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 coccolid, oscillatoriaceous, 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–PO4, N–NH4 and Ca2+ (soil surface habitats), and NO3, 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 phycocllora 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 coccolid, oscillatoriallean, 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 Arieckammen. 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 water-saturated 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, Plagiommium ellipticum, Sanionia uncinata, Tetrapodion mnioides, and Dicranum sp. (Sites 1–3) or with P. crispa, Chrysosplenium tetrandum, Cochlearia groenlandica, Poa alpina var. vivipara, Cerastium arcticum, Salix polaris, Plagiommium
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;

**Fig. 1** The location of the study area in Hornsund Fjord, West Spitsbergen (A), marine terrace Fuglebergsletta, and the Fuglebekken catchment area (B). Points 1–77 denote research sites (for detailed description see Tab. 1).
### Tab. 1 Cyanobacteria and green algae composition in the studied habitats (Sites 1–77). Study sites are described in the text.

| Species | Symbol | Sites |
|---------|--------|-------|
| **CYANOBACTERIA** |
| **Coccoid or colonial cyanobacteria** |
| *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) Kom.-Legn. 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 |
| *Aphanocthece 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 tormensis* Skuja | Glo.tor | 22–28, 31–34, 36–39, 63 |
| *Gloeocapsa* sp. | Glo.sp | 38–42, 74 |
| *Gloeocapsopsis* cf. *pleurocapsoides* (Nováček) Kom. et Anag. | Glo.ple | 68–70 |
| *Gleothecae* cf. *palea* (Kütz.) Rabenh. | Glo.pal | 74, 77 |
| *Gleothecae* sp. 1 | Gle.sp1 | 4–6 |
| *Merismopedia* sp. | Mer.sp | 1–6 |
| *Merismopedia* cf. *marssoni* Lemm. | Mer.mar | 9, 11–16 |
| *Woronichinia* sp. 1 / small cells | Wor.sp1 | 52, 54, 59 |
| *Woronichinia* sp. 2 / with aerotopes | Wor.sp2 | 40, 55, 60, 61 |
| *Woronichinia compacta* (Lemm.) Kom. et Hindák | Wor.com | 74 |
| **Heterocytous filamentous cyanobacteria** |
| *Calothrix* cf. *parietana* (Näg.) Thuret | Cal.par | 33–35, 47, 51, 52, 54, 55, 57, 62–64, 68–70, 77 |
| *Calothrix* 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 |

Nonheterocytous filamentous cyanobacteria

| Species | Symbol | Sites |
|---------|--------|-------|
| Geitlerinema acutissimum (Kufferath) Anagnostidis | Gei.acu | 4, 7, 8, 20, 21, 23, 55, 57, 59–61, 65–67, 69, 70 |
| Gloeocapsa sp. | Gla.sp | 57 |
| Homoeothrix 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 |
| Leptolyngbya foveolarum (Raben. ex Gomont) Anagn. et Kom. | Lep.fov | 4, 5, 8, 10, 27, 33, 34, 36–39, 76 |
| Leptolyngbya sieminskae Richter & Matula | 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 |
| Leptolyngbya sp. 1 / cells with grains | Lep.sp1 | 4, 6, 7, 9, 13, 18–21, 40–42, 52, 62–67, 73 |
| Leptolyngbya 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 |
| Lyngbya aestuarii Liebman ex Gamont | Lyn.aes | 59–61, 69, 70 |
| Lyngbya sp. 1 | Lyn.sp1 | 16 |
| Lyngbya sp. 2 / wide filaments | Lyn.sp2 | 44, 45 |
| Microcoleus autumnalis Trevisan ex Gamout (Strunecky et al.) | Mic.aut | 1–6, 8–26, 28–30, 56, 57 |
| Microcoleus vaginatus Gomont ex Gamont | 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 |
| Oscillatoria fracta 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 |
| Species | Symbol | Sites |
|---------|--------|-------|
| Oscillatoria sp. 2 / long cels | Osc.sp2 | 76 |
| Oscillatoria sp. 3 | Osc.sp3 | 21 |
| Oscillatoria sp. 4 | Osc.sp4 | 37–39 |
| Oscillatoria subbrevis Schmidle | Osc.sub | 4 |
| Oscillatoria tenuis Agardh ex Gomont | Osc.ten | 28–30 |
| Phormidium amoenum Kützing ex Anagnostidis et Komárek | Pho.amo | 28–30, 37, 39 |
| Phormidium sp. 1 | Pho.sp1 | 37 |
| Phormidium sp. 2 | Pho.sp2 | 4 |
| Phormidium foveolarum (Rabenh. ex Gomont) Anagn. et Kom. | Pho.fov | 27 |
| Phormidium irriguum (Kütz. ex Gomont) Anag. et Kom. | Pho.irr | 28–30, 56 |
| Planktothrix cf. limnetica (Lemm.) Kom.-Leg. et Cronberg | Pla.lim | 5, 6, 57, 62, 65 |
| Planktothrix 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 |
| Schizothrix cf. lacustris A. Braun ex Gomont / subaerophytic form | Sch.la1 | 5, 40, 42, 43, 45, 49, 51 |
| Schizothrix cf. lacustris A. Braun ex Gomont / aerophytic form | Sch.la2 | 33–39, 46–48, 74–77 |
| Schizothrix cf. lacustris A. Braun ex Gomont / plankton form | Sch.la3 | 41, 42, 53–55 |
| Schizothrix sp. | Sch.sp | 3–6 |
| Stigonema cf. mamillosus (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 Breb. | Cos.gra | 71–76 |
| Cosmarium holmiiense P. Lundell | Cos.hol | 20, 22, 49, 50, 52, 59–61, 68–74, 76, 77 |
| 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 Breb. | 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 |

