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ALGAL COMMUNITIES OF POLAR WETLANDS

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SUMMARY

Freshwater algae are of great importance in biocenoses of polar and subpolar regions. They colonize extreme biotopes in cold and arid areas, and play a significant role in polar wetlands. They are main producers in glacial streams, deglaciated soils, tundra communities, and in periodical swamps and pools occurring commonly during the polar summer seasons. Algal communities of the main biotopes of humid polar regions, recognized in the Arctic (Svalbard, Ellesmere Island) and on subantarctic islands (South Shetland Islands), are reviewed and shortly characterized in the article.

KEY WORDS

Algae - algal biocenoses - polar regions - microphyte communities - ecology - wetlands - Arctic - Antarctica

Algae are oxyphototrophic organisms which colonize and populate the high polar regions. Ecological significance of their communities increases with increasing latitude and with marginality of polar conditions. In these circumpolar, very specialized biotopes some of the most prolific producers and ecologically important organisms are the oceanic phytoplankton (Holm-Hansen et al., 1977; Gallegos et al., 1983; Economou- Amilli et al., 1995; etc.), cryosestonic algae developing on or near the surface of summer snow-fields and on glaciers (Komárek et al., 1973; Wharton et al., 1981; Smith et al., 1988; Ligowski, 1993; etc.), epi- and endolithic algae (Friedmann, 1980, 1982; Friedmann et al., 1988; Golubic et al., 1981; etc.), and benthic algal mats in continually or almost continually frozen Antarctic lakes (Komárek, Růžička, 1966; Parker et al., 1981; Love et al., 1983; etc.). However, the most abundant algal vegetation has developed in circumpolar wetland biotopes (Broady, 1982, 1987, 1988; Elster et al., 1995; Elster, Svoboda, 1995; etc.).

Polar wetlands are particularly characterized by distinct seasonality (severely changing climatic factors, polar day/night changes). In summer, the algal microflora communities develop under the continual input of light energy. The source of liquid water during this period is important: at this time the vegetation cycles of different species can terminate. In the later part of the growing season, the otherwise continuously running algal vegetative cycle enters a new phase, that of the production of diaspores in preparation for winter dormancy and regeneration at the start of the next season.

The main sources of liquid water are melting snow and ice, and, to a lesser degree, direct precipitation, summer snow fluries, rain and mist. Tidal spray provides the needed moisture along the sea shores. In summer, a complex system of streams and rivulets draining various pools, lakes and swamps form seepages in valleys, lowlands and polar coastal areas. Here, special algal mats and crusts develop (often after periodic floodings) in a relatively pure form or as a component of bryophytic and (in the Arctic) vascular plant communities. While the bryophyte and macrophytic vegetation has been studied in detail (e.g., Longdon, 1988; Svoboda, Freedmann, 1994), the ecology of algal biocenoses of the same biotopes remains mostly unknown.

Polar wetlands are created by melting water, which feeds streams during the summer season, saturates muddy soils and produces "secondary" springs. The bottom of all shallow water bodies (seepages) is cold because of the presence of underlying permafrost. All these seasonal biotopes therefore depend on the energy input for their heat supply via direct radiation warming or turbulent heat transfer from the air. When the air temperature drops below the freezing point, or when there is a significant loss of reradiated heat, the shallow pools quickly freeze or freeze-dry. As a result the continuity of the stream flow is often broken even during the season. The areas covered with soil deposits (e.g. newly deglaciated morains and coastal terraces with pools and ponds) with special soil and wetland algae pioneers, belong also to this category of biotopes. Specialized algal assemblages develop in brackish pools and salt marshes associated with the coastline.

Interesting, yet uncommon in polar regions, are geothermal springs (e.g., Krawczyk, Pulina, 1980). They differ from the previously described biotopes by having the whole year throughflow of water with a constant above-freezing temperature (usually from 6 to 25 °C). Consequently, the fluctuating air temperatures do not play any significant role during the year. However, the seasonality of the light intensity is important, since it determines the rate of photosynthesis and consequently the quantity of the biomass present during the year.

