for 2 h with 1 M KCl (1:5 soil:extracting agent) or water (1:5 soil:water), respectively, and filtered through Whatman 42 filter paper (Merck, Poland). The extracts were frozen at  $-20^{\circ}$ C in order to store for subsequent analysis. Soil water content was measured gravimetrically by drying in an oven at 60°C to a constant mass. N-NH<sub>4</sub><sup>+</sup>, N-NO<sub>3</sub><sup>-</sup>, and P-PO<sub>4</sub><sup>3-</sup> concentrations were determined using a flow-injection analyzer (FIA-Compact, MLE GmbH, Germany). The remaining parts of soil samples were air dried and sieved to remove coarse fragment, roots, and biota. Dry samples were digested with nitric acid (65% pro analysis) and hydrogen peroxide (30%) in an open system. The digests were then diluted with distilled water to 50 mL. Soil Na<sup>+</sup>, K<sup>+</sup>, Ca<sup>2+</sup>, and Mg<sup>2+</sup> content was determined using FAAS (Avanta PM, Atomic Absorption Spectrometer, GBC Scientific Equipment, Australia). The physicochemical properties of the studied sites are shown in Tab. 2. The following moisture scale (index of wetness) was used to determine moisture of the soil and index of wetness for water-saturated habitats: dry - 1, periodically dry - 2, moderately wet - 3, permanently supplied with water i 4, wet - 5 (for water biotopes).

#### Statistical analysis

Statistical analyses were performed using the program CANOCO 4.5, and ordination diagrams were created using CanocoDraw software [63].

). Study sites are described in the text.
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Variab	le	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
			Sites 1-3			Sites 4-6			Sites 31–36			Sites 37-39		•	Sites 46-48	
$N-NH_4^+$	mg kg <sup>-1</sup>	10.70	24.34	15.59	8.98	10.90	9.92	0.59	1.11	0.94	0.17	0.19	0.18	0.41	0.96	0.66
N-NO <sub>3</sub> -		106.21	285.08	167.04	110.00	154.46	126.71	1.85	2.27	2.03	0.11	0.11	0.11	0.00	0.00	0.00
$P-PO_4^{3+}$		36.64	47.10	40.59	38.20	49.57	42.25	0.00	00.0	0.00	0.00	0.00	00.0	0.00	0.00	0.00
Na⁺		0.35	0.69	0.54	0.40	0.56	0.50	0.20	0.32	0.28	1.50	1.70	1.63	0.19	0.20	0.20
$\mathrm{K}^+$	;	56.32	101.64	77.08	45.60	49.20	47.23	4.79	5.40	5.11	1.20	2.00	1.53	9.66	14.67	11.44
Ca <sup>2+</sup>		150.84	240.16	192.67	160.00	200.00	183.00	35.00	55.20	39.81	38.20	41.40	39.97	14.97	15.20	15.06
$\mathrm{Mg}^{\scriptscriptstyle +}$		11.76	14.14	13.10	10.80	12.80	11.50	5.68	7.43	6.57	4.90	5.30	5.13	4.89	4.96	4.92
Reaction	Hq	3.83	4.15	4.03	4.00	5.20	4.68	7.02	8.20	7.65	5.00	5.50	5.20	6.78	7.19	6.99
Conductivity	μS cm <sup>-1</sup>	79.40	139.70	101.73	68.30	110.01	94.47	64.50	82.20	71.28	68.20	70.90	69.70	16.01	37.20	23.70
Organic matter	${\rm g~kg^{-1}}$	47.43	91.27	75.64	88.99	92.30	90.53	6.19	14.10	10.18	6.10	6.80	6.37	6.20	6.68	6.41
			Sites 7–11		S	ites 12-15		•	Sites 16–19			Sites 20-22		U,	Sites 23–27	
NO <sup>2-</sup>	mg L <sup>-1</sup>	0.00	0.12	0.07	0.00	0.07	0.02	0.02	0.22	0.13	0.00	0.03	0.02	0.02	0.04	0.03
$NO_{3}^{-}$		15.04	20.03	17.49	14.29	22.74	17.81	15.04	21.89	19.74	1.13	3.69	2.33	0.63	3.69	2.35
$\mathrm{NH_4^+}$		0.00	0.13	0.04	0.00	0.06	0.01	0.00	0.19	0.05	0.00	0.05	0.02	0.00	0.08	0.05
$\mathrm{SO}_4^{2-}$		2.93	12.38	7.32	1.73	8.97	6.13	5.71	7.73	6.76	1.07	3.73	2.80	3.59	10.18	5.79
Ч-		0.00	0.07	0.03	0.00	0.02	0.01	0.03	0.12	0.07	0.00	0.02	0.01	0.00	0.02	0.01
CI		4.68	12.51	10.15	4.74	11.41	7.56	9.80	13.73	11.50	4.47	9.32	7.01	5.13	9.32	7.33
Na <sup>+</sup>		4.18	8.11	6.86	2.11	6.51	3.87	5.10	7.81	6.68	3.19	5.61	4.32	4.11	5.61	4.58
$\mathrm{K}^+$		0.00	3.61	1.11	0.59	1.59	1.04	0.72	1.19	06.0	0.45	0.53	0.49	0.45	0.90	0.62
Ca <sup>2+</sup>		18.72	36.82	29.82	8.75	26.64	15.54	16.54	31.07	23.57	19.79	25.31	22.55	19.79	25.91	23.62
$\mathrm{Mg}^{+}$		0.87	2.81	1.41	0.68	1.82	1.05	0.61	2.81	1.24	0.48	0.89	0.67	0.48	1.46	0.92
Reaction	Hq	6.31	7.93	7.51	6.03	7.18	6.63	6.77	7.93	7.35	6.26	7.89	7.28	7.70	7.98	7.87
Conductivity	$\mu S \ cm^{-1}$	79.49	227.00	185.38	70.91	180.10	117.13	165.00	217.00	190.68	67.97	161.00	117.92	124.80	161.00	146.74