Filamentous green algae

| Species | Symbol | Sites |
|---------|--------|-------|
| Klebsormidium 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 algae

| Species | Symbol | Sites |
|---------|--------|-------|
| 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 |
| Scotiella antarctica Fritsch f. svalbardensis E. Kol et S. Eurola | Sco.onf | 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 Boufr. | Sco.tub | 7–10, 12–14, 17–19 |
| Sciotellopsis terestris (Reisigl) Punčoch. & Kalina | Sco.ter | 7–10, 12, 14, 18, 19 |
| Scotiella oocystiformis (Lund) Punčoch. & Kalina | Sco.ooc | 4, 5 |
| Tetracystis sp. | Tet.sp | 4, 6 |
| Trochiscia granulata (Reinsch) Hansg. | Tro.gra | 5, 6 |
• 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-cm² 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 μm; Millipore; Merck, Poland). Water samples were analyzed in the Polish Polar Station's laboratory, NH₄⁺, NO₃⁻, NO₂⁻, PO₄³⁻, S–SO₄³⁻, K⁺, Ca²⁺, Mg²⁺, 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–NH₄⁺ and N–NO₃⁻ 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°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–NH₄⁺, N–NO₃⁻, and P–PO₄³⁻ 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⁺, K⁺, Ca²⁺, and Mg²⁺ 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].
Tab. 2 Minimum, maximum, and mean values of physicochemical properties in the water and soil in studied habitats (Sites 1–77). Study sites are described in the text.

