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PRODUCTION STRATEGIES IN ANTARCTIC INLAND WATERS: PHYTOPLANKTON ECO-PHYSIOLOGY IN A PERMANENTLY ICE-COVERED LAKE[1]

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Abstract. Three distinct population strategies were observed within the summer algal plankton of Lake Fryxell (Taylor Valley, South Victoria Land, 77°35′S, 163°15′E). Phytoplankton immediately under the ice (*Ochromonas* and *Chlamydomonas*) were adapted to relatively bright light but were limited by nitrogen availability. A deep maximum of *Chroomonas* and *Pyramimonas* was recorded at the bottom of the euphotic zone. This community did not respond to nitrogen or phosphorus enrichment. It was highly shade adapted but at this depth ambient irradiance was below that required to saturate photosynthesis. Net population increases in both the upper and lower euphotic communities occurred very early in the season. Flagellated algae in the middle of the oxygenated water column swam up to depths of greater light during the day and returned to lower depths of greater nutrient supply at night. These mid-euphotic populations continued to grow throughout midsummer. Comparisons with other Dry Valley lakes suggest that nutrient supply, rather than in situ light or temperature, determines the large lake-to-lake and depth variations in primary productivity. Nutrient availability appears to control algal biomass, but in contrast to arctic ecosystems, low light rather than low temperature dampens algal photosynthesis to cellular rates that are well below those recorded at lower latitudes. The complexity of production strategies in Lake Fryxell, and the occurrence of population maxima early in the season when sampling is logistically difficult, challenge the view that the desert lakes of Antarctica offer ideal and simple systems for limnological study.

Key words: algal production; Antarctica; Arctic; chlorophyll; flagellates; fluorescence; photosynthesis; phytoplankton; polar lakes; production.

INTRODUCTION

The desert lakes of Antarctica have long been described as simple systems that offer unique opportunities for ecological study. These meromictic water bodies lie in the Dry Valley region of South Victoria Land where the recession of the antarctic continental ice sheet has left deep valleys largely devoid of snow and ice cover. The lakes are permanently capped by thick ice which prevents direct wind-induced turbulence. They are further stabilized by temperature and salinity gradients. As a consequence, their phytoplankton are distributed down pronounced and relatively stable gradients of light, temperature, and nutrient regime. These waters contain many fewer plant and animal species than temperate lakes, and many authors have emphasized the extreme simplicity of community structure (e.g., Goldman et al. 1967, Koob and Leister 1972). However, the absence of some groups, such as crustaceous zooplankton, may reflect the geographical isolation of South Victoria Land rather than a particularly severe lacustrine environment (Heywood 1977).

The controlling factors for algal production under the ice have been little explored in Antarctica by comparison with the detailed International Biological Program investigations of north polar lakes. In arctic ice-covered waters biomass levels appear to be under the control of nutrient supply, but productivity per unit biomass (P/B) is dampened by temperature (Rigler 1978). Some arctic algae, however, maintain very rapid rates of metabolism and growth at low temperatures when nutrient supply and light availability are optimal, e.g., generation times of 1.8–1.9 d for *Gymnodinium* at 0°C (Kalff et al. 1975). High arctic lakes therefore respond rapidly to rich nutrient inputs such as sewage (Schindler et al. 1974).

Antarctic lakes offer a useful test of the factors controlling polar production. Water bodies in the Dry Valley region provide an unusual range of physicochemical conditions, including nutrient and temperature regimes that are more typical of temperate latitudes. The present investigation focused on Lake Fryxell, a relatively productive water in the Taylor Valley, to examine experimentally the relative importance of light, temperature, and nutrient supply for strategies of primary production by antarctic phytoplankton.

STUDY SITE

Lake Fryxell (77°35′S, 163°15′E) lies in the lower Taylor Valley at an altitude of 22 m. The lake is permanently covered by 3.8–4.6 m of ice and has an area of 7 km², a maximum recorded depth relative to the upper ice surface of 19 m, and a mean depth of 8 m.

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All sampling was at a midlake station (depth 18 m) over the austral summer of 1979–1980.

Materials and Methods

Holes were bored through the ice with a 10-cm diameter sipre ice auger. Temperature, conductivity, and dissolved oxygen were measured with in situ probes. Light was recorded beneath the ice with a Lambda submersible quantum probe. Water samples were removed from the lake with a hand-operated semirotary force pump.

In vivo fluorescence of chlorophyll was measured with a Turner 111 fluorometer modified with an externally operated shutter over the excitation beam. This instrument was fitted with a blue excitation filter (Corning CS5-60) and a red emission filter (Corning CS2-64). Fluorescence was measured initially (F_a) and after (F_b) the addition of 3-(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU). Chlorophyll concentrations were estimated by a linear regression against F_b values (Slovacek and Hannan 1977). This calibration curve was derived from spectrophotometric determinations of chlorophyll *a* (not corrected for degradation products; Talling and Driver 1963) in methanol extracts of the plankton from a range of depths in Lake Fryxell. The absorbance (A) of these extracts was measured at 480 nm and 663 nm; the ratio of A_{480} to A_{663} provides an approximate estimate of carotenoid content (Strickland and Parsons 1968).

