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ALGAL DIVERSITY, SEASONALITY AND ABUNDANCE IN, AND ALONG GLACIAL STREAM IN SVERDRUP PASS, 79°N, CENTRAL ELLESMERE ISLAND, CANADA

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Abstract: This study examines the diversity, seasonality and abundance of cyanoprocaryota (cyanobacteria) and algae, in and along a glacial stream ecosystem in Sverdrup Pass 79°N, Central Ellesmere Island, Canada. Seasonal course and seasonal values of Relative Species Occurrence, Frequency and Abundance were calculated for the glacial stream, merging with a studied section of Sverdrup River. In the stream the values were calculated separately for the upper "new" moraine section which was poorly vegetated, and for the lower, "old" moraine section with a fuller vegetation cover. Three distinct algal life-strategies were described. Two of them, representing mostly filamentous types, *i.e.* floating filamentous forms and mucilaginous films had smaller species diversity with 7 and 9 species respectivelly. These types occupied mainly the "new" moraine section of the creek and produced high biomass there. These organisms started the process of plant life invasion in the newly deglaciated parts of the moraine and did not show any noticeable seasonal trend. The third life-strategy group, suspended metaphyton (the algal flora which is present between the epiphytes as a loose collection of non-motile or slightly motile organisms, without any obvious mode of attachment), displayed higher species diversity (53 species) and occupied mainly the "old" moraine section. This group occurred less regularly and showed sharp seasonal peak.

1. Introduction

In the terrestrial Arctic and Antarctic Cyanoprocaryota (Cyanobacteria) and algae are the primary colonizers of areas, exposed to revegetation after the disappearance of ice cover (WYNN-WILLIAMS, 1986, 1993; HOWARD-WILLIAMS *et al.*, 1986; SMITH, 1990, 1993; VINCENT and HOWARD-WILLIAMS, 1986; ELLIS-EVANS and WALTON, 1990; ELSTER and SVOBODA, 1995; ELSTER *et al.*, 1997).

At Ellesmere Island, Northwest Territory, Canada, several outlet glaciers descend from the Agassiz icecaps into the deglaciated Sverdrup Pass. Glacial streams which flow from the glacial fronts in Sverdrup Pass are rich in Cyanoprocaryota and algal species diversity. Similar types of strems have been also studied in the Antarctic (BROADY, 1982, 1989a, b; HIRANO, 1979, 1983). In the stream, chosen for this study, 9 community types which produced macroscopically visible biomass were recognized (ELSTER *et al.*, 1997). All these communities have also been described in the maritime and continental Antarc-

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tica (BROADY, 1981, 1989a; VINCENT and HOWARD-WILLIAMS, 1986; HAWES, 1989).

The glacial stream ecosystem in Sverdrup Pass experienced marked variations in the physico-chemical parameters. Stream-water temperatures showed amplitudes from 0 to 11°C, the irradiance ranged from high, continuous sunlight in peak summer to low-light intensity short days in late August. Studied stream discharge also showed variable volumes of water flow from 0 to 14 *l*/s (ELSTER and SVOBODA, unpublished). Flushes of high discharge may be very erosive and clear much of the existing periphyton and metaphyton microflora. They occur mainly when warm air masses deliver warm rain, or during calm sunny days. Another important cause of algal biomass loss is sloughing, physical scraping and peeling of the periphyton and metaphyton. Also this phenomenon has been documented in Antarctic streams (HOWARD-WILLIAMS *et al.*, 1986; VINCENT and HOWARD-WILLIAMS, 1986; HAWES, 1989).

Chemical water parameters also fluctuated widely. We measured a wide range in concentrations of the nitrate- and ammonia-nitrogen(5–38 and 0.2–23 μg/*l*, respectively); of the orthophosphate and total phosphate (0.3–11 and 2–20 μg/*l*, resp.); of Ca and Mg (90–5950 and 20–3960 μg/*l*, resp.). Also conductivity ranged 1.4–82.6 μS cm^{-1}; alkalinity 0.07–0.3 mmol/*l*; and pH 4.6–7.0 (ELSTER and SVOBODA, unpublished). Great variations in the above parameters were reported in continental and maritime Antarctic streams by HOWARD-WILLIAMS *et al.* (1986), VINCENT and HOWARD-WILLIAMS (1986), HOWARD-WILLIAMS *et al.* (1989), HAWES (1989) and HOWARD-WILLIAMS and VINCENT (1989).

Grazing pressure was not studied in the glacial stream but no macroscopic herbivorous insects or crustacean arthropods were observed in the algal mat samples. These mats contained various microscopic ciliates, flagellates, nematodes, rotifers and tardigrades but their effect in terms of herbivory was probably minimal. No significant grazing have been reported from Antarctic glacial stream either (VINCENT and HOWARD-WILLIAMS, 1986; HOWARD-WILLIAMS *et al.*, 1986; HAWES, 1989).

Fluctuations of physico-chemical parameters are consistent with the "river continuum concept" of VANNOTE *et al.* (1980). This concept suggests that stream ecosystems are in a continual state of change along temporal and spatial axes, never attaining the sort of climax seen in terrestrial ecosystems.

VINCENT and QUESADA (1996) proposed three potential life-strategies for polar regions. These allow aqutic microorganisms to grow and survive in spite of great seasonal variation in physical and chemical parameters. According to this hypothesis (1) specialized genotypes occupy narrow niches, (2) generalist genotypes grow suboptimally while, (3) they experience broadly variable conditions.

Given the physical and chemical instability of the Sverdrup Pass glacial streams, it is evident that microbial succession depends upon their broad and flexible environmental tolerance (*cf.* life-strategy type 3). This tolerance may be an important factor in the competitive success of these assemblages.

The main aim of this paper is to describe the seasonality and abundance of cyanoprokaryotes and algae in, and along, the studied glacial stream with respect to their ecological variability and life-strategy. An extended list of species identified in the glacial stream was compiled (*cf.* also ELSTER *et al.*, 1997), and their abundance quantified. This list and the quantitative data were used to calculate indexes of Relative Species Occurrence, Frequency and Abundance with respect to the species seasonality and distance from the glacial front.

2. Materials and Methods

2.1. *Site description*

In Sverdrup Pass (79°N), Ellesmere Island, during the summer glacial ablation, numerous streams run down the Teardrop glacier. These streams saturate the floor of a gravelly granitic "new" ground moraine left behind by the recent retreat (max 150 year) of the glacier. They continue down the gentle slope to a much more vegetated "old" moraine and merge with Sverdrup River at about 500 m distance from the glacial front.

The N-facing stream chosen for this study originated on the eastern side of the glacier's front (Fig. 1). It was 474 m long from the point of its origin at 397 m a.s.l. to its merge with Sverdrup River at 363 m a.s.l. It was 20–200 cm wide, 5–70 cm deep and formed several shallow pools along its flow. The substrate varied in structure from fine sands to gravel and large boulders.

For the purpose of spatial analysis the stream was divided into 14 sections (A–N) according the slope, rate of flow, and vegetation cover (Fig. 1). For further ecological information concerning the stream see ELSTER and SVOBODA (1995).

2.2. *Field and laboratory procedures*

In 1991 algal samples* were collected 6 times (1–5 vials from every section of the stream fixed in 4% formalin) during the arctic summer in 14 sections of the stream and in the Sverdrup River (Fig. 1). In total, 218 samples were collected and analysed. In the laboratory relative representation of each taxon observed in unsorted mixed samples was subjectively classified for the Index of Relative Species Abundance : 5–very common; 4–common; 3–occasional; 2–rare; 1–very rare. Observations were made on slides (n=1–8) prepared from the material preserved in vials.

These data were further used for determination of algal diversity and seasonality along the stream. In addition, seasonal algal Relative Species Occurrence (ratio between the number of taxa in groups such as Cyanoprocaryota, Chlorophyceae, etc., and the number of all determined taxa in all groups on a particular sampling day) and Relative Species Frequency (ratio between the sum of individual taxa occurrences and a sum of all algal taxa occurrences determined on a particular sampling day) in all sections of the stream were calculated.

Indexes for particular sampling dates and their mean seasonal values were calculated for the entire glacial stream and the Sverdrup river, and separately for the "new" and "old" sections. Further calculations were made for all identified species together, then separately for species which produced macroscopically visible biomass, and for species which occurred only occasionally.