Varia	ıble	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
			Sites 28-30			Sites 40-42			ites 43-45			Sites 49–52			Sites 53–55	
NO <sup>2-</sup>	${ m mg}\ { m L}^{-1}$	0.09	0.10	0.10	0.01	0.03	0.02	0.07	0.10	0.09	0.00	0.02	0.00	0.00	0.00	0.00
$NO_{3}^{-}$		22.03	23.40	22.78	0.00	0.00	0.00	1.00	1.30	1.13	0.00	2.05	0.69	1.05	1.90	1.52
$\mathrm{NH_4^+}$		0.13	0.20	0.16	0.00	0.00	0.00	0.00	00.0	0.00	0.00	00.00	0.00	0.00	0.00	0.00
$SO_4^{2-}$		12.38	16.00	13.73	2.90	3.41	3.17	4.44	4.70	4.58	1.17	2.21	1.55	1.18	1.29	1.23
- L		0.05	0.07	0.06	0.00	0.01	0.01	0.09	0.10	0.10	0.00	0.05	0.02	0.00	0.01	0.00
G		11.10	12.00	11.61	13.00	16.00	14.72	6.80	7.03	6.88	3.11	5.92	4.71	3.70	4.78	4.35
$\mathrm{Na}^+$		7.90	8.40	8.14	3.90	4.50	4.16	5.30	6.00	5.70	2.70	7.90	5.71	3.70	5.15	4.21
$\mathrm{K}^+$		2.87	3.89	3.46	4.08	4.67	4.28	0.77	0.98	0.88	0.45	0.95	0.70	0.42	0.78	0.63
Ca <sup>2+</sup>		25.60	30.85	28.38	22.48	23.09	22.69	16.35	17.53	16.93	33.25	35.82	34.04	3.25	3.87	3.47
$\mathrm{Mg}^{+}$		0.89	1.00	0.95	0.97	1.03	1.00	1.34	1.80	1.61	0.58	4.64	2.51	0.62	2.10	1.14
Reaction	Hq	9.45	10.11	9.81	6.90	7.50	7.13	7.50	7.80	7.62	7.01	7.54	7.23	6.80	7.02	6.94
Conductivity	$\mu S  cm^{-1}$	132.00	140.00	136.67	137.30	143.00	140.10	135.80	141.00	138.33	117.15	183.33	139.28	117.15	120.00	118.94
			Sites 56-58			Sites 59-61			ites 62-64		•	Sites 65-67			Sites 68-70	
NO <sup>2-</sup>	${ m mg}~{ m L}^{-1}$	0.15	0.50	0.38	0.00	0.00	0.00	0.00	0.04	0.02	0.06	0.09	0.07	0.00	0.00	0.00
$NO_{3}^{-}$		1.30	2.17	1.64	06.0	1.00	0.96	0.42	0.50	0.47	0.00	00.00	0.00	0.19	0.49	0.30
$\mathrm{NH_4^+}$		0.00	0.00	0.00	0.00	0.00	0.00	0.00	00.0	0.00	0.00	00.00	0.00	0.00	0.00	0.00
$\mathrm{SO_4}^{2-}$		4.45	6.85	5.73	4.66	5.00	4.82	3.44	4.00	3.63	3.57	4.80	3.99	3.47	4.29	3.85
- Ľ		0.06	0.08	0.07	0.09	0.12	0.10	0.06	0.09	0.08	0.09	0.10	0.10	0.05	0.09	0.07
G		9.10	10.00	9.62	7.53	8.00	7.71	8.99	10.00	9.52	8.38	9.70	9.03	6.02	8.27	7.30
Na⁺		5.25	6.20	5.82	4.10	4.50	4.34	5.80	7.00	6.28	4.98	5.50	5.19	3.03	4.37	3.80
$\mathrm{K}^+$		0.00	0.75	0.25	0.46	0.60	0.52	0.98	1.40	1.15	0.41	39.00	13.30	0.58	0.70	0.64
Ca <sup>2+</sup>		19.21	20.00	19.69	19.54	22.00	20.98	20.00	22.00	20.97	14.41	17.00	15.47	11.36	26.69	18.98
$\mathrm{Mg}^{+}$		1.46	2.62	2.06	0.98	1.10	1.03	0.91	1.00	0.96	0.70	06.0	0.80	0.97	1.10	1.02
Reaction	Ηd	8.91	9.20	9.10	8.90	10.00	9.30	6.80	7.30	7.03	7.60	8.00	7.83	7.20	7.60	7.37
Conductivity	μS cm <sup>-1</sup>	143.00	180.00	165.00	110.00	120.00	115.30	55.00	67.00	59.51	149.22	154.00	151.07	115.40	120.30	118.57

