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Phytoplankton dynamics in the stratified water column of Lake Bonney, Antarctica

I. Biomass and productivity during the winter–spring transition

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Abstract Phytoplankton populations in perennially ice-covered Lake Bonney, Antarctica grow in a unique non-turbulent environment. The absence of turbulence generated by winds or major streams, combined with strong vertical gradients in temperature and nutrients, create vertically stratified environmental conditions that support three discrete phytoplankton populations in the east lobe of this lake. Phytoplankton biomass and photosynthesis were measured in the east lobe of Lake Bonney during the winter–spring transition (September) to mid-summer (January). During this period, irradiance beneath the ice increased from 0.03 to 1.9 mol quanta $m^{-2} d^{-1}$. Chlorophyll *a* concentrations ranged from 0.03 to 3.8 $\mu g l^{-1}$ within the trophogenic zone (just beneath the permanent ice cover to 20 m) and photosynthesis ranged from below detection to 3.2 $\mu g\ C\ l^{-1}\ d^{-1}$. Our results indicate: (1) phytoplankton photosynthesis began in late winter (before 9 September, our earliest sampling date); (2) maxima for phytoplankton biomass and production developed sequentially in time from the top to the bottom of the trophogenic zone, following the seasonal increase in irradiance; and (3) the highest photosynthetic efficiencies occurred in early spring, then decreased over the remainder of the phytoplankton growth season. The spring decrease in photosynthetic rates for shallower phytoplankton appeared to be related to nutrient availability, while photosynthesis in the deeper populations was solely light-dependent.

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Introduction

Phytoplankton populations at high latitudes experience extreme and rapid transitions in day length and incident irradiance during winter-spring and autumn-winter periods. Among the most southerly phytoplankton populations are those inhabiting perennially ice-covered lakes in the dry valleys region adjacent to McMurdo Sound, Antarctica. At this latitude (77 °S), day length increases from 0 to 24 h over 2 months, after which light is continuous for 3 months. Here we present the first data on the initiation and development of phytoplankton production in Lake Bonney during the period of transition from darkness to continuous daylight (September to January).

The water column of Lake Bonney is dominated by molecular diffusion rather than turbulent eddy diffusion. Approximately 4 m of perennial ice shelters the water column from wind mixing, stream input is low (occurring only 4–6 weeks per year), and strong vertical density gradients virtually eliminate turbulence (Spigel et al. 1990). Phytoplankton populations grow in stratified layers in this low-light (< 50 μmol quanta $m^{-2} s^{-1}$) environment under a variety of chemical and temperature regimes (Koob and Leister 1972; Parker et al. 1982; Lizotte and Priscu 1992a). Strong stratification and low irradiance in Lake Bonney support layered phytoplankton populations that resemble a vertical series of deep chlorophyll maxima (Lizotte and Priscu 1992a, 1994). A low abundance of heterotrophic protists and the absence of crustaceous zooplankton (Parker et al. 1982) reduce phytoplankton losses due to grazing.

Previous studies have examined how nutrient enrichments, temperature and irradiance affect photosynthesis in phytoplankton of the dry valley lakes (e.g. Goldman et al. 1967; Vincent 1981; Vincent and Vincent 1982; Priscu 1989; Priscu et al. 1989; Lizotte and Priscu 1992a, 1994). However, there have been few time series studies on the seasonal development of these

phytoplankton populations. Vincent (1981) reported that phytoplankton biomass in Lake Fryxell did not increase during spring/summer (November to January) and NH_4^+ additions stimulated photosynthetic carbon fixation by under-ice phytoplankton populations but not by deeper populations. Later studies showed that phytoplankton production was supported by regenerated nitrogen in Lake Fryxell at this time of the year (Priscu et. al. 1989).

In Lake Bonney, the distance from the nutricline was a good predictor of the maximum quantum yield of photosynthesis (Lizotte and Priscu 1994). This evidence implies that nutrient availability may control the photosynthetic efficiency of shallow phytoplankton populations. Because photosynthesis-irradiance relationships for all populations in Lake Bonney show that photosynthesis is not saturated by in situ irradiance (Lizotte and Priscu 1992a, 1994), nutrient limitation of photosynthetic efficiency in shallow populations means that in situ photosynthetic production is limited by availability of both light and nutrients. To the extent that primary productivity in the dry valley lakes is limited by nutrient availability, enhanced production would be expected to occur after periods when the remineralization of organic matter exceeds photoautotrophic uptake of inorganic nutrients (e.g. following a long, dark winter). One possible scenario is that nutrients regenerated over winter are exhausted by shallow phytoplankton populations during the initiation of photoautotrophic growth in early spring, after which the phytoplankton depend primarily on nutrients supplied by diffusion from below and by the seasonal flow of glacial melt streams.

