

# Submerged Aquatic Bryophytes in Colour Lake, a Naturally Acidic Polar Lake with Occasional Year-Round Ice-Cover

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**ABSTRACT.** Colour Lake is a small, naturally acidic (pH 3.7) lake on Axel Heiberg Island (Canadian High Arctic) that experiences occasional year-round ice cover. We investigated the benthic vegetation of this lake, with a specific aim of determining whether the annual growth of benthic bryophytes reflects the state of summer ice cover. We found the bed of the lake to be almost completely covered by mosses or liverworts to a depth of 22 m. The mosses showed annual growth bands 10–30 mm in length, visible as changes in leaf density and size. Four to five bands retained recognizable leaves and measurable amounts of chlorophyll-*a* (chl*a*), and up to 12 bands were recognizable from leaf scars. We could not find a consistent relationship between band length and persistence of ice cover for a given year. We suggest that this lack is due to the complex effects of ice cover on moss growth conditions, specifically on the water temperature and irradiance at depth. Photosynthetic characteristics of *Calliergon* over a range of light and temperature conditions, determined using pulse amplitude-modulated fluorometry, are presented in support of this argument. We conclude that moss banding patterns are an unreliable method of hindcasting episodic failure of ice to melt in Arctic lakes.

**Key Words:** Arctic lakes, aquatic bryophytes, photosynthesis, light, temperature

**RÉSUMÉ.** Le lac Colour est un petit lac de l'île Axel Heiberg, située dans l'Extrême-Arctique canadien, dont l'acidité (pH = 3,7) est naturelle et qui reste parfois englacé toute l'année. On a étudié la végétation benthique de ce lac, dans le but précis de déterminer si la croissance annuelle des bryophytes benthiques reflète l'état de la couverture de la glace en été. On a trouvé que le lit du lac est presque entièrement recouvert de mousses ou d'hépatiques jusqu'à une profondeur de 22 m. Les mousses affichaient des bandes de croissance annuelles de 10 à 30 mm de longueur, visibles sous la forme d'un changement dans la densité et la taille de la feuille. De 4 à 5 bandes conservaient des feuilles reconnaissables et des quantités mesurables de chlorophylle-*a* (chl*a*), et jusqu'à 12 bandes étaient reconnaissables d'après les cicatrices foliaires. On n'a pu trouver de rapport constant entre la longueur de la bande et la persistance du manteau glaciaire pour une année donnée. On suggère que ce manque est dû aux effets complexes du manteau glaciaire sur les conditions de croissance de la mousse, en particulier sur la température de l'eau et l'irradiance en profondeur. Les attributs photosynthétiques de *Calliergon* pour une gamme de conditions d'éclairage et de température données, déterminés par fluorimétrie par impulsions à amplitude modulée, sont présentés à l'appui de cette thèse. On conclut que les schémas de rubanement de la mousse constituent une méthode peu fiable de prévision a posteriori des interruptions épisodiques de fonte de la glace dans les lacs arctiques.

**Mots clés:** lacs arctiques, bryophytes aquatiques, photosynthèse, lumière, température

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## INTRODUCTION

Benthic photosynthetic communities, often containing a high proportion of bryophytes, can contribute a high proportion of whole-lake primary production in High Arctic lakes (Welch and Kalff, 1974). High abundance of bryophytes is also seen in Maritime Antarctic lakes that experience similar prolonged seasonal ice cover (Priddle, 1980a, b). These early studies showed that the highly seasonal light climate in high-latitude lakes strongly influenced the productivity of bryophyte communities, as did low ambient temperatures. However, there have since been few quantitative investigations of benthic bryophytes

in polar lakes. In July–August 2000, we had the opportunity to sample the benthic communities in Colour Lake, in the Canadian High Arctic (79°25' N, 90°45' W). To date, limnological studies of this lake have focused on two unusual properties, the naturally low pH, less than pH 4 (Schiff et al., 1991), and the variation in ice cover, which in some years persists year-round and in others melts out during summer (Doran et al., 1996). Variability in summer ice cover potentially results in variability in the irradiance reaching the lake's phototrophs, and Doran et al. (1996) argued that the occasional failure of ice to clear could have profound effects on lake ecology. Ice covers, even in the absence of snow, reduce the penetration of light by up to

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80%. In years with persistent ice cover, the annual dose of light is likely to be less than in ice-free years (Hawes, 1985; Welch et al., 1987; Howard-Williams et al., 1998). While interannual variations in light will potentially affect all phototrophs, persistent effects are most likely to be evident in plants with multiannual life cycles. In polar lakes, this is primarily the benthic plants of the littoral zones, usually dominated by bryophytes, which in shallow lakes also contribute most to the organic carbon fixation (Welch and Kalff, 1974).

It has recently been recognized that the strongly annual irradiance climate experienced by Arctic aquatic plants results in clearly definable annual growth bandings (Sand-Jensen et al., 1999). Such bandings are likely to reflect the growth conditions for each year, which in the case of Colour Lake we expect to be related to the presence or absence of ice cover. In this report, we examine the benthic bryophytes of Colour Lake along a depth gradient. First, we describe the species present and the biomass and annual growth features of the dominant moss species. We then compare the observed banding patterns with ice-cover records to determine the extent to which banding patterns of mosses reflect the duration of ice cover. Finally, we also make preliminary observations of the photosynthetic characteristics of this moss in relation to irradiance and temperature, to assist with interpretation of banding patterns.