Photochemical capacity was assessed by the cellular fluorescence capacity (CFC) index, defined as $(F_b - F_a)/F_b$. It ranges on a theoretical scale from 0 to 1.0 and is a relative measure of maximum photochemical capacity per unit chlorophyll (details given by Vincent 1980).

Rates of photosynthetic carbon fixation were assayed by the ^{14}C technique of Goldman (1963). Samples were incubated in 60-mL light or dark Pyrex bottles at the depths of collection with ^{14}C-HCO_3^- (1.1 MBq [30 μCi] per bottle). After 4 or 24 h the bottles were retrieved and stored in the dark until filtration (2 h maximum). The labeled cells were filtered onto 0.22-μm Millipore filters which were then acid-fumed for 24 h to remove ^{14}C-carbonates. The filters were air-dried and counted by liquid-scintillation spectrometry. Dissolved inorganic carbon levels were measured within 3 h of collection by acidification and infrared CO_2 analysis.

Samples for phytoplankton enumeration were preserved immediately after collection with Lugol's iodine solution or buffered (50 mmol/L Tris, pH 8.2) glutaraldehyde. Phytoplankton cells were sedimented and counted by inverted microscopy (Utermohl 1958).

To test for algal heterotrophy, samples were incubated in 60-mL light and dark bottles in situ with 1-^{14}C-acetate (37 kBq per bottle, $\approx$8 mg acetate-C/m^3 final concentration) with and without the noncyclic electron flow inhibitor DCMU. After 1 h (1445–1545) 10-mL portions of each sample were filtered through 0.22-μm Millipore filters which were air dried and counted by liquid scintillation spectrometry (incorporated ^{14}C). Each filtered sample was transferred to a 200-mL flask fitted with a Suba-seal (A. Gallenkamp and Co. Ltd.) from which a rectangle of filter paper, folded concertina-style and soaked in β-phenethylamine, was suspended. The samples were injected with HCl and shaken for 1 h to drive off the ^{14}C-CO_2, which was trapped by the β-phenethylamine. Tests with ^{14}C-HCO_3^- added to filtered Lake Fryxell water demonstrated that the efficiency of the CO_2 release and trapping was >97%. The filter papers were transferred to scintillation cocktail and counted (catabolized ^{14}C).

Water samples for nutrient analysis were filtered through acid-washed fine glass-fiber filters (grade GF/F, Whatman Ltd.) immediately after collection and were stored frozen. All analyses were performed on a Technicon AutoAnalyzer II. Nitrite, and nitrate after reduction by hydrazine, were analyzed by the method of Downes (1978*a*), ammonium by the method of Crooke and Simpson (1971), and dissolved reactive phosphate by a modified molybdenum-blue method (Downes 1978*b*).

As a first test of nutritional state of the plankton, populations were assayed for in vivo fluorescence before and after they were exposed to direct sunlight ($\approx$1500 $\mu E \cdot m^{-2} \cdot s^{-1}$) for 2 min. Bright light promotes the spillover of excitation energy from photosystem II (fluorescent) to photosystem I (nonfluorescent) which results in a decrease in fluorescence yield (Vincent 1979). This response to light becomes more pronounced under conditions of nutrient deficiency (Kiefer 1973).

Nitrogen deficiency was measured by the ammonium enhancement assay of Yentsch et al. (1977). When algal cells deficient in nitrogen are enriched with ammonia they rapidly accelerate protein biosynthesis. This places an increased demand on carbon skeletons, which can be replenished by a pathway involving dark CO_2 fixation. Ammonium enhancement is therefore measured as the percentage increase in dark CO_2 uptake upon addition of ammonia. Samples were incubated in duplicate dark bottles at 2°C for 4 h with and without ammonium added at a final concentration of 50 mg NH_4-N/m^3. Dark inorganic carbon uptake over this period of incubation was measured with ^{14}C-HCO_3^- as above.

To examine nutrient deficiency further, samples from 4.5 m and 9.0 m were incubated in situ in duplicate light bottles with and without enrichments of nitrogen (50 mg NH_4-N/m^3) and nitrogen plus phosphorus (50 mg NH_4-N/m^3, 10 mg PO_4-P/m^3). Photochemical capacity (CFC) was measured initially and after 15 h of incubation.

