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Photosynthate distribution by microplankton in permanently ice-covered Antarctic desert lakes[1]

Abstract—The distribution of ^{14}C-labeled photosynthate by microplankton in Lakes Vanda and Fryxell, Antarctica, was measured during the 1984–1985 austral summer. Both lakes had conspicuous deep chlorophyll maxima near the bottom of the oxygenated zone. DCMU sensitivity experiments revealed that photosynthesis below the chlorophyll maximum in Lake Fryxell was partially due to photosynthetic bacteria. These bacteria had notably higher protein and lower lipid labeling than overlying oxic microalgae. Protein labeling in the oxic microalgae had lower I_k and higher α values than for other photosynthetic end products, indicating that protein is synthesized more efficiently at low photosynthetic photon flux density than the other metabolites. The I_k values for complete photosynthesis (<20 μEinst m^{-2} s^{-1}) are among the lowest yet recorded for phytoplankton.

Antarctica is characterized by a paucity of liquid water. Much of the water that exists in the liquid state is in lakes of the dry desert valleys of southern Victoria Land. The permanent ice caps on these lakes, in concert with the highly seasonal regime of photosynthetic photon flux density (PPFD) (i.e. continuous darkness in winter and continuous sunlight in summer) impose globally unique constraints on the growth of photoautotrophic microplankton in these ecosystems.

The first investigations of photosynthetic properties in the dry valley lakes were conducted by Goldman more than 20 yr ago (Goldman 1964). His studies focused on the influences of light and nutrients on complete phytoplankton photosynthesis within their littoral and shallow pelagic zones. Goldman concluded that the organisms were adapted to extremely low light levels and were N deficient. Since then, research has focused on the factors influencing phytoplankton photosynthesis (e.g. Vincent 1981; Vincent and Vincent 1982; Parker et al. 1982). Vincent's work has shown that the phytoplankton in these lakes is physiologically adapted to environmental conditions in discrete strata down the water column, which supports the earlier contentions of Goldman. We report here the first data on the distribution of photosynthate by phytoplankton and photosynthetic bacteria living in the upper and lower portion of the euphotic zone in two permanently ice-covered Antarctic desert lakes during the austral summer.

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Studies were conducted on Lakes Vanda (77°35'S, 161°40'E) and Fryxell (77°35'S, 163°15'E), two permanently ice-covered lakes in the Wright and Taylor Dry Valleys of southern Victoria Land. Lake Vanda has a surface area of 5.2 km^2, a maximum depth of 68 m, and is covered by 3.5 m of permanent ice; Lake Fryxell has an area of 7 km^2, maximum depth of 19 m, and an ice cover of 4.6 m. Because of the permanent ice cover, these lakes have extremely stable water columns and distinct microbial layering (Vincent 1981; Vincent and Vincent 1982). The deep chlorophyll layer exists at

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the bottom of the trophogenic zone between 1.0 and 0.1% of the PPFD incident on the ice cap. Anoxia, relatively warm water, and high salinity (>10 times that of seawater in Lake Vanda) occur in the water layer below the deep chlorophyll maximum (Parker et al. 1982). Further details of the general physical, chemical, and biological properties of these lakes can be found elsewhere.

Sampling and in situ measurements and incubation were done through a 10-cm-diam hole in the permanent ice cap made with a SIPRE coring device over the deepest portion of the lake. Samples were collected with a 1-liter, nonmetallic, discrete-depth water sampler in December 1984. All depths refer to the piezometric water level.

In situ measurements of ^{14}C incorporation were conducted on lake water samples collected from selected depths and incubated with $NaH^{14}CO_3$ (final concn = 0.25 μCi ml^{-1}) in 60-ml screwcap bottles at the depth of collection for about 8 h (~1300–2100 hours). Labeled organisms, harvested by filtration of the entire sample onto Whatman GF/F glass-fiber filters followed by a 10-ml rinse with filtered lake water, were (wet) frozen until analysis.

Past work on lake Fryxell (Vincent pers. obs.) has shown that a distinct band of purple-pigmented organisms, presumably purple sulfur bacteria, exist in the H_2S-rich layer just below the oxycline. To determine the magnitude and physiological characteristics of bacterial photosynthesis in Lake Fryxell, we inoculated a separate set of bottles with 2×10^{-4} M 3-(3,4-dichlorophenyl)-1, 1-dimethyl urea (DCMU), a known inhibitor of eucaryotic oxygenic photosynthesis (Cohen et al. 1975). This concentration of DCMU is higher than that used to distinguish algal from bacterial photosynthesis in other studies (e.g. Priscu et al. 1982 used 10^{-5} M DCMU). Cohen et al. (1975) showed that concentrations of DCMU $>10^{-5}$ M may inhibit anoxygenic bacterial photosynthesis in certain organisms by about 10% at high sulfide concentrations. Inhibition of bacterial photosynthesis by 10^{-4} M DCMU was not evaluated.

