# FRESHWATER MICROBIOLOGY IN THE ANTARCTIC: I. MICROBIAL NUMBERS AND ACTIVITY IN OLIGOTROPHIC MOSS LAKE, SIGNY ISLAND

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ABSTRACT. The planktonic bacteria of oligotrophic Moss Lake (Signy Island, South Orkney Islands), were investigated as part of the first full seasonal study of freshwater microbial ecology undertaken in Antarctica. The lake is ice-covered for 8–10 months each year, extremely nutrient-poor, with a sparse phytoplankton (range 0.5–8.0 μg chlorophyll-*a* $l^{-1}$), but a well-developed benthic plant community. Seasonal fluctuations in the microbial population were monitored with direct microscopic counts and by plate counts of total heterotrophs and exo-enzyme producing bacteria. Microbial activity was assessed through division rate experiments and by uptake studies using $^{14}C$-labelled bicarbonate, glucose and acetate. The data suggest that the microbial population was relatively inactive in winter, but responded quickly to the onset of spring thaw, with both numbers and activity increasing to maximum values in December–January when the ice-cover disappeared. Photosynthetic production followed a similar pattern, being undetectable in winter and increasing rapidly in spring before stabilizing during the summer open-water period.

Heterotrophic uptake of glucose (0.8–7.6 ng $l^{-1}$ $h^{-1}$) and acetate (2–26 ng $l^{-1}$ $h^{-1}$) was comparable with the lowest values recorded in Arctic systems. A significant relationship ($P < 0.001$) between acetate $V_{max}$ and direct counts ($6.97 \times 10^{-11}$ μg $h^{-1}$ $cell^{-1}$) indicated little seasonal change in the physiological activity per bacterium. Estimates of total bacterial production were obtained both from $^{14}CO_2$ dark-uptake (using the 6% factor of Romanenko (1964)) and from changes in biomass values with time, measured by direct microscopical methods. Annual bacterial production was calculated as 18–35% of total algal production and, using further empirical formulae, estimates of bacterial decomposition accounted for 63–117% of algal production. Estimates derived from $^{14}CO_2$ dark-uptake were approximately double those obtained by direct microscopic methods and are considered over-estimates of actual bacterial activity. Nevertheless, it is clear that in Moss Lake, the majority of phytoplankton production was utilized by the bacterial population.

OF the wide range of freshwater and saline lakes reported from Antarctica (Heywood, 1977), very few have as yet been affected by human activity, and they therefore provide a unique opportunity to make baseline measurements, study ecological processes and develop models with applications to more complex lake environments. The maritime Antarctic (Holdgate, 1964) is especially rich in lake types, but with few exceptions (see Heywood, 1977), research has been restricted to Signy Island, South Orkney Islands (see Fig. 1) where virtually all these lake types can be found (Heywood and others, 1980). Continuous monitoring of various physicochemical parameters in Signy Island lakes (Heywood and others, 1980) has provided the background for several studies of phytoplankton (Light, 1977; Light and others, 1981), benthic plants (Priddle, 1979, 1980*a, b*) and animals (Heywood, 1970*a, b*; Weller, 1977; Dartnall, 1979). Microbiological research in the maritime Antarctic has been restricted to two preliminary studies. Stanley and Rose (1967) reported low numbers of heterotrophic bacteria in several pools and lakes of volcanically active Deception Island, South Shetlands. Isolates from these water bodies were capable of utilizing a wide range of carbon sources and 30% appeared to be obligate psychrophiles (as defined by Ingraham and Stokes, 1959). In more recent work, Herbert and Bell (1973) isolated various bacterial groups involved in nutrient cycling from mud and water samples taken in three freshwater lakes on Signy Island (lat. 60°45′S, long. 45°38′W), South Orkney Islands (Fig. 1). It was concluded that all the biological components necessary for cycling of carbon, nitrogen and sulphur were present in these lakes. The present programme investigated seasonal fluctuations in microbial numbers and activity of the same three lakes (oligotrophic Moss Lake, mesotrophic Heywood Lake (Ellis-Evans, 1981) and eutrophic Amos Lake) over a two-year period and results for Moss Lake are reported here.

## THE STUDY AREA

During 1976–78, monthly mean air temperatures varied between +2.2°C and −10.4°C (range of extremes, +10.7°C to −30.0°C) with an annual mean of −3.2°C in 1976 and −2.1°C in 1977.

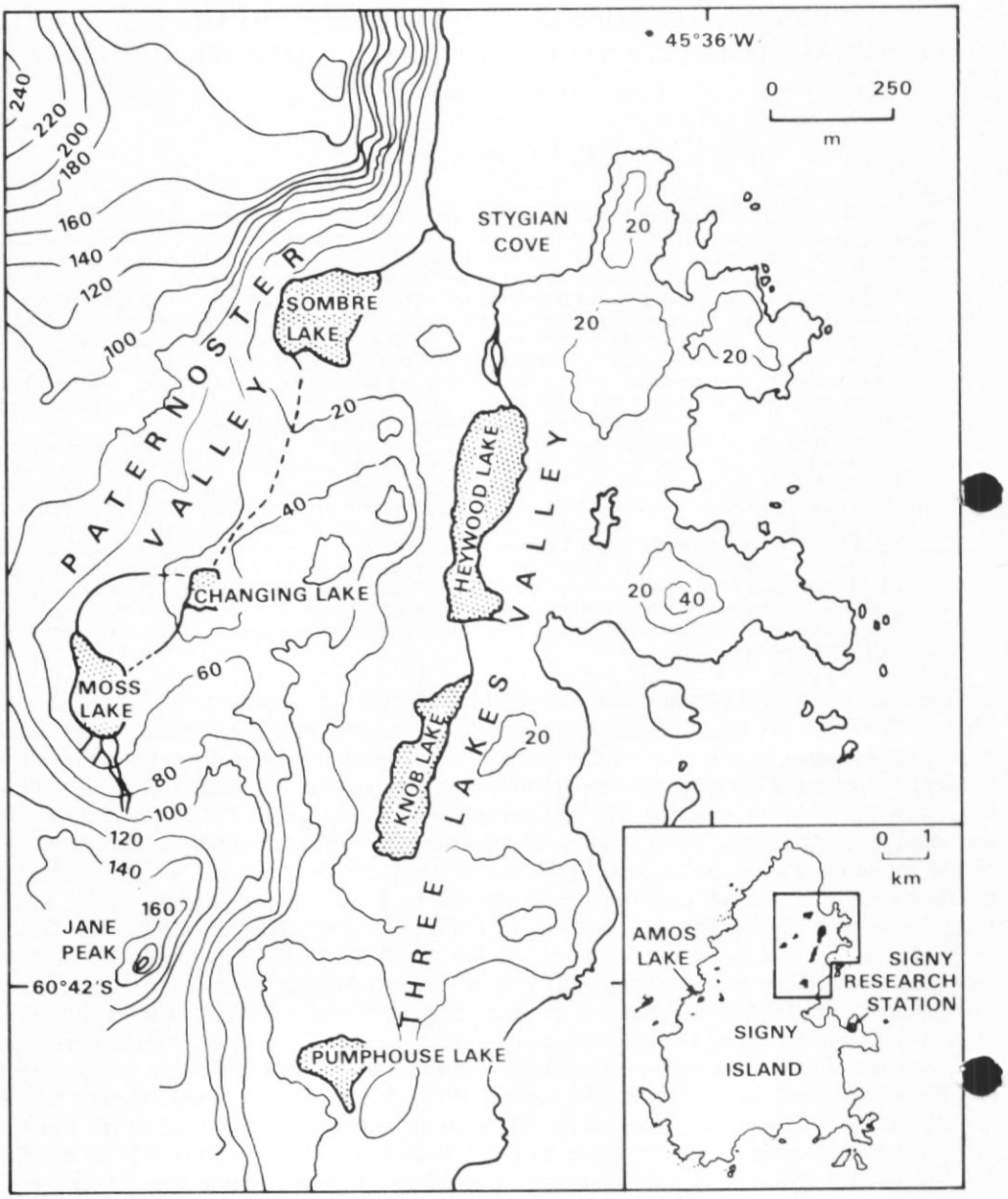



Fig. 1. Map of Signy Island showing position of the study lakes in Paternoster Valley and Three Lakes Valley. Contours at 20-m intervals. ····· Subterranean drainage through moraine, - - - - - stream flowing under ice sheet, ——— surface stream.

The annual mean wind speed was 13.5 knots (25.0 km $h^{-1}$) and annual precipitation was only 273 mm water equivalent. During the winter months, the surrounding sea froze to a depth of 1 m giving 154 days of fast ice in 1976 and 54 days in 1977. These periods were characterized by stable weather conditions. Precipitation during winter (May–October) was 111.5 and 85.2 mm, respectively, for the two years. Annual mean cloud cover of 7 oktas greatly reduced the annual daylight duration to 647 h in 1976 and 498.6 h in 1977, 17.2 and 13.3%, respectively, of the maximum possible for this latitude (D. W. S. Limbert, unpubl. data).