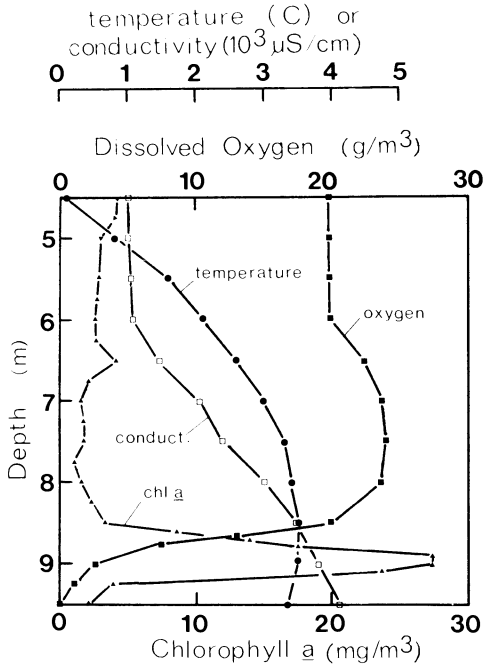

FIG. 1. Characteristics of the water column of Lake Fryxell, 20 November 1979.

RESULTS

General features of the water column

Throughout the period of sampling (November-January) the water column was strongly stabilized by gradients of temperature and salinity (Fig. 1). Temperatures ranged from 0°C immediately beneath the permanent 4.5-m ice cap to a maximum of 3.6°C midway down the water column. Dissolved oxygen levels were above saturation in the surface waters of the lake; concentrations were maximal in the region 6.5–8.0 m and declined abruptly below 8.5 m to zero at 9.5 m and below. Chlorophyll *a* concentrations were typically mesotrophic near the surface of Lake Fryxell (3–4 mg/m^3) but rose to a sharply defined maximum of 27 mg/m^3 at 9.0 m.

Irradiance immediately beneath the ice was ≈1% of the surface light level (Fig. 2). Extinction coefficients for photosynthetically available radiation markedly increased with increasing depth. For layers that were more or less optically homogeneous the coefficients were: 0.09 m^{-1} (5.0–6.5 m), 0.25 m^{-1} (6.5–8.0 m), 0.73 m^{-1} (8.0–9.5 m), and 1.80 m^{-1} (9.5–10.5 m). Below 9.5 m the light-scattering properties of the water increased because of a white suspension that was visually obvious. Minimum irradiance values at "night" were approximately one-fifth of those recorded at midday.

Distribution of phytoplankton

Four distinct regions could be recognized down the water column of Lake Fryxell with respect to algal content (Table 1). In the surface 4.5–6.5 m stratum the dominants were *Ochromonas nannos* (170 µm^3) and a small-celled *Chlamydomonas* sp. (6.2 µm^3). The latter species was equally abundant in the stratum 6.5–8.5 m where the biomass dominant was an unidentified ovoid biflagellate (308 µm^3). The 8.5–9.5 m stratum contained the deep chlorophyll maximum which was due to a red-pigmented cryptomonad, *Chroomonas lacustris* (177 µm^3), and the quadriflagellate *Pyramimonas* sp. (335 µm^3). Population counts for the flagellates declined abruptly below 9 m, and the fourth and deepest region of the lake, 9.5–19.0 m, was devoid of algae.

Over the period of sampling there was a consistent decline in the population densities of *O. nannos* and, to a much greater extent, *C. lacustris* (Table 1). *Chlamydomonas* densities peaked in December whereas the mid-euphotic biflagellate population continued to increase up to January. *Pyramimonas* cell concentrations remained more or less constant between November and January, and by 7 January this species was the biomass dominant at the bottom of the euphotic zone.

Photosynthetic characteristics

Photochemical capacity ranged from 0.21 to 0.60 CFC units down the oxygenated portion of the water column (Fig. 2, 20 November). Below 9.25 m an abrupt decline in CFC marked the bottom of the euphotic zone.

During both day and night, in situ rates of photosynthesis increased with increasing depth to a pronounced maximum at the bottom of the euphotic zone (Fig. 3). Lesser peaks were recorded higher in the water column at 6.5 m (day) and 7.5 m (night). The vertical shift in this mid-column peak suggests a downward migration of algae at night. This is consistent with the mid-euphotic distribution of chlorophyll *a*, which also appeared to shift downwards at night (Fig. 4). Integral photosynthetic rates dropped from 2.10 mg·m^{-2}·h^{-1} during the day to 0.63 mg·m^{-2}·h^{-1} at night.

The potential "energy limitation" at 9.0 m in Lake Fryxell may be partially overcome by an increase in light-capturing ability. The ratio of chlorophyll *a* to cell volume is similar for both the 4.5-m population (4.9 fg/µm^3) and the deep chlorophyll maximum (3.7 fg/µm^3). However, the 480 nm to 663 nm absorbance ratio in methanol extracts is high for the 9.0-m samples (3.2) relative to samples from immediately under the ice (2.5). These ratios suggest that the deep-living cells are richer in accessory carotenoid pigments. The cryptomonads from this lower depth also contained a red pigment which could not be extracted with boiling methanol. This was possibly phycoerythrin, which is a non lipid soluble "antenna" pigment that transfers excitation energy to the reaction centers of photosys-