Tab. 2 Continued

Max Mean													
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Mean	7	0.00	0.06	0.00	0.37	0.01	3.78	3.80	2.30	8.64	2.40	6.92	66.64
Max	Sites 74-7	0.00	0.08	00.0	1.17	0.02	4.07	4.98	5.00	13.07	5.00	7.28	81.47
Min		0.00	0.04	0.00	0.00	0.00	3.36	2.49	0.00	5.00	0.80	6.68	51.59
Mean	3	0.00	3.83	00.0	0.00	0.00	5.41	5.02	0.94	48.41	1.68	7.66	197.69
Max	Sites 71-7.	00.0	4.00	00.0	00.0	00.0	5.90	5.10	1.00	52.00	1.80	8.00	200.00
Min		0.00	3.60	0.00	0.00	0.00	5.14	4.97	0.89	43.24	1.59	7.49	195.08
ble		${ m mg}~{ m L}^{-1}$								. :		Hq	$\mu S \ cm^{-1}$
Varia		$NO^{2-}$	$NO_{3}^{-}$	$\mathrm{NH_4^+}$	$\mathrm{SO}_4^{2-}$	- H	CI	Na⁺	$\mathbf{K}^+$	Ca <sup>2+</sup>	$\mathrm{Mg}^{\scriptscriptstyle +}$	Reaction	Conductivity

In order to determine the appropriate technique of ordination, detrended correspondence analysis (DCA) was conducted [64]. The lengths of the gradients represented by the first DCA canonical axes was >3 SD for both analyzed habitat groups; therefore, canonical correspondence analysis (CCA) was chosen to assess the impact of habitat variables on the cyanobacterial and algal assemblages of the studied habitats. Forward selection was used in order to determine parsimonious subsets of significant explanatory variables for the species data and to rank environmental variables according to their importance in the ordination [63]. The statistical significance of the CCA ordinations was estimated using Monte Carlo permutation tests (with 499 permutations) [63].

Shannon's diversity index (H') [65] and evenness index (J') were used to describe species diversity.

