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Microscopic analysis on eukaryotic algae and cyanobacteria in nine seasonal lakes and ponds in Vestfjella, Dronning Maud Land, Antarctica

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Abstract Antarctic continental lakes and ponds are among the most impoverished aquatic environments on earth but many of them support flourishing populations of cyanobacteria, eukaryotic algae, protozoans, and some multicellular animals. In this study, we present results of a microscopic analysis of cyanobacteria and eukaryotic algae from nine diverse types of Antarctic continental water bodies during one austral summer. The results supplement and enlarge our previous studies on the limnological characteristics of the epiglacial and supraglacial lakes and ponds in Dronning Maud Land, an area that has received little attention from limnologists. The taxon with highest frequency among the samples (n=79) was *Mesotaenium* cf. *berggrenii*, a eukaryotic Zygnematophyceae, which occurred in 82% of the samples with a maximum cell density of 68 cells·mL^{-1}. The taxa with second and third highest frequency were the prokaryotes *Gloeocapsopsis* (60%) and *Leptolyngbya* (41%), followed by *Chlamydomonas* (34%) and *Cyanothece* (29%). The number of taxa varied between 7–21 among the lakes and ponds, being highest in a supraglacial lake, and lowest in an epiglacial lake. The results did not reveal any obvious correlation between the abundance of any taxa and the water chemistry, but water bodies with inorganic sediments had higher cell densities and biomasses than those without sediment. This suggests the importance of sediment in supporting biological diversity in these ultraoligotrophic lakes and ponds.

Keywords **Antarctic continental lakes, Antarctic continental ponds, cyanobacteria, algae, protozoa, rotifers, tardigrada**

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1 Introduction

In Antarctica, epiglacial and supraglacial lakes and ponds are common especially in the vicinity of the boundary between the ocean and the land, close to the nunataks (e.g., Hodgson, 2012; Menzies, 1995). On the Vestfjella mountain ridge on Basen, Plogen and Fossilryggen nunataks, close to the grounding line of Riiser-Larsen Ice Shelf, a few supraglacial and epiglacial lakes exist on the top of the ice sheet. The supraglacial lakes in this area are typically situated on the lee side of the dominant wind, i.e. southeast from the nunataks, while the epiglacial lakes are situating around the nunataks, in places where the ice shelf meets the mountains (Leppäranta et al., 2020). In addition, several temporary ponds and rock pools exist on the top of the nunataks. Since their location reflects the pattern of snow melt, they are not as long lived as the epi- and supraglacial lakes, which are fed by melt water from the glacier. The thermodynamics of epi- and

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supraglacial lakes are governed by the surface radiation balance and penetration of irradiation into the ice (Leppäranta et al., 2013), while the thermodynamics of small ponds and pools are controlled by the surface radiation balance and the penetration of heat into the bottom sediments. During a sunny day the ice above the ponds and pools may melt though they may be frozen at night-time (Leppäranta et al., 2020). Such water bodies differ from the permanently stratified, deep lakes of Antarctica (Vincent et al., 2008) which have perennial ice-cover or their meromictic properties due to high salinity concentration (Izaguirre et al., 2021; Vincent et al., 2008).

In summer, temporary ponds and rock pools are exposed to very intense irradiation, including UV, and their bottom sediments also store more heat since the water bodies are very shallow. As a result, temperature fluctuations can be extreme when compared to those recorded in epiglacial and supraglacial lakes (Leppäranta et al., 2020; Quesada et al., 2008).

Low nutrient concentrations and low algal biomasses prove that extremely low biological activity is a typical phenomenon in Antarctic continental water bodies (Izaguirre et al., 2021) and most are characterized by short and simple food webs. Under such conditions, the most productive habitat is thought to be the microbial mat communities (Heath, 1988; Izaguirre et al., 2021; Quesada et al., 2008). In our study area, the only documented study of a microbial mat community is that published by Keskitalo et al. (2013).

Regardless of their harsh physical conditions, many Antarctic continental lakes and ponds have surprisingly diverse nanoplankton and microplankton communities (Izaguirre et al., 2021; Kaup, 1994; Keskitalo et al., 2013; Lizotte, 2008; Vincent et al., 2008). The adaptive strategies of Antarctic phytoplankton include mixotrophy, formation of resistant cysts, starch accumulation, pigment adaptation, motility, and small size (Izaguirre et al., 2021).

This study is an extension of previous work on the primary producers of epiglacial and supraglacial lakes in western Dronning Maud Land, Antarctica (Keskitalo et al., 2013). Here, we collected samples and measurements over a longer period, and we also visited more sites. Although our primary focus is on cyanobacteria and eukaryotic algae, multicellular rotifers and tardigrada animals are also considered since they are the top grazers. Prevailing physical and chemical conditions of the water bodies are given as supporting information, to highlight the differences between the water bodies and the factors that regulate the dynamics of the organisms. Since the facilities available at the Aboa Research Station are limited, our biological observations were confined to a microscopic examination of the organisms. These were sufficient to demonstrate that each water body supports a unique microscopic community dominated by a variety of cyanobacteria and eukaryotic algae.

2 Material and methods

The results presented here are based on the analysis of material collected from eight epiglacial and supraglacial lakes and ponds, and one rock pool in the Vestfjella nunataks in the western Dronning Maud Land, Antarctica. All the sites were located either on or close to the Basen, Plogen and Fossilryggen nunataks (Figure 1). Three nunatak ponds (Top Pond1, Top Pond2 and Rock Pool1) were situated on top of Basen and one on Fossilryggen (Fossilryggen Pond). Three epiglacial ponds (Velodrome, Penaali and Ring Pond) were located between the glacier and Basen. One supraglacial lake (Suvivesi) was situated close to Basen and another (Plogen), 20 km from Basen. Except Suvivesi, all lakes and ponds, including Rock Pool1, are small and shallow water bodies (Table 1). Along the summer season, water depth may vary, however depending on the weather conditions.