The influence of PPFD on photosynthate distribution patterns was determined on lake water samples (3 liters) collected from just beneath the ice cap and from the deep chlorophyll layer of both lakes. The samples were mixed in a 5-liter carboy and distributed into 100-ml bottles that were inoculated with $NaH^{14}CO_3$ (final concn = 0.1 μCi ml^{-1}). They were incubated (in a tent or a small hut) under a range of PPFD levels, obtained with neutral-density screens, for about 8 h. Incident illumination was from natural light. It was necessary to incubate the samples "indoors" to avoid freezing. The "indoors" temperatures ranged from ~0°C to ~8°C which, except for the 57.5-m sample from Lake Vanda, is within the range of ambient lake temperatures from which the samples were collected (i.e. Lake Fryxell: 4.6 m = 0.9°C, 9 m = 3.0°C; Lake Vanda: 3.5 m = 5.2°C; 57.5 m = 19.2°C). The reactions were ended by filtration and rinsing as described above. The initial slope of the PPFD curves, α, and the rate of ^{14}C incorporation per unit chlorophyll at saturating PPFD ($P_m{}^B$) were calculated by the hyperbolic tangent function of Jassby and Platt (1976). We did not include an intercept term (R^B) because visual inspection indicated that the curves passed through the origin and because, in practice, R^B would be a small term subject to a large error (Platt and Jassby 1976). The parameter values of the equation were estimated by nonlinear regression with Marquardt's algorithm. The hyperbolic tangent function without R^B was chosen because our curves had no region of inhibition and only two parameters had to be fitted, which maximized df in the regression analysis.

The major end products of photosynthesis in samples obtained from these ^{14}C experiments were determined by the techniques outlined by Priscu and Priscu (1984). This procedure allows the incorporated ^{14}C to be apportioned into methanol-water-soluble metabolites of low molecular weight (LMW), as well as chloroform-soluble (lipid), hot-trichloroacetic-acid-(TCA)-soluble (polysaccharide), and TCA-insoluble (protein) fractions. Although treatment with hot TCA can hydrolyze nucleic acids in eucaryotic algae, Morris et al. (1974) showed that isotopic labeling of this component is low

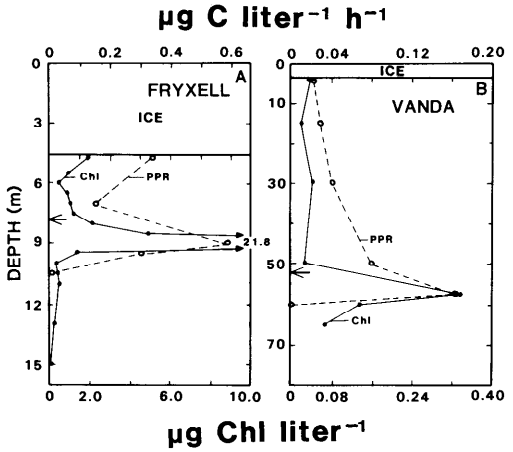

Fig. 1. Vertical profiles of photosynthesis (μg C liter^{-1} h^{-1}) and chlorophyll *a* (μg Chl liter^{-1}). The arrows on the *y*-axes mark the approximate depths of 1.0% PPFD.

relative to polysaccharide. Therefore, we refer to the hot-TCA-soluble fraction as polysaccharide.

Rates of complete photosynthesis were obtained by summing the ^{14}C incorporated into each of the fractions. Comparisons with whole-cell incorporation indicated that virtually all ($X \pm SD = 97.9 \pm 9.2\%$, $n = 10$) of the ^{14}C assimilated by the algae could be accounted for by summing the metabolite fractions. The accuracy and precision of our biochemical fractionation procedure have been given elsewhere (Priscu and Priscu 1984). Concentrations of dissolved inorganic carbon (DIC) in Lake Fryxell were determined on samples that were collected in 30-ml hypovials (previously flushed with N_2) which were frozen in the field. Analysis was by infrared gas analysis of acidified, N_2-sparged samples. DIC values for Lake Vanda were obtained from Parker et al. (1982). Because of the extreme hydraulic stability of Lake Vanda, we suspect that DIC levels vary little from season to season.

Samples for chlorophyll *a* (pheophytin corrected) analysis were filtered onto Whatman GF/F filters and stored frozen until analysis (within 1 month). The filters were thawed and extracted overnight at 4°C in the dark in DMSO which was then diluted 1:1 with 90% acetone. After centrifugation, the fluorescence of the supernatant (pure and acidified) was measured with an Aminco spectrofluorometer calibrated with standard amounts of pure Chl *a*. PPFD was measured with a cosine-corrected quantum sensor (LiCor).

Deep chlorophyll and associated photosynthetic maxima were conspicuous features of both lakes (Fig. 1). The deep maxima in Lakes Fryxell and Vanda were located at a depth where about 0.1% and 1.0%, respectively, of the PPFD incident on the ice cap penetrated, and about 2 m above the oxycline. The deep chlorophyll maximum in Lake Fryxell was very sharp, exceeding the concentration at most other depths in the water column by an order of magnitude. Photosynthetic profiles usually reflected those for chlorophyll and were maximal in the deep chlorophyll layer. Dissolved oxygen was virtually absent below the deep chlorophyll maxima in both lakes. All sampling was done at discrete depths, and fine features of the profiles may have been missed.