Geothermal springs are sometimes very different due to specific composition of dissolved salts. Although they may be counted among polar wetlands by geographical position, they really represent atypical biocenoses and maintain for polar regions uncharacteristic living conditions. Consequently, also the algal microflora is atypical having little in common with that of a typical polar, temperate or even tropical wetland.

The major characteristics of algal microphytes in polar wetlands:

1. The organisms are adapted or at least tolerant to cold environment. Their photosynthetic activity starts at temperatures close to 0 °C with maxima usually around 8-10 °C (Hindák, Komárek, 1968). Both algal types, those thriving at, and those tolerating low temperatures occur in polar wetlands.

2. As ecological opportunists algae take advantage of the long or continuous photoperiod in summer. Growth of their biomass in streams and pools is visibly exponential, as long as the nutrient supply and other favourable conditions prevail.

3. The polar growing season is short, limiting the number of algal annual reproductive cycles. It is believed that freshwater algae reproduce almost exclusively asexually in polar environments.

4. Most algal species (with the exception of those found in mineral geothermal springs) are able to utilize mineral nutrients present at extremely low concentrations (in parts per billion), as long as there is a steady supply (Elster et al., 1995) while many cyanoprokaryotes are able to fix atmospheric nitrogen as well.

5. Polar algae are adapted to periodic drying associated with increase or decrease of temperature. They are able to regain their photosynthetic activity immediately after the return of favourable conditions (temperature limits, humidity).

Polar algal microflora appears to have distinctly different ecophysiological properties from microfloras of other latitudinal ecozones. Certain morphological and physiological similarities exist only with algae from alpine biotopes. However, genetic and ecophysiological separation of polar algae from their morphologically similar counterparts of the temperate zone has not yet been successfully attempted.

Polar wetlands are particularly common in low-lying areas (oases) with a more humid climate. These are primarily the coastal areas of the Arctic and Antarctic, which are often exposed to the influence of moist oceanic winds arriving from lower altitudes, or to catabatic winds descending from the glaciers. Such wetlands exist mainly between the "cool" and "cold" climate zones, as demonstrated by Stonehouse (1989). The Arctic is more open to the southern influences, and wetland communities are well developed in many localities. Special value and ecological position has Svalbard, the nature of which is influenced substantially by the Gulf stream, the principal source of the humid climate at this archipelago. However, wetland Arctic biotopes are well developed elsewhere on the edge of central Arctic region, e.g. in the Canadian and Russian Arctic and in Greenland. In Antarctica, isolated from northern warmer oceans by circumcontinental streaming, only the subantarctic South Shetland Islands and Antarctic peninsula belong to this zone, which is under the influence of winds from the SE Pacific ocean. In the climatic oases of these areas unique wetland biocenoses have developed.

However, these wetlands are often adversely affected by human activity resulting from the high number of research stations established in Antarctic coastal areas. Likewise, some areas of the Arctic have also been greatly affected by anthropogenic influences. At Svalbard, for instance, substantial wetland areas around mining encampments have been destroyed. The better protection of very special and unique wetland microphyte communities (e.g., in the Fildes peninsula of King George Island), is urgently desirable.

In the following section, selected ecological information concerning specific polar wetlands is presented. This was obtained at Spitsbergen, Svalbard (1988), in Sverdrup pass, Ellesmere Island, Canada (1991 and 1993), and at King George and Nelson islands, South Shetlands (1989), and is presented mostly as personal observations and communication of the authors.

RESULTS

Secondary springs

Meltwater from snow-fields and glaciers often sinks underground where it moves on the surface of the permafrost table before resurfacing at various points as "secondary springs" down the slope. The characteristics of these springs is directly influenced by surface and atmospheric conditions: the water temperature (outflow from glaciers) is close to 0 °C and the springs discharge with a periodicity controlled by external atmospheric conditions. As soon as the temperature decreases below zero, these springs freeze and dry up.