Moss Lake (Fig. 1) lies 48 m above sea level in a cirque basin (Type 27a, Hutchinson 1957) at the foot of the north face of Jane Peak and is the highest of a chain of three lakes in Paternoster Valley. The catchment area for Moss Lake is extremely small, consisting of rock and scree and several areas of permanent snow and ice which provide the meltwater inflow. Two outflows exist (Fig. 2): one is a surface outflow from the north-end of the lake and the other is a subterranean outflow through the moraine on the east side around the 5 m isobath. The latter outflow continues after the inflow and surface outflow streams have frozen and the winter ice cover has developed, causing a 4 m drop in lake level and a total 75% decrease in volume (Light, 1976). The ice attains a maximum thickness of 1.2 m on this lake and is present for 9–10 months each year. When the lake refills in spring, wind mixing is restricted by the presence of an ice raft which often maintains ice cover well into January. In the deeper water, the bottom is covered by a thick layer of very fine consolidated glacial sediment on which a *Tolyphothrix-Plectonema* felt and two aquatic mosses, *Calliergon sarmentosum* and *Drepanocladus* sp. form distinct communities (Priddle, 1980*a*). In contrast to the coastal lakes, seals cannot reach Moss Lake because of its isolated position (800 m from the sea) and the small tern (*Sterna vitata*) population nesting near the western shore contributes minimal enrichment (Heywood, 1967). This lake is thus considered very oligotrophic in comparison with other Signy Island lakes. Priddle and Heywood (1980) have recently proposed a sequence for the evolution of Antarctic freshwater lakes and suggest that lakes such as Moss Lake represent the pinnacle of Antarctic lake development in the absence of enrichment.

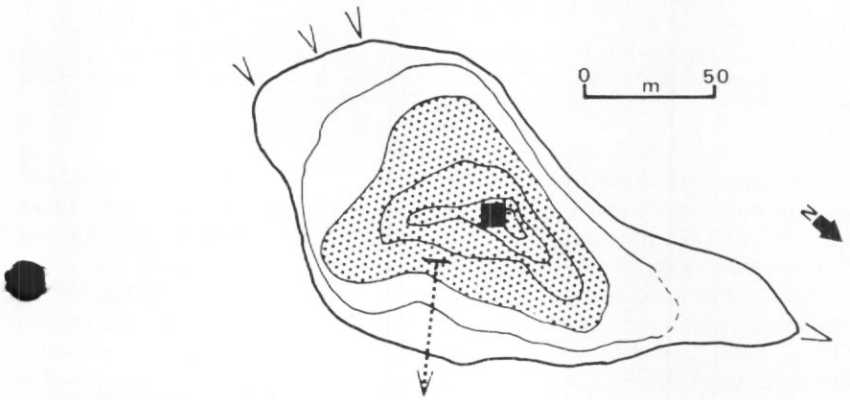



Fig. 2. Moss Lake morphometry. Arrows indicate direction of flow of the main streams. Dotted line approximates depth at which subterranean outflow is located. Bathymetric contours are at 2-m intervals. ■ Sampling station. Stippled area indicates winter lake surface area.

## Materials and Methods

Samples were obtained, weather permitting, at monthly intervals during summer and winter, and fortnightly during spring, at a station 2 m from the lake's deep spot (Fig. 2). At the main station, samples were taken at 1.5 m below the lake surface, mid-water and 1 m above the mud

surface. Sampling was carried out either from a rubber dinghy positioned on the water by mooring lines stretched across the lake or through 23-cm-diameter holes cut through the ice cover with a petrol-driven ice drill.

An autoclaveable sampler was constructed for this project from a 700-ml glass bottle with a 2 kg lead weight attached to its base (Fig. 3). After the bottle had been lowered to the required depth by a line, a sharp tug on a second line removed a rubber sealing cap to allow water to enter. A cork bung, kept inverted by a small weight, floated up inside the bottle and sealed it when full. Discrete sampling to a depth of 10 m was consistently obtained in an aseptic manner under the most arduous working conditions with this simple apparatus. All samples were returned to the Station and stored at +3°C within 1.5 h. All further manipulations were carried out at this temperature to minimize thermal shock.

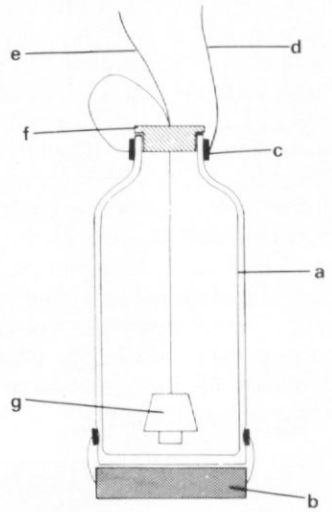



Fig. 3. Design of the water sampling bottle. The 600-ml glass bottle, a, with a 2 kg lead weight, b, attached by jubilee clip, c, is lowered by line, d, and the rubber cap, f, removed at the required depth by a sharp tug on the trigger line, e. As water enters the bottle, the inverted cork, g, floats up to seal the sample.

*Direct microscopic counts*

100-ml samples of lake water were shaken with glass beads for 2 min on a Griffin flask shaker. Known volumes of homogenized lake water (1–5 ml) made up to 10 ml with sterile filtered lake water were then filtered through 0.2-μm Sartorius cellulose acetate membranes using minimal (<20 mm Hg) suction pressure. Filters were stained with erythrosine B using the procedure described in Olah (1974). Counts were made at × 1250 magnification, with a green filter being incorporated to reduce background colour interference. As cells followed a Poisson distribution on the membrane filters, >400 bacteria were counted per membrane giving a mean value significant at 95% with an error of ±10%. Biomass carbon was calculated according to Sorokin and Kadota (1972, p. 50). To estimate percentage attached bacteria in the total count a parallel set of samples was thoroughly mixed for 10 s on a vortex-mixer and then allowed to settle for a further 1 min. Counts from vortex-mixed samples were then subtracted from counts of homogenized samples to give a rough estimate of the proportion attached. The description "attached bacteria" was taken as representing bacteria attached to inorganic and organic material. No delineation of particle size or type was attempted in this study. Population doubling times were estimated on four occasions *in situ* by the method described in Olah (1974) and using the formula given in Sorokin and Kadota (1972). Predation influences were undetectable over 24 h, so the grazing factor was omitted from the equation.

*Plate counts*

Water samples were shaken with glass beads for 2 min on a Griffin flask shaker before preparing a dilution series using sterile filtered lake water. Total viable heterotroph counts (VC) were obtained using casein–peptone–starch (CPS) spread plates (Collins and Willoughby, 1962) supplemented with 50 μg $l^{-1}$ Actidione (Upjohn Co., Mich., U.S.A.). Estimates of potential amylase-, protease- and lipase-producing bacteria in lake water were obtained using CPS spread plates (after Jones, 1971) modified with casein (4 g $l^{-1}$), starch (1 g $l^{-1}$) and tributyrin (10 g $l^{-1}$). All plate incubations were carried out at 3°C for 21 days.

*Carbon fixation*

Working solutions of 10 μCi $ml^{-1}$ NaH $^{14}CO_3$ (Amersham Radiochemical Centre) giving 3.2 μg $ml^{-1}$ of $^{14}C$ were used. Photosynthetic production was measured *in situ* using four 125-ml glass bottles at each sampling depth (2 light, 1 dark and 1 pre-fixed blank for abiotic uptake). 1-ml aliquots of $^{14}C$-solution were added to each of the four bottles and these were then incubated for 24 h at the appropriate depth. Table I demonstrates the validity of 24 h incubations compared to short-term experiments in Moss Lake. Experiments were carried out on four separate occasions and typical results are presented. Duplicate light bottle values never differed by more than 5% from the mean value. Light damage was minimized by carrying out all manipulations under a black polythene sheet. After incubation, samples were filtered through 0.2-μm membranes, washed with 50 ml of sterile filtered lake water, fumed with HCl to remove inorganic $^{14}C$ and then frozen for return to the United Kingdom. To measure algal extra-cellular production, the filtrates from several algal fixation experiments were acidified and 50-ml aliquots were frozen for subsequent counting. Carbon fixation by bacteria was studied in the laboratory essentially using the method described in Sorokin and Kadota (1972). Three 125-ml bottles were employed at each depth (2 dark, 1 pre-fixed blank), and each bottle inoculated with 2 ml of the $^{14}C$-stock solution after first prefiltering the water through a 5.0-μm membrane to remove zoo- and phytoplankton and equilibrating for 2 h. Microscopic preparations revealed bacteria still attached to algae after prefiltering. A correction was therefore applied, based on differences in $^{14}C$-acetate uptake rates measured in prefiltered and unfiltered water samples. It was assumed that algae did not contribute to uptake at the low-substrate concentrations used. Some 10% to 30% of the bacterial activity was commonly retained by the prefilter. Incubations of 24–48 h were carried out in a cooled water bath at ambient lake temperature and then filtered through 0.2-μm filters. The samples were then washed with 50 ml of sterile filtered lake water and fumed with HCl before freezing for return to the United Kingdom. Carbon fixation (both algal and bacterial) was calculated using the formula described in Vollenweider (1969, p. 72). Calculation of total production by heterotrophic bacteria was based on the assumption that dark carbon fixation represented 6% (Romanenko, 1964; Sorokin, 1970; Overbeck, 1972, 1974). Decomposition rates were also calculated from an empirical relationship given by Sorokin (1973).