Partitioning of photosynthate varied down the water column in Lake Vanda (Fig. 2A). The average (±SD) percent ^{14}C incorporation into the lipid, LMW, polysaccharide, and protein fractions in the light was 19.9±4.6, 14.9±1.9, 25.3±1.3, and 39.9±5.9, whereas that during dark incubation was 16.2±2.9, 14.3±1.9, 24.1±1.5, and 45.5±3.2. Although the proportion of ^{14}C incorporated into protein increased by 5.6% on average during dark incubation—primarily at the expense of ^{14}C flow into lipid—no significant differences ($P > 0.10$) existed between light and dark ^{14}C-labeling patterns in Lake Vanda.

The vertical pattern of ^{14}C incorporation into photosynthate in Lake Fryxell (Fig. 2B) was more variable than in Lake Vanda. The average (±SD) percent ^{14}C incorporation in the light into the lipid, LMW, polysaccharide, and protein fractions was 24.9±15.5, 7.4±1.5, 16.0±6.0, and 51.7±13.2; dark incorporation was 5.4±3.7, 8.7±6.1, 28.0±16.8, and 57.8±17.2%. ^{14}C incorporation into the LMW and polysaccharide fractions in the light was significantly ($P < 0.001$) lower in Lake Fryxell than in Lake Vanda. The only significant differences in dark ^{14}C incorporation between the two lakes

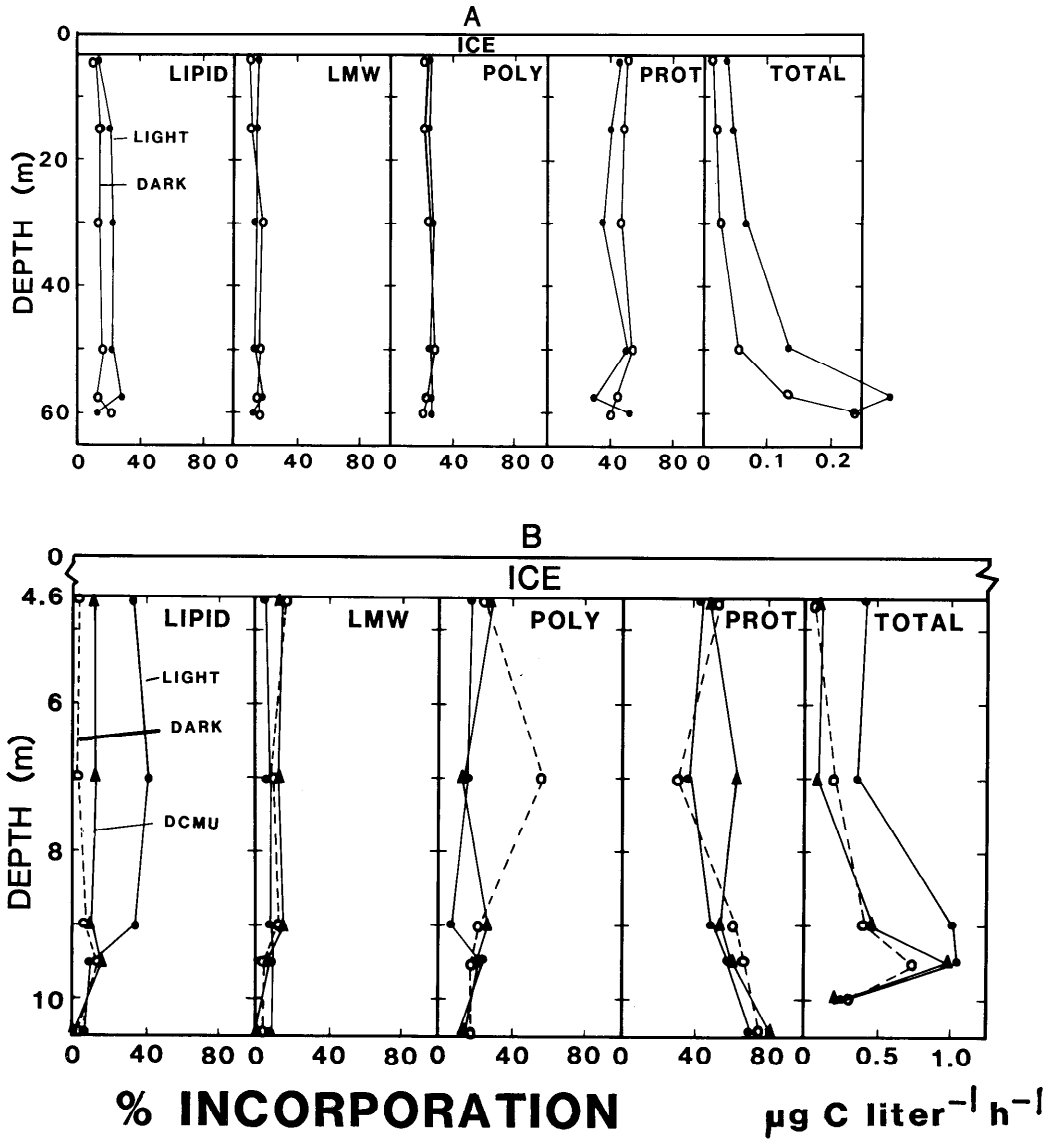

Fig. 2. Vertical profiles of the percent ^{14}C incorporation into lipid, low molecular weight metabolites, polysaccharide, protein, and the rate of total cellular incorporation in light bottles, dark bottles, and in light bottles amended with 2×10^{-4} M DCMU. A. Lake Vanda. B. Lake Fryxell.

occurred in the lipid fraction, which was on average 67% lower in Lake Fryxell ($P < 0.001$). The incorporation of ^{14}C into protein increased below 9 m in Lake Fryxell at the expense of lipid synthesis.