### STUDY SITE

Colour Lake is a small (10.2 ha; 24.1 m maximum depth, 10.1 m average depth), naturally acidic lake located in the High Arctic (79°25' N, 90°45' W) at 176 m altitude on Axel Heiberg Island, Nunavut, Canada (Fig. 1). The region is characterized by polar desert conditions, with cold dry winters and maximum precipitation occurring during July. Doran et al. (1996) report the mean annual temperature at Colour Lake to be -15.2°C, with about 500 thawing degree-days. Till deposits suggest that the lake basin formed as a result of the retreat of a side arm of the White Glacier. The catchment provides water primarily via snowmelt and accumulated water released from the seasonal active soil layer. Drainage from the lake is towards the southwest via a marsh and then through a cut in a basalt dyke that leads to Wolf Creek. The lake is ice-free for a short period in summer, but occasionally retains its ice cover year-round (Doran et al., 1996). Typically the water temperature increases to over 5°C during the ice-free summer, from 2–3°C under spring ice cover. Thick snow cover is present during winter, but it melts in spring before ice melt (Doran et al., 1996). The lake is oligotrophic, and the average pH of the water column is low (3.7). The low pH is thought to result from oxidation of Fe-S minerals dissolved in groundwater entering the lake from within the catchment (Schiff et al., 1991).

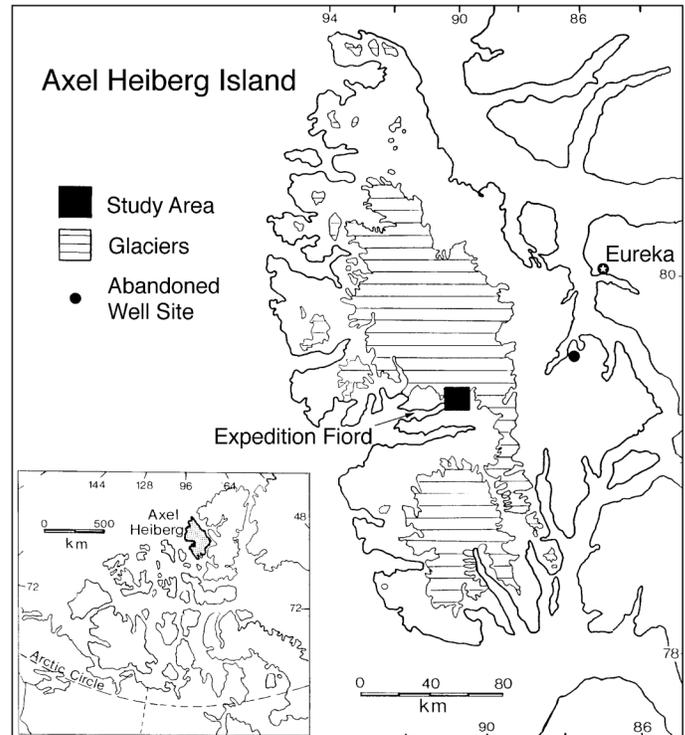


FIG. 1. The study location at the head of Expedition Fiord, Axel Heiberg Island.

### METHODS

We sampled the lake between 14 July and 5 August 2000. At the beginning of this period, the lake had a 70% cover of ice approximately 60 cm thick, which was heavily canded and close to disintegration. This ice cover was not strong enough to walk on and prevented profiling in the deeper part of the lake at that time. Strong winds on 23–24 July resulted in the overnight loss of this remnant ice cover.

#### *Water Column Measurements*

The water column was profiled using a Yellow Springs Instruments (YSI) 6600 multi-parameter sonde, fitted with probes to measure temperature (°C), conductivity (mS cm<sup>-1</sup>), depth (m), pH (units), and dissolved oxygen (g m<sup>-3</sup>). Probes were calibrated according to the manufacturer's instructions, using appropriate buffers and standard solutions. Recordings were taken at approximately 0.25 m intervals. Photosynthetically available radiation (PAR) was determined using a LiCor Li194 submersible cosine-corrected sensor connected to an appropriate meter. Under ice, this was a LiCor meter housed in a waterproof case, which was operated by divers. Once ice cover had melted, profiling was done from a raft positioned close to the centre of the lake. The vertical extinction coefficient for downwelling PAR ( $K_d - \ln$  units m<sup>-1</sup>) was estimated from linear regression of log-transformed PAR values against depth. Irradiance incident to the lake surface was obtained from a data logging station situated on the shore of the lake.

### Plant Community Descriptions

Plant sampling was conducted by SCUBA divers. Initially, they swam a series of transects perpendicular to the lakeshore to the maximum depth of plants. At 1 m vertical intervals, the cover of plants was estimated on a modified Braun-Blanquet scale of 0–6, where 0 is absent, 1 = 0–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, and 6 = 100%.

At depths of 3, 6, 9, 12, 15, and 20 m, four circular quadrats, each 8 cm in diameter, were cleared, and all plants were collected into bags. Quadrats were taken at least 1 m apart to reduce pseudo-replication. The plants were returned to the surface and processed as follows. The total number of shoots of the dominant moss was counted, and 10 plants were selected at random. Annual growth markers were identified in these mosses, according to the method of Sand-Jensen et al. (1999), and each of the four most recent years of growth was cut off and placed in a separate vial. The 10 moss shoots from each quadrat were pooled into a single sample. These plants were preserved in 5 ml of 90% ethanol and kept cool until returned to New Zealand for analysis. It was not possible to freeze these samples. Chlorophyll-*a* in 1 ml aliquots of the alcohol extracts was analyzed spectrophotometrically. The plants and the remaining volume of ethanol were dried at 60°C and then weighed. Chlorophyll-*a* content was expressed as mg g<sup>-1</sup> dry weight.