Our study is the first to examine phytoplankton dynamics in the lakes of the McMurdo dry valleys during the winter–spring transition. While previous studies established an ecophysiological context for examining phytoplankton production in the dry valley lakes (reviewed by Priddle et al. 1986), the seasonal and spatial development of these phytoplankton populations have not been reported. The purpose of our study was to follow the development and temporal variability of phytoplankton photosynthesis in Lake Bonney and, more specifically, to determine how these polar phytoplankton respond to increasing irradiance during the spring and summer.

Materials and methods

Study site

Lake Bonney is located at the head of the Taylor Valley in southern Victoria Land, Antarctica (77°43′S, 162°23′E). The lake has distinct east and west lobes connected by a narrow, shallow (12 m) channel. The lake is approximately 7 km long and has a maximum width of about 1 km. During our studies, maximum depths were 38 m in both lobes and the ice thickness was 3.7–4.2 m. All samples were collected from a sampling site in the center of the east lobe (site E30 in Spigel et al. 1990). Profiles of conductivity and temperature (Spigel et al. 1990; Lizotte and Priscu 1992a, 1994), oxygen (Lizotte and Priscu 1992a, 1994), light (Lizotte and Priscu 1992a, 1992b) and nutrients (Sharp and Priscu 1990; Sharp 1993; Lizotte and Priscu 1994; Priscu 1995) have been published.

Sampling

Our studies were conducted over two field seasons: 31 October 1990 to 22 January 1991 (the 1990 season) and 9 September to 1 December 1991 (the 1991 season). Holes in the ice of Lake Bonney were drilled with an ice auger (25-cm or 10-cm diameter) and maintained or enlarged by melting with a copper pipe through which heated ethylene glycol was circulated. All depths were measured from the piezometric water level in the ice hole (ca. 30 cm below the ice surface). Water was collected using a 2.2-l Niskin bottle with a Teflon-coated spring. Routine sampling depths were 4.5, 6, 8, 10, 13, 15, 16, 17, 18 and 20 m. During the 1991 season, samples were also collected from 3.9 m. The entire sampling procedure took about 1 hour and was done under a tent to prevent exposure to high light.

Irradiance measurements

Photosynthetically active radiation (PAR; 400–700 nm) was monitored continuously at the surface of the lake (2 m above the ice) with a Li-Cor 2π quantum sensor and under ice at 10 m with a Li-Cor 4π quantum sensor. Data were averaged over 10-min intervals and stored electronically on data loggers.

Water column transparency was determined from irradiance profiles taken at approximately weekly intervals. Diffuse attenuation coefficients for the water column were estimated by a linear regression between log-transformed irradiance and depth. The relationship was linear between 6 and 20 m. Diffuse attenuation coefficients were used to extrapolate irradiance from the 10-m mooring to other depths.

Phytoplankton identification and enumeration

Water samples were preserved with acid Lugol's solution (1% final concentration) immediately upon collection. Samples were allowed to settle for at least 5 days in 100-ml Utermöhl chambers and cells were identified following Seaburg et al. (1979) and enumerated using the inverted microscope technique.

Chlorophyll *a* measurement

Chlorophyll *a* (chl *a*) concentrations were determined from samples of lake water (100–300 ml) filtered to collect particles on 25-mm Whatman GF/C glass-fiber filters. GF/C filters are virtually as efficient as GF/F filters for collecting chl *a* samples from Lake Bonney (Lizotte and Priscu 1992b). Filters were frozen immediately for analysis later (<2 months). Each sample filter was placed in 10 ml 90% acetone, vortexed for 1 min and allowed to extract for 12–24 h at 4 °C in the dark. The efficiency of this extraction procedure was similar to that for samples homogenized in a glass-Teflon tissue grinder. Chl *a* was measured fluorometrically in a Turner Designs model 10 fluorometer calibrated with standard concentrations of purified chl *a* (Sigma Chemical). Extracts were read before and after acidification with 0.2 ml 1N HCl to correct for phaeopigment fluorescence (Holm-Hansen et al. 1965).