The flow of ^{14}C into storage products (i.e. lipid and polysaccharide) was >40% in both lakes. If ^{14}C flow into protein is considered as a relative indicator of growth (cf. Morris 1981), then our data imply that lipid is the immediate storage product for photoautotrophic growth in these lakes. Variation in the patterns of ^{14}C allocation among the photosynthetic end products is clear (Fig. 3). Relatively strong negative correlations exist between ^{14}C flow into lipid and protein (Vanda: $r = -0.95$, $P = 0.003$; Fryxell: $r = -0.95$; $P = 0.01$) compared to that between polysaccharide and protein (Vanda: $r = -0.04$, $P = 0.93$; Fryxell: $r = 0.10$, $P =$

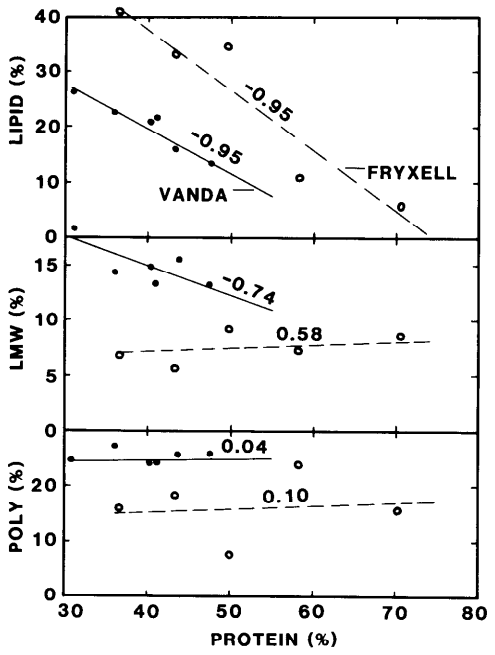

Fig. 3. Relationships between percent ^{14}C incorporation into lipid, low molecular weight metabolites, and polysaccharide and that into protein. (Data from the vertical profiles of light bottle incorporation shown in Fig. 2.) Correlation coefficients are given for each regression line to indicate the intensity of association between the variables.

0.88). Correlations between the LMW and protein fractions from the vertical profiles were not statistically significant ($P > 0.10$) in either lake. Standardized partial regression coefficients (Table 1) from multiple regression analysis of the lipid, LMW, and polysaccharide fractions on protein indicated that, in relative terms, lipid allocation was >3 times more important than polysaccharide or LMW allocation with respect to the pattern of in situ protein synthesis during the incubation period.

The addition of DCMU in Lake Fryxell inhibited photosynthesis (light minus dark inorganic carbon uptake) by 93% at 4.6 m, 100% at 7.0 m, 83% at 9.0 m, and 37% at 9.5 m. Photosynthesis was not measurable at 10 m. The relatively low inhibition of photosynthesis by DCMU at 9.5 m (Fig. 2B) indicates that anoxygenic photosynthesis was the predominant photoautotrophic process in the bottom stratum of the euphotic zone. Consequently, the patterns of

Table 1. Standardized partial regression coefficients from multiple regression analysis of protein (dependent variable) on lipid, low molecular weight metabolite, and polysaccharide (independent variables) labeling in Lakes Vanda and Fryxell. (Data from light bottle profiles shown in Fig. 2.)

	Lipid	LMW	Poly
Lake Vanda	−0.78	−0.31	−0.22
Lake Fryxell	−1.18	−0.11	−0.45

carbon flow in the DCMU-treated samples from 9.5 m would primarily represent photosynthate biosynthesis by photoautotrophic anaerobes. The percent ^{14}C incorporation into the lipid, LMW, polysaccharide, and protein fractions by these anaerobes was 11.5, 6.9, 22.9, and 58.7. This labeling pattern is quite different from the labeling patterns of the aerobic photoautotrophs located above 9.5 m, in which the average (±SD) ^{14}C incorporation in the light into the same constituents was 36.0±4.2, 7.1±1.8, 13.1±5.8, and 43.2±6.6. Protein (+36%) and polysaccharide (+75%) labeling was distinctly higher in the anoxygenic photoautotrophs, predominately at the expense of ^{14}C flow into lipid which was 68% less than for the oxygenic photoautotrophic populations.

