Slow growth and decomposition of mosses in Arctic lakes

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Abstract: Aquatic mosses are often the exclusive form of macrophytic vegetation in Arctic lakes. Despite the cold nutrient-poor water and the short ice-free summer, the mosses form dense stands on the lake bottom down to great depths. The environmental conditions suggest that moss growth and decomposition are extremely slow, but logistical and methodological difficulties have so far precluded direct measurements of the processes. Here, we use temporal changes in the size and density of leaves along the axis of moss shoots collected from different depths in Char Lake and North Lake in the Canadian High Arctic to reconstruct the annual growth and decomposition of the mosses during the past 10–17 years. Our results show low but remarkably constant annual elongation rates (about 10 mm·shoot^{-1}) in the long-lived shoots that carry green leaves for several years and decompose slowly. Cold temperatures and low nutrient supply in combination with the short Arctic growing season can account for the low growth rate, the low decomposition rates, and the unprecedented longevity of these moss communities relative to other submerged macrophytes.

Résumé : Les mousses aquatiques sont souvent la seule forme de macrophytes dans les lacs de l'Arctique. Malgré que les eaux soient froides et pauvres en nutrients et que les lacs soient déglacés durant seulement une courte période dans l'Arctique, les mousses forment des peuplements denses sur le fond des lacs jusqu'à de grandes profondeurs. Les conditions environnementales dans cette région laissent penser que la croissance et la décomposition des mousses y sont extrêmement lentes, mais des difficultés logistiques et méthodologiques ont à ce jour empêché la mesure directe de ces processus. Nous avons utilisé les changements temporels dans la taille et la densité des feuilles le long de la tige des pousses de mousses recueillies à différentes profondeurs dans les lacs Char et North, dans le Grand Nord canadien, pour reconstruire la croissance et la décomposition annuelles des mousses au cours des 10 à 17 dernières années. Nos résultats montrent que les taux d'élongation annuels sont bas mais remarquablement constants (environ 10 mm·pousse^{-1}) chez les pousses longévives qui portent des feuilles vertes durant plusieurs années et se décomposent lentement. Les basses températures et la faible quantité de nutrients, de pair avec la courte saison de croissance dans l'Arctique, peuvent expliquer le faible taux de croissance, les faibles taux de décomposition, et la longévité de ces communautés de mousses, qui dépasse celle des autres macrophytes submergés.

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Introduction

Mosses are common in unproductive terrestrial and aquatic habitats and are mainly regarded as stress-selected, slow-growing organisms (Furness and Grime 1982). In temperate regions, aquatic mosses dominate the vegetation in nutrient-poor, acid lakes (Grahn 1977; Toivonen and Huttunen 1995), and in transparent alkaline lakes, they grow at very low irradiance and temperature at depths below the rooted vegetation (McIntire et al. 1994; Middelboe and Markager 1997). In Arctic and Antarctic lakes, mosses are typically the only macrophytes present (Bodin and Nauwerck 1968; Welch and Kalff 1974; Priddle 1980).

Aquatic mosses can extend to great water depths and can apparently survive at only 0.1–2% of the surface irradiance (Frantz and Cordone 1967; McIntire et al. 1994). The deep-growing mosses have been suggested, based on short-term measurements of photosynthesis and respiration, to grow extremely slowly and live for many years (Bodin and Nauwerck 1968). These suggestions have not been confirmed due to the lack of direct measurements of growth and longevity of mosses in the natural environment. Short-term measurements of photosynthesis and respiration during summer cannot provide reliable data for evaluating the annual growth and longevity in Arctic lakes, which are covered by ice for more than 10 months a year (Schindler et al. 1974). Field incubation techniques are also difficult to apply because the mosses grow in a dense quilt of live and dead shoots that is disturbed by experimental manipulation. Moreover, the Arctic lakes are difficult to study because of the adverse climate and the remote location. Measurement of the long-term growth and decomposition of aquatic mosses would, however, be rewarding because this could help deter-