Analysis of variance (ANOVA), with Tukey honest significant difference (HSD) post-hoc testing, was used where appropriate to examine for differences between depths in the various biomass determinants. Statistica 2.0 for Windows (Statsoft Inc.) was used for all statistical analyses.

### Plant Photosynthetic Activity

Logistical constraints prevented us from making observations of photosynthesis using changes in concentrations of dissolved oxygen, or using uptake of radio-labelled <sup>14</sup>C. These would normally be methods of choice for photosynthesis measurements. Instead, photosynthetic competency of the plants in the lake was determined using Pulse Amplitude Modulated (PAM) fluorometry (Schreiber et al., 1994). A Walz Diving-PAM was used throughout. This system uses the ratio of variable to maximal fluorescence of photosystem II (PSII) under a given light regime to indicate the quantum yield of PSII (electrons produced per photon absorbed). By combining this with measured irradiance, it is possible to estimate the relative electron transport rate (RETR) as a proxy for photosynthesis (Schreiber et al., 1994). Two types of measurement were made, in situ measurements of PSII activity and laboratory measurements at a range of irradiances.

In situ measurements of moss fluorescence were made under ambient light conditions. Measurements were made at approximately 1 m vertical depth intervals, on a number

of days, and the data were pooled. At each set of measurements, the ambient PAR was measured using a LiCor Li194 sensor connected to a LiCor meter mounted in a waterproof housing. The measuring fibre of the Diving PAM was located a fixed distance from the moss shoot to be measured, at an angle that did not interfere with ambient irradiance. The fluorescence of PSII under this light regime ( $F_s$ ) was determined. Afterwards, a short pulse of saturating white light (0.4 s of > 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was provided to measure  $F_m'$  and the variable fluorescence ( $F_v$ ) was calculated as ( $F_m' - F_s$ ). The photosynthetic yield was calculated as  $F_v'/F_m'$  (Schreiber et al., 1994). RETR was then estimated by multiplying the photosynthetic yield, as estimated using the PAM fluorometer, by PAR. The relationship between PAR and RETR in the in situ data was explored by fitting a modification of the hyperbolic tangent photosynthesis irradiance curve of Jassby and Platt (1976) to the data;

$$\text{RETR} = \text{RETR}_{\text{max}} \cdot \tanh(\alpha \cdot E / \text{RETR}_{\text{max}}) \quad (1)$$

where  $\text{RETR}_{\text{max}}$  is the maximum electron transport rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) of photosynthesis, and  $\alpha$  the slope of the RETR vs. PAR curve as PAR ( $E$ ) approaches zero. This curve was fitted by least-squares iteration, using the curve-fitting function of Sigmaplot (Jandel Corporation, Chicago, USA). The photon flux at which electron transport began to saturate ( $E_k$ ) was estimated as  $\text{RETR}_{\text{max}}/\alpha$ . The Sigmaplot routine provides best estimates of variance of the two model parameters, from which a 95% confidence interval was calculated.

The effect of temperature on RETR was determined by carrying out a series of “rapid light curves” (RLCs) using the Diving PAM, at temperatures of 4.5°, 10°, and 17°C. We conducted these experiments on site at the McGill University High Arctic field station at Expedition Fiord, using large water baths to maintain chosen temperatures. Apical shoots (current year’s growth) of *Calliergon*, collected from 10 m depth, were incubated at the experimental temperature, under approximately 50  $\mu\text{mol m}^{-2} \text{s}^{-1}$  irradiance, for one hour. Rapid light curves were then undertaken. This involved placing the shoots in a darkened chamber, then inserting the fibre-optic of the Diving PAM into the chamber and aligning it with the shoot. The yield was measured after 5 s of darkening. Then a known, low-intensity actinic light source was provided for 10 seconds, and the yield measured again. The actinic light was then increased to a second programmed irradiance for 10 seconds, and the yield measured again. The process was repeated at steadily increasing actinic irradiance until nine yield measures were obtained. RETR was calculated, RETR vs. irradiance plots were constructed, and hyperbolic tangent curves were fitted as described above. Five replicate curves were obtained at each temperature, using separate moss shoots, and the data were pooled to calculate curve parameters.