TABLE I. COMPARISON OF 5-h AND 24-h CARBON FIXATION EXPERIMENTS IN MOSS LAKE

| *Production during time period* 0–5 h | *Production during time period* 5–10 h | *Production during time period* 10–15 h | *Total* 15-h *production* |
|---|---|---|---|
| 7 mg C $m^{-3}$ | 15 mg C $m^{-3}$ | 4 mg C $m^{-3}$ | 26 mg C $m^{-3}$ |
| Algal production over 24 h (15 h daylight, 9 h darkness) | | | Total 24-h production |
| | | | 24 mg C $m^{-3}$ |

The experiment was carried out at 1.5 m depth on 17 January 1978. Triplicate light bottles were used and standard deviation was always <6% of the mean value.

*Heterotrophic uptake of organic solutes*

The kinetic approach developed by Wright and Hobbie (1965, 1966) was employed to assess the heterotrophic potential of the lake bacteria populations. High activity uniformly labelled $^{14}$C-acetate (Amersham) were diluted to give stock solutions of 0.01 and 0.10 μCi ml$^{-1}$, respectively (0.47 μg glucose ml$^{-1}$ and 0.14 μg acetate ml$^{-1}$). For each depth, microlitre quantities of the solutes were micro-pipetted into two series of six dark bottles each containing 50 ml of lake water. $^{14}$C-glucose was added to give a concentration range of 0.2–4.0 μg l$^{-1}$, whilst $^{14}$C-acetate additions gave a range of 1.3–5.2 μg l$^{-1}$. Two bottles per series were pre-fixed with Lugol's acetic acid (Nauwerck, 1963) and incubations of 3–7 h at ambient lake temperatures were then carried out. Activity was stopped by the addition of Lugol's acetic acid at the end of incubation, and the samples were then filtered through 0.2-μm membranes, washed with 50 ml of sterile filtered lake water and the filter frozen for later counting in the United Kingdom. At a later stage in this study, chemicals became available which enabled microbial respiration to be measured. This is a potentially significant source of error in Wright and Hobbie's original method. The technique described by Hobbie and Crawford (1969) was therefore employed but using 25-ml volumes at ambient lake temperatures for 3–7 h incubations. Resulting filters were frozen. Kinetic experiments were repeated at all depths in winter and at the bottom depth only in summer in light bottles using 125-ml volumes to assess potential photoheterotrophy. Both light- and dark-bottle data (including respiration values) were analyzed using the modified Michaelis–Menten equation given in Wright and Hobbie (1965) and the results plotted as a linear transformation against substrate concentration in a modified Lineweaver–Burk plot. Solute uptake rates were expressed as $V_{max}$ the maximum uptake velocity (or heterotrophic potential) and the time taken to utilize the natural concentration of the substrate ($S_n$) expressed as turnover time ($T_t$). An estimate of the maximum substrate concentrations was obtained from the expression ($K_t + S_n$) where $K_t$ (a transport constant) is the substrate concentration at $V_{max}/2$ and may represent a measure of substrate affinity.

*Radioisotope counting*

All radioactive filters and filtrates (1-ml sub-samples) were counted in 10-ml volumes of dioxane-based NE-250 liquid scintillant (Nuclear Enterprises). The majority of samples were counted on a Packard Tricarb 2425 liquid scintillation counter. The remaining samples and some recounts were dealt with using a Searle model 6880 Mk. 3 liquid scintillation counter. All samples were standardized by channels-ratio (checked by internal standardization using $^{14}$C-labelled hexadecane from Amersham Radiochemical Centre) and the efficiency of the two systems estimated to be 72% and 84%, respectively.

*Physico-chemical analyses*

A long-term programme monitoring seasonal variations in physical and chemical parameters in Signy Island lakes was the source of much of the data used in this study. For consistency, all additional chemical analyses including chlorophyll-*a* (as a measure of algal biomass) were carried out using the same methodology. Details of the methods used are given in table I of Heywood and others (1980).

Water samples were filtered through 0.2-μm membranes using sterile apparatus and 100-ml aliquots frozen for subsequent analysis of dissolved organic carbon (DOC). Total inorganic carbon (TIC) for production studies was calculated from values of total alkalinity and temperature using the pH-related factor of Saunders and others (1962). A significant source of error in $^{14}$C-productivity measurements may be introduced when using this method in low alkalinity/low pH environments. In the Signy Island lakes, the problem was confined to winter, when, in any case, uptake of labelled $CO_2$ was minimal (Light and others, 1981).

## Results

*Physico-chemical and algal data*

Moss Lake was characterized (Fig. 4) by a restricted temperature range (0.6–3.7°C), high dissolved oxygen levels (notably in summer) and extremely low water-column chlorophyll-*a* concentrations (0.5–8.0 μg $l^{-1}$). During open water periods (January–March), wind-mixing resulted in a relatively homogeneous water column, but under ice cover distinct chemical and thermal stratification occurred. Winter sampling revealed an inverse thermal gradient of 1–2°C in the vertical profile (*c.*5 m) and oxygen levels as low as 2 mg $l^{-1}$ were recorded at the bottom of the water column. With the opening of the inflow in October and the disappearance of snow cover, both temperatures and oxygen levels increased throughout the lake, although stratification remained until the ice cover broke up in late January. This suggested that the inflowing melt water flowed through the lake over the winter water body and thus the top 2–3 m of the lake under the spring ice cover consisted almost entirely of melt water.

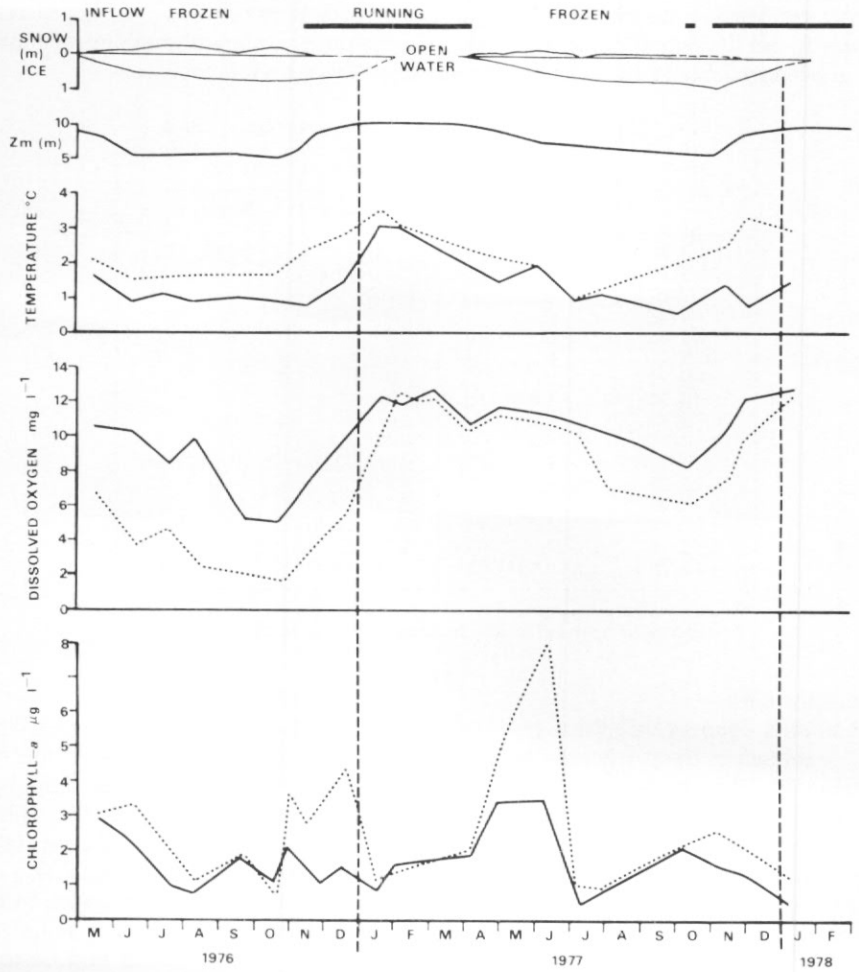



Fig. 4. Seasonal physico-chemical characteristics of Moss Lake and variations in algal biomass as estimated by chlorophyll-*a*. Continuous line indicates top-water samples, a broken line indicates bottom-water samples.