In Svalbard we have found communities of diatoms and later cyanoprokaryotes in these secondary upwellings (compare Longdon, 1988). In the Canadian Arctic, at Ellesmere Island, in early spring *Tribonema minus* and later in the season filamentous green algae (such as *Klebsormidium crenulatum, Klebsormidium rivulare* and *Zygnema* cf. *leiospermum*) were found (Elster et al., 1995).

In Antarctica, *Schizothrix frigida* and several *Nostoc*-species often dominated and have been seen to produce mats with reddish or blackish surface in secondary springs and seepages.

Glacial streams and rivers

The occurrence of streams and rivers (influenced by melting snow-fields and glaciers) is high in glaciated areas. The length and slope of the glacial streams are influenced by the distance from the glacial front and by its elevation above the sea level. As a result, streams with various rates and speed of flow exist, some eroding deep channels. Those on more gentle slopes meander widely, often temporarily flooding the surrounding terrain, forming characteristic seepages with rich algal vegetation (Oscillatorialean species in Svalbard, *Schizothrix*- and *Nostoc*-species in South Shetland Islands, etc.). Extensive development of algal vegetation appears particularly in shallow, slow moving glacial streams, and the characteristic zonation develops, if the stream is long enough (Svalbard 1988).

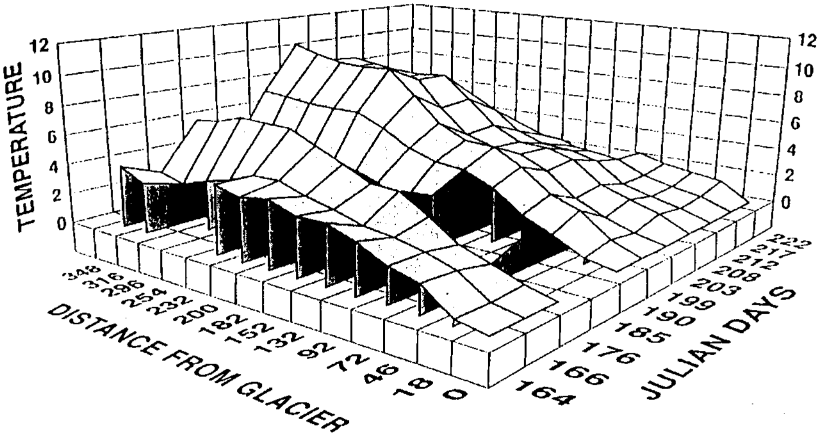

Fig. 1. Seasonality of water temperature along the glacial stream, Canadian Arctic, Ellesmere Island, Sverdrup Pass, 1991 (Orig. Elster, Svoboda, 1995)

In 1991 at Ellesmere Island we noticed a striking phenomenon. In the zone closest to the glacial front, mostly cyanoprokaryotes were present (*Phormidium autumnale* morphotype *"amoenum"*, *Dichothrix* cf. *gypsophila, Scytonema myochrous, Coleodesmium wrangelii*, among others). As the water warmed up to 10 °C (Fig. 1) with increasing distance from the glacier, green filamentous algae took over and filled the stream with their floating mass. These were mainly *Klebsormidium crenulatum, Klebsormidium rivulare, Ulothrix mucosa,* and *Zygnema* cf. *leiospermum.* Biomass of these algae gradually culminated at about 130 m from the glacial front and then diminished in the lower section of the creek, and, even lower, virtually vanished (Fig. 2). The gravelly bottom of the lower section of the stream became free of any visible algal life. Interestingly, also the measured concentration of nitrate-nitrogen in the stream water reached maximum at about 120 m from the edge of the glacier, and diminished to trace values down the stream from which we conclude that green