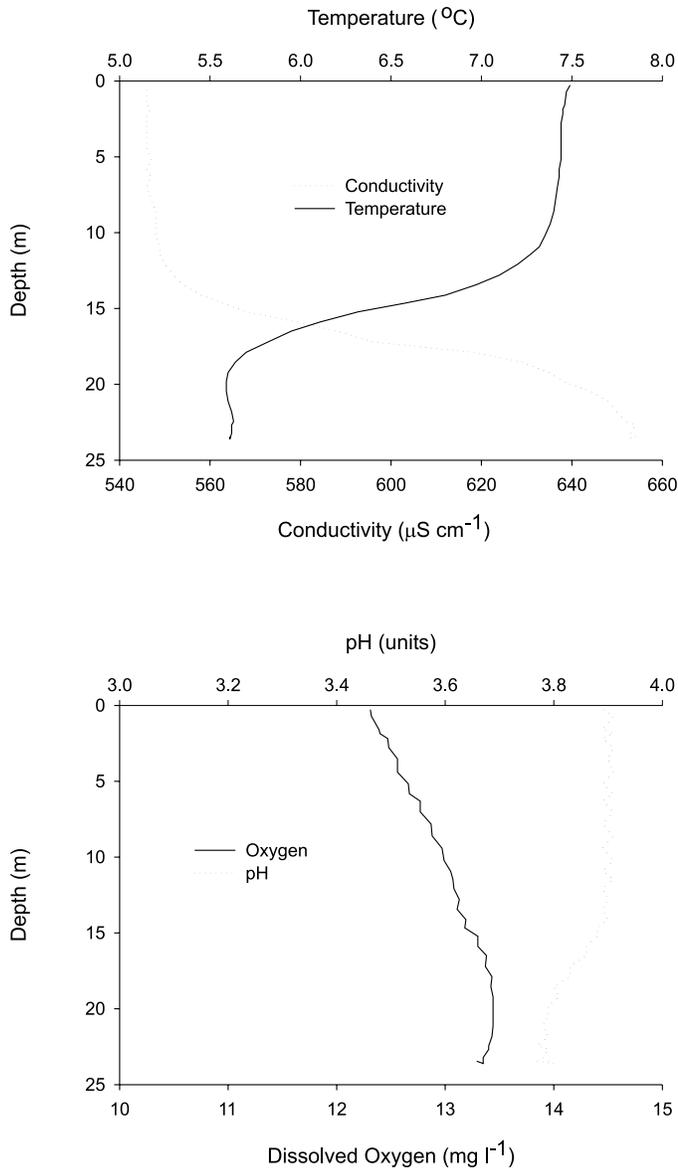


FIG. 2. Profiles of conductivity and temperature (upper panel) and dissolved oxygen and pH (lower panel) in Colour Lake on 3 August 2000.

## RESULTS

### Water Column Structure

On 3 August 2000, the lake was weakly stratified at 16 m, where temperature fell from 7° to 5.5° C and conductivity increased from 550 to 670  $\mu\text{S cm}^{-1}$  (Fig. 2). Dissolved oxygen was fully saturated throughout the water column, resulting in a slight rise in concentration of oxygen with depth due to the temperature decline. The water pH was 3.6 to 3.7 units throughout. On 21 July, SCUBA divers had recorded that under ice cover the temperature in the lake was 4°C from 20 m depth upwards, falling to 3°C only immediately below the ice cover.

Beneath the ice, the water was exceptionally clear. On 21 July, SCUBA divers using the submersible LiCor instrument recorded a  $K_d$  of 0.06  $\text{m}^{-1}$ . On this day the ice

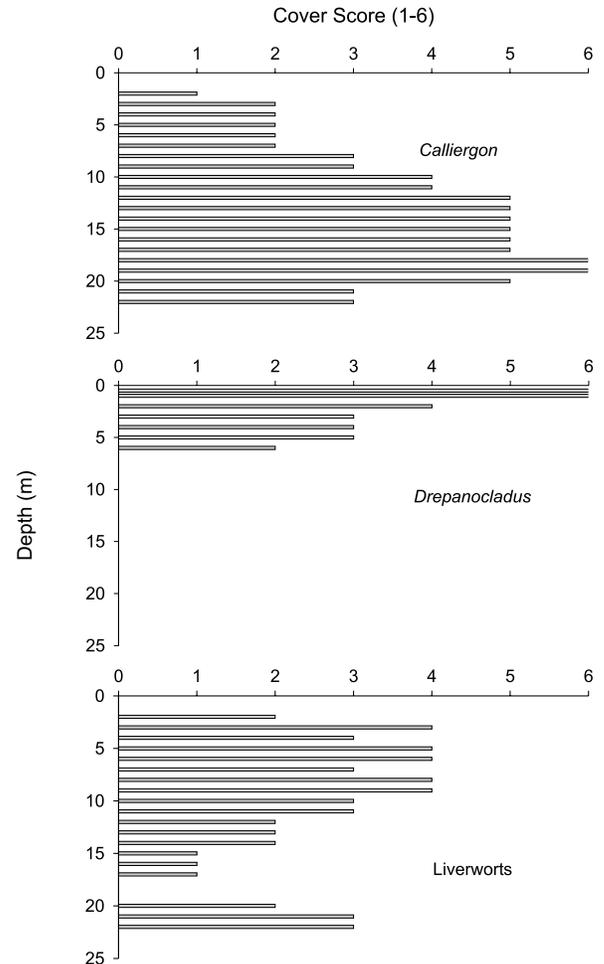


FIG. 3. Cover of the three most common bryophyte types at 1 m depth intervals. Cover scores: 0 = absent, 1 = 0–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, 6 = 100%. Median values for five transects spaced around the lake are shown.

transmitted 47% of incident irradiance. The strong wind event that ultimately cleared the lake of ice also resulted in the re-suspension of a considerable amount of material, reducing water clarity. On 2 August,  $K_d$  had increased to 0.13  $\text{m}^{-1}$ , falling to 0.11  $\text{m}^{-1}$  by 5 August, after a period of calmer weather.