Data for autumn 1976 suggested that stratification quickly became re-established if snow cover was consistently present from an early stage in winter. In autumn and early winter 1977, snow cover was sparse and patchy and the inflow continued running intermittently for some time after ice formation. This, and possible associated algal activity, as reflected in the relatively high chlorophyll-*a* concentrations (Fig. 4) and measurable $^{14}C$-$CO_2$ fixing activity (Table II), maintained oxygen at high levels throughout the water column. Thermal stratification did not develop. Only with the first heavy snow falls in late July did the anticipated water pattern emerge and, as a result, oxygen concentrations, even in bottom-water samples, never dropped below 6 mg $l^{-1}$. Such variations between years were not usually so marked in chlorophyll-*a* measurements which showed little seasonal pattern. The most obvious response was observed in bottom-samples where maxima appeared to be associated with periods of snow-free ice cover. The chlorophyll-*a* maxima may reflect the development of algae with high chlorophyll-*a* per cell to optimize use of the low light levels available. The presence of ice cover (as in ice raft) until late January markedly reduced wind-mixing and would obviously limit algal development in the upper water layers (Table II). There is also evidence, however, that the upper layer of the lake comprised melt-water with a short residence time in the lake, and this implies a poor supply of algal cells. Some evidence was found of a small maximum (Fig. 4) in the upper water column during autumn a[illegible] the lake had been well mixed all summer with through-flow rates relatively low.

TABLE II. PHYTOPLANKTON PHOTOSYNTHESIS IN MOSS LAKE

| *Date* | *Carbon fixation* (mg C $m^{-3}$ $d^{-1}$) | | |
|---|---|---|---|
| | *Top water* | *Mid water* | *Bottom water* |
| 18/4/77 | 20.0* | 12.0 | 12.0 |
| 24/5/77 | 13.0 (7.04) | 11.0 (11.83) | 8.0 (29.12) |
| 5/7/77 | 4.0 | 4.0 | 0 |
| 29/7/77 | 0 | 0 | 0 |
| 1/9/77 | 0 | 0 | 0 |
| 20/9/77 | 0 | 0 | 0 |
| 29/9/77 | 0 | 0 | 0 |
| 6/10/77 | 1.0 | 0 | 0 |
| 24/10/77 | 5.0 | 0 | 0 |
| 2/11/77 | 6.0 | 4.0 | 3.0 |
| 11/11/77 | 9.0 (17.20) | 6.0 (2.99) | 5.0 (21.46) |
| 28/11/77 | 9.0 | 3.0 | 4.0 |
| 30/12/77 | 28.0 | 21.0 | 17.0 |
| 17/1/78 | 24.0 (9.14) | 22.0 (11.40) | 14.0 (35.61) |
| 15/2/78 | 27.0 (9.05) | 23.0 (9.24) | 21.0 (39.09) |
| 14/3/78 | 16.0 (11.05) | 14.0 (9.02) | 11.0 (18.78) |

*Particulate algal production
(7.04) Extracellular production as a percentage of total production

*Total bacterial counts*

Direct bacterial counts (DC) fluctuated little throughout the study period (range (0.5–2.8) × $10^8$ cells $l^{-1}$) though a trend towards higher counts was apparent during November–January each year (Fig. 5). These findings were supported by results obtained in population doubling time experiments (Table III). Rates were extremely low throughout the year with the slowest time (347 h) recorded in winter and the fastest (201 h) recorded in early summer. Intermediate values were measured in spring (220 h) and autumn (256 h). The direct count data also revealed virtually no variation in numbers throughout the water column on each occasion. In contrast, distinct peaks for viable counts (VC) were detected under ice in upper water samples during November and December each year (Fig. 5). Viable counts for mid-depth and bottom-water samples showed no significant fluctuations throughout the study period, except for small increases in bottom-water counts in autumn.

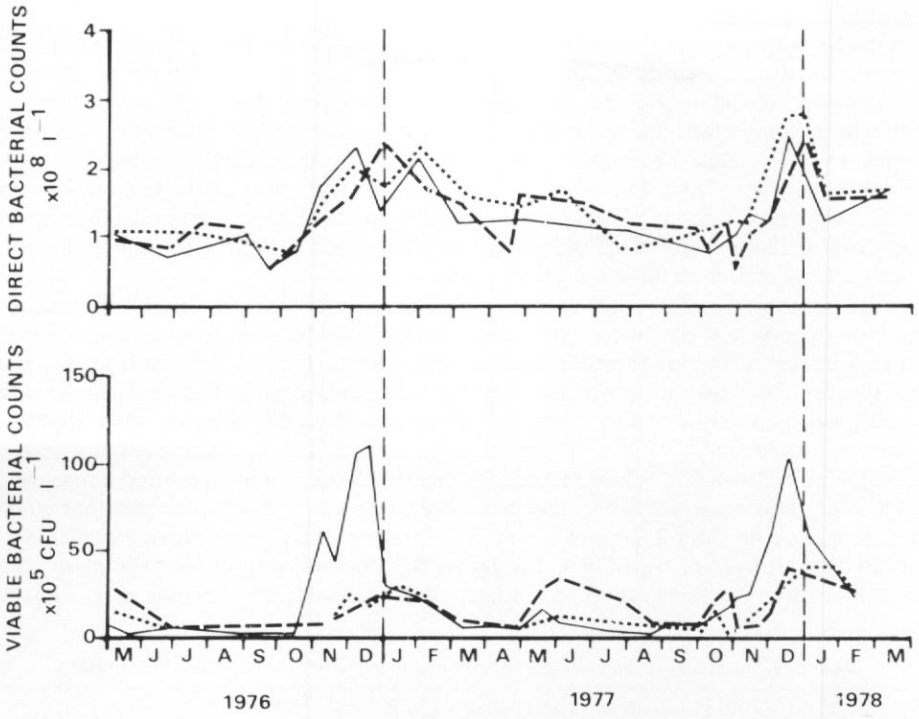



Fig. 5. Direct microscopic counts and viable aerobic plate counts. Top-water counts, ————, mid-water counts, – – – –, and bottom-water counts —— —— ——.

*Attached bacteria*

Bacteria attached to both inorganic and organic particles represent a significant proportion of total bacteria in Moss Lake and the results of four experiments to measure the percentage attached are given in Table III. Bottom-water populations showed very little variation throughout the year with a range of 17.0–26.5% in the four experiments. In contrast, top-water populations contained few attached bacteria in winter (4.5%, SE = 1.8), reflecting the low incidence of particulate material under ice cover. The percentage values increased in spring as the inflow swept material into the lake. Mid-water samples revealed consistently low percentages attached through winter and spring, reflecting the lack of mixing during these periods. However, when wind mixing did occur during the summer open-water period, remarkably similar values of 17.0% (SE = 3.8) and 17.0% (SE = 4.1) were calculated for the top- and mid-water levels, respectively.

TABLE III. SEASONAL VARIATIONS IN PER CENT ATTACHED BACTERIA AND TOTAL POPULATION DOUBLING RATES IN MOSS LAKE

| *Sampling depth* | *Percentage bacteria attached to larger particles* ± 1 S.E. | | | |
|---|---|---|---|---|
| | *Winter* | *Spring* | *Summer* | *Autumn* |
| Top water | 4.5 ± 1.8 | 21.8 ± 5.7 | 15.0 ± 3.8 | 16.0 ± 5.5 |
| Mid water | 6.5 ± 2.6 | 9.7 ± 4.1 | 17.0 ± 4.1 | no data |
| Bottom water | 17.0 ± 4.7 | 21.7 ± 4.8 | 26.5 ± 5.0 | 19.4 ± 4.4 |
| Total population doubling rate (hours) ± 1 S.E. | 347 ± 35 | 220 ± 35 | 201 ± 35 | 265 ± 27 |

*Spring population changes*

The morphological similarity between bacterial populations on CPS plates from the shelf and trough regions and the extremely low counts recorded from inflow samples suggests that the inflow was sweeping shelf-region bacteria into the trough during the spring period (Table IV). In contrast, winter populations differed markedly at the two lake stations judging by the appearance of colonies on CPS plates. The high counts recorded in the shelf region compared to the trough surface water samples (Table IV) in early spring suggest that most of the bacterial activity was located in the shallow regions of the lake during this and the pre-melt period. This can be attributed to several factors including the proximity of the sediment, higher temperatures due to black-body effects and, even possibly, greater algal activity.