Photosynthetic rate measurement

Photosynthetic rates were measured by the ^{14}C method (Parsons et al. 1984). Incubations in situ lasted 24 h and were started between 0600 and 0800 hours local time (sunrise over the mountains). Rates measured with a 24-h incubation were identical to the sum of three 8-h incubations (Sharp 1993). Incubation bottles (acid-washed, 145-ml, Pyrex glass, screw-top), two clear and one opaque, were rinsed three times with the water sample, filled gently to avoid gas exchange, and placed in a darkened box until the entire profile was collected. ^{14}C-bicarbonate (ICN Pharmaceuticals), dissolved in distilled water and stored as a sterile ampulated working solution (120 μCi ml^{-1} in 1990; 121 μCi ml^{-1} in 1991), was added to the samples as a tracer to measure photosynthesis. In the 1990 field season, ^{14}C-bicarbonate solution was added to samples from 4.5 to 10 m and from 13 to 20 m to yield final activities of 0.18 and 0.58 μCi ml^{-1}, respectively. Routine final activities in the 1991 field season were 0.18 μCi ml^{-1} for samples from 3.9 to 10 m and 0.48 μCi ml^{-1} for samples from 13 to 20 m. On 9 September 1991, the final activity was 0.37 μCi ml^{-1} in samples from 3.9 to 10 m, and 1.09 μCi ml^{-1} in samples from 13 to 20 m. Higher activities were used when photosynthetic rates were low and where ambient concentrations of dissolved inorganic carbon (DIC) were high. Following incubation, samples were filtered through Whatman GF/C filters under low vacuum (<0.5 atm). Filters were placed in 20-ml glass scintillation vials, 0.5 ml 3 N HCl was added to volatilize unassimilated ^{14}C-bicarbonate, and the contents were dried on a hot plate at 50 °C.

The radioactivity of seston collected on the filters was measured by liquid scintillation spectrometry. Ten milliliters of CytoScint ES (ICN Pharmaceuticals) liquid scintillation cocktail was added to each scintillation vial. Counts per minute were converted to disintegrations per minute based on sample quench detected by the external standard method. Quench standards were prepared using standard amounts of ^{14}C-toluene quenched with acetone.

DIC was measured using infrared absorption following acidification and sparging with high purity N_2. The instrument was calibrated with a freshly prepared standard of $NaHCO_3$. Peak areas were integrated and converted to mg l^{-1} by means of a standard curve.

Results

Seasonal variation of under-ice irradiance

Daily under-ice irradiance was determined from the diel irradiance logged at 10 m. Examples from the winter–spring transition in 1991 and the latter part of our 1990 field season illustrate the seasonal variation (Fig. 1). Between 14 September and 14 November 1991, daily irradiance at 10 m increased more than 20-fold, maximum irradiance increased 10-fold, and day length increased from 10 to 24 h. The highest irradiance level beneath the ice was 1.9 mol quanta $m^{-2}\,d^{-1}$ (measured in 1990) in mid-November (see Fig. 4); irradiance decreased in late November and early December due to the decreased transparency of the overlying ice (Priscu 1991; Lizotte and Priscu 1992b), despite the steady increase in incident irradiance up to 20 December. Glacial flour from meltstreams, in late December and early January, reduced water column transparency further (Lizotte and Priscu 1992b).

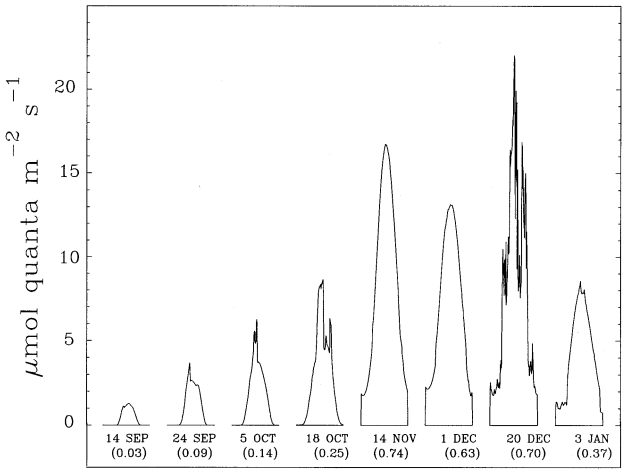

Fig. 1 Selected recordings of diel irradiance (0000 to 2400 hours local time) from 10-m depth in Lake Bonney. Data up to 1 December are from 1991; latter dates are from 1990–1991. Daily flux (mol quanta $m^{-2}\,d^{-1}$) is in parentheses

Vertical distribution of phytoplankton

Microscopic examination of lake water samples revealed three distinct assemblages of phytoplankton within the trophogenic zone (under the ice to 20 m) in the east lobe of Lake Bonney (detailed in Sharp 1993). The abundance of each phytoplankton taxon changed gradually with depth. Phytoplankton composition determined by microscopy was comparable with previous reports for Lake Bonney (e.g. Koob and Leister 1972; Parker et al. 1982). Analyses of pigment composition by HPLC also showed three distinct maxima, each dominated by algae from a different taxonomic group (Lizotte and Priscu 1992c; Lizotte unpublished data).