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Fig. 1. Annual shoot elongation of *Drepanocladus revolvens* at depth in Char Lake. Mean elongation rate was reconstructed for every annual segment 8–10 years back in time based on measurements on 26–48 shoots from each depth. The 95% CL is only shown one-sided for the highest and the lowest values to ensure clarity. The 95% CL averaged 12% of the mean annual growth rate. ●, 3.8 m depth; ○, 6.8 m depth; ■, 10.8 m depth; □, 13.5 m depth.
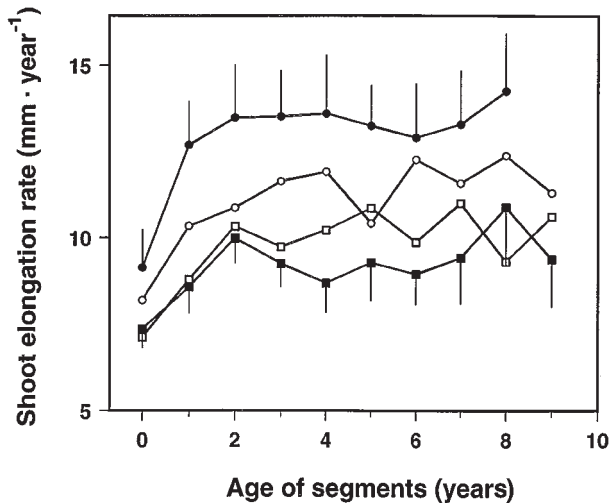
mine their role in carbon and nutrient cycling in the Arctic lakes and in the many acidified lakes at lower altitudes where mosses have become more abundant (Grahn 1977; Roelofs 1983).

Here, we reconstruct the growth and life span of *Drepanocladus revolvens* var. *intermedius* (Schimp.) Anderson et al. and *Calliergon giganteum* Schimp. at depth in Char Lake and neighbouring North Lake, High Arctic Canada (74°42′N, 94°50′W), based on seasonal changes in morphology using methods analogous to those recently developed for mosses in a temperate lake (Riis and Sand-Jensen 1997) and previously applied to terrestrial plants and seagrasses (Callaghan et al. 1978; Duarte et al. 1994). The reconstruction technique has the advantage that a large representative sample of moss shoots can be collected from different sites and depths on a single occasion to determine growth and demographic variables.

Study sites and methods

The two Arctic lakes are located in a polar region with low annual precipitation (average 136 mm·year^{-1}, McCann et al. 1972) and relatively high annual irradiance (average 6240 mol photons· m^{-2}·year^{-1}, 400–700 nm, Schindler et al. 1974). Lakes in the region are alkaline, poor in nitrogen and phosphorus, and have low phytoplankton biomasses and transparent water (Schindler et al. 1974). Char Lake (53 ha, 28 m deep) was intensely studied over several years in the 1970's, and the temperature, light climate, and water chemistry of the lake are the best known for any High Arctic lake (Schindler et al. 1974). During collection of mosses in August 1995, we determined water temperature and the spectrally averaged light attenuation coefficient (K_d, per metre) for photosynthetically active radiation (400–700 nm at 10-nm intervals) recorded with a LiCor 1800 spectroradiometer at depths of 2–20 m in Char Lake and 1–6 m in North Lake. We also determined the chlorophyll concentration at 0.5 m depth on triplicate filtered water

samples followed by fluorometric measurements according to the method of Strickland and Parsons (1972). The chlorophyll concentration was 0.46 µg·L^{-1} and K_d was 0.14·m^{-1} in Char Lake. The K_d closely resembled the values encountered in the earlier studies. Therefore, we used continuous measurements of surface irradiance for the last 10 years at a metereological station located close to Char Lake but the earlier comprehensive 3 years of measurements of light attenuation through snow, ice, and water (Schindler et al. 1974) to estimate the mean annual irradiance reaching moss populations at depth in the lake. Likewise, we used the 3 years of measurements of water temperature at depth to determine the mean degree-days integrated over the year at the different water depths.

North Lake (70 ha, 12 m deep) is more shallow, has higher phytoplankton concentration (0.90 µg chlorophyll a·L^{-1}), and is less transparent ($K_d = 0.29$·m^{-1}) than Char Lake. To obtain a crude estimate of the irradiance reaching the mosses at depth in North Lake, the light attenuation through ice and snow was assumed to be the same as for Char Lake. Char Lake is covered by ice and thin snow for most of the year, apart from a brief summer period (<8 weeks) between July and September, and mean annual water temperatures are close to 1°C (Schindler et al. 1974). Mean annual water temperature in North Lake likely resembles that in Char Lake, but maximum water temperatures in August 1995 were higher in the shallower North Lake (6°C) than in the deeper Char Lake (4°C).