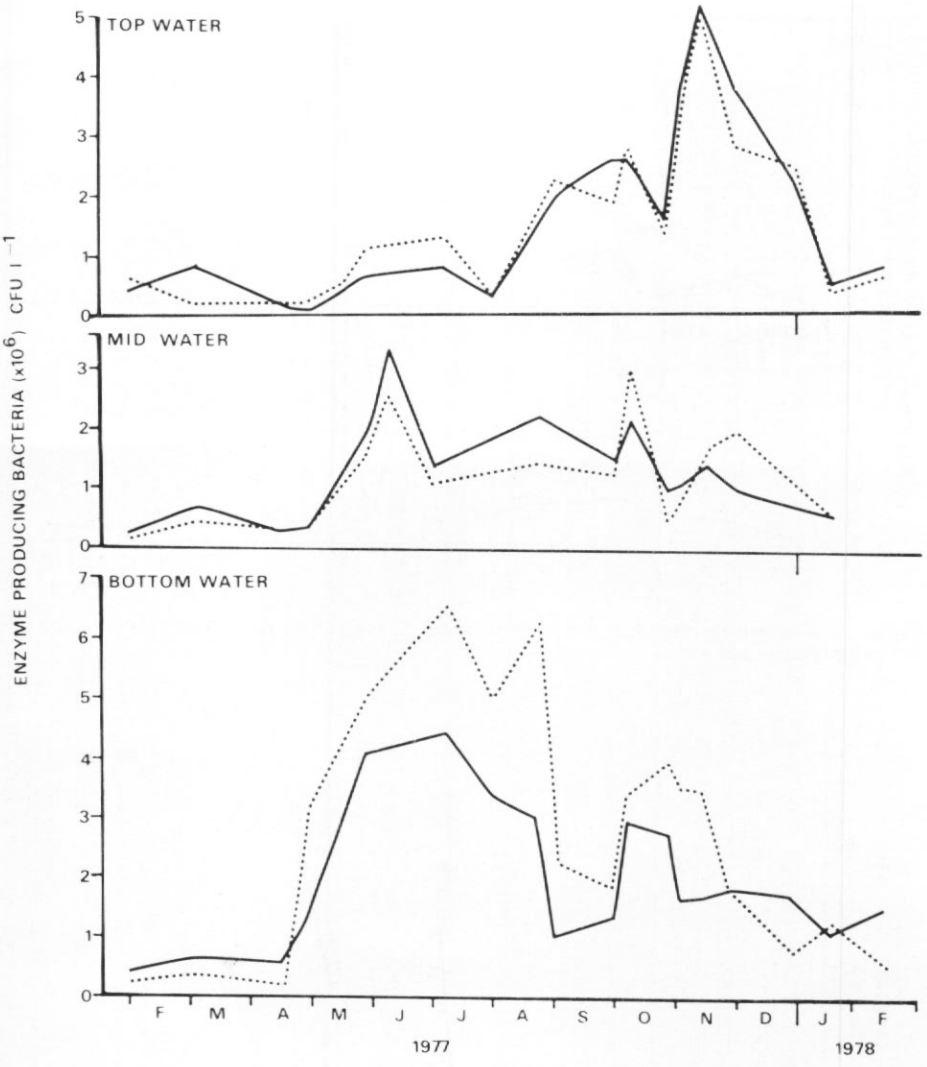
As spring proceeded, inflow rates decreased and the effect of the shelf region diminished. With the onset of open-water conditions and wind mixing, numbers decreased in the upper water column to the level of the lower water column populations. The DC:VC ratio for the top-water samples also fell into line with ratios for the other sample depths at this time. Both counts and ratios remained relatively constant over the summer, with viable numbers at a slightly higher level than was recorded in winter. However, in autumn and early winter, bottom-water viable counts increased to twice the values recorded in the overlying water layers and a marked change in the DC:VC ratio emerged. This may have been related to the higher chlorophyll-*a* values recorded at this depth during the same period. Work currently being carried out on algal productivity in similar lakes of Signy Island suggests that the majority of the bottom-water chlorophyll-*a* may in fact be phaeophytin-*a*, indicative of a senescing population (I. Hawes, pers. comm.).

TABLE IV. VIABLE BACTERIA POPULATION INCREASE IN MOSS LAKE DURING SPRING MELT

| *Date* | *Viable bacteria counts* CFU $ml^{-1} \pm$ S.E. | | | Comments |
|---|---|---|---|---|
| | *Inflow site* | *Shelf site* | *Trough site* | |
| 15/10/76 | frozen | 2 158 ± 336 | 185 ± 17 | Winter status |
| 2/11/76 | 212 ± 26 | 6 950 ± 529 | 6 160 ± 162 | Spring melt with high inflow rates |
| 16/11/76 | 850 ± 121 | 7 976 ± 171 | 4 307 ± 614 | |
| 3/12/76 | 675 ± 91 | 7 136 ± 340 | 10 530 ± 485 | Lake ice cover has decreased and inflow rates slowed |
| 27/12/76 | 420 ± 137 | 5 130 ± 212 | 3 067 ± 850 | |
| 27/1/77 | 972 ± 52 | 3 027 ± 325 | 2 665 ± 370 | Open water |

*Enzyme-producing bacteria*

Plate-counts of exo-enzyme producing bacteria revealed a distinct variation in seasonal pattern with depth (Fig. 6). Top-water samples gave highest numbers of exo-enzyme producers in November before decreasing steadily in December and remaining low (80 colony forming units (CFU) $\times 10^3$ $l^{-1}$) until September or October. Bottom-water counts, in contrast, peaked during May to August, dropped sharply in September and recovered during October before decreasing again to low counts during the summer months. These variations appear to reflect the same influences as total viable counts, namely the input of active shelf-region bacteria in spring and the activity of bottom-water phytoplankton and benthic plants in autumn and early winter. When exo-enzyme producing bacterial counts were expressed as percentages of the total viable counts in both top and bottom water (Fig. 7), protease and amylase producers each comprised <20% of the total numbers between October and April increasing to 20–60% during May to September. This was consistent with a possible increase in macromolecular nutrient sources as algal activity decreased in winter (Table II) and the population senesced. Corresponding mid-water values were relatively constant, barely exceeding 30% throughout the twelve-month study.




6. Viable plate counts of exo-enzyme-producing bacteria at three sampling depths. ———— protease producers and – – – – – amylase producers.

Lipolytic bacteria never exceeded 8% of the total counts and no seasonal pattern was discernible at any depth.

*Heterotrophic uptake of glucose and acetate*

Heterotrophic potential ($V_{max}$) data for the uptake of glucose and acetate in Moss Lake are summarized in Fig. 8. Problems were encountered when analysing the raw data as only 25% of the results obtained with glucose have significant correlation even at $P<0.10$ when the linear transformation of the kinetic data was made. The results of acetate uptake experiments proved only slightly more amenable to least-squares analysis (60% were significant at $P<0.10$). As only four data pairs were analysed for each kinetic plot, calculation of a best-fit line was complicated by deviation of even a single point. All results reported here were therefore derived from plots

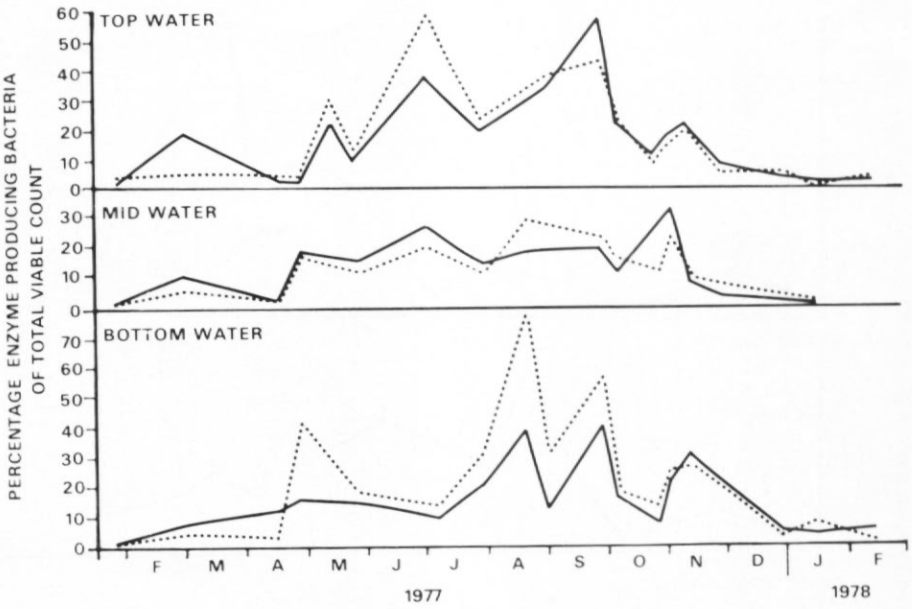



Fig. 7. Viable counts of exo-enzyme-producing bacteria expressed as a percentage of total viable counts. ——— protease producers and – – – – – amylase producers.