From beneath the ice to 8 m, *Chroomonas lacustris* (Cryptophyceae) and *Chlamydomonas* sp. (Chlorophyceae) dominated the assemblage; pigment analyses showed dominance by cryptophytes. A middle phytoplankton layer extended from 8 to 16 m, where *Ochromonas* sp. (Chrysophyceae) and an unidentified coccoid alga (<4 μm) were most common; pigment analyses showed dominance by chrysophytes. From 16 to 20 m, the phytoplankton assemblage was composed of *Chlamydomonas subcaudata* (Chlorophyceae), *Ochromonas* sp. and unidentified coccoid algae. Within this layer, the number of the *Ochromonas* sp. remained relatively constant, while the number of *Chlamydomonas subcaudata* increased from November 1990 to January 1991; pigment analyses confirmed dominance by chlorophytes.

Seasonal and vertical distribution of chlorophyll

Three vertical chlorophyll maxima developed during spring (Fig. 2), corresponding to the three taxonomically

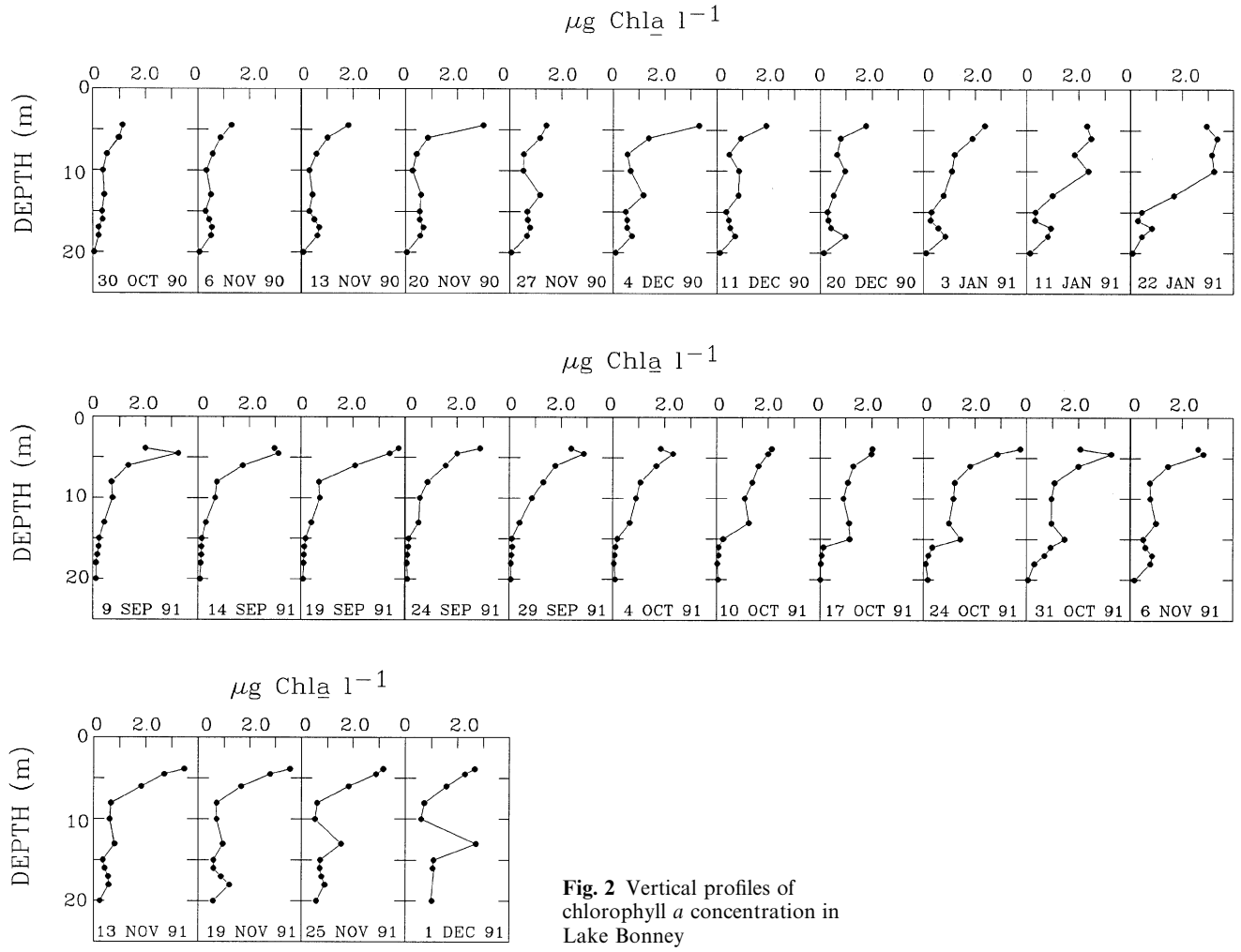

Fig. 2 Vertical profiles of chlorophyll *a* concentration in Lake Bonney

distinct phytoplankton assemblages described above. Chl *a* profiles showed that the vertical extent of the three maxima typically ranged from immediately under the ice to 8 m (shallow), 8 to 16 m (mid-depth), and 16 to 20 m (deep). Chl *a* concentrations within the surface, middle and deep phytoplankton layers ranged from 0.42 to 3.8, 0.10 to 3.3, and 0.03 to 1.2 μg l^{-1}, respectively.

Depth-integrated chl *a* concentrations for each of these layers (Fig. 4) indicated that initial development of the mid-depth maxima, and later, the deep maxima, followed increases in under-ice irradiance. Early season chl *a* data for the shallow population did not show any clear increase. Late spring increases in chl *a* were apparent in both shallow and mid-depth populations at the end of the 1990 field season. These late spring blooms followed several weeks of high stream flow that raised the level of the lake by more than a meter.

Phytoplankton photosynthesis

Photosynthetic maxima always occurred at the same depths as chl *a* maxima (Figs. 2, 3). When the closest dates from each year are compared, photosynthetic profiles show more similarity between years than do chl *a* profiles. The series of profiles (Fig. 3) and the seasonal trends for depth-integrated photosynthetic rates (Fig. 4) indicate that the three major photosynthetic maxima develop sequentially in order of depth (from shallowest to deepest). On the earliest sampling date (9 September 1991), measurable photosynthesis occurred only immediately below the ice. By the end of September [Julian Day (JD) 273], photosynthetic rates were greatest just beneath the ice and decreased exponentially with depth to 15 m. During October (JD 274 to 305) and November (JD 305 to 334), photosynthetic rates within the surface phytoplankton layer did not increase despite increasing irradiance. In October, the