Moss shoots were collected with a rake from several water depths in the two lakes. From each depth, between 10 and 50 live shoots were pressed and dried between water-absorbent paper for later investigations in the laboratory. The shoots had distinct annual segments presumably because leaves were larger and were produced more frequently in summer than during the rest of the year. Such annual growth segments are common among many temperate and Arctic plants as a result of periodicity in irradiance and temperature (Callaghan et al. 1978; Havström et al. 1995; Riis and Sand-Jensen 1997). Likewise, we regard the periodic growth segments of the mosses as annual segments due to the extreme annual periodicity of light availability in the Artic lakes. This kind of perodicity in environmental variables other than irradiance and temperature is not known. The distinct seasonal pattern of the Arctic mosses permitted us to determine the length, the dry mass, and the content of carbon, nitrogen, and phosphorus of every annual segment for 8–10 years back in time for most shoots and up to 17 years for particularly long shoots. Measurements of carbon and nitrogen were made on a Carbo-Erla CHN analyzer. Phosphorus was determined by means of oxidation with peroxidisulphate (Koroleff 1976).

Results

Both species of mosses grew at low rates in Char Lake and North Lake. The two recent annual growth segments in shoots of *D. revolvens* from Char Lake were shorter than the older segments, and they had not finished elongation (Fig. 1). The leaves remained green for at least 4 years, and the length of annual segments was remarkably constant between 2 and 9 years. The mean elongation rate of the fully grown annual segments of *D. revolvens* declined slightly but significantly at depth in Char Lake from 13.2 mm·shoot^{-1}· year^{-1} at 3.8 m depth to 10.3 mm·shoot^{-1}·year^{-1} at 13.5 m depth (Table 1). Shoots of *C. giganteum* elongated at a similar rate as *D. revolvens* at 10.8 m depth in Char Lake. Low annual mean shoot elongation was also observed for *C. giganteum* in North Lake between 17.9 mm·shoot^{-1}·year^{-1} at 4.5 m depth and 11.4 mm·shoot^{-1}·year^{-1} at 6.5 m depth (Table 1). Annual segments of *C. giganteum* reached their fi-

390

Can. J. Fish. Aquat. Sci. Vol. 56, 1999

Table 1. Annual irradiance, degree-days, and shoot demography of two moss species at depth in Char Lake and North Lake in the Canadian High Arctic.

Lake and species	Depth (m)	Irradiance (mol photons·m^{-2}·year^{-1})	Degree-days	Elongation rate (mm·shoot^{-1}·year^{-1})	Growth rate (mg dry weight·shoot^{-1}·year^{-1})	Longevity (years)	Decomposition rate (year^{-1})
Char Lake							
D. revolvens	3.8	1245	260	13.2±0.6*d*	2.8±0.3*d*	9.4±0.8*cd*	–0.13±0.05*ab*
	6.8	820	290	11.5±0.6*c*	2.0±0.2*b*	8.8±0.7*bc*	–0.11±0.06*a*
	10.8	485	305	9.3±0.4*a*	2.3±0.2*bc*	9.1±0.8*cd*	–0.11±0.06*a*
	13.5	340	325	10.3±0.5*b*	1.3±0.1*a*	10.1±1.3*d*	
C. giganteum	10.8	485	305	9.9±0.8*ab*	2.6±0.3*cd*	8.8±2.0*abcd*	–0.11±0.08*a*
North Lake							
C. giganteum	4.5	780	—	17.9±1.4*e*	2.7±1.3*cd*	7.0±1.5*a*	–0.18±0.12*ab*
	5.5	670	—	13.6±0.8*d*	1.0±0.1*a*	8.1±1.2*abc*	–0.32±0.14*b*
	6.5	580	—	11.4±0.6*c*	1.2±0.2*a*	7.5±1.6*ab*	–0.32±0.30*b*

Note: Mean elongation rate and growth rate based on weight are given as the annual rates for fully grown shoots. Longevity represents the mean age of shoots still with distinct annual segments formed by the dead leaves. Decomposition rate was calculated from an exponential fit to the decline of dry mass of annual segments older than 4–6 years in *Drepanocladus revolvens* and 3–4 years in *Calliergon giganteum*. The ±95% CL is given for 26–48 shoots for *D. revolvens* and 9–28 shoots for *C. giganteum*. Values followed by different letters are significantly different among rows within columns ($P < 0.05$, ANOVA).

nal length already after the first year, and similar to *D. revolvens*, there was little interannual variability in shoot length.