The response of complete photosynthesis in these lakes to PPFD resembled saturation curves at all depths tested (Fig. 4). The initial slopes of the curves (α) were higher in Lake Fryxell than in Lake Vanda (Table 2). Within Lake Fryxell, α for the 4.6-m population was on average 25% greater than that at 9 m. The parameter P_m^B was quite different between lakes and between populations within Lake Fryxell. The highest P_m^B value was observed in the 57.5-m community of Lake Vanda followed by the 4.6- and 9-m communities in Lake Fryxell. I_k, calculated by the identity $I_k = P_m^B/\alpha$, represents the PPFD level where extrapolations of α and P_m^B intersect. As such, I_k is a single photosynthetic parameter that is influenced by both P_m^B and α. Talling (1957) introduced this parameter for use as an index of photoadaptation for complete photosynthesis. In addition to this, we have used it to assess the response of photosynthate allocation to varying PPFD levels (dis-

cussed below). I_k for complete photosynthesis was nearly two orders of magnitude greater in the 57.5-m populations that form the deep chlorophyll layer in Lake Vanda than in the deep chlorophyll populations (9 m) of Lake Fryxell. I_k for the phytoplankton populations just beneath the Lake Fryxell ice cap (4.6 m) was about 8-fold that at 9 m in the deep chlorophyll layer of the same lake; I_k for the 4.6-m populations in Lake Fryxell was still nearly an order of magnitude less than that measured at 57.5 m in Lake Vanda. These data imply that the photosynthetic mechanisms of the Lake Fryxell populations can apparently operate more efficiently at low PPFD levels than those in Lake Vanda, consistent with the fact that maximum photosynthesis in Lake Fryxell occurs at a PPFD level about 10 times lower than in Lake Vanda (Fig. 1). Owing to the low sample number in these experiments and to incubation temperatures that differed from in situ temperature, we cannot make further quantitative interpretation of these parameters.

Photosynthate labeling patterns of all the experimental populations exposed to a gradient of PPFD levels showed a similar trend in that protein labeling decreased with increasing PPFD, primarily at the expense of ^{14}C incorporation into lipid (Fig. 5A, B). This redistribution of photosynthate occurred above ~2 μEinst m^{-2} s^{-1} in the 57.5-m community of Lake Vanda, between 18 and 50 μEinst m^{-2} s^{-1} in the 4.6-m community of Lake Fryxell, and between 0.9 and 18 μEinst m^{-2} s^{-1} in the 9-m community of Lake Fryxell. The patterns remained relatively constant above 10 μEinst m^{-2} s^{-1} in Lake Vanda whereas photosynthate redistribution appeared to continue above 18 μEinst m^{-2} s^{-1} in Lake Fryxell, although a paucity of data above 0.9 μEinst m^{-2} s^{-1} in the Lake Fryxell experiments makes this conclusion tentative. Labeling patterns in Lake Fryxell were relatively constant between 0.1 and 0.9 μEinst m^{-2} s^{-1} at both depths examined. That protein label-

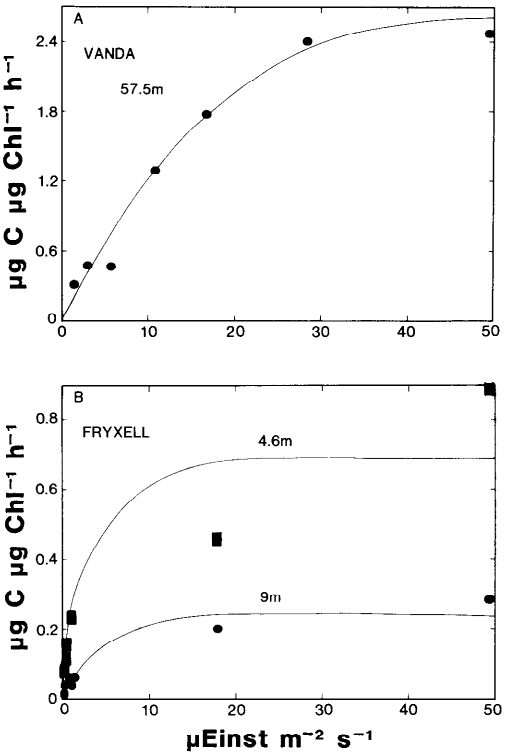

Fig. 4. Relationships between chlorophyll specific carbon assimilation [μg C (μg Chl a)$^{-1}$ h^{-1}] and PPFD (μEinst m^{-2} s^{-1}). A. Lake Vanda community at 57.5 m. B. Lake Fryxell communities at 4.6 and 9 m. The curve was fitted with a hyperbolic tangent function using Marquardt's algorithm.

Table 2. Photosynthetic parameters estimated from the curves shown in Fig. 4 using a hyperbolic tangent function fitted by nonlinear regression with Marquardt's algorithm. α is the initial slope of the curve [μg C (μg Chl a)$^{-1}$ h^{-1}] (μEinst m^{-2} s^{-1})$^{-1}$, P_m^B is photosynthesis per unit chlorophyll at saturation [μg C (μg Chl a)$^{-1}$ h^{-1}], and $I_k = P_m^B/\alpha$. Errors are given as standard deviations. The errors on I_k were obtained by propagation of the variances according to Parratt (1961), assuming independent errors.