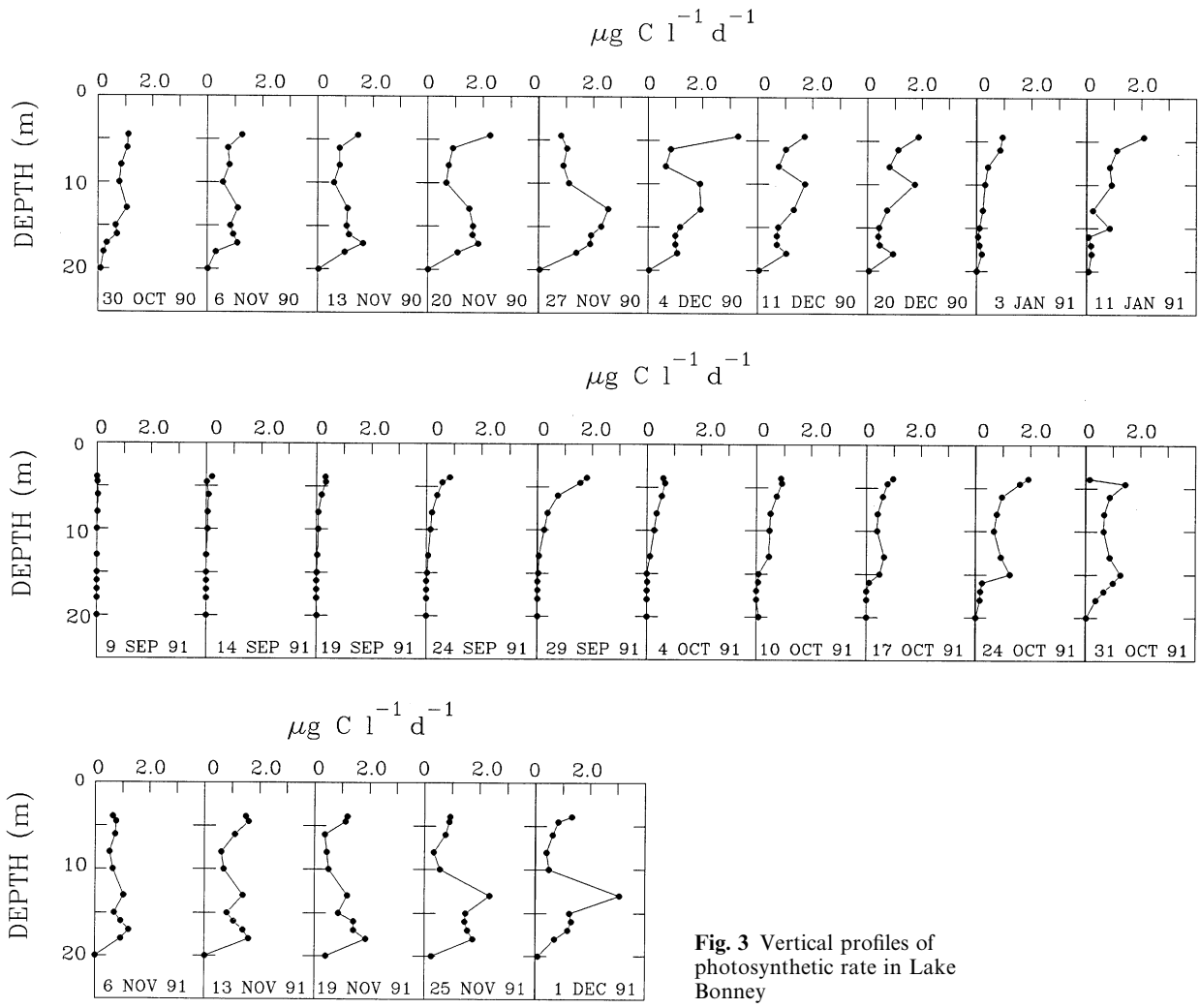

Fig. 3 Vertical profiles of photosynthetic rate in Lake Bonney

mid-depth photosynthetic maximum developed with a peak at 13 m, and the deep layer began to show measurable productivity. In November, the deep peak was well developed at 17–18 m. Photosynthesis profiles changed relatively little through December 1990. In January 1991, photosynthetic rates in shallow and mid-depth populations began to increase after a high stream input event, following the trend observed for chl *a* concentrations.

For each of the three phytoplankton layers, integrated photosynthesis was normalized to integrated chl *a* and to daily irradiance reaching the top of the layer. This measure of photosynthetic efficiency, the light utilization index [Φ, g C (g chl *a*)$^{-1}$ m^2 (mol quanta)$^{-1}$] varied seasonally (Fig. 5). In general, Φ increased over depth with each layer showing distinct seasonal trends. The highest value for the surface layer (Φ_s) was 2.5 in late September. The Φ values in the middle layer (Φ_m) peaked at a value of 3.1 in November. The Φ values in the deep layer (Φ_d) peaked at 4.9 when photosynthesis was first detected in mid-October, but afterwards fluctuated between 2.5 to 3.0. All three layers showed declining Φ values through December, with Φ_s declining earliest.