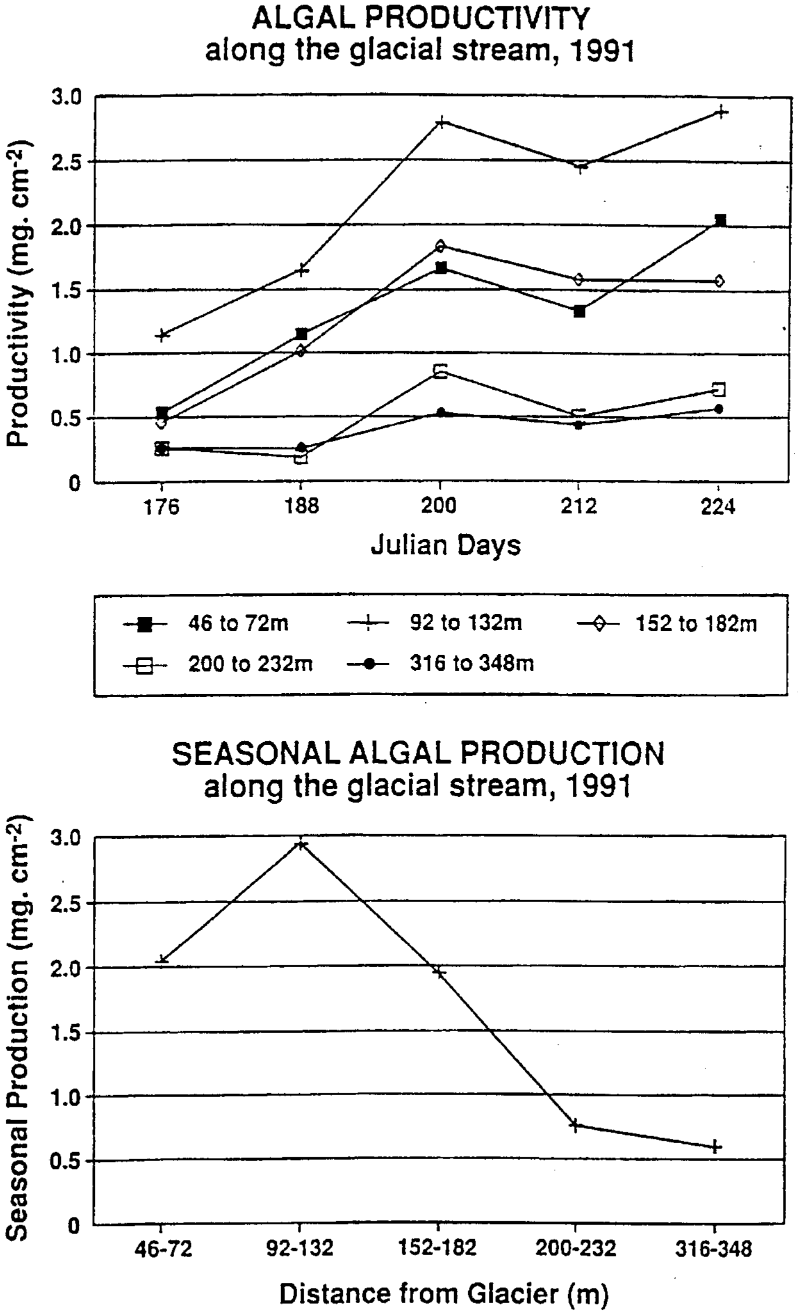

Fig. 2. Productivity of algae along the glacial stream, Canadian Arctic, Ellesmere Island, Sverdrup Pass, 1991 (Orig. Elster, Svoboda, 1995)