Mean species diversity and abundance were calculated for all groups of oxyphototrophic microorganisms and for fungi parasitizing on algae. These ecological parameters were also calculated for the three life-strategies groups. All these values were calculated for

* In order to avoid numerous duplications of terms, and unless further specified, "algae" and "algal" in the paper includes also Cyanoprokaryotes.

all section of the stream.

These indexes presented in this paper are based on a non-random sampling, *i.e.* visible colonies of algae present in the stream were sampled in order to obtain sufficient

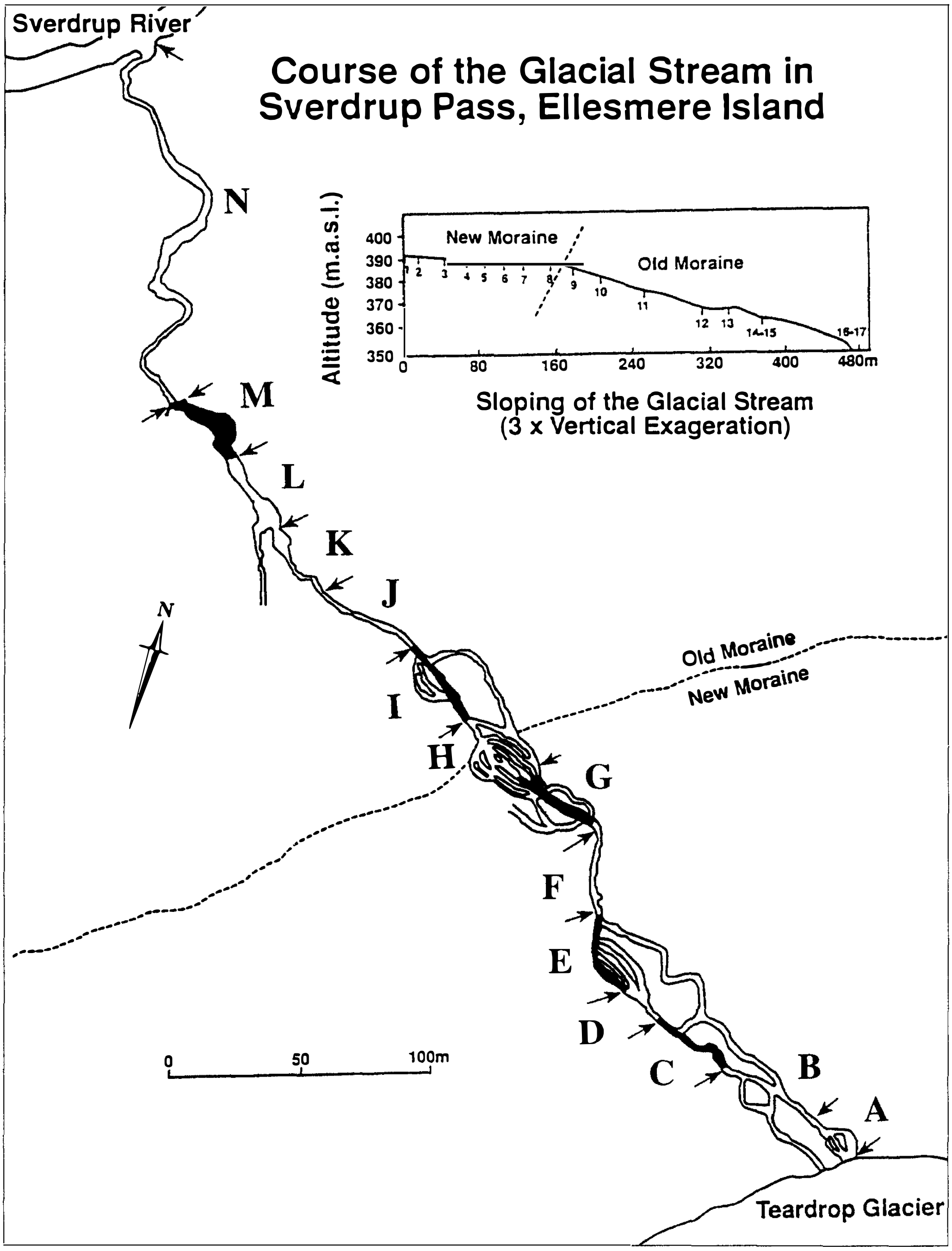


Fig. 1. Course of the glacial stream from its origin at the front of the Teardrop Glacier to its merger with Sverdrup River, Central Ellesmere Island, Canada. Note the meandering and spreading of the stream, and change of its sloping at the boundary between the "new" and "old" moraine (insert). Capital letters A–N mark the studied sections of the stream.

quantity for analysis. They represent a ratio among the many identified species in the collected material, and are, nevertheless, useful indicators of the algal groups distriution along the glacial stream during the growing season. The true actual abundance, expressed as a dry biomass and seasonal production, however, was also studied, and these results are being prepared for publication (ELSTER and SVOBODA, unpublished).

3. Results

3.1. An overview of algal diversity and seasonality in the glacial stream

An overview of algal diversity and seasonality in the glacial stream as it changes with the distance from glacial front and in the Sverdrup River is presented in Table 1. In total, 24 species of Cyanoprocaryota, 2 of Xanthophyceae, 22 of Bacillariophyceae, 7 of Chlorophyceae, 11 of Conjugatophyceae (Zygnematales), 3 of Euglenophyceae, and 2 species of fungi parasitizing on algae were identified here and described in more detail in ELSTER *et al.* (1997). Cyanoprocaryota, Bacillariophyceae and Conjugatophyceae had more than 10 species in a group while Xanthophyceae, Chlorophyceae and Euglenophyceae had less than 10 species per group.

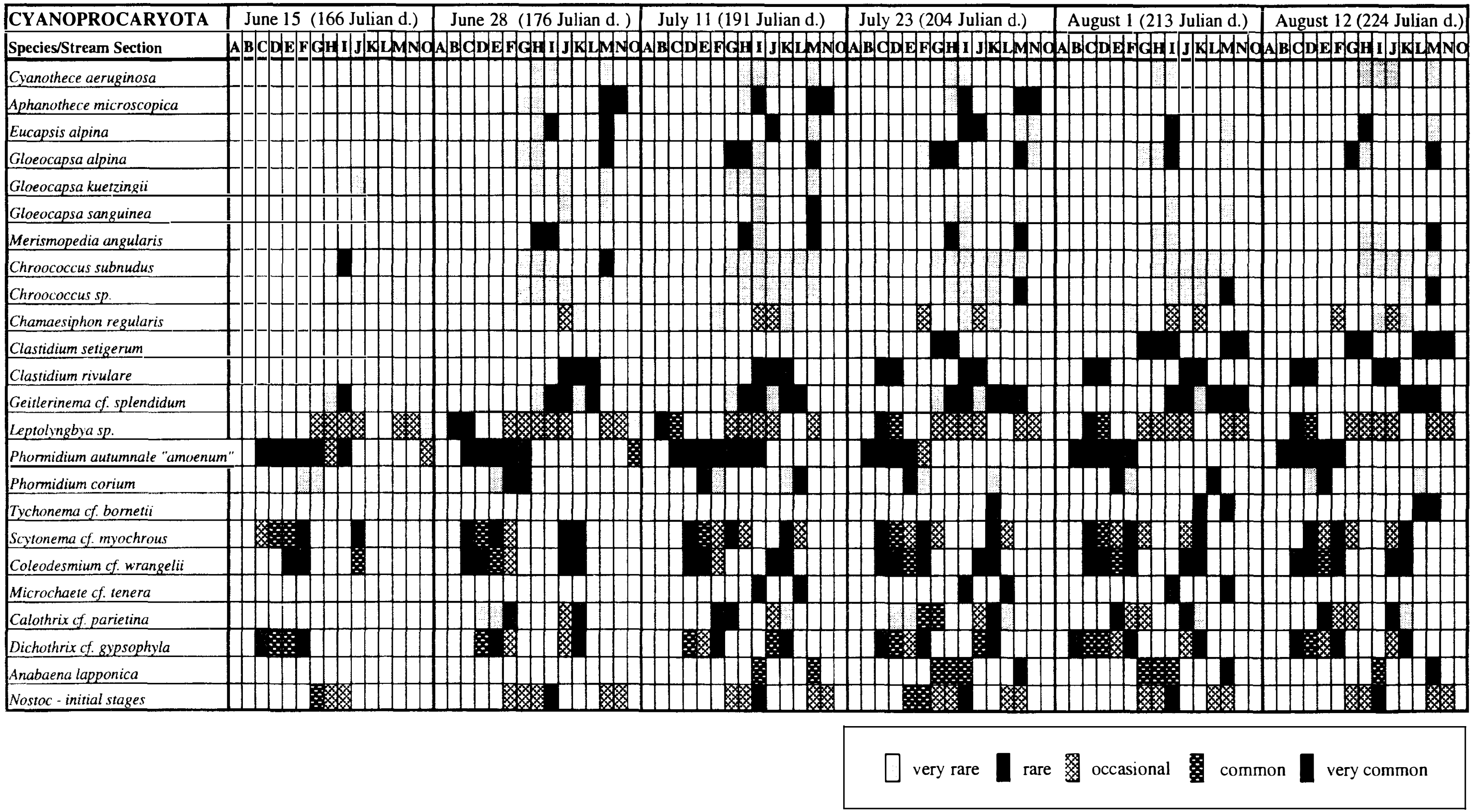
Relative Species Occurrence of all described species in the glacial stream (from site A to N) is show in Fig. 2 (left column). All groups had higher than 50% occurrence throughout the summer except for Cyanoprocaryota and Euglenophyceae at the beginning of the season. Xanthophyceae with only two species found and identified (*Chlorobotrys polychloris, Tribonema vulgare*) were present during the entire season. Other groups showed seasonal peaks, *e.g.* Bacillariophyceae in the early part (June 15 to July 23), Cyanoprocaryota in the later part of season (June 28 to August 12). Euglenophyceae had the lowest occurrence and sharply peaked in the middle of the season (July 23).