The dry mass of the annual segments changed markedly with age along the shoot axis of *D. revolvens* (Fig. 2). The annual segments reached the maximum dry mass in the second to third year at 3.8 m depth, while they reached the maximum weight later at greater depth. The dry mass of fully grown annual segments was markedly higher in shallow water than in deep water (Fig. 2) because the size and density of leaves along the shoot axis were higher in the shallow-water than in the deep-water populations. Beyond the age of maximum dry mass, the annual segments gradually lost weight (Fig. 2) along with a visual change of the leaves from fresh green to pale green, then to brown, and finally to black, showing an ongoing senescence. Senescence was postponed to gradually older segments of the shoots at increasing depth. In populations of *D. revolvens* between 3.8 and 10.8 m depth with sufficient annual generations included in the material, the dry mass of annual segments declined exponentially from the age of maximum dry mass to the age of 10–15 years at a rate of 0.11–0.13·year^{-1} (half-life about 6 years), while no mass decline was apparent at 13.5 m (Fig. 2; Table 1). The mass decline is primarily due to loss of leaf material, while the stem is more resistant.

The annual growth rate in dry mass of *C. giganteum* at 10.8 m in Char Lake was not significantly different from the annual growth rate of *D. revolvens* at the same depth (Table 1). Likewise, the dead annual segments of *C. giganteum* in Char Lake lost mass at the same rate as in *D. revolvens*. Similar growth rates of *C. giganteum* in North Lake were observed at 4.5 m, while rates were twofold lower at 5.5 and 6.5 m (Table 1). The rate of mass loss in old segments of *C. giganteum* in North Lake was markedly higher (0.18–0.32·year^{-1}, Table 1) than in Char Lake.

The moss tissue was poor in nitrogen and phosphorus at all ages and depths, but the contents of carbon, nitrogen, and phosphorus were higher in the youngest apical segments than in older parts (Table 2). The nitrogen content was particularly low in mosses from Char Lake, showing C:N mass

ratios of 32–46, while ratios were 17–24 in mosses from North Lake (Table 2). The nitrogen concentrations in Char Lake mosses are among the lowest reported for submerged macrophytes and markedly lower than the critical concentrations proposed for nitrogen-limited growth (Duarte 1992). Phosphorus concentrations in the mosses were also low, although the C:P ratios (164–410) were within the range of critical phosphorus concentrations proposed for macrophyte growth (Duarte 1992). The low N:P ratios, particularly in mosses from Char Lake (6.4–9.4), also suggest that nitrogen rather than phosphorus may limit the rates of moss growth and decomposition.

Discussion

The reconstruction technique allowed determination of the annual mean shoot elongation about 9 years back in time with a high reproducibility at every depth (i.e., 95% CL of mean annual elongation rate was 12% for *D. revolvens* and 22% for *C. giganteum*). The mosses grew slowly in length and at slightly lower rates at increasing depth, while the mean values did not change significantly among years at any depth (Fig. 1). This result suggests that differences in growth conditions among years were small or, alternatively, that mosses allocated resources between annual segments of different ages maintaining a relatively constant elongation rate every year independent of the suitability of growth conditions in any particular year. The extensive variation in dry mass of annual segments at depth shows that the suitability of growth conditions is indeed variable, but the mosses can maintain about the same annual elongation by varying the size and density of the leaves (Table 1; Fig. 2).

We found no relationship between the annual surface irradiance and the growth rate of the mosses, but the interannual changes in light availability for the mosses in the lakes are also much more dependent on the variable light attenuation through snow, ice, and water than on the incident irradiance, and these attenuation components are not measured routinely. The perennial nature of the moss shoots presumably has the advantage that storage and allocation of resources