Discussion

Development of maxima for phytoplankton biomass and photosynthesis proceeded sequentially from shallower to deeper phytoplankton populations in a manner that implies a seasonal descent of the threshold irradiance required for net production. In many pelagic systems, a spring phytoplankton bloom is triggered by an increase in the average daily irradiance in the mixed layer due to decreasing mixed layer depth and increasing incident irradiance (Sverdrup 1953; Smetacek and Passow 1990). In the non-turbulent waters of Lake Bonney, initiation of the development of the spring

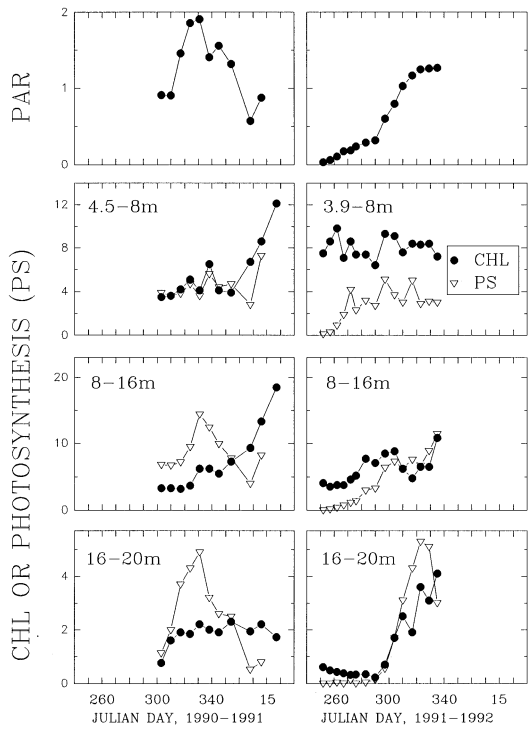

Fig. 4 Time courses of *PAR* (mol quanta $m^{-2} d^{-1}$) immediately beneath the ice, and of chlorophyll *a* (*chl*) concentrations ($mg\,m^{-2}$) and photosynthetic rates (*PS*, $mg\,C\,m^{-2}\,d^{-1}$) integrated for shallow, middle and deep phytoplankton populations in Lake Bonney. Note that different *scales* are used for each vertically distinct population

