Nitrogen transformations in Lake Bonney, Antarctica : dynamics in a non-turbulent environment
by Christopher Dee Woolston

A thesis submitted in partial fulfillment of the requirements of the degree of Master of Science in Biological Sciences
Montana State University

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NITROGEN TRANSFORMATIONS IN LAKE BONNEY, ANTARCTICA: DYNAMICS IN A NON-TURBULENT ENVIRONMENT

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A thesis submitted in partial fulfillment
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Christopher Dee Woolston

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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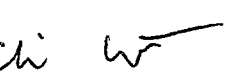
Signature 

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TABLE OF CONTENTS

TABLE OF CONTENTS, CONT.

TABLE OF CONTENTS, CONT.

LIST OF TABLES

LIST OF TABLE, CONT.

Table Page

LIST OF FIGURES

LIST OF FIGURES, CONT.

Figure Page

NITROGEN TRANSFORMATIONS IN LAKE BONNEY, ANTARCTICA

Christopher D. Woolston, 1994

ABSTRACT

This study was designed to determine sources of dissolved inorganic nitrogen (DIN) and microbial strategies for DIN utilization in a non-turbulent environment (perennially ice-covered Lake Bonney, Antarctica).

Water samples were inoculated with ^{15}N labeled DIN and incubated either in situ or in an incubator. Experiments were designed to test DIN uptake over a range of substrate concentrations, irradiances, and incubation periods. Additional experiments were designed to measure in situ NH_4^+ regeneration, as well as the effects of free amino acids, ambient NH_4^+ concentration , and phytoplankton on NH_4^+ regeneration rates.

Experiments designed to measure in situ NH_4^+ regeneration rates were inconclusive; apparently rates were below the detection limits of the method. The efficiency of conversion of serine to free NH_4^+ increased with depth. Removal of phytoplankton had no discernible effect on regeneration rates.

NH_4^+ was the preferred source of DIN at all depths. In situ uptake rates of NH_4^+ in the trophogenic zone generally exceeded the rate of supply of NH_4^+ by diffusion, indicating that NH_4^+ regeneration was a major source of DIN in the trophogenic zone. Three mechanisms for enhancing uptake of DIN (particularly NH_4^+) in relatively nutrient poor waters were observed: increased microbial affinity for NH_4^+, surge uptake of DIN within minutes of DIN enrichment, and increased affinity of DIN uptake for irradiance.

Microplankton in the shallow, relatively nutrient poor waters of Lake Bonney appear well acclimated and adapted to utilize the ambient supply of DIN.

INTRODUCTION

It has long been recognized that supply of dissolved inorganic nitrogen (DIN) often controls productivity of marine phytoplankton (e.g. Dugdale and Goering 1967). Recently, it has become increasingly evident that phytoplankton growth can be limited by nitrogen in freshwater systems as well (Dodds et al. 1991; Priddle et al. 1986; Priscu and Priscu 1984).

The ecological importance of DIN has been thoroughly documented, but the complexity of most environments has confounded attempts to isolate physiological responses to nutrient supply in natural systems (Smetacek et al. 1990). Turbulence and grazing pressure create conditions of disequilibrium which prevent maximal utilization of nutrients and add significant complexity to phytoplankton dynamics (Smetacek et al. 1990).

Even in some relatively quiescent Antarctic lakes (e.g. Heywood Lake, Signey Island) during ice-cover, minor turbulence and subsequent fluctuations in the light field greatly complicate determination of the factors that control productivity (Hawes 1983). Similarly, losses due to grazing must be considered in most investigations of aquatic nutrient cycles and phytoplankton productivity. Grazing rates must be quantified for accurate calculations of critical depth and nutrient control of primary productivity (Smetacek et al. 1990). Furthermore, Lynch and Shapiro (1981) found that grazing significantly affects community succession in response to nutrient additions. Like turbulence, but to

a lesser extent, grazing creates disequilibrium that inhibits phytoplankton acclimation or adaptation to nutrient resources.