### Plant Distribution

Bryophytes covered the bottom of the lake, from the lake edge to the 22 m depth contour. The bryophytes were poorly attached to the sediment surface, and typically, a red-brown, iron-rich precipitate coated the plants at the sediment-moss interface. The dominant bryophyte was *Calliergon giganteum* Shrimp, with a second moss species, *Drepanocladus revolvens* var *intermedius* (Shrimp), present at shallow depths. The other common bryophyte was an unidentified leafy liverwort “lawn” seen at most depths, but particularly on steeper slopes where mosses were patchy. Median cover values (Fig. 3) indicate that there was a zonation of the *Calliergon* and *Drepanocladus*,

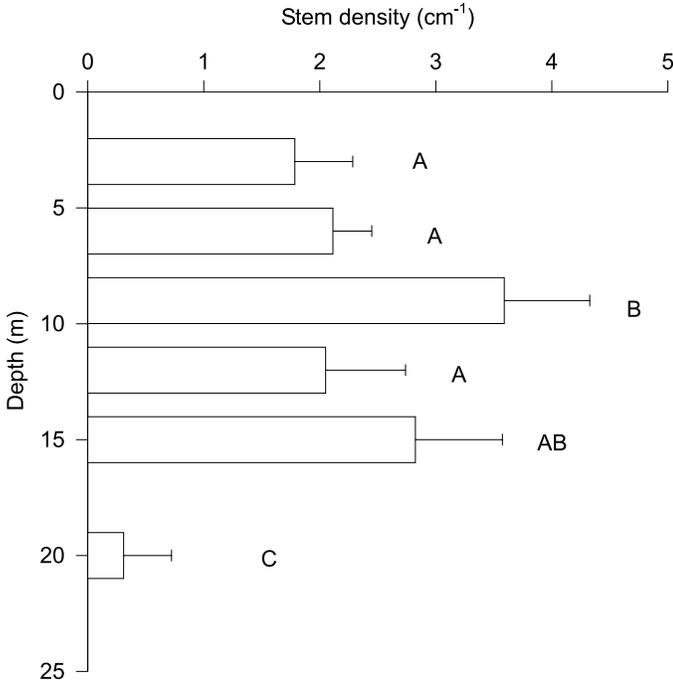


FIG. 4. Shoot density of *Calliergon* in Colour Lake in August 2000. Letters indicate ANOVA groupings within the data (n = 4).

with the former dominant below 6 m, and the latter at depths shallower than 2 m. The “liverwort lawn” had a bimodal distribution, and was found both at depth and in the shallower parts of the lake.

*Shoot Density and Biomass*

Shoot density of *Calliergon* was low close to the maximum depth limit, but showed only minor variations at other depths (Fig. 4). ANOVA suggested that there were three significant groupings, with the 20 m samples less dense than all other depths, 9 m samples denser than all others except 15 m, and 3, 6, 12, and 15 m samples being similar. We suggest that the significantly higher density at 9 m may be an anomaly of the low number of samples at each depth, and we consider shoot density to be similar at all depths above 20 m. The average shoot density for all samples shallower than 20 m is 2.5 cm<sup>-2</sup>.

Biomass was estimated by multiplying the shoot density by the dry weight of the upper four years of moss growth. In general, it was found that almost all shoots had four years’ growth preserved, but few had more than this; hence, four years was taken as representing viable biomass. Depths from 6 to 15 m showed no significant differences from each other, while both 3 m and 20 m samples had significantly lower biomasses than this mid-water band (Fig. 5).

*Annual Growth Increments*

Annual growth increments could be readily identified in the mosses from Colour Lake, with up to 12 years’ growth visible from leaf scars. Growth for the 2000 summer was

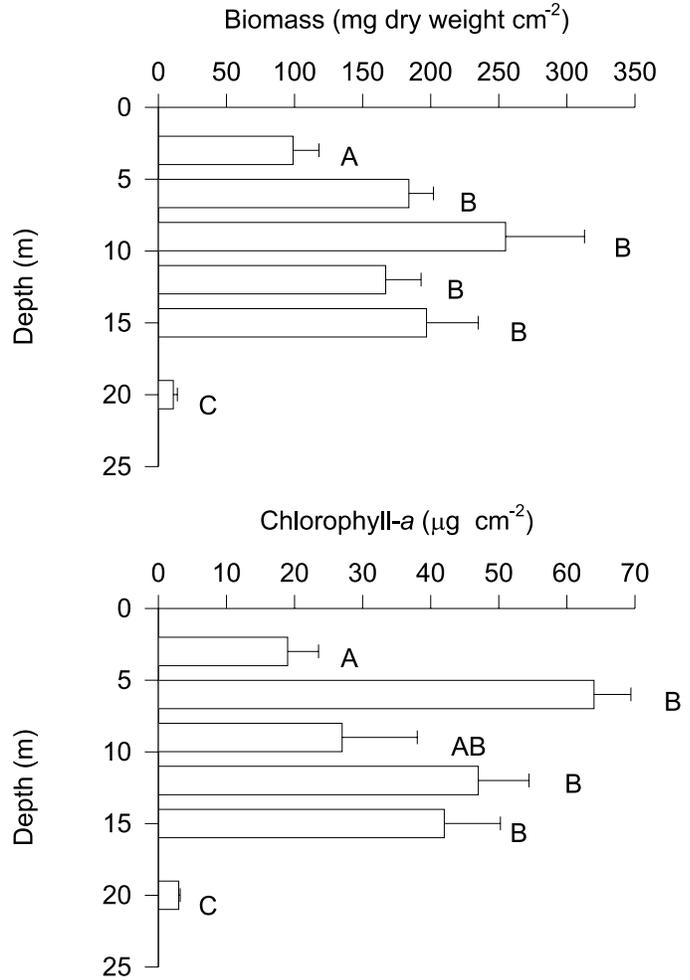


FIG. 5. Areal active biomass of *Calliergon* in Colour Lake (derived from shoot density) and dry weight and chlorophyll-a content of the most recent four years of growth. Letters indicate ANOVA groups within the data.

incomplete at the time of sampling, so extension of the most recent growth band at all depths was less than in other years. Annual extensions were similar (approximately 15 mm per year) at 3 m and 6 m depth, and extension at these two depths was similar for all years before and including 1998. At 9–15 m, shoot elongation was greater, reaching maxima of 25–30 mm in 1997 and tending to be less in earlier years. At 20 m, however, shoots reached maximum extension in 1994, and this depth showed an interannual pattern quite different from all others. Variability within each year, at each depth, is indicated in Figure 6 by 95% confidence intervals, and in many cases, these do not overlap, suggesting statistically significant differences.