| Variable | Sites 1–3 | Sites 4–6 | Sites 31–36 | Sites 37–39 | Sites 46–48 |
|----------|-----------|-----------|-------------|-------------|-------------|
| N–NH₄⁺  | mg kg⁻¹   |           |             |             |             |
| Min      | 10.70     | 24.34     | 8.98        | 1.11        | 0.17        |
| Max      | 15.59     | 24.34     | 9.22        | 1.11        | 0.18        |
| Mean     | 15.59     | 24.34     | 9.22        | 1.11        | 0.18        |
| N–NO₃⁻  |           |           |             |             |             |
| Min      | 106.21    | 285.08    | 110.00      | 2.27        | 0.11        |
| Max      | 167.04    | 285.08    | 126.71      | 2.27        | 0.11        |
| Mean     | 167.04    | 285.08    | 126.71      | 2.27        | 0.11        |
| P–PO₄³⁻  | mg kg⁻¹   |           |             |             |             |
| Min      | 36.64     | 47.10     | 38.20       | 0.28        | 0.17        |
| Max      | 47.10     | 47.10     | 42.25       | 0.28        | 0.17        |
| Mean     | 40.59     | 47.10     | 42.25       | 0.28        | 0.17        |
| Na⁺      | mg L⁻¹    |           |             |             |             |
| Min      | 0.35      | 0.69      | 0.40        | 0.50        | 0.19        |
| Max      | 0.69      | 0.69      | 0.50        | 0.50        | 0.19        |
| Mean     | 0.54      | 0.69      | 0.50        | 0.50        | 0.19        |
| K⁺       | mg L⁻¹    |           |             |             |             |
| Min      | 56.32     | 101.64    | 45.60       | 1.20        | 0.00        |
| Max      | 101.64    | 101.64    | 47.23       | 1.20        | 0.00        |
| Mean     | 77.08     | 101.64    | 47.23       | 1.20        | 0.00        |
| Ca²⁺     | mg L⁻¹    |           |             |             |             |
| Min      | 150.84    | 240.16    | 160.00      | 1.07        | 6.78        |
| Max      | 192.67    | 240.16    | 183.00      | 1.07        | 6.78        |
| Mean     | 167.04    | 240.16    | 183.00      | 1.07        | 6.78        |
| Mg²⁺     | mg L⁻¹    |           |             |             |             |
| Min      | 11.76     | 14.14     | 10.80       | 4.90        | 4.89        |
| Max      | 14.14     | 14.14     | 11.50       | 4.90        | 4.89        |
| Mean     | 13.10     | 14.14     | 11.50       | 4.90        | 4.89        |
| Reaction pH |        |           |             |             |             |
| Min      | 3.83      | 4.15      | 4.03        | 5.00        | 6.78        |
| Max      | 4.15      | 4.15      | 4.03        | 5.00        | 6.78        |
| Mean     | 4.03      | 4.15      | 4.03        | 5.00        | 6.78        |
| Conductivity µS cm⁻¹ |             |           |             |             |             |
| Min      | 79.40     | 139.70    | 68.30       | 4.90        | 4.89        |
| Max      | 192.67    | 139.70    | 71.28       | 4.90        | 4.89        |
| Mean     | 101.73    | 139.70    | 71.28       | 4.90        | 4.89        |
| Organic matter g kg⁻¹ |             |           |             |             |             |
| Min      | 47.43     | 91.27     | 88.99       | 6.19        | 6.20        |
| Max      | 75.64     | 91.27     | 90.53       | 6.19        | 6.20        |
| Mean     | 75.64     | 91.27     | 90.53       | 6.19        | 6.20        |
| Variable | Sites 28–30 | Sites 40–42 | Sites 43–45 | Sites 49–52 | Sites 53–55 |
|----------|-------------|-------------|-------------|-------------|-------------|
| NO$_2$ (mg 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$_3$ | 2.03, 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 |
| NH$_4$ | 0.13, 0.20, 0.16 | 0.00, 0.00, 0.00 | 0.00, 0.00, 0.00 | 0.00, 0.00, 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 |
| Cl | 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 |
| Ca$^{2+}$ | 11.10, 12.00, 11.61 | 13.00, 16.00, 14.72 | 3.11, 5.92, 4.71 | 3.70, 4.78, 4.35 | 3.70, 5.15, 4.21 |
| Mg$^{2+}$ | 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 |
| Na$^+$ | 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 |
| K$^+$ | 25.60, 30.85, 28.38 | 22.48, 23.09, 22.69 | 16.35, 17.53, 16.93 | 33.25, 35.82, 34.04 | 32.5, 3.87, 3.47 |
| F$^-$ | 0.09, 0.10, 0.08 | 0.09, 0.10, 0.08 | 0.09, 0.10, 0.08 | 0.09, 0.10, 0.08 | 0.09, 0.10, 0.08 |
| 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 |
| K$^+$ | 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 |
| Mg$^{2+}$ | 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 pH | 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 |
| Conductivity µS 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 |

| Variable | Sites 56–58 | Sites 59–61 | Sites 62–64 | Sites 65–67 | Sites 68–70 |
|----------|-------------|-------------|-------------|-------------|-------------|
| NO$_2$ (mg 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 | 0.90, 1.00, 0.96 | 0.42, 0.50, 0.47 | 0.00, 0.00, 0.00 | 0.19, 0.49, 0.30 |
| NH$_4$ | 0.00, 0.01, 0.00 | 0.00, 0.00, 0.00 | 0.00, 0.00, 0.00 | 0.00, 0.00, 0.00 | 0.00, 0.00, 0.00 |
| 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 |
| Cl | 0.06, 0.08, 0.07 | 0.07, 0.12, 0.10 | 0.06, 0.09, 0.08 | 0.09, 0.10, 0.09 | 0.05, 0.09, 0.07 |
| Na$^+$ | 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 |
| K$^+$ | 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 |
| Mg$^{2+}$ | 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 |
| Mg$^{2+}$ | 1.46, 2.62, 2.06 | 0.98, 1.10, 1.03 | 0.91, 1.00, 0.96 | 0.70, 0.90, 0.80 | 0.97, 1.10, 1.02 |
| Reaction pH | 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$^{-1}$ | 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 |
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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).