The perennially ice-covered lakes in the McMurdo dry valley region of South Victoria Land, Antarctica, provide an opportunity to observe natural transformations of DIN in the absence of turbulence or grazing pressure. This study focuses on Lake Bonney, a meromictic lake located in the upper Taylor Valley.

Like other lakes in the McMurdo dry valleys, Lake Bonney is characterized by extreme hydraulic stability. In this lake, mixing occurs almost exclusively on a molecular scale and turbulent mixing is nearly non-existent (Spigel et al. 1990). There are two main causes for this stability. Firstly, the perennial 4 m ice-cover prevents direct wind-induced mixing. Secondly, chemical gradients within the lake lead to strong density stratification (Spigel et al. 1990).

Grazing pressure in Lake Bonney is limited by the near absence of upper trophic levels. Some zooplankton have been recorded, including ciliated zooplanktors of the genus *Strombidium* and *Sphaerophyra* (Parker et al. 1982). These organisms are primarily associated with benthic mats and are rare to absent in the pelagic environment (Parker et al. 1982).

In the absence of grazing pressure, phytoplankton production can be more directly related to temperature, light, and nutrient availability (Cullen 1990). These three factors have a complex regulatory effect on productivity, and much controversy has surrounded attempts to isolate one factor as the cause of seasonal succession of phytoplankton populations (McCombie 1960, Cullen 1990). At a physiological level, they are not mutually exclusive: all organisms require nutrients for biosynthesis, and temperature and

light govern the ability of phytoplankton to utilize available substrate. Observation of nutrient control of primary productivity could therefore most readily be accomplished in a system where light and temperature remain relatively constant over the doubling time of an organism.

For these reasons, Lake Bonney is an ideal site for monitoring phytoplankton utilization of nutrients. The hydraulic stability of Lake Bonney prevents rapid temporal variation in temperature. Due to the perennial 4 m ice-cover, which provides insulation as well as prevents turbulence, changes in temperature at a given depth are very gradual. Even in relatively turbulent marine habitats, seasonal temperature changes in Antarctic waters do not significantly affect microbial heterotrophic activity (Ellis-Evans 1982).

Furthermore, during the austral spring and summer, microplankton in Lake Bonney grow in a relatively constant light regime. In all aquatic systems, the light regime fluctuates according to first order effects (factors that govern solar flux, e.g. latitude, weather, and light extinction within the water column) and second order effects (e.g., turbulent displacement of phytoplankton and phytoplankton migration). In Lake Bonney, these effects combine to form temporal stability in the light regime over the life span of microplankton. At high latitudes, there is little diel variation in irradiance; four months of darkness and four months of daylight are separated by two month periods of twilight. The intensity of light that reaches the water column of Lake Bonney varies with cloud cover and the changing transparency of the ice, but these variations are minor compared to the diel light/dark cycles found in low latitude systems. Hydraulic stability minimizes second order effects

and thus provides phytoplankton a relatively constant light environment.

The stability of the water column has shaped the structure and composition of planktonic communities. Most of the phytoplankton in Lake Bonney are flagellates (principally *Chlamydomonas subcaudata*, *Cryptomonas* sp., and *Ochromonas* sp.) (Sharp 1993), while diatoms are rare (Parker and Simmons 1983; Parker et al. 1977, Sharp 1993). Apparently, natural selection strongly favors motile algae in this quiescent environment.

In addition to shaping community composition, the stability of the water column has allowed for specialized growth and survival strategies. As previously described, these strategies include motility and efficient photosynthesis at low irradiance (Priscu et al. 1990). Potentially, water column stability could also allow for efficient utilization of inorganic nutrients by phytoplankton and efficient regeneration of NH_4^+ by bacteria.