	α	P_m^B	I_k
Lake Vanda			
57.5 m	0.131±0.013	2.66±0.179	20.31±2.44
Lake Fryxell			
4.6 m	0.311±0.131	0.689±0.091	2.22±0.973
9 m	0.248±0.030	0.068±0.022	0.27±0.095

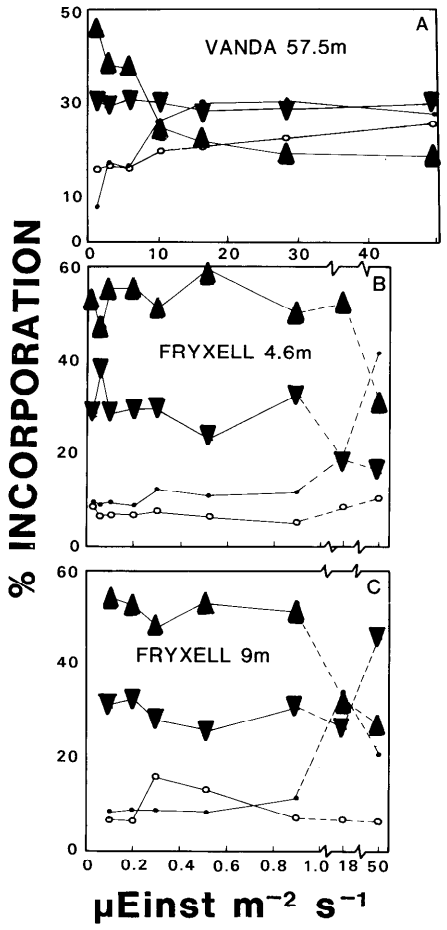

Fig. 5. Percent ^{14}C incorporation into protein (▲), polysaccharide (▼), lipid (•), and low molecular weight metabolites (○) as a function of PPFD (μEinst $m^{-2} s^{-1}$). Samples are from the experiment shown in Fig. 4.

ing and lipid labeling showed the strongest negative correlations in these experiments supports the in situ patterns of photosynthate distribution, which revealed a similar trend. The only major deviation from this pattern was in the 9-m Lake Fryxell experiment where the polysaccharide fraction increased at 50 μEinst $m^{-2} s^{-1}$ at the expense of ^{14}C incorporation into the protein and lipid fractions.

The incorporation of ^{14}C into the major end products of photosynthesis as a function of PPFD followed saturation kinetics. The photosynthetic parameters from these experiments (Table 3) revealed several consistencies. First, protein had the lowest I_k value in all experiments, indicating that ^{14}C incorporation into protein saturates at lower PPFD than does incorporation into storage products and LMW metabolites. Second, the slope of initial ^{14}C incorporation, α, was greatest for protein, particularly in Lake Fryxell. This trend in α implies that protein is synthesized more efficiently at low levels of PPFD than the other metabolic fractions. Finally, P_m^B was highest in the storage products and LMW metabolites whose relative synthesis was stimulated by increasing PPFD.

Studies of the distribution of photosynthate by microplankton growing under ice are relatively rare. By virtue of the variable patterns reported, the studies that have been conducted indicate that low PPFD (<10% of incident PPFD penetrates the ice cap) is not the only major factor contributing to the pattern of photosynthate distribution. For example, Priscu and Goldman (1983*a*) observed that 20.9% of the ^{14}C assimilated by phytoplankton just beneath the ice in a subalpine lake was incorporated into protein, and Palmisano and Sullivan (1985) measured 7.9 and 30.1% ^{14}C incorporation into protein in the congelation ice and platelet ice communities from McMurdo Sound, Antarctica. The major end product in these studies was generally polysaccharide. Our present study reveals that the labeling patterns vary considerably between two Antarctic dry valley lakes. Because prevailing PPFD is not significantly different among the phytoplankton growing in these freshwater systems, other factors must be invoked to explain the variation observed in photosynthate distribution.

The water temperature in Lake Vanda ranged from 5.2°C just beneath the ice cap (3.5 m) to 19.2°C at the depth of the deep chlorophyll maximum (57.5 m), whereas water temperatures in Lake Fryxell ranged from 0.9°C just beneath the ice cap (4.6 m) to 3.0°C in the region of the deep chlorophyll maximum. Despite these temperature variations, no conspicuous relationships between temperature and vertical profiles of the labeling patterns was evident in either lake, indicating that temperature alone did not have a major influence on these patterns. In addition to temperature, the major

Table 3. Photosynthetic parameters for ^{14}C incorporation into the metabolite fractions. (Data from curves shown in Fig. 4.) Errors are given as standard deviations. The errors on I_k were obtained by propagation of the variances about α and P_m^B according to Parratt (1961), assuming independent errors. (Dimensions on α, P_m^B, and I_k as in Table 1.)