The measurements and samplings were carried out between 4 December 2014 and 28 January 2015, with each site being visited on a minimum of three occasions. The *in situ* measurements included water temperature (T_w) and dissolved oxygen (DO) concentration with YSI Professional Plus device fitted with an optical DO sensor. The pH of the samples was determined on return to the laboratory using an Orion (Model, 201) pH meter. Additional measurements on frozen samples were conducted after we returned to Finland at the laboratory of the Lammi Biological Station (LBS), University of Helsinki. These determinations included total nitrogen (TN) and total phosphorus (TP) after wet oxidation with a Gallery Plus Thermo Scientific Analyser (Koroleff, 1983), cation concentrations with Varian SpectrAA 220/FS atomic absorbance spectrophotometer, absorbance properties of aqueous samples with a Shimadzu Spectrophotometer (UV-2100), as well as electrical conductivity (EC) with YSI 3200 meter. Drilling through the ice was made as gentle as possible and water samples were removed using a small Limnos tube sampler. Further details of the procedure are given in Leppäranta et al. (2020) together with some supplemental observations.

In addition, photosynthetically active radiation (PAR) measurements were taken with LiCor sensors (air, spherical and underwater) in Suvivesi, Plogen Lake and Fossilryggen Pond. PAR sensors made by MDS-L, Alec Electronics Co. Ltd. were used in Top Pond1, Top Pond2 and Rock Pool1 for measuring the incoming PAR at the lake surface and at depth of 5 cm in the ice. Global radiation (400–2800 nm wavelengths) measurements were carried out with Middleton EP-16 pyrano-albedometer system on the ice of Lake Suvivesi and at the Aboa Research Station.

Acid Lugol was added to the plankton samples immediately after the samples were taken, and the samples were examined at a magnification of 400 times using a Carl Zeiss inverted microscope. The initial sample volumes varied from 0.5 L up to 7.5 L, and all samples were concentrated by using a 10 μm mesh size polyamid plankton net (KC

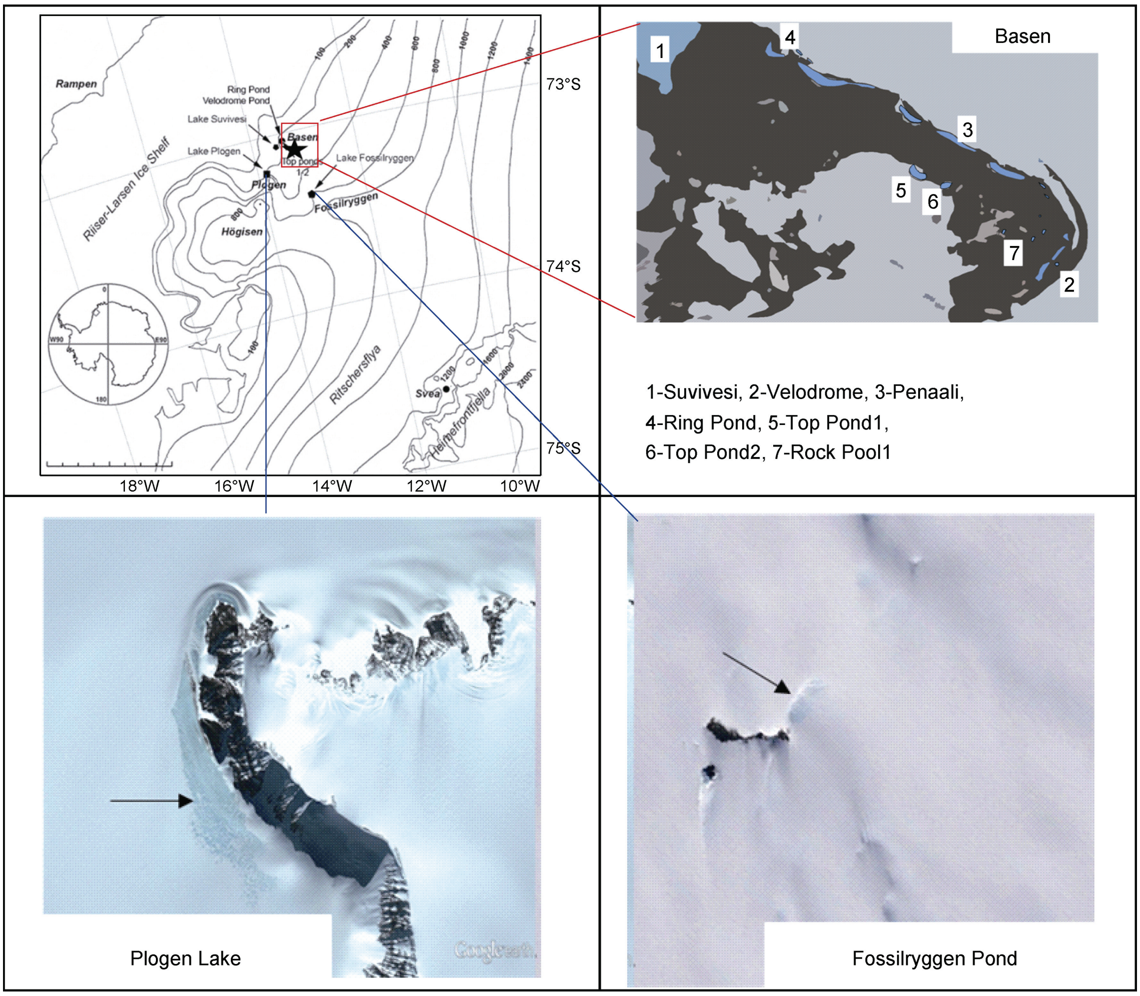

Figure 1 Map of the study area in western Dronning Maud Land, Antarctica.