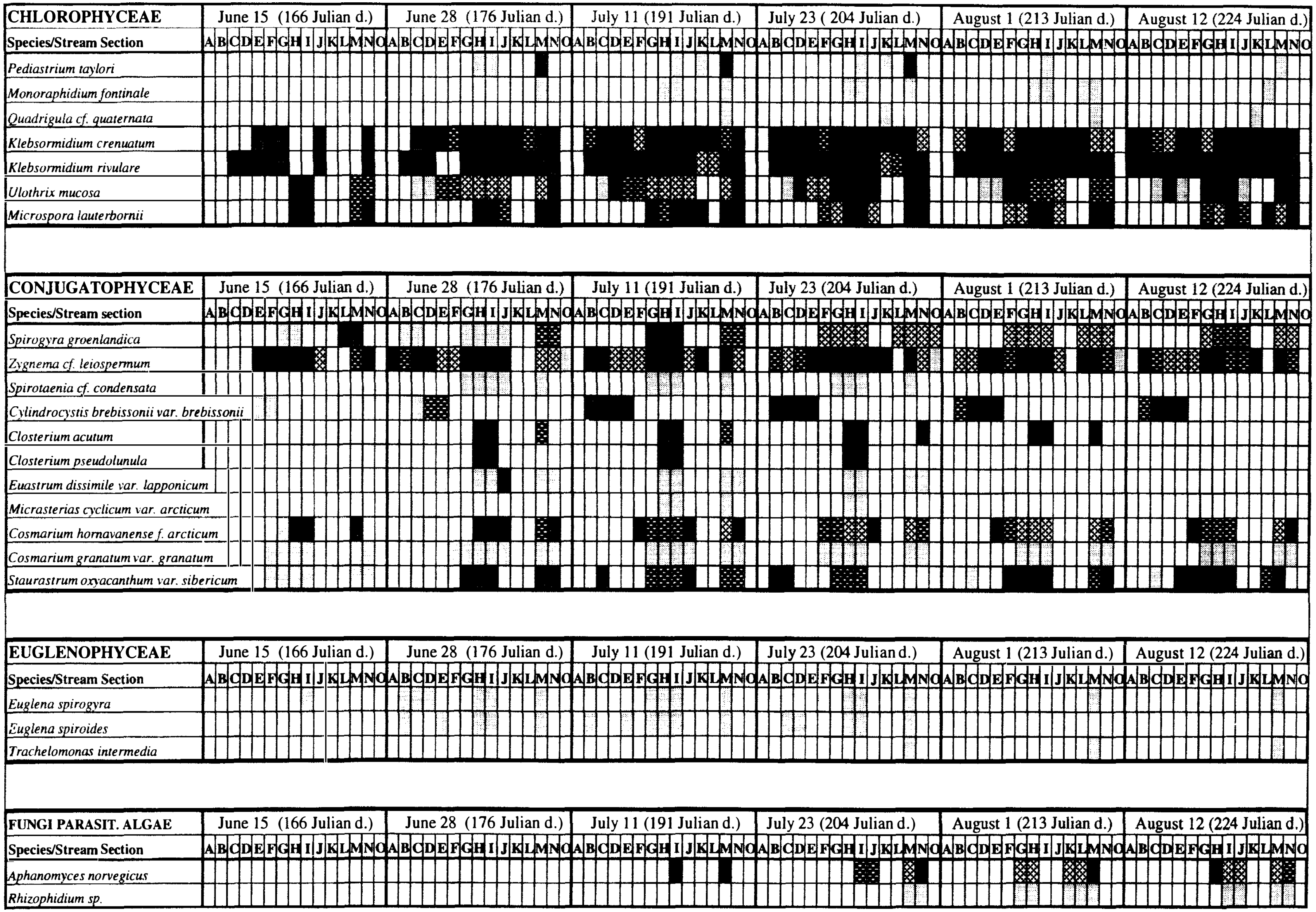
Species which produced visible biomass (Relative Abundance 2–5) showed 100% occurrence throughout the season (Fig. 2, left column). Only Cyanoprocaryota increased their occurrence from 80% to 100% in the early summer period and this was due to gradual progression of the *Anabaena* community.

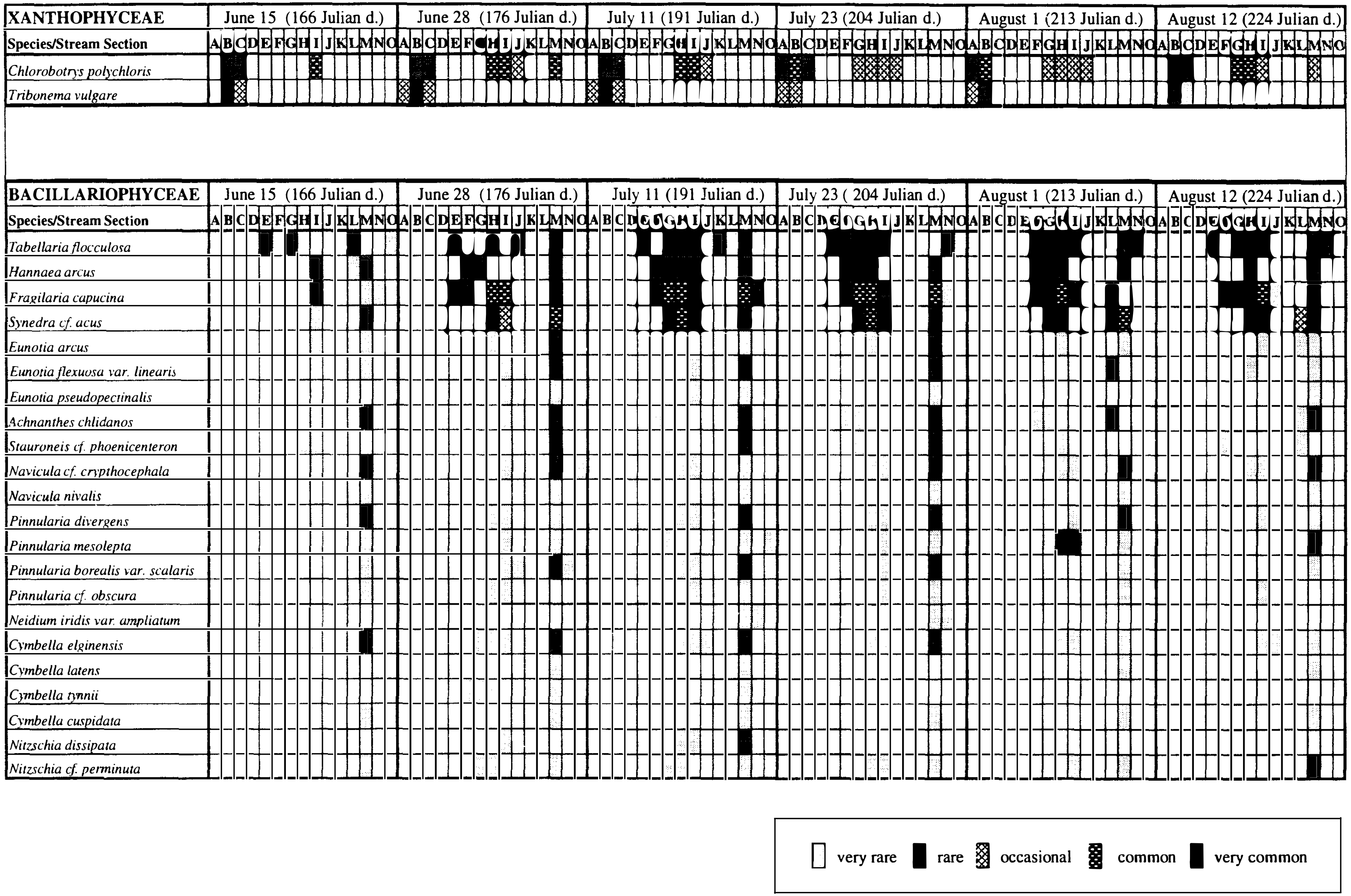
Complementary species (Relative Abundance 0–2), *i.e.* species with scattened biomass, showed sharp seasonal increase in occurrence (Fig. 2, left column). Bacillariophyceae maintained high presence over the whole season with a peak in mid-June. The other groups showed an increase trend from 0% (coccal green algae) to 20–40% (Cyanoprocaryota, Euglenophyceae and Conjugatophyceae) from the beginning of the season. Fungi parasitizing on algae peaked in the second half of the season (July 23 to August 12).