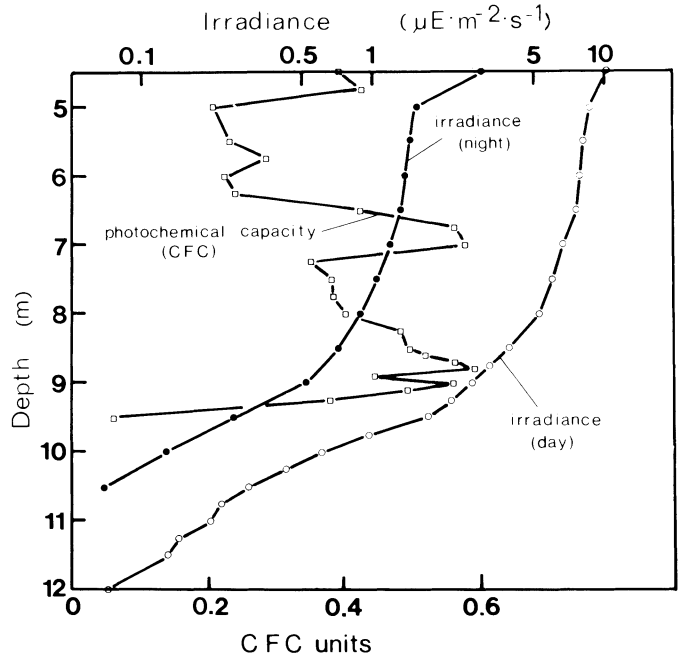

FIG. 2. Depth profiles for midday irradiance (23 November), midnight irradiance (27 November), and photochemical capacity as measured by the CFC index $[(F_b-F_a)/F_b]$ (20 November). All dates were in 1979.

tem II with high efficiency (Govindjee and Braun 1974).

A further adaptation to shade in Lake Fryxell may be a high efficiency of conversion of absorbed light to photosynthate. Assimilation numbers (photosynthetic rates per unit chlorophyll) were lowest at 5 m, but at greater depths were more or less constant at ≈ 100 μg C·mg chlorophyll $a^{-1}\cdot h^{-1}$ (Table 2). However, photosynthetic efficiency (photosynthesis per unit chlorophyll per unit irradiance) markedly increased with increasing depth to a maximum at the bottom of the euphotic zone (Table 2).

As a further guide to light-capturing efficiency down the water column, samples were collected from 4.5, 7.0, and 9.0 m and were incubated in light and dark bottles with ^{14}C-HCO_3^- for 24 h at the top (4.5 m) and bottom (9.0 m) of the euphotic zone. The approximately four fold decrease in light availability down this portion of the water column had a much greater effect on 4.5-m populations than on those samples from greater depths (Table 3). Photosynthesis by algae from the deep chlorophyll maximum was reduced by only 28% despite the large reduction in ambient irradiance.

A more detailed investigation of the shade charac-

TABLE 1. Average concentration (10^9 cells/m^3) of algal dominants in euphotic strata of Lake Fryxell. Each value is derived from discrete samples at depth intervals of 0.5 m or less. A dash indicates $<1.0 \times 10^8$ cells/m^3.

Algal species	Layer (m)	20 November	14 December	7 January
Ochromonas nannos	4.5–6.5	1.8	1.0	0.5
	6.5–8.5	—	—	—
	8.5–9.5	—	—	—
Chlamydomonas sp.	4.5–6.5	0.9	1.8	1.1
	6.5–8.5	1.0	2.4	1.2
	8.5–9.5	—	—	—
Biflagellate (unidentified)	4.5–6.5	0.4	0.3	0.4
	6.5–8.5	0.9	1.4	1.7
	8.5–9.5	—	—	—
Chroomonas lacustris	4.5–6.5	—	—	—
	6.5–8.5	0.8	0.7	—
	8.5–9.5	17.40	6.51	0.17
Pyramimonas sp.	4.5–6.5	—	—	—
	6.5–8.5	—	0.29	1.16
	8.5–9.5	2.59	1.44	2.02

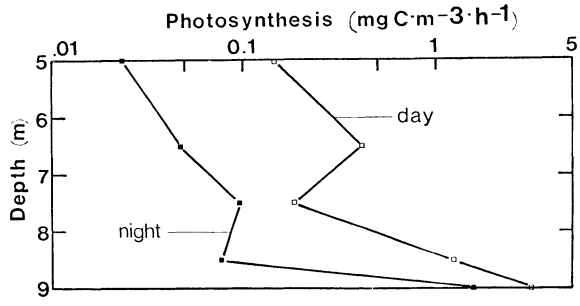

FIG. 3. In situ photosynthetic rates during the day (1340–1740, 23 November) and the night (2315–0315, 27 November). Note logarithmic scale for productivity values.