# Results

# Diversity of cyanobacteria and green algae in different types of habitats

In the first (I) group of habitats, the lowest values of the diversity index (H') and evenness index (J') were recorded at soil sites located on mountain slopes in the vicinity of bird (Alle alle) colonies (Sites 1-3), i.e., at sites rich in nitrogen and phosphorus. Low J' values result from the dominance of nitrophilous Prasiola crispa, and from low abundances of other taxa. The further the distance from the nests, the higher the diversity of cyanobacteria and green algae observed. The highest diversity was recorded at sites with the initial stage of cyanobacteria-moss communities (Sites 37-39). In this case, heterocystous species and an aerophytic form of Schizothrix lacustris were the main components of the phycoflora assemblages. A relatively high J' index shows that these communities are balanced (Tab. 2).

In Group II habitats, a much higher species diversity was recorded compared to Group I. In the majority of the cases, both H'and J' indices reached extremely high values, suggesting the balanced nature of cyanobacterial and algal assemblages in these habitats. The differences in biodiversity between particular habitats of Group II are not as clear as those in soil surface habitats (Group I). However, a slight upward tendency can be observed in the gradient of decreasing seabird colony influence (Tab. 3). **Tab. 3** Values of Shannon's diversity index (H'), evenness index (J'), and the number of species for sampling sites. Grey area – soil surface habitats, white area – shallow water habitats.

Sample	No. of spec.	Diversity $H'$	Evenness J'	Sample	No. of spec.	Diversity H'	Evenness J'
1	6	0.375	0.209	28	20	2.698	0.901
2	6	0.448	0.250	29	17	2.466	0.870
3	6	0.476	0.265	30	18	2.647	0.916
4	18	1.856	0.642	40	11	1.683	0.702
5	17	1.797	0.634	41	7	1.136	0.584
6	17	1.803	0.636	42	7	1.197	0.615
31	5	1.403	0.872	43	15	2.436	0.900
32	5	1.368	0.850	44	22	2.901	0.938
33	16	1.848	0.667	45	21	2.828	0.929
34	13	1.751	0.683	49	15	2.449	0.904
35	11	1.760	0.734	50	13	2.220	0.866
36	14	1.871	0.709	51	11	1.984	0.827
37	21	2.120	0.696	52	13	2.321	0.905
38	13	1.914	0.746	53	15	2.394	0.884
39	16	2.078	0.749	54	15	2.458	0.908
46	10	1.487	0.646	55	21	2.789	0.916
47	12	1.641	0.660	56	11	2.173	0.906
48	10	1.571	0.682	57	12	2.322	0.935
7	13	1.973	0.769	58	15	2.458	0.908
8	15	2.412	0.890	59	10	2.064	0.896
9	13	2.394	0.933	60	9	1.946	0.886
10	10	1.987	0.863	61	10	2.272	0.987
11	13	2.226	0.868	62	17	2.114	0.746
12	11	2.150	0.896	63	14	1.931	0.732
13	9	1.924	0.876	64	16	2.174	0.784
14	12	2.240	0.902	65	18	2.137	0.739
15	10	2.083	0.905	66	16	2.047	0.738
16	6	1.667	0.931	67	17	2.301	0.812
17	9	1.958	0.891	68	20	2.726	0.910
18	11	2.013	0.839	69	21	2.466	0.810
19	12	1.811	0.729	70	24	2.808	0.884
20	12	2.281	0.918	71	12	2.219	0.893
21	19	2.729	0.927	72	16	2.736	0.987
22	8	1.769	0.851	73	15	2.510	0.927
23	9	1.886	0.859	74	22	2.862	0.926
24	7	1.663	0.855	75	11	2.213	0.923
25	6	1.661	0.927	76	15	2.597	0.959
26	10	2.057	0.893	77	16	2.348	0.847
27	11	2.114	0.882				

# Cyanobacterial and green algal assemblages in relation to environmental gradients

**Group I** – soil surface habitats. CCA showed that environmental factors significantly affected the structure of cyanobacterial and algal assemblages. The eigenvalues for Axes 1 and 2 were 0.986 and 0.341, respectively. The cumulative percentage variance explained by these axes was 51.8% (38.5% + 13.3%). According to the forward selection results,  $P-PO_4^{3-}$  (F = 9.71, p = 0.002),  $N-NH_4^+$  (F = 3.79, p = 0.06), and  $Na^+$  (F = 2.95, p = 0.002) were the best predictors of species composition. Although other variables ( $N-NO_3^-$ ,  $Mg^{2+}$ ,  $Ca^{2+}$ ,  $K^+$ , pH, conductivity, soil moisture, and organic matter) were not included in the model, they might also have a significant influence on the phycoflora assemblages because they strongly correlate with the best predictors.