Table 1 The locations and morphometric data of the studied lakes and ponds

Lake/pond name	Lake type	Location	Area/km^2	Max depth/m	Other information
Suvivesi	Supra	73°02.84'S, 13°28.66'W	3.6100	2.00	Water at the surface of a glacier, ice-covered.
Velodrome	Epi	73°00.91'S, 13°22.00'W	0.0007	0.75	Water between ice layers; meltwater also from nunatak and ice-sheet; rocky shores.
Penaali	Epi	73°01.02'S, 13°24.04'W	0.0150	0.75	Water between ice layers; meltwater also from nunatak and ice-sheet; rocky shores.
Ring Pond	Epi	73°01.65'S, 13°26.39'W	0.0047	1.50	Water between ice layers; meltwater also from nunatak and ice-sheet; rocky shores.
Top Pond1	Npo	73°01.40'S, 13°24.03'W	0.0002	0.50	Water under ice-cover; meltwater from ice-sheet; inorganic bottom sediment.
Top Pond2	Npo	73°01.28'S, 13°23.71'W	0.0005	0.20	Water between ice layers and inorganic sediment; occasionally ice-covered during the day; water from ice-sheet.
Rock Pool1	Npo	73°01.00' S, 13°22.72'W	0.00002	0.20	Inorganic sediment; occasionally ice-covered during the day; meltwater from snow; rocky shores.
Plogen Lake	Supra	73°11.90'S, 13°48.51'W	0.1350	1.00	Water between ice layers; meltwater also from nunatak and ice-sheet.
Fossilryggen Pond	Npo	73°23.50'S, 13°02.17'W	0.0011	1.00	Inorganic sediment; ice-covered; receives water also from melting snow.

Notes: Supra, supraglacial lakes; Epi, epiglacial ponds; Npo, nunatak ponds; types are according to Leppäranta et al. (2020).

Denmark A/S). Finally, the samples were settled and counted from 50 fields according to Utermöhl (1958). In addition, fresh samples were investigated with a microscope. The identification of species and taxa were thus based entirely on their morphological characteristics, without the use of more specific molecular biology tools. Samples from the Rock Pool1 were taken directly to the sample bottles due to a dense microbial mat community which prevailed there. As a result, these samples contained water and fragments of the microbial mat. Species identification was based on publications by Starmach (1985), Krammer and Lange-Bertalot (1986, 1988, 1991), Komárek (2000), Komárek and Komárková (2004), Komárek and Anagnostidis (2005), Coesel and Meesters (2007), and Remias et al. (2009). Due to shortage of laboratory facilities at Aboa Research Station, the identification of species/taxa was based only on morphotypes. Therefore, the list of species/taxa, which has been constructed, may include some unrelated taxa.

Statistical analyses were performed with SigmaPlot12.5 software and the relationships between the environmental variables and the plankton were established by Pearson product-moment correlations.

3 Results

3.1 Cyanobacteria and eukaryotic algae

From 79 samples, 25 eukaryotic algal taxa, 8 prokaryotic cyanobacterial taxa, 3 ciliate taxa, 2 heterotrophic flagellate taxa, 1 rotifer and 1 tardigrade were found, making a total of 40 different taxa. The most common eukaryotic taxon was *Mesotaenium* cf. *berggrenii* (Zygnematophyceae), which occurred in 82% of the samples, and also had highest cell density (maximum 68 cells·mL^{-1}, in Suvivesi BAV55 site collected on 16 December 2014). *Gloeocapsopsis* (Cyanophyceae) had the second highest frequency (60%) and was followed by *Leptolyngbya* (Cyanophyceae), *Chlamydomonas* (Chlorophyceae) and *Cyanothece* (Cyanophyceae) (Table 2, Figure S1). In the water bodies, the number of taxa varied between 7 and 17 per site, being highest in Suvivesi H1 and Velodrome sites, and lowest in Plogen Lake and Rock Pool1 (Figure 2). In Suvivesi, the highest diversity of plankton was found at the beginning of December 2014, when four dinoflagellate and seven diatom taxa were present. At that time, diatoms were more abundant than during other sampling times.

Mesotaenium cf. *berggrenii* occurred in all lakes and ponds except in Rock Pool1. In Suvivesi, its density was higher than that in the other water bodies (Figure 3), but its cell numbers varied between the sampling sites, being highest in Suvivesi BAV55. *Mesotaenium* had its maximum cell density in the middle of December 2014 (Figure 4), two weeks after the lake started to expand due to the ice melt. Another chlorophyte, *Chlamydomonas,* had its density maximum during the third week of January 2015. Among the cyanobacteria, *Gleocapsopsis* had the density peak in the middle of December 2014, while *Phormidium* peaked twice; the first one at the beginning of December 2014 and the second one at the end of January 2015. *Cyanothece* peaked only once at the beginning of January 2015.

Table 2 Frequency of taxa found from the samples. Those with less than 0.02 are not given. The genus *Phormidium* also includes the genus *Planktothrix*

	Taxon	Class	Frequency
Eukaryotic algae	*Mesotaenium* cf. *berggrenii*	Zygnematophyceae	0.82
	Chlamydomonas	Chlorophyceae	0.34
	Diatoma/Tabellaria	Bacillariophyceae	0.17
	Cyclotella	Mediophyceae	0.12
	Chrysochromulina	Coccolithophyceae	0.12
	Peridinium sp.	Dinophyceae	0.09
	Navicula sp.	Bacillariophyceae	0.05
	Staurastrum sp.	Zygnematophyceae	0.04
	Pinnularia sp.	Bacillariophyceae	0.04
	Dinoflagellata sp. (small)	Dinophyceae	0.02
	Monoraphidium	Chlorophyceae	0.02
Prokaryotic cyanobacteria	Gloeocapsopsis	Cyanophyceae	0.60
	Leptolyngbya	Cyanophyceae	0.41
	Cyanothece	Cyanophyceae	0.29
	Phormidium sp.	Cyanophyceae	0.27
	Nostoc	Cyanophyceae	0.05
		Phylum	Frequency
Ciliates and multicellular animals	Ciliata1	Ciliata	0.16
	Ciliata3	Ciliata	0.13
	Philodina gregaria	Rotatoria	0.11
	Tardigrada	Tardigrada	0.05