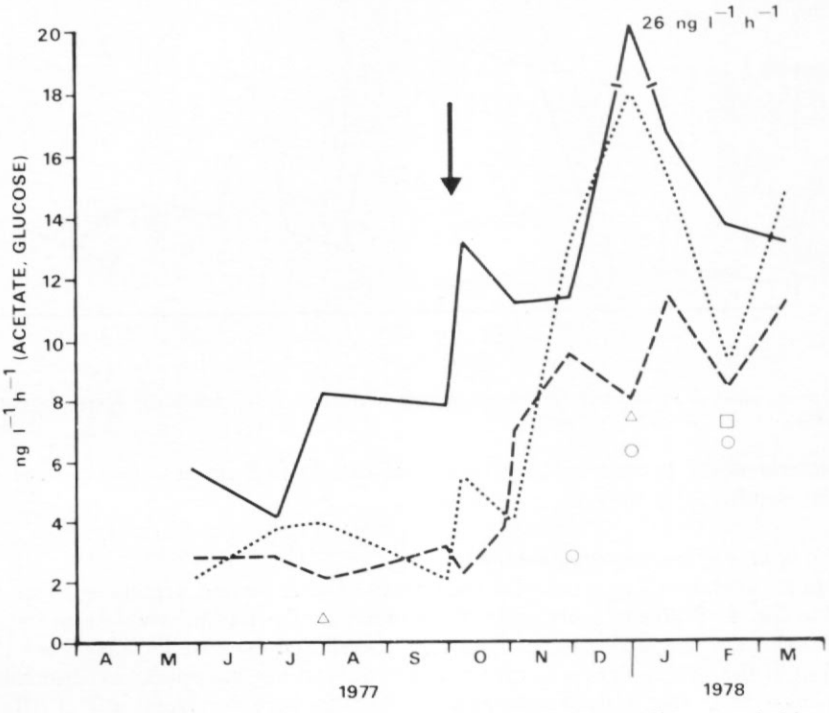



Fig. 8. Seasonal patterns of heterotrophic uptake rates ($V_{max}$) of $^{14}$C-glucose and $^{14}$C-acetate in Moss Lake. Acetate uptake: top water (——————), mid water (– – – – –) and bottom water (—— —— ——). Glucose uptake: top water △, mid water □ and bottom water ○. Arrow indicates date inflow started running.

fitted by eye. Such plots comprised 60% and 10% of the total data obtained for acetate and glucose, respectively. The limited kinetic data revealed that the heterotrophic potential ($V_{max}$) in Moss Lake was extremely low, ranging from 2–26 ng acetate $l^{-1}$ $h^{-1}$ and 0.8–7.6 ng glucose $l^{-1}$ $h^{-1}$. The highest acetate $V_{max}$ values were consistently obtained from bottom-water samples, but the seasonal pattern of low winter activity rising in spring to a summer peak was essentially the same throughout the vertical profile. Data for glucose $V_{max}$ values were sparse with only 6 plots sufficiently clear to permit a fit by eye. This was largely attributable to the low $^{14}C$ activity necessarily employed to simulate natural substrate concentrations which resulted in large counting errors despite long incubation periods. The limited data nevertheless suggested that glucose uptake was of a similar order to that of acetate and followed a similar seasonal pattern. Estimated respiration of the two solutes also proved difficult to obtain with only two of the results differing significantly from blank values. This was attributable in part to the low counts, but the main error was in the high blanks probably due to decomposition of traces of substrate during heat sterilization or storage. Stock solutions were acidified before autoclaving to prevent this, but the procedure only reduced the error. Respiration was estimated as 11% and 18% of total acetate assimilation in two bottom-water samples for January 1978.

Despite sampling difficulties, limited $^{14}C$-acetate uptake studies were made on the shelf site. These indicated that before the melt began on October 5, 1977, activity in the shelf water column (1.5 m) was almost twice (6.2 ng acetate $l^{-1}$ $h^{-1}$) the corresponding trough top-water value and comparable to the trough bottom-water $V_{max}$ value (7.8 ng $l^{-1}$ $h^{-1}$). This would seem to indicate further the significance of the proximity of the sediment surface to bacterial activity and support the hypothesis of the shelf providing the initial inoculum of active bacteria to trough upper water layers in spring.

Fifteen separate attempts to measure photoheterotrophic uptake of organic solutes failed to show any evidence that this process was operating at detectable levels in Moss Lake during 1977–78.

Turnover times for the natural substrate of 85–1 300 h for acetate and 135–1 650 h for glucose indicate that activity was negligible for a major part of the year throughout the trough water column (Table V). Bacteria in the bottom-water layer were most active from September to March, whereas in the mid-water layer, activity was effectively restricted to the November to March period. Microbial populations in the upper water never gave turnover times less than 405 h although turnover times were shortest during spring and summer as in the other water column sampling depths.

$K_t + S_n$ is an estimate of the maximum natural substrate concentration ($S_n$). Values were in the range 2–6 μg $l^{-1}$ acetate and 1–2.5 μg $l^{-1}$ glucose, indicative of low, relatively stable con-

TABLE V. KINETIC DATA FOR HETEROTROPHIC UPTAKE OF $^{14}C$-ACETATE AND $^{14}C$-GLUCOSE

| | *$T_t$-Turnover times* (h) | | | *$K_t+S_n$* (μg $l^{-1}$ Solute) | | |
|---|---|---|---|---|---|---|
| *Date* | *Top water* | *Mid water* | *Bottom water* | *Top water* | *Mid water* | *Bottom water* |
| May | 1 080 | 1300 | 665 | 2.8 | 2.6 | 4.0 |
| July | 1 005 | 850 | 835 | 2.9 | 3.2 | 3.5 |
| July | 1 480 | 840 | 580 (1 650) | 3.1 | 3.5 | 4.9 (2.4) |
| Sept | 980 | 1205 | 595 | 3.1 | 2.6 | 4.9 |
| Oct | 1 400 | 675 | 365 | 3.2 | 3.6 | 5.0 |
| Oct | 895 | 810 | 390 | 3.2 | 3.7 | 4.5 |
| Nov | 640 | 890 | 490 | 4.4 | 3.4 | 5.7 |
| Nov | 495 (1200)* | 350 | 430 | 4.7 (3.4) | 4.5 | 5.0 |
| Dec | 585 (370) | 230 | 852 (135) | 4.8 (2.4) | 4.5 | 2.2 (1.0) |
| Jan | 405 | 240 | 245 | 4.5 | 4.0 | 4.4 |
| Feb | 525 | 505 (310) | 330 (140) | 4.4 | 4.6 (6.6) | 4.8 (7.1) |
| Mar | 435 | 285 | 360 | 4.7 | 4.6 | 4.9 |

*Data in brackets—glucose kinetics values.

centrations of these two substances in the lake water throughout the year (Table V). The results also imply a relatively high substrate affinity for the two solutes within the microbial population since $K_t$ (the transport constant) was also necessarily low. No seasonal pattern for $K_t + S_n$ was discernible except that generally higher values were recorded in the bottom-water layer.

The physiological activity per average bacterium throughout the year ($V_{max}$ cell$^{-1}$) was calculated from the regression of $V_{max}$ data on direct microscopic counts. The limited number of glucose $V_{max}$ values proved statistically unacceptable, but the acetate data gave a $V_{max}$ cell$^{-1}$ of $6.97 \times 10^{-11}$ µg h$^{-1}$ cell$^{-1}$, significant at $P < 0.001$ ($r = 0.62$, $n = 36$). No significant relationship was demonstrated between plate counts and $V_{max}$ data.

Dissolved organic carbon values for the lake were obtained at intervals throughout the year. Highest DOC concentrations were recorded in late winter when 6.8 mg l$^{-1}$ DOC was measured in top-water samples and 4.5 mg l$^{-1}$ in bottom-water samples. The high surface value probably reflects increased concentration due to "freezing out". When the inflow started, DOC levels decreased (3.1 mg l$^{-1}$ in top water) and with the disappearance of ice cover a well mixed water column was in evidence with a uniform value of 2.7 mg l$^{-1}$ throughout the entire profile. Clearly, DOC was never particularly high in Moss Lake water, and this can be explained by the low allochthonous input from melt water and low biological activity.