Strongly eutrophic sites (1–6) were grouped on the right side of the diagram, i.e., at the high concentrations of all nutrients. In Sites 1–3, a massive development of nitrophilous green algae *Prasiola crispa* in the form of cracked lamelliform macroscopic thallus, accompanied by filamentous *Klebsermidium* cf. *montanum*, were observed. Among green algae, there were loose filaments of *Microcoleus autumnalis*. The developing microflora assemblages were characterized by low diversity, the dominance of one species (*Prasiola crispa*), and a small contribution by other taxa, such as aerophytic cyanobacteria. At Sites 4–6, a larger number of species were recorded, among which *P. crispa*, coccoid green algae, and filamentous cyanobacteria were dominant.

In contrast, the Sites 31–39 and 46–48 (areas not affected by seabird colonies) were situated on the left side of the diagram. They were characterized by considerably lower concentrations of all nutrients and lower conductivity but higher values of pH and humidity. Extremely low concentrations of nutrients, especially nitrogen and phosphorus, in these habitats qualitatively determine cyanobacterial assemblages. On the CCA diagram, cyanobacteria and green algae species had a relatively wide dispersion. In all these sites (31–39 and 46–48), the microfloral crusts were formed mainly by the aerophytic form of *Schizothrix* cf. *lacustris* with a large contribution of heterocystous cyanobacteria: *Nostoc* spp., *Petelonema crustaceum*, *Sacconema* sp., *Tolypothrix tenuis*,



**Fig. 2** Correlation triplot based on canonical correspondence analysis (CCA) depicting the relationship between the main physicochemical characteristics of the soil and the cyanobacterial and green algal assemblages. Site descriptions are in the text. Full cyanobacteria and green algae taxa names are given in Tab. 1. The diagram shows only the most important (forward-selected) environmental variables.

accompanied by filamentous species Leptolyngbya spp., coccoid Chroococcus turgidus, and Gloeocapsa spp. At more humid sites (46-48), snowbeds and small depressions in the ground periodically supplied with water from melting snow and rain, cyanobacteria formed black and brown, thick, cylindrical, nodular firm colonies, mats and leathery crusts. They were accompanied by clumps of mosses. At Sites 31-36, moderately wet habitats on patterned ground, gray-olive and brown thick crusts of cyanobacterial assemblages occurred. At Sites 37-39, crusts of cyanobacterial assemblages with a large contribution of desmids were found; although they occurred in low abundance, it was a distinctive feature (Fig. 2).

**Group II** – water-saturated habitats. CCA results showed that environmental factors significantly affected the structure of cyanobacterial and algal assemblages. The eigenvalues for Axes 1 and 2 were 0.623 and 0.488, respectively. The cumulative percentage variance explained by these axes was 13.6% (7.6% + 6%). According to forward selection, the strongest effect was exerted by NO<sub>3</sub><sup>-</sup>, (F = 4.24, p = 0.002), moisture (wet index), (F = 3.49, p = 0.002), and pH (F =2.87, p = 0.002).