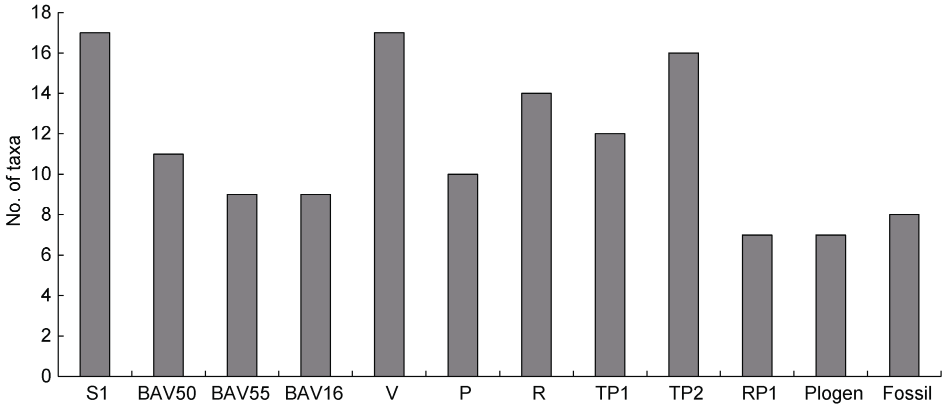

Figure 2 Total number of taxa, including protists as well as rotifers, in the water bodies. S1=Suvivesi H1, BAV50=Suvivesi BAV50, BAV55=Suvivesi BAV55, BAV16=Suvivesi BAV16, V=Velodrome, P=Penaali, R=Ring Pond, TP1=Top Pond1, TP2=Top Pond2, RP1=Rock Pool1, Plogen=Plogen Lake, Fossil=Fossilryggen Pond.

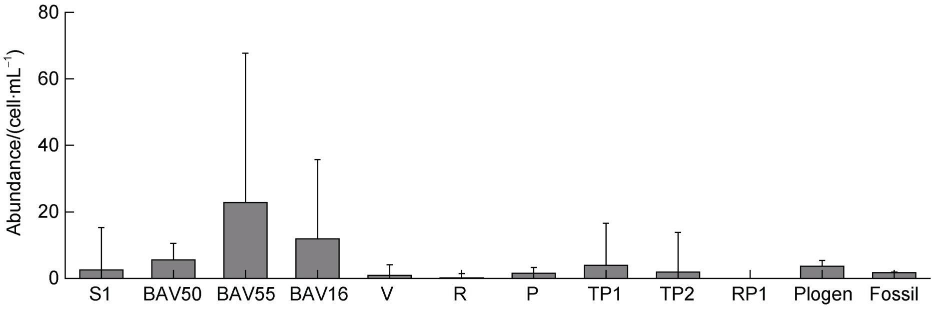

Figure 3 The mean abundance of *Mesotaenium* cf. *berggrenii* (Zygnematophyceae, Charophyta) in the studied lakes and ponds from the beginning of December 2014 until the end of January 2015. The error bars indicate the maximum observed density of each water body. S1=Suvivesi H1, BAV50=Suvivesi BAV50, BAV55=Suvivesi BAV55, BAV16=Suvivesi BAV16, V=Velodrome, R=Ring Pond, P=Penaali, TP1=Top Pond1, TP2=Top Pond2, RP1=Rock Pool1, Plogen=Plogen Lake, Fossil=Fossilryggen Pond.

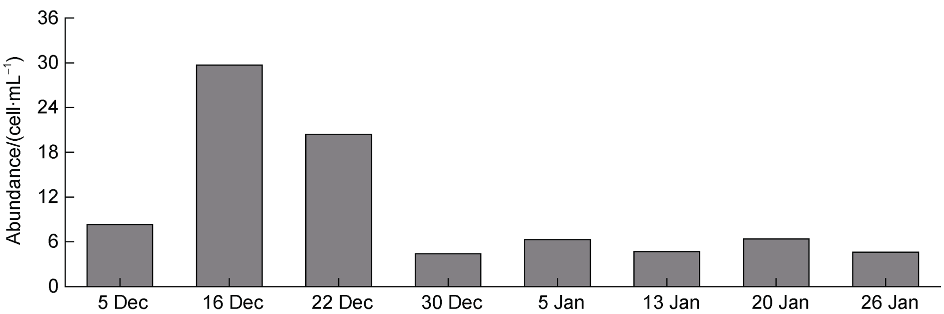

Figure 4 The succession of *Mesotaenium* cf. *berggrenii* (Zygnematophyceae, Charophyta) in lake Suvivesi. The cell abundances represent the average from four sampling sites. The coefficient of variation varied between 0.7–1.3.

3.2 Microbial mat communities

By far the most abundant taxon, in terms of cell number and biomass, was the cyanobacteria *Leptolyngbya*, which produced a very high biomass in Rock Pool1. Even if the mat structure itself is ignored, the number of "freely living" trichomes (typically less than 300 μm in length), reached >40000 mL^{-1}. The biomass of this community varied within a wide range depending on the location of the pool (Figure 2). In pools where the mat covered most of the surface, the biomass sometimes accounted for several kilograms per square meter as fresh weight. In most studied waterbodies, similar mat communities existed but equally rich communities were only found in some small rock pools nearby Rock Pool1 which had not been examined in detail. In larger ponds and lakes, the mat communities existed on the bottom sediments (Fossilryggen) and/or in the shoreline (Velodrome, Ring Pond, and Suvivesi) which were again not investigated in detail. This was because the top surface of all water bodies, except Top Pond2 and Rock Pool1, was frozen so the structure of their microbial mat communities was more difficult to investigate.

Besides *Leptolyngbya*, two genera of cyanobacteria were abundant in the mat communities, namely *Nostoc* and *Phormidium*. However, we did not find any eukaryotic algae living therein. In contrast, ciliates (at least three taxa) were abundant as well as two rotifer species, *Philodina gregaria*, a bdelloid rotifer, and one taxon of *Lecane*. The largest animals belonged to the group of Tardigrada, which were most numerous in the Rock Pool1.

In addition, few small colonies of unidentified organisms, which might be fungi, were found from different water bodies but not studied in more detail.