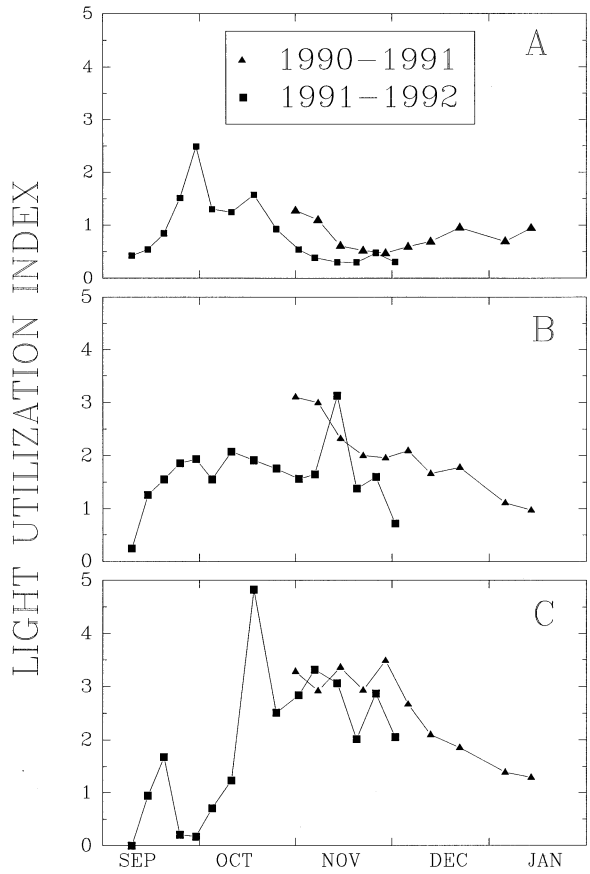

Fig. 5A–C Time courses of the light utilization index [Φ, g C (g chl *a*)$^{-1}$ m^2 (mol quanta)$^{-1}$] in **A** the surface, **B** the middle, and **C** the deep phytoplankton layers in Lake Bonney during the 1990 (1990–1991) and 1991 (1991–1992) field seasons

phytoplankton blooms is solely a function of the seasonal increase in incident irradiance. Increases in photosynthetic rates were usually followed by increases in chl *a*, often with a lag of a few weeks. This temporal separation in the development of maxima for photosynthesis and algal biomass, combined with the distinct taxonomic segregation we observed, implies that the phytoplankton maxima developed from in situ production and not from sinking or vertical migration of cells. Chl *a* profiles measured at 4-h intervals over a 24-h period during November also showed that no significant vertical migration occurred (Priscu, unpublished data).

After photosynthesis was initiated within a layer, photosynthetic rates generally increased with irradiance. However, the surface layer was an exception. Photosynthetic rates within the surface layer did not increase coincident with irradiance after Φ_s began to decrease in October. Because these phytoplankton are always light-limited (Lizotte and Priscu 1992a), lowered photosynthetic efficiency, combined with little increase in biomass and less dramatic increases in irradiance after October, led to stagnation in primary production. The seasonal trend for Φ_s implies that another factor, in addition to irradiance, begins to limit primary production immediately beneath the ice in Lake Bonney during late October/early November.

Several lines of evidence suggest that phytoplankton immediately beneath the ice of Lake Bonney may become nutrient limited, starting in early November. Firstly, concentrations of inorganic P and N are at least an order of magnitude lower within the surface layer, relative to the deeper layers (Sharp and Priscu 1990; Sharp 1993; Lizotte and Priscu 1994; Priscu 1995). Ambient ratios of dissolved inorganic N:P, and estimates of the relative upward diffusion rates for these nutrients imply that phytoplankton in Lake Bonney are P-deficient (Priscu 1995). Secondly, maximum photosynthetic quantum yields decreased with distance from the nutricline, with the shallowest populations having extremely low maximal quantum yields that are indicative of nutrient stress (Lizotte and Priscu 1994). Thirdly, phytoplankton in the upper water column showed a positive growth response following a large influx of glacial meltwater in late December 1990 and January 1991, which caused the lake level to rise at least 1 m and introduced glacial flour particles to at least the 12-m depth (Lizotte and Priscu 1992b). This large advective stream influx was followed by increases in chl *a* concentrations, photosynthetic rates,

photosynthetic efficiencies (this study) and maximal quantum yields (Lizotte and Priscu 1994). Finally, nutrient enrichment experiments on shallow populations in November and December showed significant increases in photosynthetic rates upon the addition of inorganic P and N; such increases were not as pronounced in deep-water populations (Sharp and Priscu 1990; Sharp 1993; Priscu 1995).