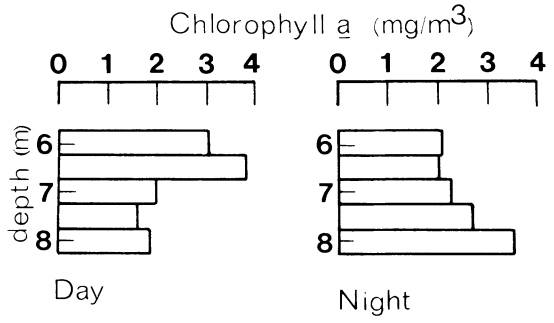

FIG. 4. Distribution of chlorophyll *a* during the day (23 November) and night (27 November) in the mid-euphotic zone. Each bar is the average concentration of chlorophyll *a* in 0.5-m layers, derived from discrete samples at 0.25-m intervals.

teristics of deep-living phytoplankton in Lake Fryxell was performed with a 24-h displacement incubation at 9.0-m water at six depths. Maximum photosynthetic rates were recorded at 6.5 m (Fig. 5). Photosynthesis was measurable at the incubation depths of 9.5 m (where it was 73% of that at 9.0 m) and 10.5 m (34% of that at 9.0 m). Both of these depths lie in anoxic waters where CFC is negligible; the sharp cutoff of the trophogenic zone at 9.25 m must therefore be due to factors other than light availability. The I_k value (a measure of the onset of light saturation of photosynthesis; Talling 1957) was 0.1% of surface irradiance, indicating adaptation to extreme shade conditions.

Test for algal heterotrophy

A mechanism which might further aid algal growth in the deep euphotic zone is supplemental heterotrophic nutrition. In an in situ incubation with 1-^{14}C-acetate, light significantly stimulated both incorporation (14% increase) and catabolism (9%) of the ^{14}C label (Table 4). This light response was not observed in samples incubated in transparent bottles with the photosystem II inhibitor, DCMU. Algal species at this depth may therefore be capable of photoheterotrophic uptake of at least one organic compound at low ambient substrate concentrations.

TABLE 2. Assimilation numbers and photosynthetic efficiencies. Values calculated from daytime photosynthetic data in Fig. 3 and average irradiance ($\mu E \cdot m^{-2} \cdot s^{-1}$) at each depth over the period of incubation.

Depth (m)	Assimilation number*	Photosynthetic efficiency†
5	48.4	5.6
6.5	97.6	12.8
7.5	111.1	18.5
8.5	81.3	25.4
9.0	111.6	41.3

* μg C fixed·mg chlorophyll $a^{-1} \cdot h^{-1}$.
† μg C fixed·mg chlorophyll $a^{-1} \cdot h^{-1}$·unit irradiance^{-1}.

TABLE 3. Displacement experiment. Photosynthetic rates (mg $C \cdot m^{-3} \cdot d^{-1}$) for samples incubated at the top (4.5 m) and bottom (9.0 m) of Lake Fryxell's euphotic zone. Each figure is calculated from the difference between duplicate light and dark bottle incubations, 6 December 1979.

Collection depth (m)	Incubation at 4.5 m	Incubation at 9.0 m	Percent reduction
4.5	1.02	0.42	68
7.0	0.78	0.54	31
9.0	101.52	73.20	28

Nutrient status of the plankton

The ratio of chlorophyll fluorescence before and after 2 min of bright light on 10 December decreased from 1.56 (range for duplicate assays of ±0.07) at 4.5 m, to 1.28 (±0.07) at 7.0 m, and 1.16 (±0.002) at 9.0 m. The same trend of decreasing depression of fluorescence with increasing depth was also observed earlier in the season (20 November). These data suggest that nutrient deficiency was most pronounced in the surface *Ochromonas*-dominated community.

Inorganic nitrogen and phosphorus concentrations increased with increasing depth down the water column (Table 5). Immediately within the anaerobic zone, ammonium and phosphate levels rose by two orders of magnitude. Dissolved inorganic N:P ratios at all depths were low relative to the 10:1 ratio found in algal cells (Vollenweider 1968).

Ammonium enhancement assays were performed on plankton material from throughout the euphotic zone on 4 December to assess nitrogen deficiency. Dark carbon uptake in samples from 4.5 m and 6.5 m was significantly stimulated by addition of ammonium ($P < .05$, Table 5). Samples from 7.5 m and below did not respond to ammonium additions.

The photochemical capacity of 4.5-m samples as measured by CFC also responded to the addition of nitrogen. After 15 h of in situ incubation on 14 December the CFC increased by 0.166 units (50 mg NH_4-N/m^3 added vs. no addition: $t = 6.87$, $.025 > P > .01$, df = 2). On the same date there was no greater response to nitrogen plus phosphorus (50 mg NH_4-N/m^3, 10 mg PO_4-P/m^3 final concentration; N + P vs. N: $t = 1.96$, $P > .1$, df = 2). In a repeat of this experiment with 9.0-m water there was no significant CFC response to either N or N + P.