3.3 Environmental conditions

At the end of November 2014, when sampling started, all studied lakes and ponds were still frozen, but less than a week later, 4 December 2014, some water appeared in Suvivesi and the epiglacial lakes. Soon, the ice at a depth of 0.5–1.0 m was melting which was then hastened by the high irradiance (Figure 5). At the end of December 2014, the weather changed and from the beginning of January 2015 the incident irradiation declined so the rate of ice-melt slowed down. During the second half of December 2014, Top Pond2 and Rock Pool1 were frozen only during nights, but in January 2015 they were partially or completely frozen during the day as well.

Our measurements showed that there were some striking differences in the irradiance/air temperature variations recorded in the lakes. For example, in Suvivesi (Figure 6), T_w fluctuated diurnally within a range of 0.1–1.5 ℃ and in Rock Pool1 within 3.0 and 11.7 ℃. The highest mean water temperature (T_w) (4.7 ℃) was found in Rock Pool 1 and Top Pond 2 while in the rest of the lakes and ponds the mean water temperature was only 0.3–0.5 ℃. However, Fossilryggen was an exception since there it was 3.6 ℃ (Table S1). On 21 January 2015, T_w was 7.6 ℃ above the bottom, however, which was the highest measured temprature in Fossilryggen during the study period. Only in Rock Pool1 the DO data logger measured higher temperatures, with a maximum of 11.7 ℃ in the late afternoon, 28 December 2014.

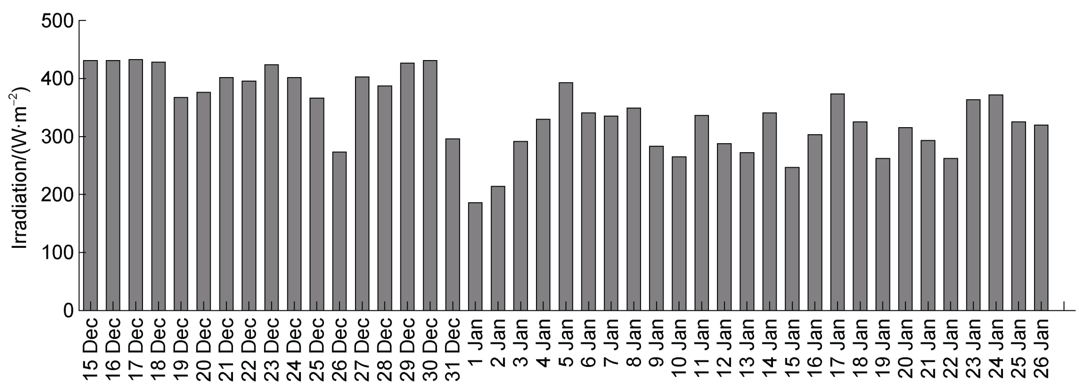

Figure 5 Daily mean total irradiation at the Aboa Research Station.

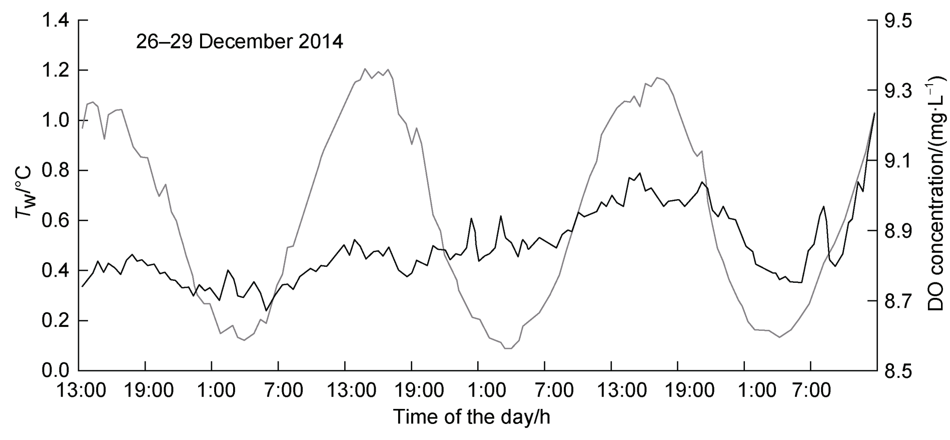

Figure 6 Water temperature (grey line) and dissolved oxygen (DO, black line) concentration in lake Suvivesi in the end of December 2014. The measurements were taken at the depth of 0.8 m.

In the studied lakes and ponds, DO concentrations (and saturations) generally varied within a relatively narrow range (Table S1) with DO saturation remaining below the equilibrium with atmosphere. In Rock Pool1, there were three peaks of DO value given by the data logger. The secondary level of the two maximum DO concentrations and saturations were 21.4 mg·L^{-1} and 174% on 27 December, 2014; 17.4 mg·L^{-1} and 144% on 3 January 2015. The highest DO concentration and saturation was 24.9 mg·L^{-1} and 176% respectively, recorded at noon 28 December 2014.

Except in three lakes and ponds (Top Pond1, Rock Pond1 and Fossilryggen Pond), the mean water pH varied between 7.0 and 7.8 (Table S1). The highest pH values were found in Rock Pool1, and the second and third highest in Top Pond1 and Fossilryggen Pond. The lowest pH (5.9), was measured in Suvivesi, a value identical with the pH of snow.

TN and TP concentrations varied substantially between the water bodies, with the highest concentrations being measured in Rock Pool1. The lowest TN concentrations were recorded in Suvivesi, Ring Pond and Plogen and the lowest TP concentrations in Top Pond1 and Top Pond2, and in Fossilryggen Pond and Ring Pond (Table 3). EC varied in a wide range, being lowest in Suvivesi, Penaali and Plogen, and highest in Rock Pool1, Fossilryggen and Top Pond1 and Top Pond2.