Relative Species Frequency of the studied algal groups is show in Fig. 2 (central column). Although Chlorophyceae had a lower species diversity, this group showed the highest species frequency. The most common was the mainly filamentous group of green algae (*Klebsormidium, Ulothrix, Microspora*) present in the stream over the entire season. Cyanoprocaryota and Conjugatophyceae had a lower frequency. Xanthophyceae, represented by only two species, had a high frequency, while Bacillariophyceae were the lowest. The algal groups showed little seasonal variation with the exception of Euglenophyceae, which peaked in early in the season.

Table 1. *Species Diversity and Relative Abundance of Cyanoprocaryota and representative algal groups as they occurred the 1991 summer season in studied sections of the glacial stream (A–N) and in Sverdrup River (O), Sverdrup Pass, Centrale Ellesmere Island, Canada. See legend for the five Abundance classes.*




CHLOROPHYCEAE
Species/Stream Section
June 15 (166 Julian d.)
June 28 (176 Julian d.)
July 11 (191 Julian d.)
July 23 (204 Julian d.)
August 1 (213 Julian d.)
August 12 (224 Julian d.)
A B C D E F G H I J K L M N O
Pediastrium taylori
Monoraphidium fontinale
Quadrigula cf. quaternata
Klebsormidium crenuatum
Klebsormidium rivulare
Ulothrix mucosa
Microspora lauterbornii
CONJUGATOPHYCEAE
Species/Stream section
Spirogyra groenlandica
Zygnema cf. leiospermum
Spirotaenia cf. condensata
Cylindrocystis brebissonii var. brebissonii
Closterium acutum
Closterium pseudolunula
Euastrum dissimile var. lapponicum
Micrasterias cyclicum var. arcticum
Cosmarium hornavanense f. arcticum
Cosmarium granatum var. granatum
Staurastrum oxyacanthum var. sibericum
EUGLENOPHYCEAE
Species/Stream Section
Euglena spirogyra
Euglena spiroides
Trachelomonas intermedia
FUNGI PARASIT. ALGAE
Species/Stream Section
Aphanomyces norvegicus
Rhizophidium sp.


XANTHOPHYCEAE
June 15 (166 Julian d.)
June 28 (176 Julian d.)
July 11 (191 Julian d.)
July 23 (204 Julian d.)
August 1 (213 Julian d.)
August 12 (224 Julian d.)
Species/Stream Section
A B C D E F G H I J K L M N O
Chlorobotrys polychloris
Tribonema vulgare
BACILLARIOPHYCEAE
June 15 (166 Julian d.)
June 28 (176 Julian d.)
July 11 (191 Julian d.)
July 23 (204 Julian d.)
August 1 (213 Julian d.)
August 12 (224 Julian d.)
Species/Stream Section
A B C D E F G H I J K L M N O
Tabellaria flocculosa
Hannaea arcus
Fragilaria capucina
Synedra cf. acus
Eunotia arcus
Eunotia flexuosa var. linearis
Eunotia pseudopectinalis
Achnanthes chlidanos
Stauroneis cf. phoenicenteron
Navicula cf. crypthocephala
Navicula nivalis
Pinnularia divergens
Pinnularia mesolepta
Pinnularia borealis var. scalaris
Pinnularia cf. obscura
Neidium iridis var. ampliatum
Cymbella elginensis
Cymbella latens
Cymbella tynnii
Cymbella cuspidata
Nitzschia dissipata
Nitzschia cf. perminuta
very rare
rare
occasional
common
very common

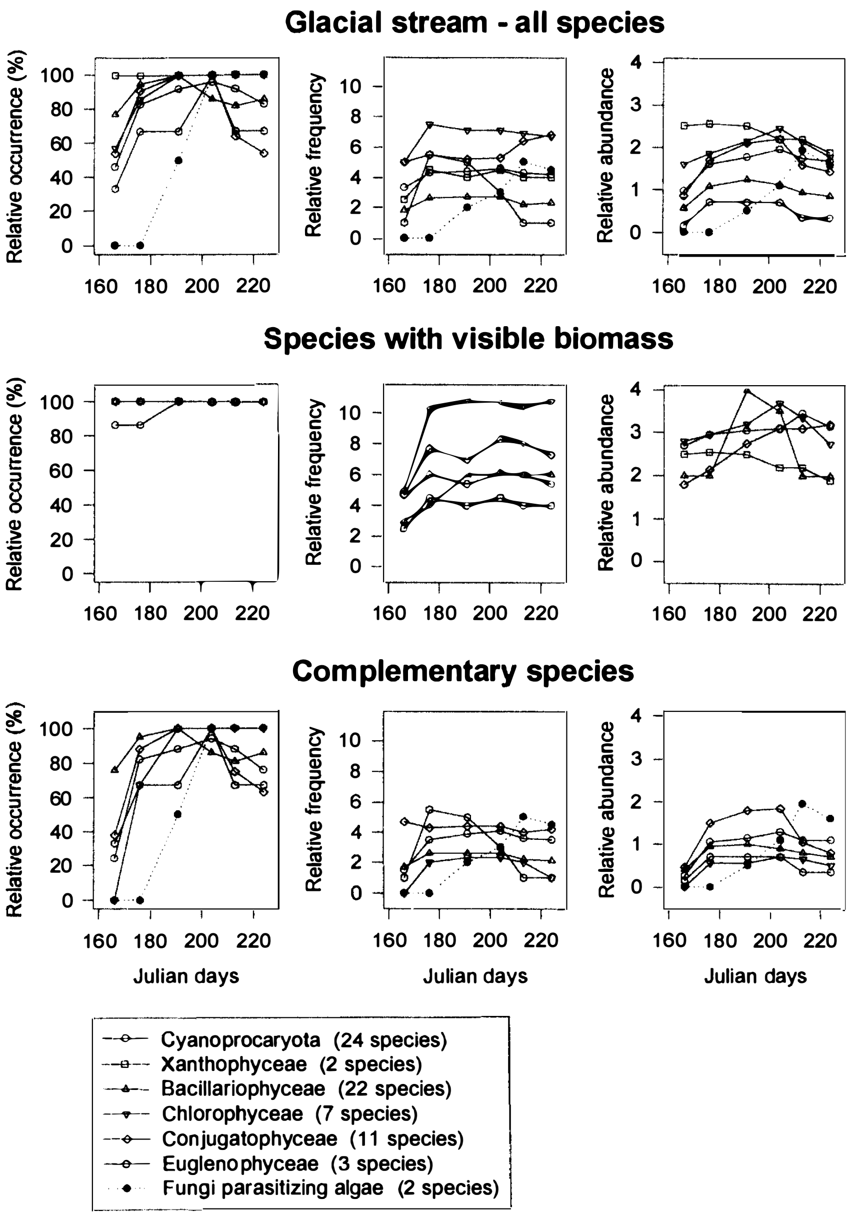


Fig. 2. Seasonal patterns of Relative Occurrence, Frequency and Abundance of identified algal groups in the entire glacial stream.