DISCUSSION

Three distinct strategies of algal production can be distinguished within the layered assemblage of autotrophs in Lake Fryxell. Immediately beneath the ice, irradiance levels are comparable with the light regime at the bottom of euphotic zones in temperate lakes and oceans. However, nutrient supply in this region is at a minimum for the water column, and the extremely low photosynthetic rates per unit chlorophyll (Table

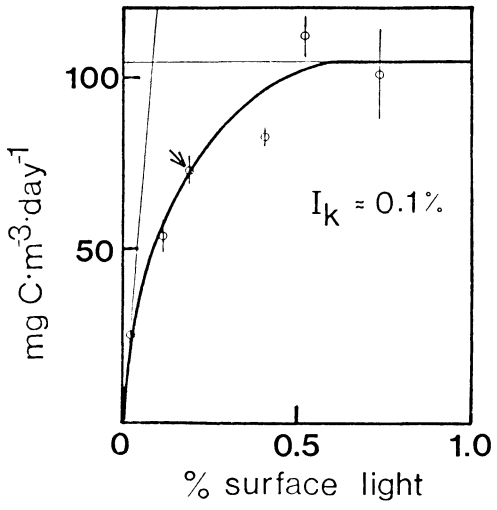

FIG. 5. Effect of displacement on photosynthesis. Water from 9.0 m incubated at six depths for 24 h, 10–11 December 1979. Arrow marks the incubation depth of 9.0 m. Bars represent range for duplicate light bottles minus dark control at each depth. I_k is the point of intersection between the initial gradient and asymptotic value of the photosynthesis/light curve.

2) may reflect severe nitrogen deficiency at this depth. This *Ochromonas*-dominated community declined over the period of sampling. Population growth must therefore be timed earlier in the season when surface nutrient levels are at a maximum after prolonged nutrient regeneration by bacteria over winter.

Nitrogen limitation may be a feature common to the algal communities of several lakes in Antarctica. Goldman et al. (1967) reported that photosynthesis in both littoral and surface pelagic waters of Lake Vanda was enhanced by additions of nitrate but not phosphate. Similar results have been obtained by Tominaga (1977) using the same bioassay on Lake Skallen Oike (69°40′S, 39°24′E). Both of these reports need to be corroborated with alternative techniques in view of recent evidence that the ^{14}C-photosynthesis bioassay is an unreliable and sometimes misleading indicator of N or P limitation (Healey 1979). In Lake Bonney, benthic algal mats contained N and P in ratios of 4.7–6.0 (Weand et al. 1977). When compared with the typical biomass ratio of 10:1, this strongly suggests a shortage of nitrogen. However, NO_3-N in the surface waters of Bonney appeared to be in abundant supply throughout summer, with dissolved inorganic N:P ratios typically ≈37:1 (Weand et al. 1977).

At the bottom of Fryxell's euphotic zone, nutrient availability may be more typical of enriched waters. The gradients in nitrogen and phosphorus concentrations from 9.0 to 10.0 m are extreme, and therefore molecular and turbulent diffusion may be important in recharging the lower euphotic zone with nutrients over winter. Bacterial biomass is maximal for the oxygen-

TABLE 4. Uptake and catabolism of 1-^{14}C-acetate by plankton samples from the deep chlorophyll maximum incubated in bottles at 9 m depth. Each value is the mean for duplicates, 25 November 1979.

Treatment	1-^{14}C-acetate uptake (10^5 decays per minute)		
	Incorporated	Catabolized	Total
Dark	2.73	2.12	4.85
Light	3.11	2.31	5.42
Light + DCMU*	2.60	1.93	4.53

* Noncyclic electron flow inhibitor.

ated water column in this region (W. Vincent, *personal observation*) and consequently nutrient resupply by bacterial mineralization may also be highest here. Primary production by the cryptomonads and *Pyramimonas* (Prasinophyceae) at the lowest euphotic depths is performed in a regime of high nutrient supply but low input of energy. The high photosynthetic efficiency and low I_k value suggest that this community is well adapted to such a dimly lit environment. The I_k value, however, may merely be the consequence of a much-reduced maximum photosynthetic rate per unit chlorophyll (Yentsch and Lee 1966), which is about an order of magnitude below values reported for freshwater plankton at lower latitudes.

Although photosynthetic rates are highest in the 8.5–9.5 m stratum (Fig. 3), dissolved oxygen levels are very low and indicate either extreme activity by heterotrophs or very high rates of respiration by the autotrophs. The transport and catabolism data for ^{14}C-acetate (Table 4) demonstrate that some algae at this depth have the potential to take up and catabolize at least one organic substrate. However, data of this type cannot be considered conclusive evidence of algal heterotrophy in situ (Vincent and Goldman 1980).

The high but rapidly declining biomass levels in the 8.5–9.5 m stratum suggest that net production by algae there begins very early in the growing season when nutrient concentrations are highest and when shading by algae within the same and overlying strata is at a minimum. Net population losses by respiration later in the season may contribute towards the low dissolved oxygen tensions in this zone.