Table 3 The chemical data for the studied lakes and ponds. The values are averages of two samples, one taken at the beginning and one at end of the study period. All the results, apart from the pH, are based on the analysis of frozen samples transported to Finland

Lake/pond name	Site	pH	EC/ ($mS \cdot m^{-1}$)	Colour/ (mg Pt·L^{-1})	TP/ ($\mu g \cdot L^{-1}$)	TN/ ($\mu g \cdot L^{-1}$)	K/ ($mg \cdot L^{-1}$)	Na/ ($mg \cdot L^{-1}$)	Ca/ ($mg \cdot L^{-1}$)	Mg/ ($mg \cdot L^{-1}$)	Mn/ ($mg \cdot L^{-1}$)	Fe/ ($mg \cdot L^{-1}$)	Cations/ ($mg \cdot L^{-1}$)
Suvivesi	H1	5.7	3.2	0	4	31	0.04	0.10	0.10	0.03	0	0.02	0.29
	BAV50	5.7	3.5	0	48	136	0.77	0.05	0.05	0.01	0	0.01	0.88
	BAV55	5.7	1.9	0	8	49	0.14	0.07	0.10	0.02	0	0.01	0.34
	BAV16	6.0	3.9	1.4	116	177	0.69	0.04	0.00	0.02	0	0.00	0.75
Velodrome		9.0	59.0	1.4	163	287	0.06	1.05	6.20	0.64	0.01	0.21	8.17
Penaali		6.4	5.4	1.7	52	109	0.06	0.35	0.35	0.06	0.00	0.02	0.83
Ring Pond		8.7	19.0	0	8	73	0.36	3.10	4.20	0.91	0.01	0.06	8.60
Top Pond1		9.3	59.0	21.0	9	192	0.50	4.19	6.15	2.50	0.01	0.54	13.90
Top Pond2		9.0	186.0	11.0	6	120	1.10	9.46	16.20	6.39	0.01	0.08	33.20
Rock Pool1		10.1	801.0	39.0	43	1798	4.52	202.60	26.80	21.70	0.01	0.08	255.70
Plogen Lake		6.5	5.4	2.3	9	38	0.02	0.11	0.40	0.06	0	0.01	0.59
Fossilryggen Pond		9.2	229.0	2.3	5	283	8.21	24.60	39.5	8.05	0.01	0.04	80.40

Notes: TN, total nitrogen; TP, total phosphorus; EC was measured at 25 ℃; cations are the sums of K, Na, Ca, Mg, Mn, and Fe concentrations.

The cation concentrations varied a lot between the sites (Table 3). The difference between the minimum and maximum values being highest in sodium (Na), magnesium (Mg) and calcium (Ca), and the lowest was that recorded in TP. Except Ca, iron (Fe), potassium (K) and TP, the rest of the chemical constituents had their highest concentrations in Rock Pool1, where also highest pH, EC and colour values were found. In contrast, the lowest values of measured chemistry variables usually existed in Suvivesi.

3.4 Organisms and environmental variables

Very few significant statistical relationships were recorded between the biota and the environmental variables. The most notable one was the negative correlation (r<–0.65, P<0.02) between the cell number of *Mesotaenium* cf. *berggrenii* and the Na, Ca, and Mg concentrations. In contrast, there was positive correlation (r>0.73, P<0.03) between the abundance of the cyanobacterium of Cyanothece and the water temperature and DO. Similarly, the abundance of another cyanobacterium *Phormidium* was positively correlated with water temperature (r=0.79, P<0.015), but not with DO.

The concentrations of the three major cations (Na, Ca, Mg) were inter-correlated among the studied sites (all at r>0.7, P<0.01), and also correlated with EC (r>0.9, P<0.0001). The relationships between other cation (K, Na, Mn, Fe) concentrations and EC were significant as well (r>0.58, P<0.05). Water pH and EC were also strongly correlated (r>0.9, P<0.0001).

4 Discussion

The results showed that all investigated water bodies had organisms which were able to survive over harsh winter conditions and grow in summer, though only few were able to produce cell densities comparable to those in temperate and boreal water bodies. In general, our results agreed with the findings of earlier studies (Izaguirre et al., 2021), which reported extremely low eukaryotic algal and prokaryotic bacterial densities in Antarctic continental water bodies due to their challenging environmental conditions. In most habitats, the organisms could only colonise liquid water and/or slush during the summer, when fluctuating irradiances and temperatures produce very changeable environmental conditions.

In comparison to phytoplankton in Lake Fryxell, which is perennially ice-covered lake (Spaulding et al., 1994), the communities and their dynamics in our lakes and ponds were very different. In deep Antarctic continental lakes, many phytoplankton species are adapted to growing under low light intensities (Vincent, 1981; Vincent and Vincent, 1982). In our shallow lakes and ponds the cells had to adapt to very high photosynthetically active irradiation and UV-radiation in summer, and also their short-term variation within minutes and hours. Although the studied water bodies share, on the annual scale, the characteristic features of Antarctic continental freshwaters, i.e. poor light regime, great annual variation in solar radiation, extremely low temperatures, and often nutrient limitation (Izaguirre et al., 2021), their environmental conditions may be even more extreme for the organisms than in deeper water bodies, with perhaps slightly more stable conditions. Anyway, all organisms must have their own adaptive strategies to survive. In deeper ice-covered Antarctic continental lakes motility is among the key strategies together with pigment adaptation and mixotrophy (Izaguirre et al., 2021; Priddle et al., 1986). In our shallow water bodies, motility has not been adopted as a key strategy, instead they have become adapted to high UV-radiation, desiccation, and highly variable temperature conditions.

However, the adaptation strategies and succession patterns of organisms during the summer varied. For example, *Mesotaenium* cf. *berggrenii*, a rare example of an alga adapted to live on bare glacial surfaces (Remias et al., 2009), is also able to live in snow (Hoham and Remias, 2020). It had already reached its maximum cell density at the beginning of the summer while *Chlamydomonas* peaked just in the middle of January. Differences in timing can be also seen among cyanobacteria. When a species is capable to persist in harsh habitats without cyst formation such as *Mesotaenium* (Remias et al., 2009), that may explain its rapid density increase in our studied lakes. The vegetative cells of *Mesotaenium* contained high amount of intraplastidal starch, which became visible by Lugol-staining. The cells can also contain cytoplasmic lipid bodies and peripheral vacuoles filled with brownish secondary pigment, providing protection to the harmful effects of high PAR and UV-irradiation (Remias et al., 2009). The amount of PAR under the ice surface can be very high (Leppäranta et al., 2020), suggesting that *Mesotaenium* cells were tolerant of high irradiance.