Among species which produced visible biomass filamentous green algae accounted for the highest frequency with the filamentous Conjugatophyceae (*Zygnema* and *Spirogyra*) being the second (Fig. 2, central column). Both groups showed higher frequency at the beginning of the season (the end of June). Cyanoprocaryota, Bacillariphyceae and Xanthophyceae had all lower frequencies.

Complementary species displayed a different scenario. Unicellular Desmids had the highest Relative Frequency throughout the season (Fig. 2, central column). Unicellular Cynoprocaryota increased at the beginning of the season (June 28–July 11). Euglenophyceae and parasitizing fungi had notable, but opposing, seasonal trends. Diatoms and coccal green algae had a low frequency with inconspicuous seasonal trends.

Relative Species Abundance in the glacial stream (Fig. 2, right column) was the highest for Cyanoprocaryota, Xanthophyceae, Chlorophyceae and Conjugatophyceae. While Xanthophyceae peaked early in the season (June 15 to July 11), Cyanoprokaryotes, Chlorophyceae and Conjugatophyceae peaked later in the season (July 23 to August 1). Bacillariophyceae and Euglenophyceae had the lowest abundance. Chlorophyceae, Conjugatophyceae and Cyanoprocaryota had the highest Relative Abundance among the groups producing visible biomass (Fig. 2, right column). Again, Xanthophyceae showed higher abundance at the beginning (June 28–July 23) while Bacillariophyceae showed higher abundance in the middle of the season (July 23). Diatoms showed the strongest seasonal peak. Complementary species showed more obvious seasonal trends in Relative Abundance. Unicellular Desmids developed a conspicuous peak while some other groups had less pronounced seasonal peaks. Parasitizing fungi were most abundant at the end of the season.

3.2. "New" and "old" moraine comparisons

In the "new" moraine section of stream (site A–G), Xanthophyceae (*Chlorobotrys*

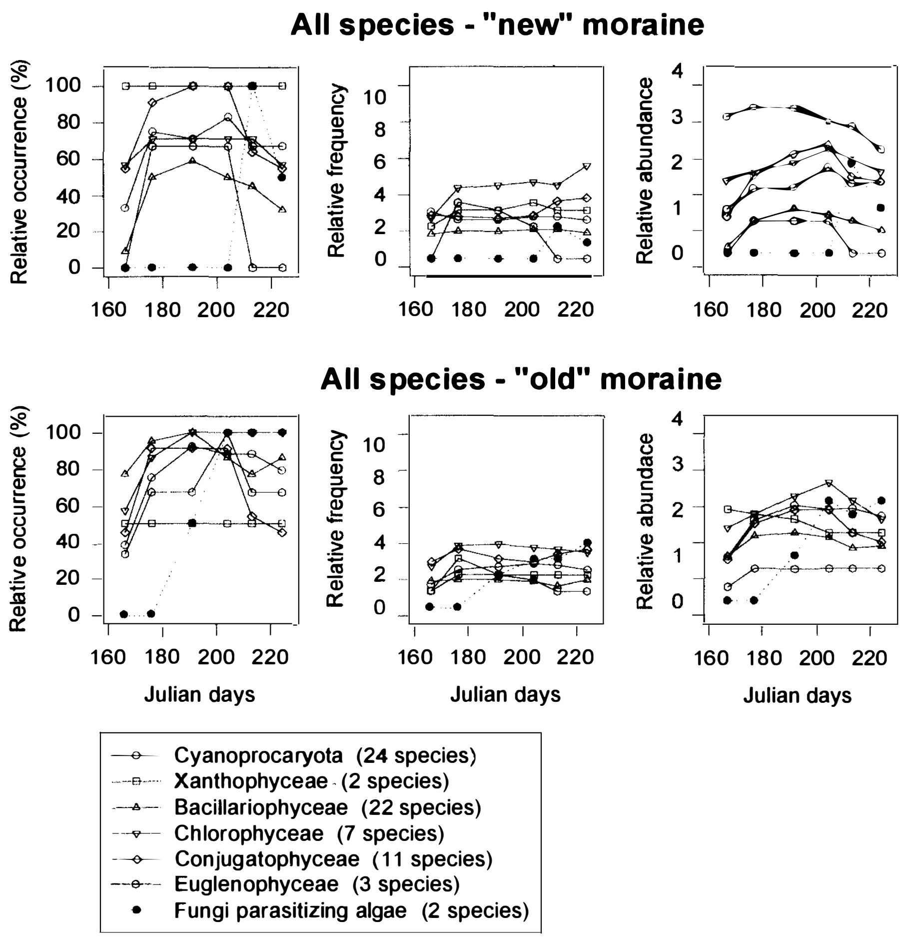


Fig. 3. Seasonal patterns of Relative Occurrence, Frequency and Abundance of all species in the representative algal groups in the "new" and "old" moraine sections of the glacial stream.

polychloris, *Tribonema vulgare*) had 100% Relative Occurrence while in the "old" moraine (site H–N), the group had only 50% occurrence throughout the season (Fig. 3, left column). Also *Zygnema* cf. *leiospermum* was more present in the "new" moraine, while Chlorophyceae and Diatoms dominated the "old" moraine. In both moraines all groups, except Xanthophyceae, showed a seasonal peak.

In both parts of the stream, Chlorophyceae had the highest Relative Frequency and Diatoms the lowest. Cyanoprocaryota and Conjugatophyceae had intermediate frequency with insignificant seasonal trends (Fig. 3, central column).

In terms of Relative Abundance, Xanthophyceae was the most prevalent group in the "new" moraine section of the stream which passed through "new" moraine (Fig. 3, right column). This was due to vigorous development of *Tribonema* in the secondary springs near the glacial front. Cyanoprokaryotes, Chlorophyceae and Conjugatophyceae were also quite abundant in both parts of the stream while Bacillariophyceae and Euglenophyceae were less prolific (Table 2). All groups showed gentle seasonal peaks, except Xanthophyceae, which decreased in abundance during the season.

Table 2. Relative Abundance of species with "visible biomass" in five algal groups in the glacial stream, Sverdrup Pass.

	Species with visible biomass	Relative abundance		
		New m.	Old m.	Sver. r.
A	*Phormidium autumnale "amoenum."*	4.2	0.7	1.2
	Scytonema cf. *myochrous*	3.6	4.3	0
	Coleodesmium cf. *wrangelii*	2.8	4.8	0
	Dichothrix cf. *gypsophyla*	3.7	3.5	0
	Anabaena lapponica	1.3	2.9	0
	Nostoc - initial stages	3.2	3.6	0
B	*Chlorobotrys polychloris*	2.7	3.4	0
	Tribonema vulgare	3.1	0	0
C	*Tabellaria flocculosa*	2.6	2.6	0.2
D	*Klebsormidium crenuatum*	3.3	2.2	0
	Klebsormidium rivulare	4.3	2.2	0
	Ulothrix mucosa	2.4	3.5	0
	Microspora lauterbornii	2.9	4.1	0
E	*Spirogyra groenlandica*	2.3	2.9	0.5
	Zygnema cf. *leiospermum*	3.6	3.8	0.3
	Cylindrocystis brebissonii var. *breb.*	3.7	0	0

A – Cyanoprocaryota, B – Xanthophyceae, C – Bacillariophycear, D – Chlorophyceae,
E – Conjugatophyceare

New m. – section of stream originated at the glacial front run down the freshly deglaciated "new" ground moraine for about 200 m.

Old m. – section of stream more vegetated ("old moraine") for about 200 m from glacial front until it merged with the Sverdrup rivuled.

Sver. r. – aprox. 2 km long section of the glacial river from the merger pointo of the studied stream, down-east the Sverdrup valley.

In the "new" moraine, species with visible biomass showed 100% Relative Occurrence throughout the season (Fig. 4, left column). In the "old" moraine Bacillariophyceae and Chlorophyceae were highly represented with the remaining groups occurring much less. Only Cyanoprocaryota showed a seasonal trend.

Filamentous green algae and Conjugatophyceae had the highest Relative Frequency in both moraines (Fig. 4, central column). Cyanoprocaryota, Bacillariophyceae and Xanthophyceae were less ubiquitous. All groups showed insignificant seasonal trends.