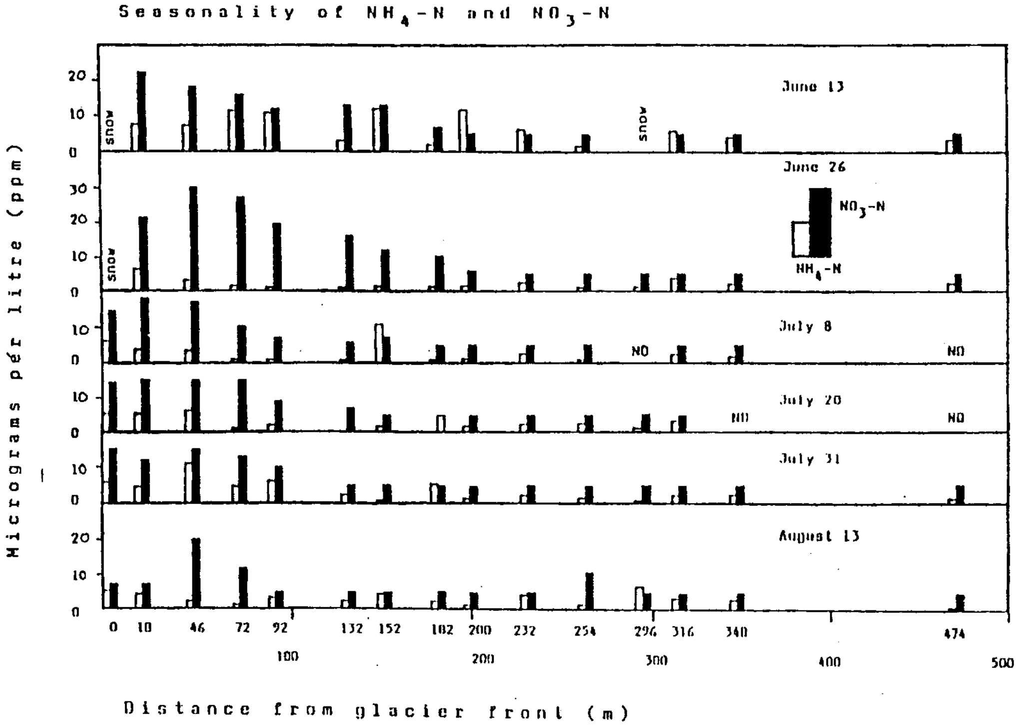

Fig. 3. Decrease of nitrogen content along the glacial stream, Canadian Arctic, Ellesmere Island, Sverdrup Pass, 1991 (Orig. Elster, Svoboda, 1995)

algae in the lower section of the creek had no nitrogen to support their growth (Fig. 3; Elster, Svoboda, 1995).

Moraine and terrace lakes

In a rugged terrain of glacial moraines, small and shallow seasonal ponds and pools fill with meltwater early in the season. Most of them lose their water due to subsurface drainage and evaporation. These pools carry sufficient nutrient load to support benthic communities of diatoms and cyanoprokaryotes which produce a high biomass (Table 1). Banks of ponds in older moraines and around shallow lakes which are enclosed behind uplifted coastal terraces are covered by mosses and (in the Arctic) by vascular plants. Algae float in a water column and grow epiphytically on submerged shoots of plants. Both types of lakes dry up and freeze during the winter season.

Wet sedge meadows

Associated with lakes margins and expanding into flat, often sickle or fan-shaped depressions are the wet sedge meadows. A thick carpet of moss slows down the movement of water, if there is an up-slope source. In this, almost stagnant water, initially tiny globules of nitrogen-fixing *Nostoc* sp. develop into massive gelatinous lumps, and thus contribute significantly to wet meadows productivity in terms of nitrogen and biomass input (Murray, Svoboda, 1989; Murray, 1991).

Wet slope seepages and algal crusts

Late and permanent snow banks feed wet seepages down slopes. These seepages are dark in colour and are densely populated with algae (*Phormidium autumnale, Leptolyngbya* sp., *Klebsormidium* sp.). Over time, soft, skin-like layers of algae, bacteria and soil particles develop which harden when dry and can be peeled off. In polar-desert landscapes algal-microbial crusts are often the only detectable life forms and source of organic carbon and nitrogen in the soil, priming the landscape for the invasion and colonization of higher plants at climatically favourable conditions.