	α	P_m^B	I_k
Lake Vanda			
57.5 m			
Lipid	0.035±0.006	0.761±0.092	21.74±4.56
LMW	0.025±0.002	0.684±0.052	27.36±3.02
Poly	0.038±0.004	0.771±0.049	20.29±2.49
Protein	0.039±0.007	0.463±0.040	11.87±2.37
Lake Fryxell			
4.6 m			
Lipid	0.035±0.027	0.349±0.120	9.97±8.42
LMW	0.017±0.015	0.069±0.011	4.00±3.59
Poly	0.102±0.028	0.120±0.015	1.18±0.36
Protein	0.282±0.219	0.120±0.040	0.43±0.36
9 m			
Lipid	0.009±0.003	0.065±0.002	7.22±2.42
LMW	0.007±0.003	0.016±0.002	2.29±1.02
Poly	0.003±0.0001	0.227±0.138	75.70±46.07
Protein	0.037±0.008	0.073±0.006	1.97±0.45

vertical differences in phytoplankton populations, nutrient levels, and PPFD (both intensity and spectral characteristics) (*see* Vincent 1981; Vincent and Vincent 1982) in these lakes seem to have had minimal effect on vertical profiles of photosynthate labeling.

The major difference in labeling patterns with depth occurred in the anoxygenic photosynthetic bacteria present at 9.5 m in Lake Fryxell. Specifically, protein labeling by anoxygenic bacterial photosynthesis was 36% greater than that observed by the aerobic populations above 9.5 m. This increase in protein labeling, with respect to the aerobic populations, was primarily at the expense of ^{14}C flow into lipid, which was 68% lower than in the aerobic populations. Such a pattern may reflect the fundamental metabolic differences that exist between oxygenic eucaryotic and anoxygenic procaryotic phototrophs. Besides the obvious difference in electron donors, photosynthetic bacteria not only fix and reduce CO_2, but can photoassimilate organic compounds anaerobically (Fuller 1979). Because we did not measure the fate or magnitude of organic carbon assimilation at 9.5 m in Lake Fryxell, we are unable to describe the pathways of total carbon assimilation. However, the preponderance of evidence suggests strongly that CO_2 reduction via the Calvin cycle is the major metabolic route of C assimilation in the light (Fuller 1979). Despite the apparent relative unimportance of organic carbon assimilation reported for these organisms, which may be ancillary to and dependent on the Calvin cycle, organic carbon assimilation may be vital to the successful growth and maintenance of these cells (Buchanan et al. 1972). The use of molecular nitrogen as a nitrogen source for growth of photosynthetic bacteria, which has been demonstrated in many species of all groups (Stewart 1973), may also have contributed to the relatively high rates of protein labeling we measured in these organisms relative to eucaryotes, although the high NH_4^+ levels that exist in the region of the photosynthetic bacteria (Vincent 1981) makes this reason for the difference unlikely in Lake Fryxell. Light quality has been shown to have little effect on photosynthate partitioning in photosynthetic bacteria (Hauschild et al. 1962); therefore we presume that the labeling pattern of the 9.5-m sample treated with DCMU is not a spectral response. Further work is needed not only on the physiology of photosynthetic bacteria in Antarctic lakes, but on the contribution that these bacteria

have on total primary production in these lakes.

The strong inverse relationship we observed between lipid and protein labeling in both the in situ vertical profiles and the PPFD experiments indicates that lipid served as the primary short-term storage product for protein synthesis, whereas the polysaccharide fraction may have acted as a long-term product or constitutive component of the organisms. However, elsewhere (e.g. Priscu and Priscu 1984) protein labeling occurred primarily at the expense of ^{14}C incorporation into polysaccharide. Variations between protein and storage-product labeling are most evident when samples are experimentally incubated at different levels of PPFD. In our study, protein labeling predominated at low experimental PPFD primarily at the expense of lipid synthesis, while high protein labeling at low PPFD in the above-mentioned marine studies was primarily at the expense of polysaccharide synthesis. This difference may be partly related to the relatively continuous sunlight that prevailed during our study, which has been shown to support photosynthesis in Antarctic lakes over a diel cycle (Vincent 1981). Until the size and turnover rate of the metabolite pools is measured and other potential pathways of carbon assimilation evaluated (e.g. anaplerotic, chemosynthetic), our hypothesis concerning protein and specific storage product interaction remains speculative.

I_k values for complete photosynthesis in the lakes we studied are among the lowest yet reported for phytoplankton and are considerably below the values of 100–200 μEinst $m^{-2}\,s^{-1}$ typically found for temperate phytoplankton (e.g. Platt and Jassby 1976). The only I_k values comparable to those we measured were observed in microalgae growing in the bottom congelation ice of McMurdo Sound (Palmisano et al. 1985) and in sea-ice microalgae from the high Arctic (Cota 1985). Palmisano et al. reported an average I_k of 5 μEinst $m^{-2}\,s^{-1}$ for this diatom-dominated community. The PPFD levels reaching both the sea-ice microalgae of McMurdo Sound and the phytoplankton of Lakes Vanda and Fryxell never exceeded 7 μEinst $m^{-2}s^{-1}$. Interestingly, Palmisano and coworkers observed strong photoinhibition above 25 μEinst $m^{-2}\,s^{-1}$, whereas photoinhibition was not evident in the Antarctic lake phytoplankton exposed to PPFD levels up to 50 μEinst $m^{-2}\,s^{-1}$. Our finding agrees with that of Cota (1985) who showed that Arctic sea-ice populations do not necessarily photoinhibit at low levels of PPFD. The lower sensitivity of the Antarctic lake phytoplankton to photoinhibition would allow effective photosynthesis during early summer when the ice caps are more transparent (Vincent pers. obs.), although photoinhibition may ultimately become a factor limiting the growth of the Antarctic sea-ice microalgae when surface snow and ice melt allow increased transmission through sea ice.