*Production studies*

Both algal (Table II) and bacterial production (Fig. 9) followed essentially similar seasonal patterns with highest activity occurring during the open-water period and negligible activity detectable for most of the winter. Maximum algal photosynthetic production was estimated as 31.0 mg C m$^{-3}$ d$^{-1}$ at 1.5 m depth on December 30, 1977, whilst bacterial production (based on the 6% factor) gave a maximum value at the same depth of 12.4 mg C m$^{-3}$ d$^{-1}$ (on February 15, 1978). Due to the high transparency of the water and the effects of wind mixing, open-water production by both these groups of organisms decreased only marginally down the water column. However, in winter, when photosynthetic activity was undetectable, bacterial production was measured in bottom-water samples, possibly reflecting the proximity of sediment and benthic plant communities. The use of a 5.0 µm prefilter gave only a crude separation of bacterial and

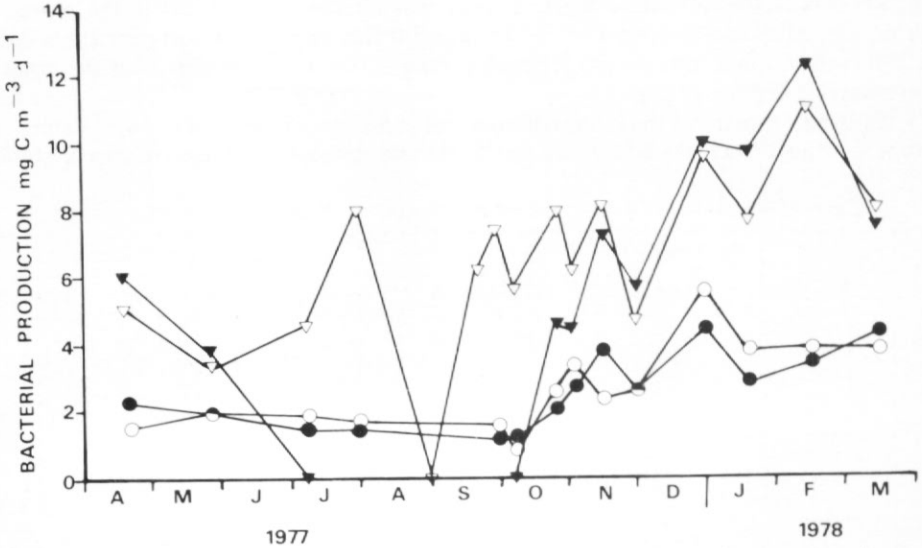



Fig. 9. Seasonal patterns of bacterial production as derived from radio-isotope uptake (▼ top water, ▽ bottom water) and microscopic count methods ( ● top water, ○ bottom water). Mid-water data has been omitted for clarity but generally followed bottom-water patterns.

algal populations since microscopic preparations revealed bacteria still firmly attached to algal particles after filtration. This leads to an underestimate of bacterial $CO_2$ fixation and was corrected by measuring $^{14}C$-acetate uptake by filtered and unfiltered samples on each occasion and assuming that algae do not assimilate DOC at low concentrations (Wright and Hobbie, 1966). The percentage of $^{14}C$-acetate assimilating bacteria not passing the filter corresponded to between 11% and 38% of the total and no clear seasonal pattern could be discerned from the data. However, comparison of corrected bacterial $CO_2$ fixation with total dark fixation suggested that bacterial activity represented *c.*88% of total dark $CO_2$ fixing activity in winter whereas in summer, this value fell to *c.*30% indicating significant algal dark fixation during this latter period.

Estimates of bacterial production derived from microscopic count data (Fig. 9) and generation rate experiments were of a similar order to, but usually somewhat lower than, values derived (using the 6% factor) from $^{14}CO_2$ dark uptake. No clear difference in production was noted between top- and bottom-water samples even in winter and seasonal variation in activity was less pronounced than in the $^{14}CO_2$ data. On an annual basis (Table VI), bacterial production was calculated as 2.65 g C $m^{-2}$ (microscopic method) and 4.99 g C $m^{-2}$ ($^{14}CO_2$ method), significantly lower than algal particulate carbon production of 12.79 g C $m^{-2}$ (including algal dark fixation, 0.19 g C $m^{-2}$). Algal extracellular production was measured (in duplicate) on five occasions during 1977–78 and the mean results (Table II) indicate that whilst top- and mid-water algal populations released 3–17% of total carbon incorporated, bottom-water populations released a significantly higher proportion (19–39%) possibly indicative of unhealthy cells. With such limited data no overall seasonal pattern was discernible, but a rough estimate of annual extracellular production gave a value of 1.5 g C $m^{-2}$ $y^{-1}$, which is about 10% of the total annual algal production (14.29 g C $m^{-2}$).

Sorokin (1973) suggested that decomposition of DOC by bacteria could be approximated using the empirical relationship, Decomposition rate (D) = (Heterotrophic $CO_2$ Fixation) × 56 (mg C $m^{-3}$ $d^{-1}$). Substituting the dark $^{14}CO_2$ fixation value (0.30 g C $m^{-2}$ $y^{-1}$) into this equation gave a value of 16.80 g C $m^{-2}$ $y^{-1}$ for bacterial decomposition . A second estimate was obtained by taking 6% of the bacterial production value derived by microscopical methods to represent heterotrophic $CO_2$ fixation (6% of 2.65 = 0.16 g C $m^{-2}$) and this gave 8.96 g C $m^{-2}$ $y^{-1}$ (Table VI). These values are of a similar order to those calculated for algal production and suggest that bacteria play a significant role in Moss Lake water column.

TABLE VI. ANNUAL ASSIMILATION AND DECOMPOSITION DATA FOR MOSS LAKE WATER COLUMN

| *Component* | g C $m^{-2}$ $y^{-1}$ |
|---|---|
| Particulate algal production | 12.60 |
| Extracellular algal production | 1.50(10.4% of total) |
| Algal dark $CO_2$ fixation | 0.19 |
| Total algal carbon production (1) | 14.29 |
| Bacterial dark $^{14}CO_2$ fixation (2) | 0.30 |
| Total fixed carbon ((1)+(2)) | 14.59 |
| Bacterial biomass production | |
| derived from microscopic counts | 2.65 |
| derived from $^{14}CO_2$ dark uptake data | 4.99 |
| Bacterial decomposition of DOC | |
| derived from microscopic counts | 8.96[a] |
| derived from $^{14}CO_2$ uptake data | 16.80[b] |
| Allochthonous C input | unknown, but probably negligible |
| Losses (outflow, sediment, grazing) | unknown, but probably small |

[a] value obtained from indirect estimate of heterotrophic $CO_2$ fixation (6% of 2.65 ± 0.16) × 56 (Sorokin, 1973).

[b] value obtained from direct estimate of $CO_2$ fixation (0.30) × 56.

## Discussion

Chlorophyll-*a* concentrations were consistently low throughout the water column with the exception of bottom-water samples during the spring and the entire column during early winter. Lowest chorophyll levels were associated with the summer and winter periods when the two extremes of light climate were encountered, whilst high chlorophyll concentrations were found under snow-free ice cover, a feature also noted elsewhere by Maeda and Ichimura (1973) and Albrecht (1964). Severe photo-inhibition at high summer-light intensities has been frequently reported from clear Antarctic lakes (Goldman and others, 1963, 1972; Tominaga, 1977). Goldman and others (1963) also reported that at lower temperatures photo-inhibition occurred at lower light intensities. Long day length as encountered in summer at high latitudes probably accentuates the degree of inhibition. Thus, Wright (1964) established that phytoplankton in Beaver Pond, Canada, migrated to deeper water in response to high light intensities and Kalff and others (1972) reported similar movements in Char Lake, High Arctic. No obvious evidence of this phenomenon was found in Moss Lake, but sampling was not sufficiently frequent or detailed to confirm or refute the possibility.

In contrast to the low biomass levels, significant algal production was measured in Moss Lake with an annual particulate carbon production about three times that of Char Lake (Kalff and Welch, 1974). However, Lorenzen (1979) has suggested that the use of glass bottles can enhance upper-water production estimates by absorbing otherwise inhibitory UV-B radiation. Fogg and Horne (1970) concluded that UV radiation may be a major factor controlling the level of production in shallow Antarctic freshwater lakes. Since very little light attenuation occurred in Moss Lake (see Priddle, 1980*a*) the possible overestimate attributable to the use of glass bottles was almost certainly significant to a considerable depth. Kalff and Welch (1974) did not indicate what type of bottle they used in the Char Lake study. In the above context it is interesting to note that benthic algae felts, in shallow areas of Antarctic lakes, contain high concentrations of carotenoid pigments which may selectively absorb the damaging wavelengths (Goldman and others, 1963; Fogg and Horne, 1970; Priddle and Belcher, 1981). In addition, CPS plates of upper-water samples in the present study were invariably dominated by orange-pigmented bacteria, a feature also noted by Anderson and Dokulil (1977) whilst studying oligotrophic Canadian mountain lakes.