The "light climate" in the studied lakes and ponds was very similar to that measured by Gorton et al. (2001) and Remias et al. (2009). High sugar and polyol concentrations of *M. berggrenii* seem to lower its intracellular freezing temperature and prevent damages of desiccation (Remias et al., 2009). In the study area, the period when melt water exists under ice lasts from late November to April (Leppäranta et al., 2013), is the maximum five months when the organisms can be metabolically active. At high latitudes, cyanobacteria cells often contain scytonemin, which is a sheath pigment against high UV-radiation (Garcia-Pichel and Castenholz, 1991; Quesada et al., 1998). In Rock Pool1, cyanobacteria had dark brownish colour, implying an abundance of such pigments.

Regarding the phytoplankton results, the large volume of water filtered through a 10 μm plankton net for the samples (except in Rock Pool1), may mean that abundance of small cells was underestimated. For the same reason, filtration may also underestimate the diversity of plankton by failing to retain some very small cells.

A bdelloid rotifer, *Philodina gregaria*, also tolerates extreme conditions such as high UV-radiation, which makes its widespread distribution in Antarctic continental water bodies possible (Allende and Pizarro, 2006; Hobbie and Laybourn-Parry, 2008; Izaguirre et al., 2003; Suren, 1990). For example, in lakes and ponds on ice shelves with microbial mats, *Philodina gregaria* has a dormancy known as anhydrobiosis, which allows the organisms to dehydrate and resist desiccation (Gilbert, 1974), a survival strategy important in temporal ponds and rock pools during freezing, melting, and drying.

Our results also revealed that the algal communities were surprisingly similar in different epiglacial and supraglacial water bodies. In all of them, the cell density was low and *M. berggrenii* was usually the most abundant species. The communities of the two ponds on Basen and Rock Pool1 and Fossilryggen were an exception. In those waterbodies cyanobacteria were distinctly more abundant than in the other habitats. The common feature of these habitats is an inorganic bottom sediment, which can be an important source of nutrients for cyanobacteria and algae in tundra ponds (Hobbie and Laybourn-Perry, 2008). In the other lakes and ponds, most of the bottom was covered with ice so there was very little contact between water and sediment. We suggest that in shallow ponds, some contact between water and sediment is essential for the organisms to thrive. This contact not only provides the organisms with nutrients but hastens their growth since the sediments absorb more heat than the ice. As a result, germination of the resting cells and growth of the microbes may be supported. Sediment may also provide suitable habitat for the resting cells to survive over harsh periods. The studied small ponds and rock pools with inorganic sediment had clearly higher water pH, and N and P concentrations than the epiglacial and supraglacial lakes, and nunatak ponds without inorganic sediment, and can be classified as specific type of water bodies in Vestfjella (Leppäranta et al., 2020).

It is likely that the availability of nitrogen and phosphorus depends, at least partially, on the presence of snow petrels nesting on the cliffs. At the beginning of summer there were around 60–70 petrels in the Basen population but only a few were left at the end of the season due to predation by south polar skuas. Obviously, the impact of snow petrels and polar skuas was highest in the epiglacial lakes below their nesting sites as well as in the ponds on top of Basen, where we saw skuas swimming and petrels flying over. In contrast in Plogen, with only few snow petrels, they are thought to have only a minor impact on the lake near the nunatak. Faucher et al. (2021) have recently argued that snow petrels may have increased allochthonous carbon inputs to ponds in Untersee Oasis.

When the ponds are ice-free, their nutrient concentrations may also be influenced by evaporation, which tends to increase element concentrations with time.

In the case of nitrate-nitrogen, dry deposition is possible since the study area lies only 150 km from the seashore. In comparison to Antarctic continental ponds measured by Wait et al. (2006), the nutrient concentrations in the lakes and ponds studied here were substantially lower.

In our group of lakes, the most extreme habitat was Rock Pool1, where microbial biomass exceeded that of other lakes and ponds by several orders of magnitude, and the abnormally high DO values suggested intense metabolic activity. The only habitat with equally high metabolic activity indicated by DO super-saturation was the bottom of Fossilryggen Pond.

Based on the results of this study, we conclude that the epiglacial and supraglacial lakes and ponds situating in the blue ice region of western Dronning Maud Land offer an extreme environment for all the freshwater organisms. This is due to a combination of factors such as high irradiation, low water temperature, low nutrient concentrations, short ice-free period and rapid changes between melting, freezing, and drying. Where inorganic bottom sediment existed, the abiotic conditions supported cyanobacteria in particular, and suggested the fundamental importance of the sediment for organisms of such oligotrophic environments.

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Supplementary Table and Figures

Table S1 Water temperature (T_w), dissolved oxygen (DO) and pH data of the studied lakes and ponds. Suvivesi includes the measurements from the four sampling sites (H1, BAV50, BAV55, BAV16). The measurements cover the study period of each lake. The number of measurements varied from three (Plogen and Fossilryggen) up to 11 (Suvivesi)