On the CCA diagram (Fig. 3), the main gradient (Axis 1) is related to the level of eutrophication. On the right side of the diagram, there are fertile, ornithogenic sites (7-19, 28-30, and 56-58 - wet turf, shallow puddles, streams, and ponds). This group of sites is predominated by nitrophilous species Prasiola crispa, Microcoleus autumnalis, and Phormidium irriguum (or Ph. amoenum in shallow ponds). The subdominant species include Leptolyngbya valderiana, which is accompanied by Pseudanabaena catenata, P. frigida, and morphospecies of the genus Leptolyngbya spp. In these habitats, a high diversity of nonfilamentous green algae (Cosmarium spp. and Scotiella spp.) were observed. In wet moss habitats, streams and ponds, there was a large abundance of filamentous green algae of Ulothrix spp. and Microspora spp. genus (shallow pond, Sites 56-58). In the center of the diagram, there are sites moderately and weakly influenced by seabirds. This group represents mesotrophic habitats such as wet turf (Sites 20-22), moderate current streams (Sites 23-27), and shallow streams (Sites 53-55). These habitats offer optimal development conditions for the following cyanobacteria: Microcoleus autumnalis (dominant; Sites 20-27), Leptolyngbya spp., and Oscillatoria fracta. Apart from that, a large abundance of filamentous green algae of Ulothrix spp. genus (Ulothrix aequalis, U. subtilis, and U. cf. oscillarina) were observed in wet moss habitat and streams. The left site of the diagrams is occupied by oligotrophic and extremely oligotrophic habitats. Cyanobacteria form assemblages, composed of distinctive species, and their quantity in assemblages were significant. At the bottom of lakes and stream (mud, sand, gravel, and fine stones), these species form thick and leathery crusts saturated with carbonates. Those habitats are characterized by a high dominance of a few taxa (Schizothrix cf. calcicola 2, Sch. lacustris 2, Pseudanabaena contorta, Microcoleus vaginatus, and Leptolyngbya spp.). They are primarily accompanied by coccoid taxa, characterized by a low contribution in cyanobacterial assemblages, e.g., large quantities of vast orangebrown nodular thalli of D. gypsophila occur in the Gloeocapsa punctata / Gloeocapsa sp. crusts at the bottom. The last group of habitats displayed in the diagram is the most diverse, as it includes a shallow stream (Sites 43–45), a moist Saxifraga spp. community







(Sites 49–52, 74–77), puddles between mosses, and erosive hollows with slow current waters (Sites 68–70, 71–73). A high contribution of N<sub>2</sub>-fixing species of cyanobacteria is a distinctive feature of these habitats. Benthic cyanobacterial assemblages in streams and hollows were mainly formed by the dominant *Microcoleus vaginatus*, subaerophytic *Schizothrix lacustris* 1, *Symplocastrum* sp. 1, *Geitlerinema acutissimum*, *Leptolyngbya valderiana* and coccoid types *Aphaocapsa* spp., *Chlorogloea purpurea*, *Gloeocapsa biformis*, *G. compacta*, and *G. punctata*. Codominants include heterocystous taxa of *Nostoc* commune (three morphotypes) forming hard, large, flat, gelatinous colonies, as well as *Tolypothrix* sp., *T. tenuis*, *Petelonema crustaceum*, *Calothrix* cf. *parietana*, and *Calothrix* sp. 1 in firm mucilaginous baggy mats of various diameters.

# Discussion

The studied part of the northern shore of Hornsund Fjord (Fuglebekken catchment) is characterized by a wide diversity of environmental conditions. It is well established that, in this area, there is a high variation in physicochemical parameters of habitats, especially in the availability of nutrients [46,47,49–52,66]. Migała et al. [55] also indicated considerable ecological heterogeneity in this area in terms of humidity, microhabitat temperature, soil type, and vegetation type. The studied habitats offer a wide spectrum of environmental conditions for cyanobacteria and algae, thus promoting the development of diverse phycoflora assemblages [11,24,26,30,31,33,66–69].

The growth of microalgae and plants in Arctic regions is limited by factors such as temperature, water availability, and nutrient supply. Therefore, these parameters are usually taken into account in studies focusing on the relationships between algae or plants and habitat conditions (e.g., [26,70–73]). Some studies conducted in polar habitats indicated the major influence of basic nutrients in the formation of cyanobacterial and algal assemblages [23,41,46]. Studies conducted in the Hornsund area also confirm the major influence of physicochemical parameters, particularly the availability of phosphorus and various forms of nitrogen (N–NO<sub>3</sub><sup>-</sup>, N–NH<sub>4</sub><sup>+</sup>), on cyanobacteria and algae. The level of these macroelements considerably diversified the studied habitats and apparently was the main factor influencing phycoflora assemblages. This is consistent with the literature showing that nitrogen and phosphorus are among the main factors limiting the growth of plants and other organisms in the polar regions [37,40,45,47,70,73,74].

The differences in the nutrient levels in Hornsund habitats are clearly associated with the occurrence of birds. Herbivorous seabird colonies fertilize the nutrient-poor terrestrial ecosystems by providing large amounts of organic material. Seabird guano is a rich source of nitrogen ( $NO_3^-$ ,  $NH_4^+$ ), potassium ( $K^+$ ) and phosphate ( $PO_4^{3-}$ ), and affects other physicochemical properties, e.g., soil/water conductivity and reactivity; thus, it is the most important driver of ecological conditions [49–52,65,72]. Hence, this factor has a strong effect on the structure of plant and phycoflora communities in the Hornsund Fjord area [46,70,71].