The only region of net production during the summer study period was the mid-euphotic zone. The success of mid-euphotic flagellates may rest on their ability to swim to lower depths of more favorable nutrient regime at night and to return to shallower depths of higher irradiance during the day. This nocturnal migration is supported by day and night profiles of photosynthesis (Fig. 3), chlorophyll *a* (Fig. 4), and CFC (W. Vincent, *personal observation*). It may explain why dark CO_2 fixation by 7.5-m populations was not enhanced by ammonium enrichment despite N levels and N:P ratios similar to those at 6.5 m (Table 5), and why 8.5-m populations demonstrated photosynthetic

TABLE 5. Dissolved nitrogen and phosphorus levels (mg/m³) and percentage ammonium enhancement for dark CO_2 uptake by duplicates from each depth, 4 December 1979. NS = no significant difference in dark CO_2 uptake between samples with and without ammonium enrichment.

Depth (m)	NH_4-N	NO_2-N	NO_3-N	Total N*	PO_4-P	N:P†	With NH_4 enhancement (% increase)
4.5	2.1	1.9	<0.3	3.0	0.8	3.7:1	36
6.0	0.9	2.1	0.3	3.3	0.8	4.1:1	22
7.0	0.9	1.9	1.4	4.2	1.1	3.8:1	NS
8.0	2.3	1.2	1.1	4.6	0.6	7.7:1	NS
9.0	2.3	0.9	3.1	6.3	2.8	2.2:1	NS
10.0‡	252	<0.3	<0.3	252	210	1.2:1	—§

* NO_3-N + NO_2-N + NH_4-N.
† Ratio of dissolved inorganic nitrogen to phosphorus.
‡ Data from S. Nakaya (Hirosaki University) for samples collected 22 November 1979 (*personal communication*).
§ Not tested.

efficiencies more comparable with 7.5-m rather than 9.0-m algae (Table 2). Vertical migration of phytoflagellates is well known in ice-covered lakes at lower latitudes in winter, as for example, in Lake Erken (Nauwerck 1963). A reverse pattern may exist in arctic Char Lake (74°42′N, 94°50′W) where the chlorophyll "center of gravity" shifts 3–4 m over the 24-h cycle, rising at night and sinking during the day (Kalff and Welch 1974).

Vertical layering of algal species is a typical feature of ice-covered waters, including temperate lakes, during winter. Wright (1964) recorded chromatic adaptation beneath the ice of humic-stained Beaver Pond, Massachusetts. Red-pigmented cryptomonads occurred immediately under the ice where the relative proportion of green light was maximal; at greater depths, where red and orange wavebands were proportionately more important, the community shifted towards yellow-green species (chrysomonads). In Lake Fryxell the most penetrating wavebands are probably green and blue, with red light very rapidly extinguished (see Goldman et al. 1967). These reverse light properties relative to Beaver Pond probably account for the reverse chromatic shift recorded in the Fryxell community, with yellow-colored *Ochromonas* beneath the ice but red-pigmented *Chroomonas* in the lower euphotic zone.

Lake Fryxell cannot be considered a simple monoculture of primary producers. Despite a euphotic zone only 4.75 m thick, the floristic and physiological differentiation of planktonic algae with depth is pronounced. This complexity of algal physiologies, in combination with peculiar hydrodynamic properties (e.g., thermohaline convection cells, wind-induced ice-cover movement), untested effects of grazing by rotifera and protozoans, marked variation in community structure of microheterotrophs with depth (e.g., Koob and Leister 1972), and the unusual importance of benthic plant and animal communities (e.g., Parker et al. 1977) challenge the widely promoted view that the inland waters of Antarctica represent uniquely simple systems.

Maximum biomass accumulated in Lake Fryxell early in the season before sampling was logistically possible. The most active period for lake metabolism in Antarctica is probably in early spring when nutrients have accumulated to a maximum and when ambient irradiance has just begun to rise above the compensation point for algal photosynthesis. The most successful strategy for a primary producer under such

TABLE 6. Photosynthetic and physicochemical characteristics of Dry Valley lakes. ND = not detectable.

	Vanda	Bonney (East Lobe)	Fryxell
Integral photosynthesis (mg $C \cdot m^{-2} \cdot d^{-1}$)	14	32*	39
Maximum photosynthesis (mg $C \cdot m^{-3} \cdot d^{-1}$)	1.6	6.1	73.2
Depth of maximum (m)	60	13	9
Temperature at P_{max} depth (°C)	20	7.3	3.6
Light at P_{max} depth (% of surface irradiance)	0.3	8*	0.2
Source of data	Goldman et al. (1967)	Koob and Leister (1972)	This study
Nutrients in upper aphotic zone (from Torii et al. 1975)			
NH_4-N (g/m³)	0.12–0.14	ND–0.37	0.84–4.10
PO_4-P (g/m³)	ND	ND	0.21–1.22

* Data from Goldman et al. (1967).

conditions may be efficient use of low irradiances early in the season to take up and store the limited supply of available nutrients. The extreme field conditions and absence of logistic support in the Dry Valleys at this time of year make these systems difficult to study when they are most active.