Winter survival of algae in alpine lakes is aided by reduced respiration rates at low temperatures, thus permitting lower compensation points (Wright, 1964; Morgan and Kalff, 1975). In Signy Island lakes, the light intensity beneath the ice around midwinter is even lower than values for alpine lakes and phytoplankton sediment out (Light and others, 1981). The onset of heavy cover in June caused a similar response in Moss Lake. Priddle (1980*a*) found that, in the clearest of the Signy Island lakes, the benthic algae recommenced net production in late August, but phytoplankton of Moss Lake did not start growth until September/October which indicated higher compensation points than those of the benthic plants. Many cold-water algae are able to survive extended periods of darkness (Bunt and Lee, 1972; Morgan and Kalff, 1975; Antia, 1976) and periodic illumination at sub-compensating light intensities (a frequent occurrence in Antarctic lakes) prolongs survival (Smayda and Mitchell-Innes, 1974). Photo-induced uptake of organic molecules may supplement energy reserves (Bunt and Lee, 1972; Wright, 1964) but experiments carried out on Moss Lake revealed no measurable photoheterotrophy. In the absence of data to the contrary, the conclusions that Signy Island phytoplankton algae probably survive winter darkness by extremely low respiration rates and by encystment (Light and others, 1981; Fogg and Horne, 1970) still provide the most likely explanation.

The range of direct bacterial counts ( $(0.5–2.8) \times 10^8$ cells $l^{-1}$) was remarkably similar to counts recorded for ultra-oligotrophic Char Lake ( $(0.1–2.0) \times 10^8$ $l^{-1}$) in the High Arctic (Morgan and Kalff, 1972) and of a similar order ($5 \times 10^8$ cells $l^{-1}$) to several East European oligotrophic lakes studied by Straŝkraba and Straŝkrabová (1967). Population generation rates were relatively low with comparatively little difference between winter and summer rates. By way

of comparison, generation rates for the least productive area of shallow Lake Balaton in Hungary varied by a factor of *c.*6.5 (Olah, 1974), although a larger temperature range probably contributed to this value. Bacterial plate counts only rarely exceeded $3 \times 10^6$ CFU $l^{-1}$ and higher counts were found only in top-water samples during November and December. The evidence indicated that very little mixing occurred during spring and that the shelf area was the most likely source of these viable cells. Schindler and others (1974) described how melt water running into Char Lake during early melt flowed under the ice raft and over the winter water body which contained high electrolyte concentrations. The two water layers only mixed at the onset of wind-induced turbulence during open water. The present study shows that the same sequence of events occurred in Moss Lake as it regained its summer level. Thus, the high numbers of viable bacteria swept into the lake trough from the shelf region during spring made only a small contribution to lake carbon cycling as the majority were swept throught the lake to the outflow. By the time mixing had begun, inflow rates had decreased markedly and maximum lake volume had been achieved, so the influence of the shelf population on the trough station was greatly reduced.

In Moss Lake there was a significant seasonal correlation ($P<0.001$) between acetate $V_{max}$ (glucose data being inadequate) and total bacterial numbers similar to the glucose $V_{max}$ correlation with direct counts shown by Morgan and Kalff (1972) in Char Lake, and by Ramsay (1978) for a range of oligotrophic and mesotrophic New Zealand lakes. This implies that physiological activity per average bacterium in these lakes changed very little throughout the year, a conclusion supported by the consistently long turnover times recorded in all these systems. Glucose uptake has been related to viable counts of bacteria by various workers (Allen, 1969; Gorden, 1969; Seki and Kennedy, 1970), but in the present study no correlation could be found between plate counts and $V_{max}$. There are two possible explanations assuming no significant sampling error; first, the Signy Island data were calculated from acetate $V_{max}$ values because an insufficient number of glucose $V_{max}$ values were available and, secondly, the fact that two different agar media were used. Wright and Hobbie (1965) noted that whilst acetate-utilizing bacteria were associated with large particles, glucose utilizers were not, implying that the acetate-utilizing and glucose-utilizing populations were different and certainly very few lake isolates from Signy Island grew well on acetate media. It was concluded from extensive tests using various media that CPS consistently gave higher counts of bacteria than commercial media such as Oxoid and Difco nutrient agars and Oxoid tryptone soya agar. Similar findings were reported for English lakes by Jones (1970). Furthermore, it was demonstrated that these latter media favoured fast-growing bacteria which were possibly the group actively metabolizing in the lake environment and measured by $^{14}C$ heterotrophic uptake experiments whilst CPS also brought out slow-growing bacteria. If so, a correlation of bacterial counts on nutrient agar with $V_{max}$ would be anticipated, but not on CPS.

Kinetic uptake of glucose by bacteria has been measured in aquatic environments of varied trophic status (Wright and Hobbie, 1965; Vaccaro and Jannasch, 1966; Allen, 1969; Hamilton and Preslan, 1970). A plot of the seasonal glucose $V_{max}$ range ($y$) against the mean daily primary production ($x$) for a range of lakes gave a direct relationship of bacterial activity with lake trophic status (Morgan and Kalff, 1972, fig. 3). Hobbie and Rublee (1977, fig. 14.7) demonstrated that this relationship was complicated when pollution and/or sediments had a strong influence. Moss Lake was kinetically comparable with Lapland lakes (Hobbie and Wright, 1968) and Char Lake (Morgan and Kalff, 1972) and, from the proposed relationship, can therefore be classified as extremely oligotrophic.

From Table VI, it would appear that algae produced 2–3 times more POC than bacteria. However, mineralization by bacteria was equivalent to 62–117% of total algal carbon production (14.29 g C $m^{-2}$) in 1977–78. The reliability of the bacterial activity estimates can be questioned since both microscopic and $^{14}CO_2$ methods rely on conversion factors. Overbeck and Daley (1973) pointed out that in laboratory studies, the assimilation ratio for heterotrophic $CO_2$ fixation could range from 0.5–12% and more recently, Jordan and Likens (1980) found that

bacterial production derived using the 6% factor was significantly higher than estimates based on organic C fluxes, $^{35}SO_4$ uptake and the microscopic count method. Production estimates based on microscopic examination generally seem to give lower values than other methods due to losses via grazing and bacterial DOC production. Grazing was not apparently important in the present study, but copious amounts of mucopolysaccharide-like material was noted in microscopic preparations. It therefore seems reasonable to suggest that true bacterial production lies between 2.65 g C $m^{-2}$ and 4.99 g C $m^{-2}$. Schindler and others (1974) established that carbon input from the catchment area was negligible in the carbon budget of Char Lake. Moss Lake input was similarly composed of melt water and derived from a far smaller catchment, so it seems probable that carbon input was again small. If so, the data presented in Table VI suggest that virtually all the carbon input (essentially allochthonous) was utilized by bacteria.

Priddle (1980*a*) estimated production values of 40 g C $m^{-2}$ and 45 g C $m^{-2}$, respectively, for the mosses and algal felts in clear Signy Island lakes. But mosses represent 10% and algal felts only 5% of the total lake surface area in Moss Lake so these values are not as significant in whole lake terms. The contribution of the shelf communities has not been assessed as yet, but was clearly restricted by ice scour. Production data given in Table VI, therefore, almost certainly represent a conservative estimate of the true production value.

Zooplankton involvement in water column carbon cycling is completely unknown due to the heterogeneous distribution throughout Moss Lake. The majority are benthic browsers, some of which (especially copepods) migrate vertically at intervals (Heywood, 1967; Weller, 1977; Dartnall, 1979). Throughout this study, animals were present in extremely low numbers and their contribution to carbon cycling in the water column is therefore unlikely to have been significant.

It is concluded that bacteria represent an important component of the planktonic population in Moss Lake, although algae were the predominant organisms. The bacteria were closely linked with the algae, reflecting nutrient dependence in the absence of allochthonous nutrient sources. Algal activity ceased under winter snow/ice cover and bacterial activity correspondingly decreased as a significant proportion of the population sedimented out attached to larger particles. Annual algal production was three times greater than in Char Lake in the High Arctic, and this may possibly be attributed to the high assimilation efficiency common to Antarctic freshwater algae (Light and others, 1981). Bacterial numbers and physico-chemical parameters, however, were comparable with those of Char Lake and bacterial uptake of dissolved organic solutes in the two systems were remarkably similar, being some of the lowest on record. Moss Lake appears to be eminently suitable as a base-line for studies of eutrophication in Antarctic freshwater ecosystems, as Char Lake is for Arctic ecosystems.

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