The purpose of this study was to assess transformations of dissolved inorganic nitrogen by several different microbial communities in Lake Bonney. The main body of this thesis has been divided into three parts. Part I describes the methods and results of routine data collection. These results are necessary for interpretation of all experiments discussed in Parts II and III. Part II includes experiments designed to assess sources of DIN as well as microbial strategies to enhance DIN utilization. Part III focuses on the role of irradiance in regulating DIN uptake and the degree to which microplankton have adapted to utilize irradiance for DIN uptake. Following Part III is an overall conclusion that briefly integrates the results of Part I, II, and III. The remainder of this

introductory section will discuss aspects relevant to all parts of the thesis: previous research on Lake Bonney and other dry valley lakes, hypotheses and objectives, and a description of the study site.

PREVIOUS RESEARCH ON LAKE BONNEY AND OTHER DRY VALLEY LAKES

Captain R.F. Scott's discovery of Lake Bonney in 1903 marked the beginning of dry valley lake research (Parker et al. 1982). Owing to their remoteness, thorough scientific investigation of the lakes did not begin until the early 1960's. Liquid water beneath the ice covers of Lake Bonney and Lake Vanda was sampled in 1961; this was the first attempt at limnological analysis of dry valley lakes (Angino and Armitage 1963).

Several early investigations of Lake Bonney focused on distribution of nutrients (Armitage and House 1962, Angino and Armitage 1963, Angino et al. 1963, Goldman 1964, Yamagata et al. 1967). The extreme salinity of Lake Bonney's deeper waters apparently caused methodological difficulties; reports of nutrient concentrations were inconsistent and often contradictory (Fortner et al. 1986, Sharp 1990).

The first studies of dynamic biological processes in dry valley lakes were conducted by Goldman (1964). Goldman's measurements of primary productivity within the lake indicated a high quantum yield of photosynthesis. He concluded that the phytoplankton had adapted to low ambient light levels.

In the 1970's, several studies documented the distribution of microplankton in dry valley lakes (Koob and Leister 1972, Parker et al. 1977, Parker et al. 1982). Koob and Leister (1972) reported three distinct zones of primary productivity and phytoplankton abundance.

Later studies attempted to correlate productivity in dry valley lakes with light and nutrient supply. Vincent (1981) suggested that nutrients played the primary role in regulation of microplankton growth. Specifically, he proposed that the phytoplankton of Lake Fryxell (located in the lower Taylor Valley) were nitrogen deficient and that regeneration of NH_4^+ in large part fueled productivity in the trophogenic zone. Green et al. (1989) noted that the allochtonous inputs of PO_4^{-3} to Lake Fryxell greatly exceeded NO_3^-, and nitrogen, compared to phosphorus, was more efficiently cycled within the lake.

Thorough investigation of the factors that control productivity in Lake Bonney began in 1989. Priscu et al. (1990) hypothesized that the photosynthetic apparatus of Lake Bonney phytoplankton should be precisely adapted to the relatively constant ambient light fields. Photosynthesis/irradiance experiments conducted initially by Priscu et al. (1988) and confirmed by Lizotte and Priscu (1992) demonstrated that phytoplankton were indeed shade adapted; however, phytoplankton in the relatively nutrient-poor surface waters appeared to harvest light less efficiently than deeper populations. Lizotte and Priscu (1993) determined quantum yield of photosynthesis through measurements of natural fluorescence, chlorophyll concentration, phytoplankton absorption spectra, photosynthetic efficiency, and spectral irradiance. Interestingly, quantum yields increased dramatically with increasing proximity to the chemocline. Models constructed in an attempt to predict primary productivity from natural fluorescence, irradiance, and quantum yields were unsuccessful. Apparently, productivity of the upper

trophogenic zone is largely influenced by nutrient supply (Lizotte and Priscu 1993).