Depending on trophic conditions, soil and shallow water habitats are dominated by two main types of phycoflora, highly contrasted in terms of species composition. In oligotrophic habitats heterocystous species prevail (e.g., Nostoc spp., Dichothrix spp., Calothrix spp., and Tolypothrix spp.). In habitats particularly poor in nitrogen compounds, a significant (around 50%) increase of heterocysts in relation to vegetative cells in filaments was observed. The important role of heterocystous cyanobacteria in providing nitrogen to nutrient-poor polar ecosystems is well understood [43-45,74-77]. An analysis of nitrogen isotope ( $\delta^{15}N$ ) from nitrogen fixation N<sub>2</sub> in soils under cyanobacteria mats [49] confirmed this role. The occurrence of heterocystous species in nitrogen-poor habitats is correlated with the increased nitrogen demand on the soil crust [28,78]. Cyanobacteria, compared to green algae, contribute less to microhabitats fertilized by seabirds, which are rich in phosphorus, nitrogen, and other nutrients. In the present study, Prasiola crispa dominates, accompanied by other nitrophilous green algae and individual nitrophilous oscillatorialean cyanobacterial taxa (e.g., Microcoleus vaginatus). The phycoflora of these habitats was shaped primarily under the influence of phosphorus and nitrogen compounds, which occur in nitrate and ammonium forms. The present study shows that high quantities of nitrogen (especially ammonium forms) limits the diversity and quantitative development of cyanobacterial assemblages, whereas in combination with abundant phosphorus compounds, they stimulate the growth of green algae taxa.

Phosphorus is pivotal in nitrogen fixation. According to Madan et al. [42], nitrogen availability is correlated with the presence of phosphorus in the tundra. Phosphorus deficiency is observed in almost every soil type and it impedes ecosystem efficiency [79–81]. Areas under the influence of seabird colonies are unique for their high concentrations of phosphorus in soluble and bioavailable forms [50,51]. The present study shows that the role of phosphorus compounds increases in low nutrient (mainly nitrogen-poor) habitats and those under the influence of herbivore populations (geese, reindeer). Phosphorus provided by feces [52] stimulates the growth of *Nostoc* sp. colonies and other heterocystous cyanobacteria on feeding, nesting, or resting sites of, particularly,

geese. The rate of nitrogen fixation is remarkably increased by geese grazing [53], which introduces phosphorus with feces and, consequently, stimulates growth of cyanobacteria, particularly heterocysts. However, in the present study, biological nitrogen fixation was inhibited by the high content of nutrients in the habitats under the cliff, where a large amount of bird droppings were supplied by colonies of seabirds that nest there.

Phosphorus availability is also considerably dependent on pH [79,80], which is a significant factor in shaping algal and cyanobacterial assemblages in the Hornsund area due to its influence on macro- and microelements availability.

Humidity is another factor strongly influencing West Spitsbergen habitats, as confirmed by research into the influence of water availability on the quantity and placement of phycoflora (e.g., [4,25,48,67]). Humidity depends on topography (elevated or flat areas, depressions) and areas with long lasting snow cover and/or stagnating water provide suitable conditions for the development of cyanobacteria and algae, consequently leading to high biodiversity. The results of the present study confirm the significance of several correlated ecological factors and habitat properties on the phycoflora of Hornsund Fjord.

# Conclusions

The study conducted in various habitats in the Hornsund Fjord area indicates the influence of physicochemical parameters on the structure of cyanobacterial and algal assemblages. Statistical analysis revealed significant relationships between the distribution of species and environmental factors (in particular, N–NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, PO<sub>4</sub><sup>3-</sup>, and Ca<sup>2+</sup> concentrations, as well as pH and moisture). In nitrogen-poor habitats, dominance of heterocystous cyanobacteria species is observed. In habitats rich in nutrients, the nitrophilous species of algae are most predominant. Our findings add to the knowledge on the formation of phycoflora assemblages under specific combinations of environmental factors.

# Acknowledgments

The authors would like to thank the reviewers for their comments and suggestions which helped to improve the original manuscript.

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