Deep oligotrophic lakes

There are numerous deep freshwater oligotrophic lakes in the circumpolar regions, such as Linné and Kongres Lakes at Svalbard, Lake Hazen at Ellesmere Island and many others in the circumpolar Arctic. In Antarctica, there are some smaller but deep lakes along the south-western coast of King George Island (Fildes peninsula) and in northern oasis of the Nelson Island in South Shetlands in Antarctica. These lakes are covered by 1 to 1.5 (2.5) m thick ice throughout several months of the year. The margins of these lakes or their entire surface area are ice free only for a short period of a year (two to four months in summer). In this type of lake phytoplankton develops primarily with the discharge of nutrients during the spring snowmelt. In spite of this nutrient supply, yearly productivity is very low (Kalff, 1970; Minns, 1977). Some limnological parameters in Linné lake (Svalbard 1988) are shown in Table 2. The shallow lakes covered by ice during the whole year and situated in coastal areas of the Antarctic continent represent a special case. On the bottom of these lakes develop massive mats of cyanoprokaryotes and algae during the summer season and ecology of these communities is well known: Komárek, Růžička (1966); Love et al. (1983); Parker et al. (1981); etc.

Brackish pools and salt marshes

In coastal areas brackish pools and marshes represent another type of algal biotopes. They are supplied by fresh water from the land (melting snow and ice), and by sea water at a high tide. Brackish lakes are mostly transient biotopes. They form behind tidal dunes (Fig. 4) or due to coastal uplift resulting from deglaciation (Dickman, Quelett, 1987). Brackish pools and marshes are colonized by specific algal microflora. The colonization of the bottom of coastal swamps and following seasonal succession starts by communities of diatoms and later is characterized by heavy mats of cyanoprokaryotes and green filamentous algae. Ecological characteristics of brackish pools from the northern part of Svalbard and their representative groups are shown in Table 1.

Biotope	stagnant waters, moraine ponds, pools, moors	springs, creeks and riv
Dominant algae	mats of cyanoprokararyotes and diatoms on the bottom *Gloeotila, Sphaeroplea, etc.*	*Ulothrix, Hydrurus* *Tribonema, Klebsormidiu* cyanoprokaryotes, diatom
temperature (°C)	3.5 - 11	3.5 - 8.5
pH	7.3 - 7.8	6.9 - 8.6
conductivity (S)	37.0 - 258.0	54.0 - 238.0
alcalinity (mmol.l^{-1})	0.92 - 1.53	0.61 - 2.35
NO_3^--N + NO_2-N (mg.l^{-1})	0.133 - 0.167	0.093 - 0.233
NH_4^+-N (mg.l^{-1})	0.08 - 0.15	0.08 - 0.15
P (mg.l^{-1})	0.010 - 0.016	0.010 - 0.049
PO_4^{3-} - P (mg.l^{-1})	0.003	0.003 - 0.035
Ca^{2+} (mg.l^{-1})	12.2 - 58.2	7.15 - 55.19
Mg^{2+} (mg.l^{-1})	2.4 - 16.1	4.96 - 8.68
SO_4^{2-} - S (mg.l^{-1})	0.007 - 3.0	0.33 - 1.32
Cl^- (mg.l^{-1})	3.4 - 9.22	3.69 - 9.22
Fe^{2+} (mg.l^{-1})	0.05 - 0.1	0.1 - 0.4
SiO_2^+ - Si (mg.l^{-1})	0.37 - 0.42	0.04 - 3.12

Table 1. Comparison of ecological parameters of selected biotopes with algae in Svalbard (July - August 1988)

Geothermal springs

Deep geothermal springs are not common. The basic ecological characteristics of these springs are: year-round constant temperature (usually only slightly higher than 0 °C, but springs with temperature over 20 °C also appear, e.g. in the high Arctic in North Spitsbergen - Bockfjord) and a constant flow rate over the year (Krawczyk, Pulina, 1980). The springs have specific stenothermal microvegetation, which is quite different from periodic glacial secondary springs.