Sharp (1993) formulated a one-dimensional light-dependent growth model of primary productivity. This model assumed that light availability, and not nutrient supply, limits growth. The model's predictions of gross chlorophyll specific growth rates did not correlate well with actual growth rates, particularly in surface waters. For example, chlorophyll specific growth rates within the chemocline exceeded growth rates in the relatively high irradiance surface waters. Once again, it was concluded that nutrient supply in the upper trophogenic zone limited photosynthesis (Sharp 1993). Nutrient bioassays conducted by Sharp (1993), designed to detect deficiency of nitrogen or phosphorus, were inconclusive; however, recent bioassays have shown that phytoplankton photosynthesis in the upper trophogenic zone can be enhanced significantly by nutrient enrichment (Priscu, unpublished data).

HYPOTHESES AND OBJECTIVES

Just as Priscu et al. (1990) hypothesized that phytoplankton should be precisely adapted to ambient light levels, I propose that the level of physiological adaptations for inorganic nitrogen uptake will reflect the nutritional status of the community. In situations where nitrogen limitation exists (if any), phytoplankton will have enhanced efficiency of inorganic nitrogen uptake, particularly uptake of NH_4^+. Specifically, this study was designed to test the following hypotheses:

1. NH_4^+ is the preferred source of DIN for all Lake Bonney planktonic communities.
2. Regeneration of NH_4^+ provides a major nitrogen source for phytoplankton in the upper trophogenic zone.
3. "Regenerated" NO_3^- and NO_2^- provide a minor source of nitrogen for phytoplankton in the upper trophogenic zone.
4. Nitrogen deficient communities are capable of rapid short term uptake of NH_4^+, and, to a lesser extent, $NO_3^-$and NO_2^-.
5. Nitrogen uptake is extremely "shade adapted," i.e., quickly saturated with respect to irradiance, particularly in nitrogen depleted surface waters.
6. Photoinhibition of nitrogen uptake, when present, occurs at an irradiance substantially above ambient levels.

The following objectives were undertaken to test the hypotheses:

1. Measure maximum uptake rates of NH_4^+, NO_3^-, and NO_2^- throughout the water column.
2. Measure the uptake response to different concentrations of NH_4^+, NO_3^-, and NO_2^-.
3. Measure rates of regeneration of NH_4^+.
4. Measure the time course uptake of NH_4^+, NO_3^-, and NO_2^-.
5. Quantify the irradiance requirements for uptake of NH_4^+, NO_3^-, and NO_2^-.

DESCRIPTION OF STUDY SITE

Geography and Geology

The McMurdo dry valleys lie between the MacKay and Koettlitz glaciers at latitude 77° 10'S to 77° 45'S, longitude 160° 20'E to 160° 00'E (Chinn 1993). At 3700 km^2, the valleys represent the largest ice-free area on the continent. The Taylor Valley was originally carved by the Taylor V glaciation approximately four million years ago, and numerous smaller glaciations have shaped the valley since then (Heywood 1984, Chinn 1993). The Taylor Valley has been largely ice-free for at least 100,000 years, and the basins of the present day Taylor Valley lakes (Lake Bonney, Lake Fryxell, Lake Hoare, Lake Chad, and Mummy Pond) were formed 100,000 to 500,000 years ago (Chinn 1993).

The major rock types found in the modern-day Taylor Valley include dolerites, marbles, granite, basalts, gneisses, schists, sandstones, and metasediments (Claridge and Campbell 1977; Heywood 1984). Ultramaphic dikes are prominent features of the land surrounding Lake Bonney, evidence of past vulcanism (Lawson, personal communication).

Climate

The McMurdo dry valleys constitute one of the driest ecosystems in the world. Precipitation in the form of snow may reach 10 cm a year, but most of the moisture is quickly lost to sublimation (Green et al. 1989). Potential ablation rates are

approximately 30 times greater than the average annual precipitation (Chinn 1993). Katabatic winds, which blow from the Polar Plateau and can exceed 130 km h^{-1}, maintain the relative humidity below 50% (Heywood et al. 1984). The annual mean temperature is between -20 to -25° C (Heywood et al. 1984).