The assimilation numbers (P_m^B) in the Antarctic lakes were relatively low. Assimilation numbers reported for temperate phytoplankton typically fall between 2 and 10 μg C (μg Chl a)$^{-1}$ h^{-1} (Falkowski 1981), while values for Arctic and Antarctic marine phytoplankton have been reported between 0.6 and 3 (Tilzer et al. 1985). Thus, the assimilation numbers reported here are comparable with those for polar marine phytoplankton but higher than those reported by Palmisano et al. (1985) for the congelation ice community in McMurdo Sound [<0.1 μg C (μg Chl a)$^{-1}$ h^{-1}] and by Cota (1985) for Arctic sea-ice microalgae. Although I_k and P_m^B values for complete photosynthesis in our study were significantly below values for temperate phytoplankton, the photosynthetic efficiencies (α) fell within the range of values reported for both temperate (Harding et al. 1982) and Antarctic phytoplankton (Tilzer et al. 1985) and both Arctic and Antarctic sea-ice microalgae (Cota 1985; Palmisano et al. 1985).

I_k values for photosynthetic end products generally ranged from 11.9 to 27.4 μEinst $m^{-2}\,s^{-1}$ in Lake Vanda (57.5 m) and 1.18 to 9.97 for both the 4.6- and 9-m populations in Lake Fryxell (a single value of 75.7 μEinst $m^{-2}\,s^{-1}$ was calculated for the 9-m polysaccharide fraction). These relatively low values confirm, as do those for complete photosynthesis, the shade-adapted nature of the phytoplankton growing in Antarctic lakes. Clearly, ^{14}C incorporation into protein showed the highest degree of shade ad-

aptation. Work with both cultures and natural populations (e.g. Morris et al. 1974) has also shown that incorporation of ^{14}C into protein saturates at a lower PPFD than does incorporation into storage products. To our knowledge, this pattern seems universal among microalgae.

Ultimately, the physiological state of an organism or population should be expressed in terms of growth rate. Based on particulate N (PN) data collected at the depths where photosynthetic end products were measured (J. C. Priscu unpubl. data), in conjunction with a particulate protein N (PPN): PN ratio of 0.34 (g : g) (Priscu and Goldman 1983*b*) and an N : C ratio for algal protein of 0.30 (g : g) (DiTullio and Laws 1983), we estimate that the average carbon-specific growth rates (μ) in Lake Vanda in terms of ^{14}C incorporated into protein C was 0.090 h^{-1} (range 0.002–0.046) and in Lake Fryxell it was 0.003 (range 0.002–0.006 h^{-1}). These rates can be translated into doublings per day as

$$\text{doublings } d^{-1} = (\mu/0.693) \times 24 \text{ h}.$$

Extrapolating hourly to daily rates through multiplication by 24 is not unrealistic for Antarctic lake phytoplankton during summer because photosynthesis and presumably growth occurs continuously, although at reduced rates during the low light period (Vincent 1981). We emphasize that the accuracy of these estimates depends on the accuracy of our initial assumptions and the degree of intracellular end product cycling. The PPN : PN ratio used for these estimates was obtained from a phytoplankton population forming a deep chlorophyll layer in a subalpine lake—an environment that experiences PPFD and nutrient levels similar to those found in our Antarctic study lakes. Furthermore, DiTullio and Laws (1983) have compiled data showing that the N : C ratio in algal protein is surprisingly constant. Because of these details, we feel that our growth estimates should be reasonably accurate. From the above relationships, average water column doublings d^{-1} of 0.308 (range, 0.069–1.59) and 0.101 (range, 0.069–0.173) were estimated for Lakes Vanda and Fryxell, respectively. The doubling times we estimate for the microplankton in these lakes generally fall within the range calculated for marine (0.050–3.80 doublings d^{-1}) (Eppley 1981) and freshwater (0.001–0.587 doublings d^{-1}) (Forsberg 1985) phytoplankton, despite the permanent ice cap and consequent low PPFD levels.

The surprisingly high microbial growth rates we estimate for Antarctic lakes may be related to extreme hydraulic stability caused by the permanent ice cover. It apparently allows the organisms to adapt precisely to a specific set of environmental conditions—in particular PPFD—that exists at a certain depth. A similar argument can be made for the spatially and temporally stable Antarctic sea-ice microbial community (Palmisano et al. 1985). Hence, from an ecological viewpoint, there appears to be a trade-off between the low levels of PPFD in the water column resulting from the permanent ice cap, which should reduce photoautotrophic growth, and the extreme stability induced by the ice cap, which allows the organisms to adapt precisely to a relatively well defined environment. Further studies on the phytoplankton dynamics in permanently ice-covered Antarctic lakes, which are perhaps the most hydraulically stable aquatic environments known, should provide new information on the relationship between the degree of water column stability and phytoplankton growth.

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