Fig. 2. Mean dry mass (± 95% CL) of annual segments up to 17 years old in 26–48 shoots of *Drepanocladus revolvens* from each of the different depths in Char Lake. The curve for dry mass versus shoot age was fitted by eye in the young segments, while the exponential rate of decline of dry mass in old segments at depths of 3.8–10.8 m was fitted by log-linear regression. The oldest annual segments have no error bars because fewer than five segments were available.
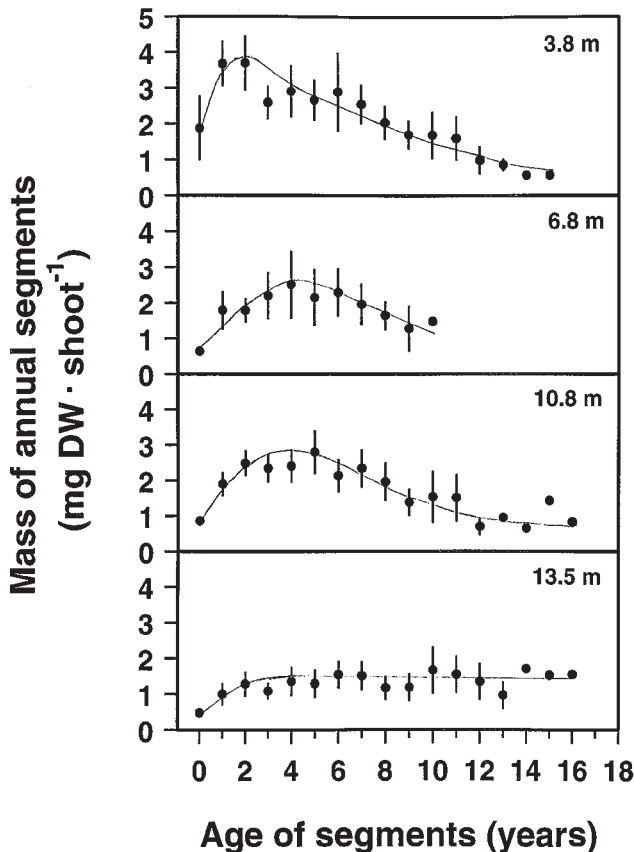
are possible such that new green tissue can be produced after the long arctic winter, and perhaps after even longer dark periods, if ice and snow cover fails to disappear every summer. Functionally, the aquatic mosses may resemble the lignified arctic heather *Cassiope tetragona* (L.) D. Don., which maintains photosynthetic leaves for about 4 years and continues to produce new shoot segments during cold arctic summers with late snow melting, although the number and size of the leaves are smaller than during more suitable warm summers (Havström et al. 1995).

The annual mean elongation of the moss shoots is low for both Arctic species, while the mean age of the shoots, still with discernible annual growth segments, is high (i.e., 7.0–10.1 years, Table 1). The low growth rates and high longevity of the Arctic mosses are unprecedented among all previous studies on freshwater rooted macrophytes (reviewed by Nielsen and Sand-Jensen 1991). The only previous measurements of aquatic moss growth and longevity are for populations of *Sphagnum subsecundum* coll. and *Drepanocladus exannulatus* (Gümbel) Warnstorf from the mesotrophic Grane Langsø in Denmark (Riis and Sand-Jensen 1997). Here, the annual shoot elongation in the thermocline and upper hypolimnion at 6–10 m depth was about 20-fold higher

(226–248 mm·shoot^{-1}·year^{-1}) and mean shoot longevity only 0.95–1.35 years. The most likely explanation for the low growth rate and the high longevity of the mosses in the Arctic lakes is the cold water, the short summer period of adequate light for net photosynthesis, and the nutrient-poor tissue. The annual irradiances received by the moss populations were low but not systematically different between the temperate Grane Langsø (144–621 mol photons·m^{-2}·year^{-1}, 400–700 nm, Riis and Sand-Jensen 1997) and the two Arctic lakes (342–1245 mol photons·m^{-2}·year^{-1}, Table 1). However, light availability is much less evenly distributed over the year in the Arctic lakes. The annually cumulative degree-days were 2069–2964 at 6–10 m depth in the temperate lake and only 261–327 in the Arctic lakes. Moreover, the nitrogen content was much higher (3.1–3.7% dry weight) in *Sphagnum* mosses from the temperate lake, with C:N ratios of 11.2–13.6; these are threefold lower than the ratios found in the mosses from Char Lake (Riis and Sand-Jensen 1997) (Table 2).