Morphology

Lake Bonney, with a surface area of approximately 4 km^2 (Chinn 1993), is the largest lake in the Taylor Valley. It consists of two lobes (the east lobe and the west lobe) which are connected by a narrow (40 m wide), shallow (14 m deep) sill. The west lobe, the smaller of the two, is abutted by the Taylor Glacier. Both lobes have a maximum depth of approximately 40 m. Several streams (runoff from the Taylor, Hughes, LaCroix, Sollas, Rhone, Calkin, Matterhorn, and Marr glaciers) flow intermittently into the lake during late austral spring and austral summer. The lake has no outflows; water is lost through ablation and sublimation of the perennial 4 m thick ice-cover (Chinn 1993).

Part I

Routine Data Collection and Overview of ^{15}N Experiments

ROUTINE DATA COLLECTION METHODS

Parameters Analyzed

Routine collections were conducted in each lobe every 10 d throughout the 1992-1993 field season (hereafter referred to as the "1992 season") and every 14 d throughout the 1993 field season. Water samples were analyzed for chlorophyll a (CHL); primary production (PPR); NH_4^+, NO_3^-, and NO_2^- (DIN); soluble reactive phosphorus (SRP) and particulate carbon and nitrogen (PC and PN). An inventory of sampling dates and depths is presented in Table 1. All depths are from the piezometric level, the level of the water surface in the sampling hole (approximately 27 cm below the top of the ice).

Water Sampling Procedure

Early in each season, sampling holes were drilled with a 10 cm or 25 cm diameter ice auger. After drilling, holes were enlarged with a "hot finger," copper tubing through which hot glycol was circulated. The hot finger was reapplied to the holes periodically throughout the season to prevent narrowing or refreezing. After application of the hot finger, holes were allowed to cool for at least 24 h before sampling. A portable structure was placed over the sampling hole.

For routine data collection, samples were collected with a 2.2 liter Niskin sampling bottle with teflon-coated springs. The bottle was fastened to metered 1/8 " aircraft cable and was lowered and raised with a manual winch. The Niskin bottle was inverted several

times before removal of water to eliminate gradients within the bottle.

Water samples were collected through a short piece of rubber tubing attached to the nozzle of the Niskin. One l from each depth was transferred into a 1 liter HDPE bottle for analysis of DIN, SRP, CHL, and CHN. Once full, each 1 liter HDPE bottle was placed in a cooler for transport to laboratories on the lakeshore. A portion of the water remaining in the Niskin was used to fill primary productivity bottles (3 145 ml Pyrex glass screw-top bottles). Two of the bottles were clear and one was opaque. The tubing on the Niskin was inserted to the bottom of each bottle to prevent intrusion of gasses into the sample. Once full, the bottles were placed in a dark box until inoculated with $^{14}C\text{-}CO_3^{-2}$. All bottles were acid washed and rinsed three times with sample water before final collection.

Chemical and Biological Measurements

Chlorophyll a

Collection of CHL and nutrient samples commenced within 2 h of collection. The laboratory was cool and dim during filtration of CHL and nutrients. For the 1992 season, 2 200 ml aliquots were each filtered onto precombusted (450° C for 2 h) 25 mm Whatman GF/F glass fiber filters under low vacuum (< 0.5 atm). The filtrate was collected in an acid washed Ehrlemyer flask. A portion of the filtrate was used to pre-rinse a 125 ml HDPE nutrient bottle; the rest was transferred to the bottle for future nutrient analysis. During the 1993 season, two 100 ml aliquots were filtered for CHL analysis, and the filtrate was collected directly into the 125 ml HDPE nutrient

bottle through the use of vacuum chambers (bell jars). Each CHL filter was gently folded in half (CHL side in) and placed in a glassine envelope. The envelopes were wrapped in aluminum foil and kept frozen until analysis at Crary laboratory, McMurdo Station. Nutrient bottles were also kept frozen until analysis. Analysis of CHL and nutrients occurred within two months of collection.