| Variable | Min | Max | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max | Mean |
|----------|-----|-----|------|-----|-----|------|-----|-----|------|-----|-----|------|
| NO$_2^-$ | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| NO$_3^-$ | 0.08 | 0.08 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| NH$_4^+$ | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| SO$_4^{2-}$ | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| F$^-$ | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Cl | 3.36 | 4.29 | 3.78 | 3.24 | 4.00 | 3.78 | 3.24 | 4.00 | 3.78 | 3.24 | 4.00 | 3.78 |
| Na$^+$ | 4.96 | 5.00 | 4.99 | 3.24 | 4.00 | 3.59 | 3.24 | 4.00 | 3.59 | 3.24 | 4.00 | 3.59 |
| K$^+$ | 0.89 | 1.00 | 0.94 | 0.00 | 5.00 | 2.30 | 0.00 | 5.00 | 2.30 | 0.00 | 5.00 | 2.30 |
| Ca$^{2+}$ | 43.24 | 52.00 | 48.08 | 5.00 | 13.07 | 8.64 | 5.00 | 13.07 | 8.64 | 5.00 | 13.07 | 8.64 |
| Mg | 4.32 | 4.59 | 4.44 | 0.80 | 5.00 | 2.40 | 0.80 | 5.00 | 2.40 | 0.80 | 5.00 | 2.40 |

**Tab. 2 Continued**

| Variable | Min | Max | Mean | Min | Max | Mean | Min | Max | Mean |
|----------|-----|-----|------|-----|-----|------|-----|-----|------|
| Conductivity µS cm$^{-1}$ | 195.08 | 200.00 | 197.69 | 51.59 | 81.47 | 66.64 | 51.59 | 81.47 | 66.64 |
| pH | 7.49 | 7.66 | 7.58 | 6.68 | 7.28 | 6.92 | 6.68 | 7.28 | 6.92 | 6.68 | 7.28 | 6.92 |
| Reaction | 1.59 | 1.80 | 1.68 | 0.80 | 1.68 | 0.80 | 1.68 | 0.80 | 1.68 | 0.80 | 1.68 | 0.80 |

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          | 0.613         |
| 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 percent variance explained by these axes was 51.8% (38.5% + 13.3%). According to the forward selection results, $P - \text{PO}_{4}^{3-}$ ($F = 9.71, p = 0.002$), $N - \text{NH}_{4}^{+}$ ($F = 3.79, p = 0.06$), and $\text{Na}^{+}$ ($F = 2.95, p = 0.002$) were the best predictors of species composition. Although other variables ($N - \text{NO}_{3}^{-}, \text{Mg}^{2+}, \text{Ca}^{2+}, \text{K}^{+}, \text{pH}, \text{conductivity}, \text{soil moisture}, \text{and organic matter}$) were not included in the model, they might also have a significant influence on the phycocloras 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 *Klebsormidium* 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* spp., *Tolyphothrix* *tenus*, 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).

**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.
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 Prasiloa 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 Sciotilla 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 streams (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 orange-brown nodular thalli of D. gypsophila occur in the Gloeocapsa punctata / Gloecocapsa 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.
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(Sites 49–52, 74–77), puddles between mosses, and erosive hollows with slow current waters (Sites 68–70, 71–73). A high contribution of N₂-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 *Tolyphothrix* sp., *T. tenuis*, *Petelonema crustaceum*, *Calothrix cf. parietana*, and *Calothrix* sp. 1 in firm mucilaginous baggy mats of various diameters.

Fig. 3 Canonical correspondence analysis (CCA) depicting the relationship between the main physicochemical characteristics of the water and the cyanobacterial and green algal assemblages. (A) The ordination of species and physicochemical parameters on the first and second ordination axes. (B) The ordination of species and sites on the first and second ordination axes. Site description is 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.
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]. Migala 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–NO₃⁻, N–NH₄⁺), 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 (NO₃⁻, NH₄⁺), potassium (K⁺) and phosphate (PO₄³⁻), 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 *Tolyphothrix* 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 (δ¹⁵N) from nitrogen fixation N₂ 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−NH₄⁺, NO₃⁻, PO₄³⁻, and Ca²⁺ 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.

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