Nutrient deficiency of shallow phytoplankton populations in early spring presumably reflects the depletion of nutrient pools produced during the winter. Upward diffusion across the chemocline and advective inputs from glacial runoff appear to be the only sources of new nutrients for these phytoplankton populations. Typically, both of these sources are meagre, owing to high water column stability (vertical diffusion coefficients are near the molecular level) and to the cold, dry climate (which limits glacial melting and runoff). However, dissolved nutrients may be restocked during the dark winter months. The long, dark winter restricts nutrient uptake related to photoautotrophy while other processes, such as microbial regeneration of inorganic nutrients and diffusion of nutrients across the chemocline, continue. These overwinter conditions can reset nutrient stocks in the trophogenic layers of the dry valley lakes each year.

The winter–spring transition during September and October was a period in which phytoplankton from all three layers increased in photosynthetic efficiency (Φ). This is also the period during which day length is increasing. Ryther (1956) first suggested that day length would have such an influence on integrated production normalized to biomass and irradiance (on an annual scale); ouput from current models (Cullen 1990) supports this contention.

An alternative explanation is that Φ is extremely low after winter because much of the chl *a* signal may be associated with inactive cells (e.g. in resting stages or dead). With the onset of light in the spring, resting cells could give rise to photosynthetically viable cells and the pigments associated with dead cells may be photooxidized. Evidence for this winter carry-over of a residual chl *a* signal can be seen by comparing the total integrated water column concentrations from the earliest sampling date with values from the last sampling date of the preceding year: 7.5 mg m^{-2} on 30 October 1990 followed 13.2 mg m^{-2} on 13 January 1990 (Sharp 1993), and 12.6 mg m^{-2} on 14 September 1991 followed 32.4 mg m^{-2} on 22 January 1991. In the latter year, the chl *a* concentrations immediately beneath the ice at the onset of spring were as high as any recorded in the previous two field seasons (Sharp 1993; Figs. 2, 4). Thus, in the 1991 field season, the "signal" of the spring bloom in the shallowest population, which in preceding years showed an increase of about 1 μg chl *a* l^{-1}, may have been lost in the "noise" of overwintering chl *a* from the preceding summer bloom (Fig. 4) that was triggered by unusually high stream inputs in January 1991. A longer temporal data set in concert with winter chl *a* profiles would be needed to test this contention.

Peak values of Φ in Lake Bonney were much higher than have been reported for temperate, marine phytoplankton (Platt et al. 1988). In part, high photosynthetic efficiency may be due to the irradiance spectrum beneath the thick ice cover of Lake Bonney, which is dominated by blue-green wavelengths (Lizotte and Priscu 1992b) that are readily absorbed by phytoplankton pigments (Lizotte and Priscu 1992b, 1994; Neale and Priscu 1995). The decrease in Φ for the middle and deep phytoplankton layers during December and January may be related partly to changes in the spectral quality of PAR (less blue, more green), resulting from increases in phytoplankton absorption and turbidity from glacial runoff (Lizotte and Priscu 1992b).

In conclusion, we observed that the development of three distinct vertical maxima for both chl *a* and photosynthetic rates in Lake Bonney largely followed the seasonal increase in irradiance from winter to midsummer. Dates for the earliest accumulation of chl *a* and the first measurable rates of photosynthesis were observed to follow a temporal sequence from shallower populations to deeper populations, implying that initiation of phytoplankton activity was light limited during the winter–spring transition. Phytoplankton immediately beneath the ice showed increased photosynthesis with increasing irradiance during September and early October, but not through November and December, implying that environmental factors other than light eventually limit their productivity. This finding is consistent with previous studies that implicated nutrient availability as a factor causing lower productivity in shallow phytoplankton populations relative to the deeper, nutrient-rich phytoplankton populations in Lakes Bonney, Fryxell and Vanda during mid-summer (Vincent 1981; Vincent and Vincent 1982; Priscu et al. 1989; Lizotte and Priscu 1994; Priscu 1995). Early spring peaks in photosynthetic rates and photosynthetic efficiency for shallow phytoplankton populations imply that sufficient nutrients are available when photosynthesis is initiated by light availability during the winter–spring transition. In contrast, phytoplankton productivity in deeper populations appears to be solely light dependent. Further study of the seasonal variation of nutrient dynamics and their role in phytoplankton photosynthesis and growth is needed to establish mechanistic links between nutrient cycling and primary productivity in the dry valley lakes.

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