In the northern part of Spitsbergen, in Bockfjorden Inlet (Jotunkjeldene and Trollkjeldene, 79°N), geothermal springs exist with a year-round constant temperature of 20-26 °C. These springs (spring area and its outlet zone) are occupied by a special algal microflora (Marti, Herzog, 1989). From the ecological and evolutionary points of view, these springs are interesting because with distance from the hot wents the water cools down, dissolved salts precipitate (forming sometimes travertine cascades and terraces) and the algal microflora changes accordingly. Ecological parameters with typical groups of main algal species are listed in Table 1.

CONCLUSION

In this short review we have tried to outline and partially characterize a variety of polar wetland biotopes. Some of them such as snowbanks, brackish pools, salt marshes and thermal springs carry distinct algal communities. Whereas, freshwater biotopes with either flowing or stagnant waters and having shallow or deep water bodies support less distinct algal communities, or their species

creeks eutrophized by bird colonies	brackish pools	hot springs	surface layer of melting snow field
cyanoprokaryotes, diatoms	mats of cyanoprokaryotes and diatoms	cyanoprokaryotes, diatoms, filamentousconjugatophytes, charophytes	coccal green algae
3.5 - 8.5	7.5 - 8.2	1.0 - 6.0	0 - 1.5
8.9	7.3 - 8.2	7.4 - 8.9	8.6
181.0	530.0 - 578.0	1460.0 - 3360.0	258.0
1.78	1.53 - 3.26	10.51 - 14.08	2.35
0.712	0.179 - 0.263	0.053 - 0.567	0.29
0.12	0.12	0.08 - 0.50	0.20
0.059	0.010 - 0.039	0.007 - 0.039	0.039
0.047	0.003 - 0.029	0.003 - 0.013	0.09
27.5	28.6 - 58.2	107.3 - 169.3	55.19
14.2	19.8 - 21.7	7.9 - 21.7	8.68
4.29	3.51 - 5.28	16.5 - 29.7	1.32
11.9	97.7 - 154.2	156.7 - 760.2	9.22
0.05	0.05 - 0.15	0.05 - 0.1	0.4
0.28	0 - 0.37	9.13 - 19.62	0.51

	O_2 (mg.l^{-1})	pH	temperature (°C)	PhAR (W.m^{-2})	DW (m.l^{-1})
			9.0	225.0	-
Water level	17.2	7.4	5.3	165.0	-
1 m	16.5	7.5	5.2	90.0	0.0455
2 m	15.3	7.5	5.2	48.0	0.0442
3 m	15.3	7.5	5.3	220.4	-
5 m	14.7	7.5	5.1	-	0.0276
6 m	-	-	-	9.6	-
7 m	-	-	-	9.0	-
8 m	-	-	-	7.5	-
10 m	14.3	7.6	5.1	-	0.0531
15 m	13.9	7.5	5.1	-	0.0359

Table 2. Main ecological parameters in the lake Linné, W. Spitsbergen, Svalbard (July 1988)

composition and ecological dominance is less known. It is therefore imperative that polar wetlands are brought to the attention of algal taxonomists and ecologists, and that research in species diversity, seasonality and productivity in coupled with measurements of microclimate and other ecological parameters. The assumed or proven algal sensitivity to increased UV radiation over both poles gives such a research special urgency. Other topics for polar algal priority research include, e.g.,