Low nutrients and cold temperatures may constrain photosynthesis and growth of the mosses in these Arctic lakes. Nutrient shortage limits capital investment in enzymes and new growth products, while low temperature limits the specific catalytic capacity per enzyme available and, thereby, the possible gain from the investment of a certain amount of nutrients. These constraints on enzymatic capacity should be particularly strong in Arctic lakes in which light is received as a single, almost continuous dose during a short 2- to 3-month period. Marine macroalgae in Arctic regions can, in contrast, obtain a higher productivity and tissue turnover because high nutrient availability in part can compensate for the low temperatures by investment in greater enzyme concentrations (Davison et al. 1991; Markager and Sand-Jensen 1994). This compensation is precluded in nutrient-poor Arctic lakes.

Cold temperatures and low nutrient concentrations can also account for the longevity of the Arctic mosses and the slow weight loss of dead tissue. Thus, rates of growth, senescence, and decomposition should be closely coupled and regulated by the same intrinsic and extrinsic factors (Enriquez et al. 1993; Cebrian and Duarte 1995). The annual rate of weight loss of dead moss tissue from Char Lake was only about 0.11–0.13·year^{-1} or 20- to 200-fold lower than the values for other freshwater macrophytes mostly obtained in experiments in temperate regions at higher temperatures (reviewed by Enriquez et al. 1993). The rates of weight loss of detritus derived from temperate reed plants are also about 10-fold faster than the rates for the Arctic mosses at similar concentrations of tissue nitrogen (Enriquez et al. 1993).

Despite the low growth rates, the Arctic mosses are capable of forming dense stands due to the slow loss rates and the longevity of the tissue (Welch and Kalff 1974). They can also contribute significantly to the pool of organic detritus because rates of microbial degradation are expected to be strongly limited by low temperature, low nutrient concentration, and low activity of invertebrate detritivores, which accelerate degradation in warmer aquatic habitats (Webster and Benfield 1986).

The reconstruction technique presented here is straightforward and allows an inexpensive and precise analysis of growth, life span, and decomposition of moss populations

392

Can. J. Fish. Aquat. Sci. Vol. 56, 1999

Table 2. Carbon content and elemental mass ratios in young and old annual segments of *Drepanocladus revolvens* and *Calliergon giganteum* at depth in Char Lake and North Lake, Canadian High Arctic.

Lake and species	Depth (m)	Carbon (% dry weight)		C:N ratio		C:P ratio		N:P ratio	
		Young	Old	Young	Old	Young	Old	Young	Old
Char Lake									
D. revolvens	3.8	30.6	26.9±0.7*bc*	43	46±2*d*	332	410±17*c*	7.7	8.9±0.3*a*
	13.5	39.9	29.7±0.8*c*	32	33±1*c*	206	302±38*ab*	6.4	9.4±1.9*ac*
C. giganteum	10.8	37.9	27.4±2.8*bc*	33	33±3*c*	266	368±47*bc*	8.1	9.2±4.2*abc*
North Lake									
C. giganteum	4.5	25.4	22.2±1.8*a*	20	20±1*a*	366	333±62*abc*	8.6	15.9±1.9*d*
	5.5	29.7	29.4±2.7*c*	18	23±1*b*	386	313±90*ab*	21.1	12.6±5.7*cd*
	6.5	26.4	26.0±3.5*b*	17	24±1*b*	164	281±76*a*	9.4	12.1±3.6*bc*

Note: Young annual segments representing the recent 1.5-year segments were pooled for all individuals of each species and depth. Old annual segments (>2 years) were pooled for each year and an overall mean was calculated for all years. Mean values (±95% CL) represent 26–48 shoots for *D. revolvens* and 9–28 shoots for *C. giganteum*. Values followed by different letters designate significantly different values among rows within columns ($P < 0.05$, ANOVA).

from remote regions with adverse climate and sites difficult to access. The formation of a dense quilt of live and dead moss shoots on the lake bottom and the slow rates of growth and decomposition of the Arctic mosses preclude traditional incubation methods, while the reconstruction technique benefits from the slow rates of the processes, allowing several years of growth and decomposition to be represented in just one collection of the moss shoots. In future use, however, independent tests are recommended to acertain that growth segments are indeed annual, although no other explanation appears likely today. With methodological improvements the broad-scale reconstruction techniques should permit better evaluations of the consequences of future changes in snow and ice cover and temperatures in Arctic lakes following proposed climate changes.

Acknowledgements

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