In the "new" moraine, all groups except Bacillariophyceae showed increasing Relative Abundance with the progress of the season (Fig. 4, right column). Diatoms peaked in the mid-season (July 11). In the "old" moraine Cyanoprocaryota, Xanthophyceae and Bacillariophyceae were more abundant.

In both moraine sections, the complementary species showed notable seasonal increase and late dropped in Relative Occurrence (Fig. 5, left column). Desmins were the highest. Parasitic fungi peaked later in the season.

In terms of Relative Frequency (Fig. 5, central column) Euglenophyceae was only group with a pronounced seasonal peak in the "new" moraine. The other groups did not

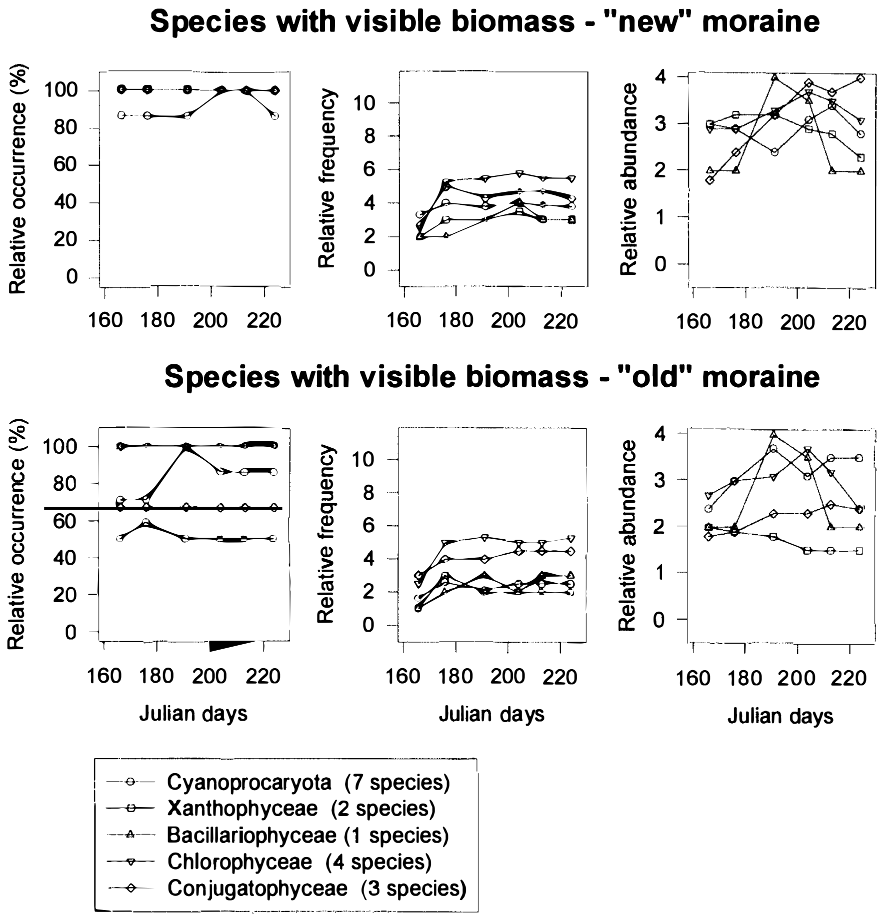


Fig. 4. Seasonal patterns of Relative Occurrence, Frequency and Abundance of species with visible biomass Relative Abundance (2–5) in the representative algal groups in the "new" and "old" moraine sections of the glacial stream.

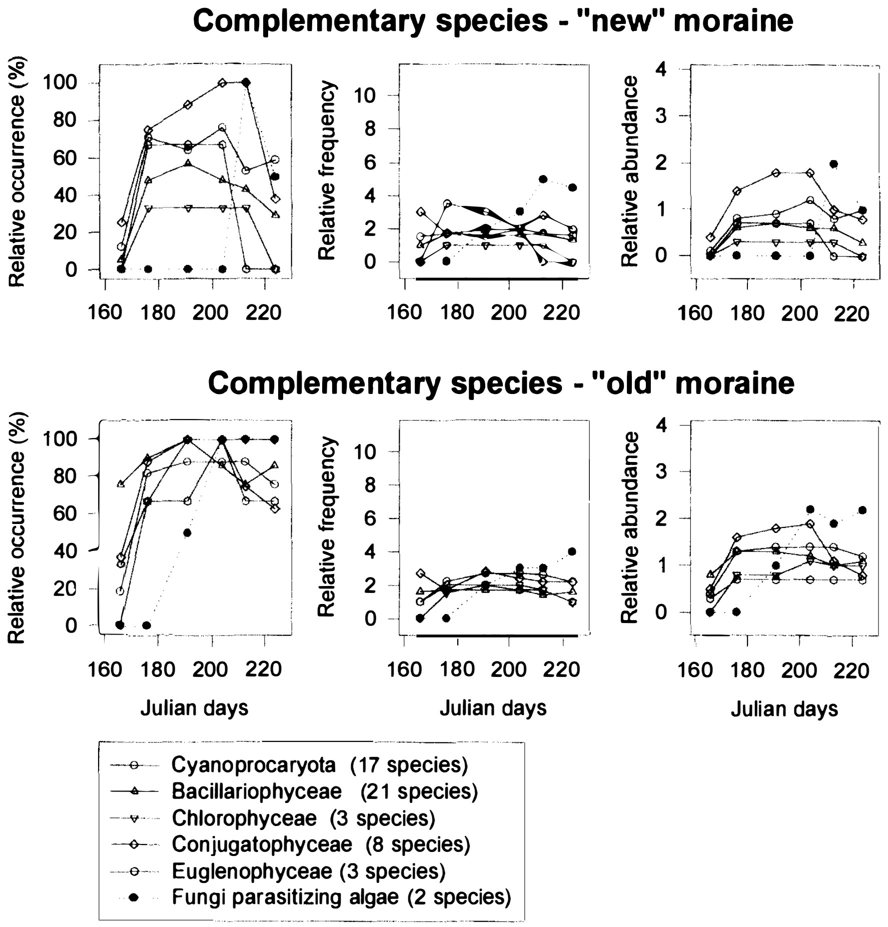


Fig. 5. Seasonal patterns of Relative Occurrence, Frequency and Abundance of complementary species Relative Abundance (0–2) in the representative algal groups in the "new" and "old" sections of the glacial stream.

show significant seasonal trend in either moraine section. Fungi increased their frequency mainly in the later part of the season.

The group with the highest Relative Abundance in the entire stream were Desmids (Fig. 5, right column). Again, parasitic fungi rose in their abundance towards the end of the season.

3.3. Sverdrup River

Only three groups, Cyanoprocaryota (*Phormidium autumnale "amoenum"* and *Leptolyngbya* sp.), Bacillariophycea (*Tabellaria flocculosa*) and Conjugatophyceae (*Spirogyra groenlandica* and *Zygnema* cf. *leiospermum*), were found at very low Relative Occurrence, Freguency and Abundance in the river (Fig. 6, Table 2). Their presence was most noticeable during the very early part of the season before the glacial streams started to run and while the river was still collecting the snowmelt water from the Sverdrup Pass valley. This water was rich in nutrients deposited on the landscape over the winter by muskoxen, caribou, arctic hare and other wildlife, and from the decomposing vegetation. Later, when the snowmelt was completed and the river was supplied only by the glacial water, the algal coating of the river gravel almost disappeared.

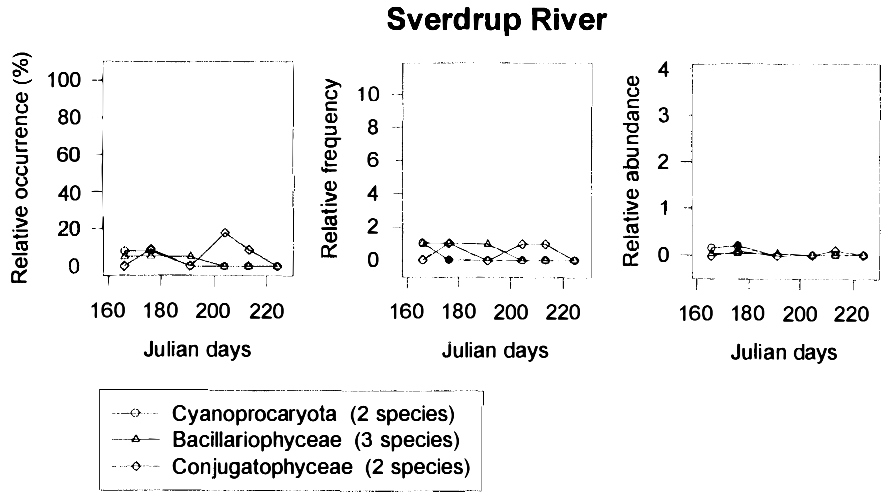


Fig. 6. Seasonal patterns or Relative Occurrence, Frequency and Abundance of three representative algal groups in Sverdrup River at the area of merger with the glacial stream.