For CHL analysis, the frozen filters were placed in 20 ml scintillation vials. Ten ml of 90% acetone were added to each vial, and the samples were vortexed for 1 min. Tests conducted in 1989 indicate that this is an appropriate method of CHL extraction for the phytoplankton in Lake Bonney (Lizotte and Priscu, unpublished data). CHL concentration of the extract was measured fluorometrically with a Turner Design model 10 AU fluorometer calibrated with standard concentrations of purified CHL (Sigma Chemical). Measurements were made before and after acidification (0.2 ml 1 N HCl) to correct for phaeopigment fluorescence.

Nutrients

Nutrient samples were thawed before analysis. All nutrient assays were conducted on 10 ml samples. For NH_4^+ analysis, samples from 15 m and deeper in the east lobe and 13 m and deeper in the west lobe were diluted 1:10 (1 ml lake water + 9 ml deionized water). This was done to prevent salt interference with the color forming reaction and to keep NH_4^+ concentrations within the linear range of the method (Sharp 1993). The blue indophenol reaction between NH_4^+, phenol, and hypochlorite at high pH was used to

determine NH_4^+ concentration (Solorzano 1969). Absorbance of the sample was measured using a 1 cm pathlength cell and a Beckman spectrophotometer.

For NO_2^- analysis, samples from 15 m and deeper in the east lobe were diluted 1:10 (1 ml lake water + 9 ml deionized water). Samples from the west lobe were not diluted. NO_2^- concentrations in the west lobe were consistently less than 1 μM; dilution of the sample could therefore decrease NO_2^- concentrations below the limit of detection. Repeated recovery tests indicate greater than 90% recovery of added NO_2^- at depths below 15 m. Concentration of NO_2^- was measured with the NED/sulfanilamide diazotization reaction (APHA 1985).

Samples for NO_3^- analysis from 15 m and deeper in the east lobe and 13 m and deeper in the west lobe were diluted 1:10. All of the NO_3^- in the sample was reduced to NO_2^- by shaking the samples with spongy cadmium and ammonium chloride EDTA buffer at pH 8.3 (Jones, 1984). The concentration of NO_2^- was then determined with the NED/sulfanilamide reaction.

Soluble reactive phosphorus samples from 15 m and deeper in the east lobe were diluted 1:2 (5 ml lake water + 5 ml deionized water). Samples from the west lobe were not diluted; recovery tests indicated greater than 90% efficiency of SRP detection in undiluted samples. SRP was measured with the ammonium molybdate/potassium antimonyl tartrate method (Downes 1978).

Following the methods of Sharp (1993), the reduction step to prevent arsenate interference was omitted.

Particulate Carbon and Nitrogen

Collection of PC and PN commenced after filtering of all CHL and nutrient samples. For each depth, one 500 ml aliquot was filtered on a precombusted 25 mm GF/F glass fiber filter at low vacuum (< 0.5 atm). Each filter was rinsed with approximately 20 ml of deionized water (DIW) to remove inorganic nitrogen from the filter. Filters were air dried for several d in aluminum weigh-boats before transport to Crary Laboratory. Upon arrival at the laboratory, filters were frozen (-45° C) until analysis. Samples from the 1992 season were transported frozen to MSU and analyzed within 6 months of collection. Samples from the 1993 season were analyzed at Crary laboratory within 3 months of collection.

Particulate filters were acidified before analysis to remove remaining inorganic carbon. Flash-combustion gas chromatography (Carlo Erba model 1500 elemental analyzer) was used to measure the nitrogen and carbon content of the filters wrapped in tin foil (combustion catalyst). Areas under chromatographic peaks were compared to areas obtained from standards of isothiourea (1992) or acetanilide (1993). Standards were weighed $\pm$ 1.0 μg with a Cahn model 35 electrobalance. All measurements were corrected for carbon and nitrogen contamination of the filters and the foil.