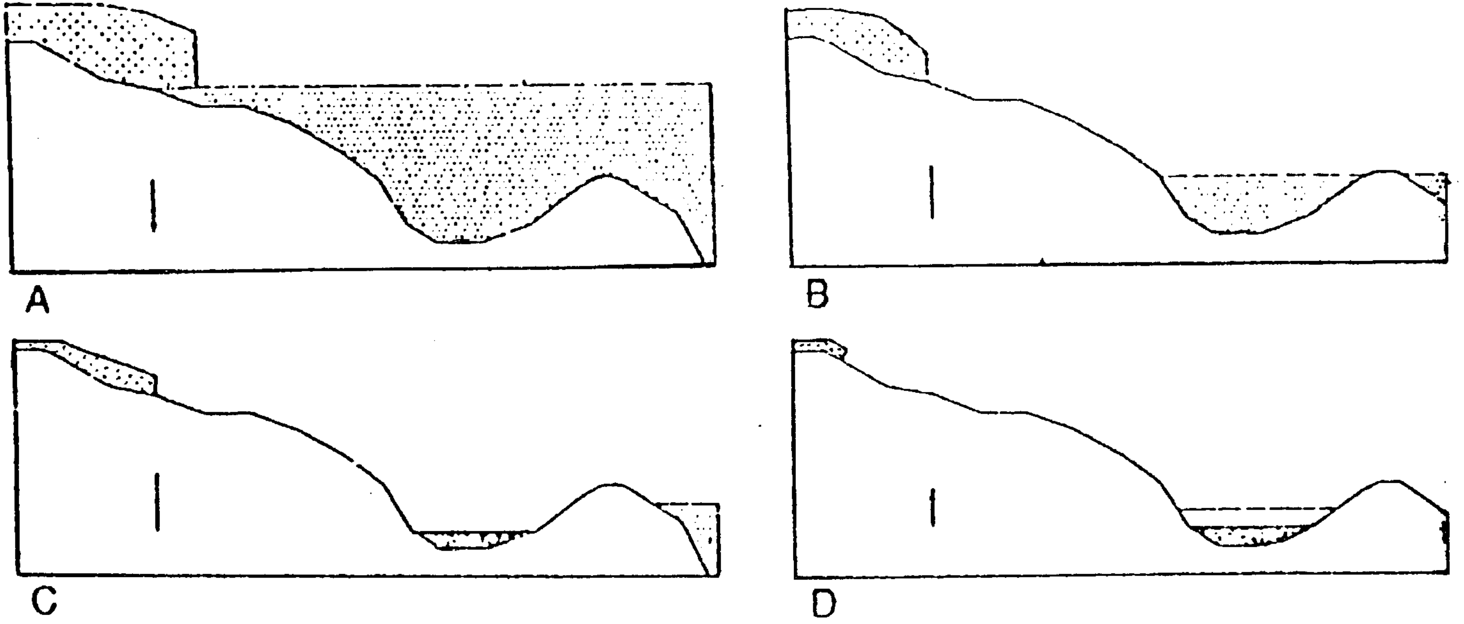

Fig. 4. Origin of coastal brackish pools and swamps after deglaciation of the sea shore (after Dickman, Quelett, 1987)

adaptations to extreme cold and low-nutrient environments, narrow niche separation along environmental gradients and continua (a result of microniche selection or competition?).

It is evident that in arctic and antarctic regions a wide spectrum of freshwater and brackish wetlands can be identified. The origin of most of these wetlands can be traced to times following deglaciation when the ice-free landscape was subjected to postglacial uplift and drainage development. It has been proposed that algae are the initiators of successional processes immediately after deglaciation. They can be dispersed over large distances, since their minute propagules are easily transported by water and by wind. While cyanoprokaryotes have played a fundamental role in introducing available nitrogen via nitrogen fixation into restauring arctic ecosystems, green algae have been efficient facilitators of the nitrogen storage and its transfers to bryophytes and vascular plants (Elster, Svoboda, 1995). Thus, algae are primary movers of fixed energy in the organic matter they produce. Their full ecological role in the process of revegetation of the deglaciated polar landscapes is, however, not well understood and is being a subject of intensive studies.

Important aim of wetland freshwater and brackish polar microflora research (i.e. the study of species diversity, seasonality and productivity in dependence on the microclimate and climate ecological conditions) is also utilization of their immense sensitivity to global climate changes.

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