Chlorophyll-a and ash free dry weight (AFDW) in each annual band showed considerable variation at all depths (Fig. 7). Maximum chl-a content was seen at most depths in the 1998 band, with the minimum in the still-growing 2000 band. Comparison of 2000 values with other years suggests that less than half of the year’s chl-a accumulation had occurred at the time of sampling. In general, maximum biomass accumulated in shoots growing at 6–12 m depth.

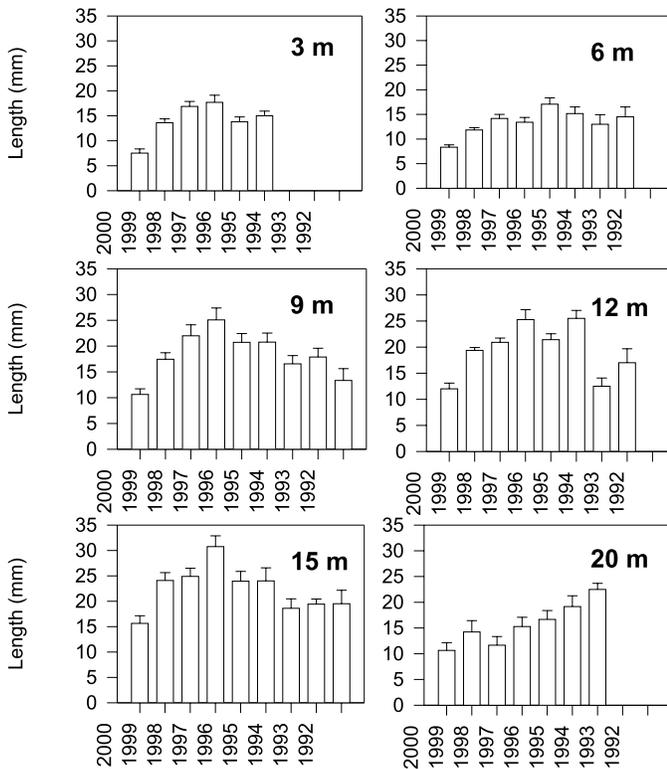


FIG. 6. Length of extension of year classes at six depths in Colour Lake. Each bar is the mean  $\pm$  95% confidence interval ( $n = 40$  for 1996–2000, less for earlier years, but always exceeding 10). Sufficient growth bands were not found at all depths in all years to allow calculation of a mean.

#### Photosynthetic Activity

The pooled in situ observations of RETR for *Calliergon* could be fitted to the hyperbolic tangent function (Fig. 8). Using the entire data set, the parameters of the irradiance vs. RETR curve were estimated (Table 1). These suggested that under in situ conditions, RETR became saturated at a photon flux density of approximately  $140 \text{ mmol m}^{-2} \text{ s}^{-1}$ .

Measurements undertaken in the laboratory, at a range of temperatures, also showed good fits to the hyperbolic tangent function (Fig. 9). Curves fitted to these data yielded the same value for  $\alpha$  (0.3) from  $4.7^\circ$  to  $17^\circ\text{C}$  and steadily increasing values of  $\text{RETR}_{\text{max}}$  with increasing temperature. The rate of increase of  $\text{RETR}_{\text{max}}$  was equivalent to a  $Q_{10}$  (proportional increase for a  $10^\circ\text{C}$  temperature rise) of 2.3. The constancy of  $\alpha$  meant that the rise in  $\text{RETR}_{\text{max}}$  with temperature was inevitably accompanied by an increase in  $E_k$  (Table 1).

#### DISCUSSION

The most abundant bryophytes in this study, *Calliergon giganteum* and *Drepanocladus revolvens*, appear to be typical aquatic macrophytes of this part of the High Arctic. They were common in wet sedge meadows of the Truelove Lowlands of Devon Island (Vitt and Pakarinen, 1977) and were the most abundant mosses in two freshwater lakes on