Lake/pond name	Index	T_w/℃	DO/%	DO/(mg·L^{-1})	pH
Suvivesi	mean	0.5	93.7	13.5	7.0
	median	0.4	96.1	13.8	7.3
	min	0.2	81.8	11.7	5.9
	max	0.9	100.6	14.7	7.7
	sd	0.3	7.4	1.1	0.6
	95% CI	0.2	5.9	0.9	0.5
Velodrome	mean	0.5	102.6	14.8	7.6
	median	0.5	103.6	14.9	7.7
	min	0.2	98.3	14.1	7.0
	max	0.6	105.4	15.1	8.1
	sd	0.2	2.7	0.4	0.4
	95% CI	0.2	3.7	0.5	0.3
Penaali	mean	0.3	86.9	12.6	7.4
	median	0.3	85.9	12.4	7.3
	min	–0.1	82.6	11.8	7.1
	max	0.6	92.0	13.3	7.9
	sd	0.3	4.2	0.6	0.4
	95% CI	0.2	3.7	0.5	0.3
Ring Pond	mean	0.3	75.4	10.9	7.7
	median	0.2	70.9	10.1	7.5
	min	0.1	68.0	9.9	7.1
	max	0.6	96.9	14.1	8.5
	sd	0.2	12.2	1.8	0.6
	95% CI	0.2	10.7	1.6	0.5
Top Pond1	mean	0.6	82.0	11.8	8.5
	median	0.5	81.1	11.8	8.5
	min	–0.1	80.3	11.6	8.4
	max	1.7	84.4	11.9	8.6
	sd	0.7	1.7	0.1	0.1
	95% CI	0.6	1.5	0.1	0.1
Top Pond2	mean	4.7	91.3	11.9	7.8
	median	4.4	91.5	11.7	7.8
	min	1.0	83.2	10.9	7.5
	max	9.3	103.5	13.6	8.2
	sd	3.0	7.8	1.1	0.3
	95% CI	2.6	6.8	0.9	0.2
Rock Pool1	mean	4.7	146.7	19.0	9.3
	median	5.7	148.3	19.0	9.3
	min	1.2	113.6	14.5	8.4
	max	6.9	175.8	24.9	10.3
	sd	2.4	22.4	3.4	0.7
	95% CI	0.2	1.4	0.3	0.5

Continued

Lake/pond name	Index	T_w/℃	DO/%	DO/(mg·L^{-1})	pH
Plogen Lake	mean	0.4	85.5	12.4	7.4
	median	0.5	85.2	12.3	7.3
	min	0.2	84.4	12.1	7.0
	max	0.5	86.8	12.6	7.8
	sd	0.2	1.2	0.3	0.4
	95% CI	0.2	1.4	0.3	0.5
Fossilryggen Pond	mean	3.6	158.9	21.0	8.5
	median	4.0	151.7	20.0	8.8
	min	0.2	128.6	18.3	7.4
	max	7.6	253.4	30.4	9.2
	sd	1.5	29.4	3.0	0.3
	95% CI	0.8	14.9	1.5	0.2

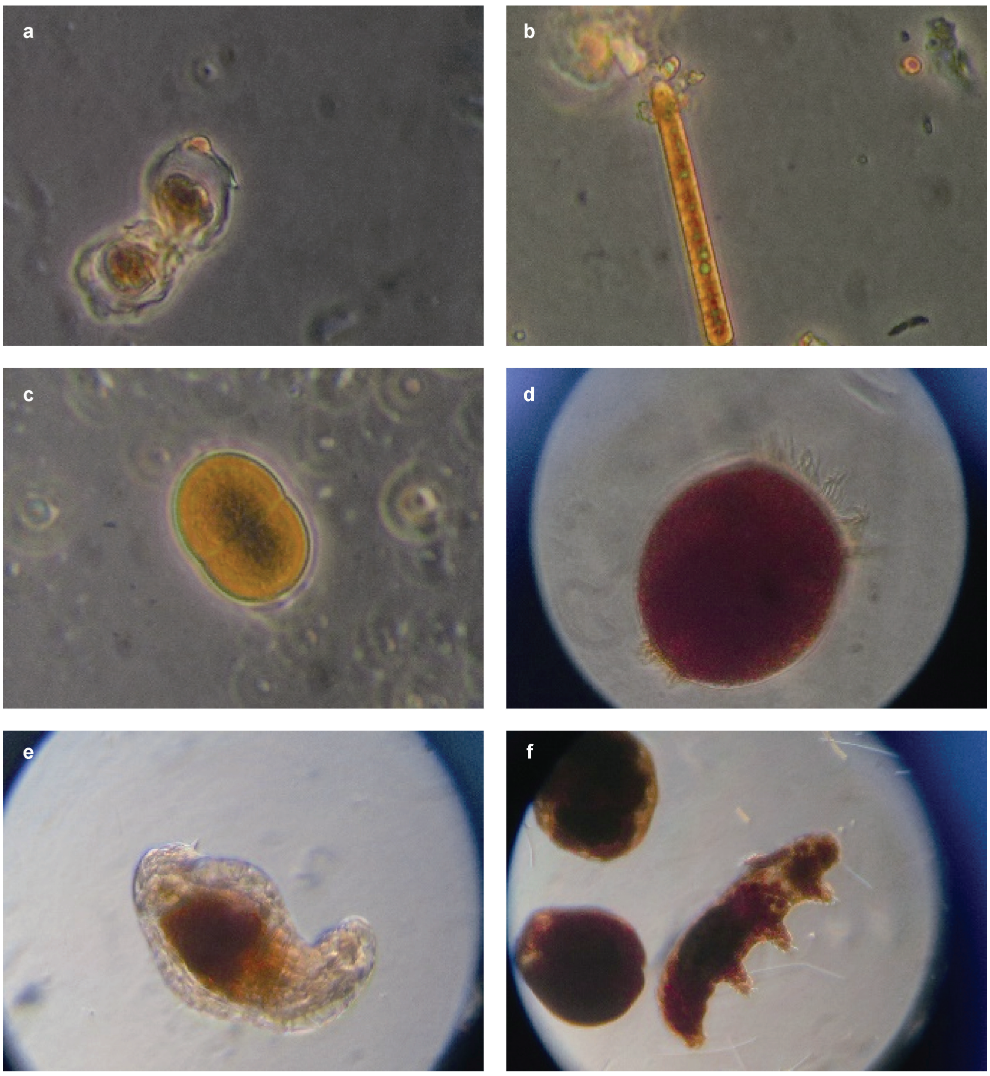

Figure S1 Photographs of the most abundant eukaryotic algae (**a**, *Mesotaenium* cf. *berggrenii*), two common cyanobacteria (**b**, *Phormidium* sp., **c**, *Cyanothece* sp.), one ciliate (**d**), two rotifers (**e**, *Philodena gregaria*, **f**, *Legane* sp.), and tardigrada (**f**).

Figure S2 Two microbial mat community photographs from Rock Pool1 taken in January 2015. The white device in the left picture is DO logger.