3.4. Means and Ranges

Mean seasonal values of the three ecological parameters Relative Occurrence, Frequency and Abundance are presented in Table 3. The glacial stream had much higher mean seasonal Rel. Occurrence (58%), Frequency (24%) and Abundance (1.5/5), than Sverdrup River where these values were extremely low (1.8%, 2.4%, and 0.04/5, respectively).

Species which produced visible biomass in the stream had Rel. Occurrence (17%), Frequency (46%) and Abundance (2.8/5) while the complementary species scored 42%, 17%, and 0.8/5, respectively.

There were small differences in these parameters between the "new" and "old" moraine section of the stream, when calculated for all species together. The "old" moraine had a higher Occurrence (54%) and Frequency (30%) than the "new" moraine (41% and 20% respectively). Both sections had the same Abundance (1.5/5) .

Species with macroscopically visible biomass had slightly higher Rel. Occurrence (16%), Frequency (48%) and Abundance (3.0/5) in the "new" moraine compared to 14%, 44%, and 2.6/5, respectively in the "old" moraine section. Complementary species had higher Rel. Occurrence (41%), Frequency (26%), and Abundance (1.0/5) in the "old" moraine. In the "new" moraine these values were 24%, 10% and 0.6/5, respectively.

3.5. Algal groups—Stream continuum

In most groups the species diversity along the glacial stream gradually increased and was generally higher in the "new" moraine (Fig. 7A). Xanthophyceae with dominant *Tribonema vulgare* propagated near the glacial front. At the beginning of the "old", vegetated moraine, diversity was still on the increase because of the presence of a greater number of metaphyton species in the stream-flooded meadow (cf. Fig. 1, section G). In lower parts of the "old" moraine, species diversity varied, depending on the abundance of higher vegetation in the stream. In places where the stream bottom was fully covered

Table 3. Mean seasonal values of algal Relative Occurrence, Frequency and Abundance in the glacial stream, and separately in the "new" and "old" moraine parts of the glacial stream and Sverdrup River.

		Species mean relative occurrence (n)	Species mean relative frequency (%)	Species mean relative abundance
Glacial stream	All species	57.8 (41–66)	24.3 (12.6–29.2)	1.5
	Species with visible biomass	16.7 (16–17)	46.0 (28.6–51.7)	2.8
	Complementary species	41.7 (24–49)	17.2 (6.6–22.5)	0.8
"New" moraine only	All species	41.0 (22–51)	19.8 (10.1–24.8)	1.5
	Species with visible biomass	16.3 (16–17)	48.3 (32.3–55.9)	3.0
	Complementary species	24.2 (5–34)	10.3 (2.4–14.4)	0.6
"Old" moraine only	All species	54.3 (37–64)	30.3 (15.9–37.9)	1.5
	Species with visible biomass	13.8 (13–15)	43.9 (27.4–48.6)	2.6
	Complementary species	40.8 (22–49)	26.3 (12.2–34.6)	1.0
Sverdrup river	All species	1.8 (0–4)	2.4 (0–5.8)	0.04

( ) values in parenthesis represent the range above and below mean.

by mosses and sedges, algal diversity was high, while in places with a gravelly bottom it diminished.

Group Chlorophyceae (mainly filamentous green algae–*Klebsormidium*, *Ulothrix*) showed the highest abundance in the "new" moraine. Similarly Cyanoprocaryota, (*e.g. Phormidium*, *Dichothrix*, *Scytonema*, *Coleodesmium* and *Leptolyngbya*) and Conjugatophyceae (filamentous *Zygnema* and *Spirogyra*) peaked in abundance mostly in the C–F sections. In the "old" moraine the Rel. Abundance varied, depending on the nature of the stream bottom.

3.6. Algal life strategies—Stream continuum

Species diversity, as related to the distinct algal life strategy groups, are plotted along the course of glacial stream (Fig. 7C). The filamentous group (which includes *Klebsormidium*, *Tribonema*, *Zygnema*, *Spirogyra*, *Microspora* and *Ulothrix*) produced mats in the stream current. The mucilaginous group, represent mainly by Cyanoprocaryota (*Phormidium*, *Dichothrix*, *Scytonema*, *Coleodesmium* and *Anabeana*) produced films on submersed stones, sandy banks and clay bottoms. (All of these species are known to be nitrogen fixers.) The metaphyton life strategy group contained many (*Cyanothece aeruginosa*, *Eunotia arcus*, *Closterium pseudolunula*, *Cosmarium hornavanense* f. *arcticum*, etc.), mostly unicellular species. Species diversity of this group varied greatly. In places where the stream bottom was covered with mosses and sedges, metaphyton diversity rose, while in places with a gravelly bottom it decreased.

Filamentous and mucilaginous groups were poor in species but had high, although decreasing Relative Abundance with the distance from the glacial front (Fig. 7D). In contrast, the metaphyton group was rich in species composition but lower in Relative

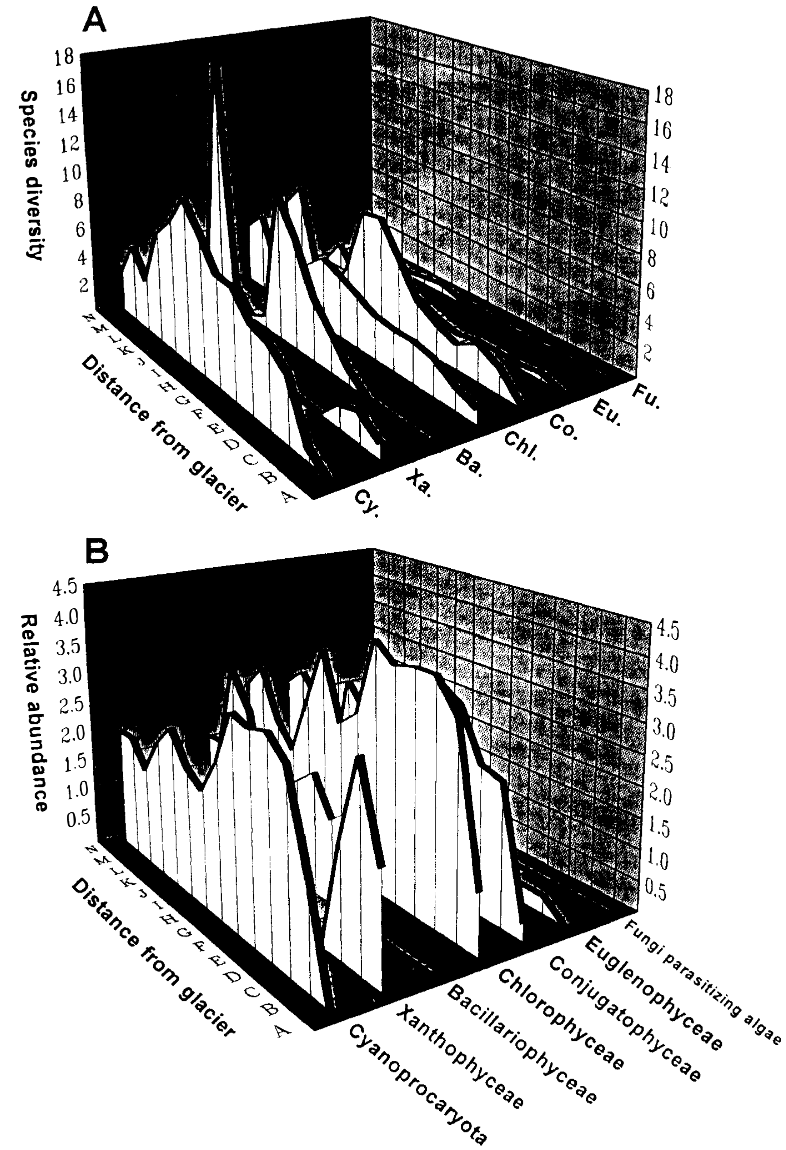


Fig. 7 (A, B). Species Diversity and Relative Abundance in the representative algal groups along the glacial stream.