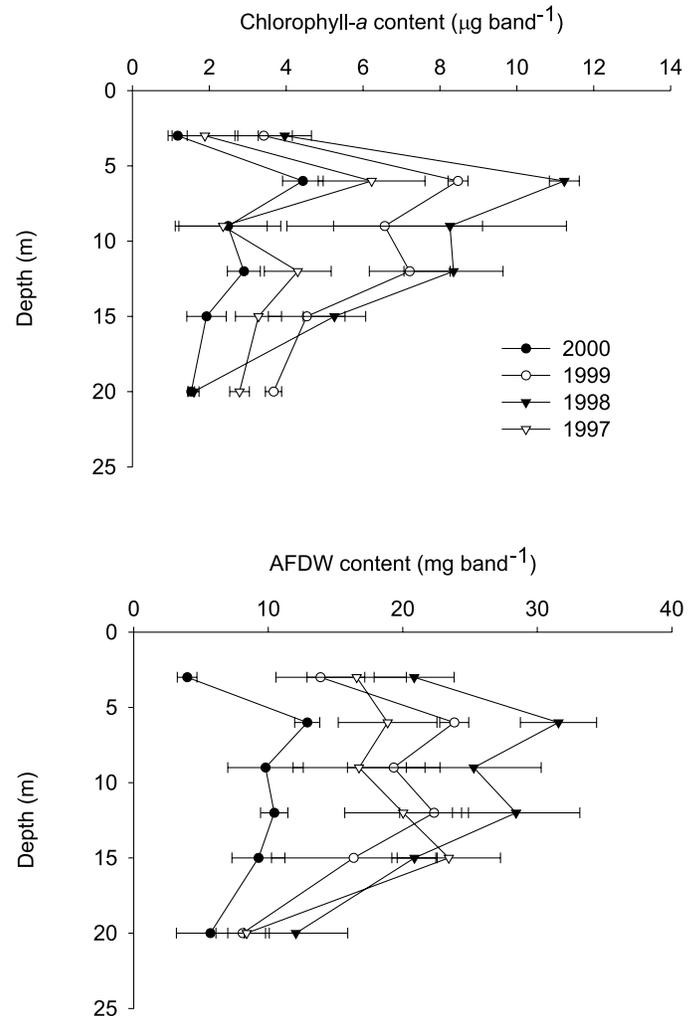


FIG. 7. Chlorophyll-*a* (top) and ash free dry weight (bottom) in each of the four most recent year bands. For each year/depth combination, the mean  $\pm$  standard deviation is shown ( $n = 4$ ).

Cornwallis Island (Sand-Jensen et al., 1999). The annual extensions measured in our study are similar to those of 9–18 mm reported for both *Drepanocladus* and *Calliergon* by Sand-Jensen et al. (1999) from a similar range of depths in two High Arctic lakes, and the dry weight that this represented was also similar to theirs ( $1\text{--}2.7 \text{ mg y}^{-1}$ ). Like Sand-Jensen et al. (1999), we found that annual growth was clearly recognizable and that leaves were retained on moss shoots for four years, with maximum chlorophyll and dry weight attained in the bands representing the previous two summers' growth. The low pH of Colour Lake (3.4 units) does not appear to have affected the submerged moss flora relative to non-acid lakes of the region.

There was clear evidence of a depth zonation of species, with *Drepanocladus* most abundant in the shallow areas of the lake. The reasons underlying this zonation were not addressed in this study, though the upper 2 m of the lake correspond with that part which undergoes seasonal ice formation. The unidentified leafy liverwort formed a tangled mat on the floor of the lake, and this was associated with steeper, less stable slopes in the lakes,

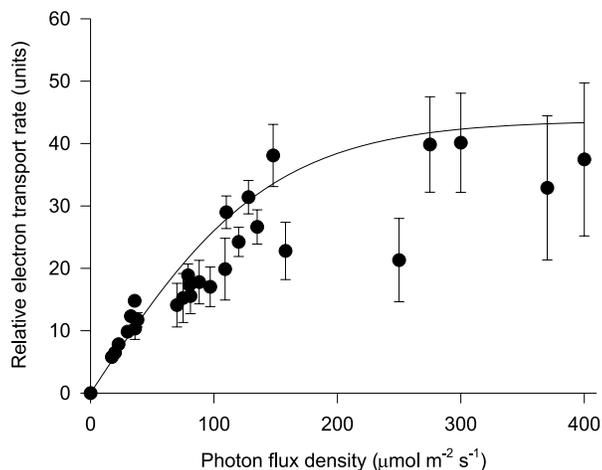


FIG. 8. In situ measurements of relative electron transport rate at a range of irradiances. Each point is the mean of 10–15 measurements at a specific depth/time combination.

suggesting that this growth form may be associated with rapid colonization.

Our data also confirm the ease with which annual markers can be used in assessing growth of mosses in Arctic lakes, but raise some cautionary notes with respect to interpretations of these bands. Etiolation has previously been noted in Antarctic bryophytes (Priddle, 1980a) and may be a complicating factor in interpretation of bandwidths. Our data (Fig. 7) indicate that in deeper water, *Calliergon* underwent shoot etiolation; thus, lower chl-*a* and AFDW contents were found there than in annual bands of similar lengths at shallower depths. However, what was most striking in the annual increment length data was the failure to show the expected pattern of lesser growth in years of persistent ice cover. Data from Doran et al. (1996) show that 1994 was an ice-covered summer, whereas all the other years covered in the moss record were ice-free. While small dips in band length are evident in the 9–15 m mosses in 1994 relative to previous and following years, at 20 m bands were longer in 1994 than in any other year. These data would suggest that, while at middle depths persistent ice cover does retard growth or elongation, at 20 m it does not. The single ice-covered summer in our data set restricts the confidence that can be placed on this observation. However, the physiological data obtained on photosynthetic responses to light and temperature allow us to generate a hypothesis to explain this apparent paradox. This relates to the unexpectedly complex effects of ice cover on growth conditions for mosses at 20 m.

In particular, we found that while ice cover reduced the penetration of light to the water column, it also protected the lake from sediment re-suspension through wind action, thus preserving high water clarity. Consideration of the actual doses of light received at the various sampling depths, in the presence and absence of ice, suggests that under open water, the increased surface penetration (95% compared to 47% under ice) was offset at depths greater than 15 m by the reduction in water clarity ( $K_d$  0.11

TABLE 1. Estimates of parameters for relationships describing RETR and irradiance. In situ measurements were obtained using the Diving PAM fluorometer on several different days and at several depths. Laboratory measurements were made on plants collected at 10 m and acclimated in the laboratory to low light, at three temperatures. In each case the best estimate of each parameter,  $\pm$  95% confidence limit, is indicated.