Integral photosynthetic rates in Lake Fryxell are higher than in two other Dry Valley lakes for which productivity data are available, Bonney (upper Taylor Valley) and Vanda (Wright Valley). This difference is more striking in terms of maximum photosynthetic rates (P_{max}) within each water column (Table 6). In each of the three lakes, a well-defined P_{max} occurs at the bottom of the euphotic zone where light is suboptimal, but temperatures, and probably nutrient supply, are at a maximum. Qualitative observations from Lake Miers (Miers Valley 78°05′S, 164°00′E) suggest a deep chlorophyll maximum in this lake also; the deep production peak similarly occurs just above the anoxic zone at ≈0.1% of surface irradiance in temperatures (≈5°C) close to the maximum for the entire water column (Baker 1967).

A comparison of physicochemical data from Lakes Vanda, Bonney, and Fryxell indicates that neither temperature nor light regime can account for the large lake-to-lake variation in productivity (Table 6). Light levels are similar in the two extremes, Vanda and Fryxell, and temperatures are lowest in the most productive water, Lake Fryxell. The Fryxell displacement experiments (Table 3, Fig. 5) suggest that light is more limiting than temperature for in situ photosynthesis. However, the temperature range is small in Lake Fryxell and the larger temperature shifts with depth may be more important within the euphotic zones of Lakes Bonney and Vanda.

Nutrient supply varies markedly both within and between the Dry Valley lakes. No comparative figures are available for total N or P content for all of these waters; however, an approximate guide to nutrient status may be obtained from dissolved inorganic N and P levels in the upper aphotic zone of each lake. Unlike nutrient concentrations at higher, euphotic depths, these values are not affected by algal uptake and therefore provide a relative measure of nitrogen and phosphorus regeneration. Furthermore, their magnitude will directly affect the rate of nutrient transfer to the euphotic zone by the molecular or turbulent diffusion. Values for the upper aphotic zone in Lakes Vanda (60–65 m), Bonney (15–22 m), and Fryxell (10–15 m) are presented in Table 6. Ammonium and phosphate levels are much higher in Lake Fryxell than in either of the less productive water bodies. Within the euphotic zone of Lake Fryxell nutrient concentrations increase with depth to a maximum in the region of P_{max} (Table 5). Similar profiles have been recorded in Lakes Bonney and Vanda where NO_3-N levels rise to a euphotic maximum in the region of the deep production peak (Torii et al. 1975). In Lake Bonney, enhanced rates of photosynthetic carbon fixation have been recorded after nutrient enrichment of the euphotic zone by upwelling (Hoehn et al. 1977, Parker et al. 1977). It is therefore probable that nutrient supply, rather than in situ light or temperature, is the primary factor controlling the large variation in productivity both between and within Dry Valley lakes.

In arctic lakes, nutrient levels regulate water column production by controlling algal biomass. Average rates of cellular metabolism, however, appear to be largely independent of nutrient supply but strongly depressed by low temperatures (Rigler 1978). In lakes of the Dry Valley region, water temperatures attain much higher values than in the arctic, but light availability is reduced by thicker, persistent ice-cover, e.g., 4.5 m of permanent ice on Lake Fryxell, but only 2 m on Char Lake, Canada, and this usually melts out in summer (Rigler 1978). Despite the higher temperatures, P/B ratios in the Antarctic are comparable to or lower than those in north polar lakes. Assimilation numbers in Lake Fryxell were typically in the range 50–120 μg C fixed·mg chlorophyll $a^{-1}\cdot h^{-1}$. In the cooler waters of less productive Char Lake, P_{max} attains 225 μg C·mg chlorophyll $a^{-1}\cdot h^{-1}$ (Kalff and Welch 1974).

A comparison between Lakes Vanda and Fryxell further illustrates the lesser importance of temperature. The cell count data collected by Goldman et al. (1967) allow for an order of magnitude estimate of biomass carbon levels in the region of P_{max} (average diameter of coccoid species estimated as 5 μm ≡ 65 μm^3/cell; *Phormidium* assumed to be *P. fragile,* the common species in Vanda as found by Seaburg et al. 1979, ≡ 314 μm^3/100-μm unit; cell volumes converted to biomass carbon by the equation of Mullin et al. 1966). P/B values are thereby estimated as 0.09 d^{-1} for the Vanda populations at 20°C, 0.3% light. A similar calculation for the deep productivity maximum in Fryxell (3.6°C, 0.2% light) on 6 December 1979 yields a P/B ratio of 0.13 d^{-1}. These values are remarkably similar despite very different temperature and nutrient regimes. Light availability at the depth of P_{max} is comparably low in both lakes suggesting that it is this factor which reduces productivity per unit biomass, not temperature. The estimated values of P/B are particularly low by comparison with temperate waters (typically >1.0; Haney 1973) but fall within the range reported from arctic Char Lake (Kalff et al. 1975). In contrast to arctic ecosystems, low light rather than low temperature appears to control cellular rates of algal production, but in polar lakes of both hemispheres nutrient supply exerts an overall control by regulating biomass.

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