Abundance. Only *Cylindrocystis*, *Tabellaria*, *Chlorobotrys* and *Nostoc* produced visible biomass in this life strategy group.

4. Discussion and Conclusions

The Sverdrup Pass glacial stream ecosystems represent algal oases in an otherwise barren polar desert terrain. Being supplied with water, nutrients and continuous light in summer, cyanoprokaryotes and algae are at the onset of life reinvasion after deglaciation (SMITH, 1993; WYNN-WILLIAMS, 1993; ELSTER and SVOBODA, 1995). The stream, enlivened by algae, function as nourishing veins, initiating the process of primary succession on the newly ice-free landscape.

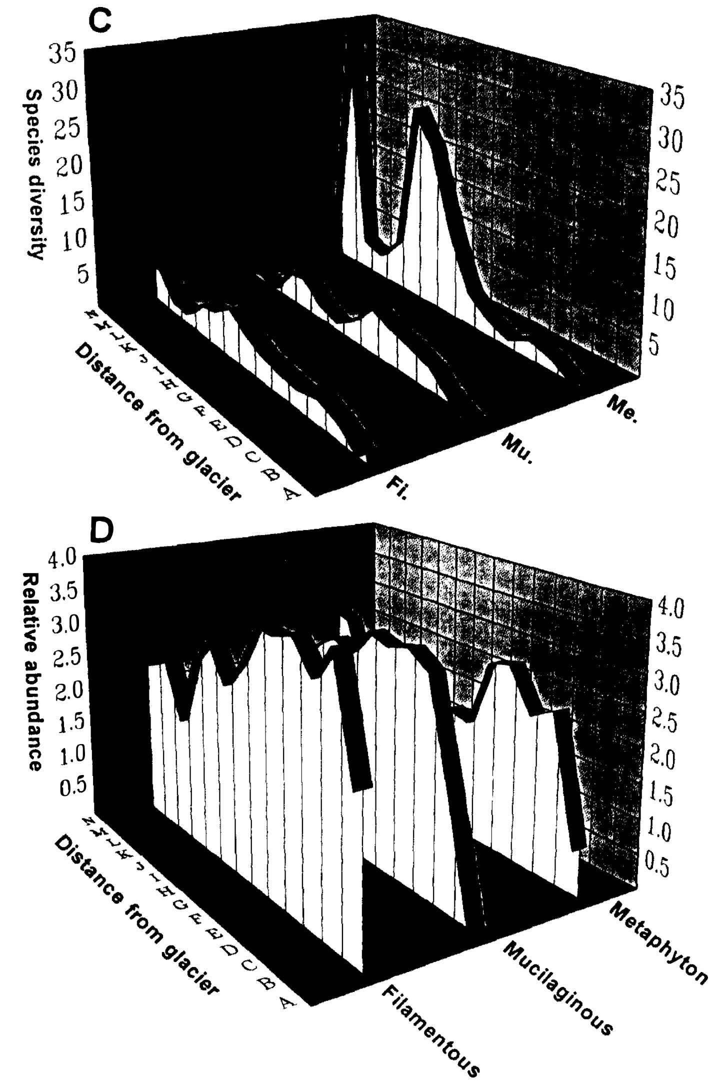


Fig. 7 (C, D). Species Diversity and Relative Abundance in the Metaphyton-, Mucilaginous- and Filamentos life strategy groups along the glacial stream.

At times of high glacial melt, the normally shallow glacial stream flooded the surrounding area, saturated the ground and created numerous temporary pools. In contrast, Sverdrup River usually had a rapid flow, with irregular high-volume peaks depending on day-to day ablation rates. At these periods it carried a high share of eroded suspensoids which made the water turbid. Physical, chemical and biological variations were also observed among the Antarctic fresh water ecosystems (VINCENT and HOWARD-WILLIAMS, 1986; HOWARD-WILLIAMS *et al.*, 1986; BROADY, 1989b; HAWES, 1989).

Cyanoprocaryota, Xanthophyceae, Chlorophyceae and Conjugatophyceae (Zygnematales), most of them represented by the filamentous form (*Klebsormidium*), were the groups with the highest Relative Abundance in the Sverdrup Pass glacial stream. Chlorophyceae were represented minly by the filamentous forms. They were low in diversity but showed the highest Rel. Frequency, and were present in the stream throughout the season.

Species diversity of the four most represented groups—Cyanoprocaryota, Xanthophyceae, Chlorophyceae and Conjugatophyceae (Zygnematales)—was lower in the "new" moraine section of the stream. Their Relative Abundance, however, was highest there, having firsthand access to nutrients carried down by the meltwater.

Three ecologically complementary life strategies were recognized as operating in the stream. The first strategy represented by, filamentous *Klebsormidium*, *Tribonema*, *Zygnema* and *Spirogyra*, produced floating mats in the stream current. The second strategy group, *Phormidium*, *Nostoc*, *Dichothrix*, *Scytonema* and *Coleodesmium*, produced mucilaginous films and flocculi on submersed stones and sandy banks. These species of Cyanoprocaryota are known as nitrogen fixers. Species producing macroscopically visible biomass showed weak seasonal trends but adopted special life strategy described already also for the Antarctic periphyton by VINCENT and HOWARD-WILLIAMS (1986), HAWES (1989), HAWES *et al.* (1992). The first algal component of this visible biomass in the continental Antarctic consisted of filamentous Cyanoprocaryota (*Phormidium*, *Nostoc*). This life strategy group was characterized as having low production but vegetative cells can survive the dark winter as dry frozen mats HAWES *et al.* (1992). These provide large inoculum for growth the following summer, thus allowing for a perennial population. The overwintering mass of cells regains a high metabolic activity after spring rehydration. The second algal component described in the maritime Antarctica consists of filamentous algae *Klebsormidium*, *Mougotia*, *Zygnema* and shows an opposite life strategy. A small number of vegetative cells survives the winter period HAWES (1990). These algae will start to propagate and will reach maximum biomass 2 to 3 months after the stream spring break-up. These are ecological opportunists which grow not only during the short polar summer but in temperate zones also in winter periods of thaw, even under snow, and in early spring and late fall. Both these life strategy groups initiate the process of primary succession on newly deglaciated Arctic and Antarctic landscapes.

Species of the third life-strategy group, mostly unicellular metaphytons, are suspended among the "higher" plants: mosses, submersed vascular plants and algal mats. They occurred mostly in the stream section of the "old" moraine. This group of algae shows sharp seasonal rise, and unicellular Desmids had the highest Rel. Abundance there. The early peak in Rel. Frequency of Euglenophyceae was probably associated with the leaching of organic compounds during the snow and soil thaw. Euglenophyceae are mixotrophs which can metabolize these organic substances as described by ELSTER and KOMÁREK (1993) in the seasonal succession in shallow polluted pool habitats from Central Europe. This niche requirement contrasts with the widely-described seasonal successions of Bacillariphyceae and Cyanoprocaryota, controlled by seasonal patterns of temperature and radiation in various freshwater habitats (BRANDL *et al.*, 1989; LEE, 1989).

We discovered that all cyanoprocaryota and algae species in the Sverdrup Pass glacial stream could be assigned into two potential niche specific groups as outline by VINCENT and QUESADA (1996). The first group, with lower species diversity and higher biomass, occupied the less vegetated "new" moraine section of the stream. This group of primary colonizers (ruderal strategy), classified as "Generalist genotypes", experience broad conditions of optimal and suboptimal growth (VINCENT and QUESADA, 1996). These oxyphototrophic microorganisms have developed special adaptations which helped them to survive dry freezing, low water temperature, high irradiance, or biomass loss through scraping or sloughing. Despite apparently adverse environment they produce a surprisingly large biomass which significantly helps to start the process of primary succession on newly deglaciated terrain. The second niche-specific group, which occupied the vegetated "old" moraine section of the steam, had a higher species diversity but did not produce biomass comparable with that in the "new" moraine. This group of "Specialized genotypes" occupied narrow niche in which they outperformed other colonizing "generalists". They grew suboptimally, but survive because of their tolerance to poor supporting conditions (VINCENT and QUESADA, 1996).

This work shows that the process of revegetation of newly deglaciated landscape and of algal primary succession is being initiated by freshwater oxyphototrophic microorganisms with a "generalist genotype" experience. These organisms are so widely adapted the changing environmental conditions that they can start the process of reinvasion in diverse habitats and after all types of disturbance.

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