Treatment	RETR <sub>max</sub> (mmol m <sup>-2</sup> s <sup>-1</sup> )	$\alpha$ (unitless)	$E_k$ ( $\mu$ mol m <sup>-2</sup> s <sup>-1</sup> )
In situ (4–7°C)	35.6 $\pm$ 4.8	0.26 $\pm$ 0.04	137 $\pm$ 36
Lab, 4.5°C	15.4 $\pm$ 0.6	0.30 $\pm$ 0.06	51 $\pm$ 18
Lab, 10°C	25.1 $\pm$ 1.4	0.29 $\pm$ 0.06	87 $\pm$ 18
Lab, 17°C	43.7 $\pm$ 1.8	0.30 $\pm$ 0.04	146 $\pm$ 18

compared to 0.06 m<sup>-1</sup> under ice). Under ice-free conditions, 32% of surface light will have penetrated to 10 m depth, 18% to 15 m, and 11% to 20 m. Under ice-covered conditions, only 24% would reach 10 m, but 18% still reaches 15 m, and 13% reaches 20 m. Increases in irradiance resulting from loss of ice cover can be rather small or nonexistent, particularly at greater depths, if they are accompanied by reduced water clarity.

Persistent ice cover has also been shown to result in lower summer water temperature, peaking at approximately 4°C (Doran et al., 1996). This compares to temperatures higher than 7°C in water above 15 m, but lower than 5.5°C at 20 m, seen during our study. Thus, banding patterns of mosses in shallow water are likely to reflect the presence or absence of ice cover, since upper waters will be warmer and better lit under ice-free conditions than under ice cover. This will not be the case, however, in waters more than 15 m deep: there, ice-free temperatures will be little higher than temperatures under ice cover because of stratification, and irradiance will be lower because of increased light attenuation. Dissolved inorganic carbon concentrations and speciation are also likely to affect growth of mosses (Riis and Sand-Jensen, 1997; Schwarz and Markager, 1999), but it is unclear from our data how these would vary with ice cover, if at all.

Laboratory and field estimates of photosynthesis, as electron transport activity through PSII, were in good agreement with each other and together suggest that both temperature and light might affect potential growth. The differences in RETR<sub>max</sub> between laboratory and field observations (laboratory values in our study were approximately half of those in the lake under similar temperatures) are likely to relate to the different types of light source used in making the measurements, the short acclimation time to the irradiance gradient in the laboratory measurements, and the range of temperatures in the field data. Such differences are commonly seen in studies of this type. The  $Q_{10}$  of 2.3 for RETR derived from the laboratory experiments is, however, similar to that reported for photosynthesis in other polar aquatic mosses (Priddle, 1980b) and clearly shows that, if irradiance is adequate, an increase in temperature will lead to an increase in photosystem activity. While an increase in temperature would appear to

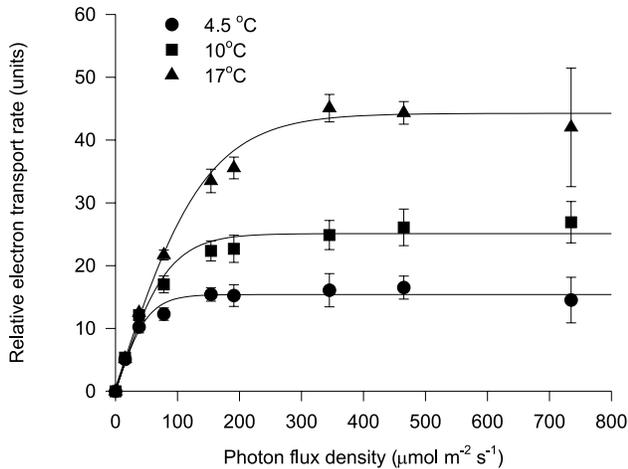


FIG. 9. Rapid light curves obtained from *Calliergon* at three temperatures in the laboratory. Plants were pre-adapted to  $50 \mu\text{mol m}^{-2} \text{s}^{-1}$  irradiance.

favour carbon accrual, we have no data on the effects of temperature on respiration rates, which could also increase with temperature and thus offset this apparent gain (Priddle, 1980b).

Insofar as estimates of RETR are surrogates for photosynthesis, and hence potential growth rates, our data suggest that in years with persistent ice, low temperatures associated with persistent ice will reduce moss growth in the upper part of the lake, but this may be offset in the deeper parts by the increased light regime. In contrast, when ice cover is lost, the higher temperature and light regime in the upper waters will favour growth, while in deeper water, low light may override any small effect of raised temperature.

The data presented in this paper confirm previous findings that bryophytes dominate the benthic flora of Arctic lakes. Even though the waters of Colour Lake have an unusually low pH, the taxa of mosses found are similar to those of other nearby freshwaters, and the performance of these mosses, in terms of annual increments of length and dry weight, is also similar. We also found, as in previous studies, that moss leaves in these high-latitude habitats generally persist for approximately four years before they finally slough. Sufficient stems retain leaves for longer than this to allow a longer history of moss growth to be recovered. However, the failure to establish a clear relationship between the growth of mosses (as recorded by annual increments) and the persistence of ice cover points to the care that needs to be taken when using internal growth markers to hindcast growth conditions. We suggest that the multiple effects of loss of ice cover on water temperature, water clarity, and light transmission combine in Colour Lake to smooth out year-to-year changes in moss growth. In addition, the ability of moss stems to etiolate under low-light conditions, and thus reduce the degree of correlation between band length and biomass, further complicates hindcasting.

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