Primary Productivity

Photosynthesis was measured by in situ uptake of ^{14}C-CO_2. A Glison 1000 ml pipette was used to inoculate primary productivity

bottles with $^{14}C\text{-}CO_3^{-2}$ stock. Bottles were sealed tightly and inverted several times after addition of $^{14}C\text{-}CO_3^{-2}$ to mix the sample.

The productivity bottles were suspended for 24 h at the depth of collection. Studies conducted by Sharp (1993) indicated that measurements of daily net photosynthesis based on a single 24 h incubation did not differ significantly from measurements based on three 8 h incubations. The incubation hole was located away from the sampling hut and was covered to prevent excess irradiance from entering the water column. The bottles were placed in the hole between 0700 h and 0800 h local time, when the sun was behind mountains. This reduced the possibility that algal photosynthetic ability would be damaged by incidental exposure to sunlight before incubation.

The bottles were returned to the lakeshore laboratory immediately after removal from the lake. All bottles were kept cold and dark before and during filtration. Samples were filtered on precombusted 25 mm GF/F Whatman glass fiber filters at low vacuum (<0.5 atm). Filters were transferred to 20 ml scintillation vials and acidified with 0.5 ml 3 N HCl to remove unassimilated ^{14}C. The vials were dried (40-50° C) for 1 to 2 d and sealed for shipment to Crary laboratory, McMurdo.

Activity of the filters was determined by liquid scintillation spectroscopy at Crary Laboratory. Ten ml of CytoScint ES (ICN Pharmaceuticals) liquid scintillation cocktail was added to each vial before analysis. Counts per min were compared to a quench curve for

conversion to disintegrations per min (DPM). Acetone was used as the quenching agent and ^{14}C-toluene was the standard.

DPM was converted to rate of carbon uptake through the following equation:

$$\text{mg C m}^{-3}\ \text{day}^{-1} = \frac{(\text{DIC})^* (\text{DPM}_C - \text{DPM}_D) * 1.06 * \mu\text{Ci} * 10^3\ \text{liter}}{(2.2 * 10^6\ \text{DPM}) * (\mu\text{Ci added})^* \text{m}^3 * t} \quad (1)$$

where DIC (dissolved inorganic carbon) is expressed in mg l^{-1} , 1.06 is a correction for isotope discrimination, DPM_C is disintegrations per min in the clear bottles, DPM_D is disintegrations per min in the dark bottle, $2.2 * 10^6$ is the DPM per µCi, 10^3 converts liters to m^3, and t is the length of incubation (d).

Physical Parameters

Lake profiles of temperature, oxygen, and irradiance were collected on the day of each routine data collection. Irradiance was measured at 1 m intervals with a Li-Cor 4π quantum sensor attached to a Li-Cor model LI-1000 data logger. In addition, irradiance on the ice surface was continuously monitored by a Li-Cor 2π quantum sensor attached to a Campbell 21 x data logger. In situ irradiance was measured every 10 min at 10 m east lobe from 17 Jan 1993 to 31 Dec 1993 by a with a Li-Cor 4π quantum sensor attached to a Campbell 21x data logger. Irradiance readings from the Campbell were calibrated to correspond with Li-Cor 1000 readings.

Table 1. Dates and depths of collection for various parameters.
EAST LOBE

Sampling Dates	CHL	PPR	SRP	DIN	PC/PN
24 Nov 1992	B	A	B	B	B
4 Dec	C	A	C	C	C
14 Dec	C	A	C	C	C
24 Dec	C	A	C	C	C
4 Jan 1993	C	A	C	C	C
27 Oct	E	D	E	E	E
10 Nov	E	D	E	E	E
24 Nov	E	D	E	E	E
7 Dec	E	D	E	E	E
21 Dec	E	D	E	E	E

A= 4, 5, 6, 8, 10, 12, 13, 15, 16, 17, 18, 20 m.

B= 4, 5, 6, 8, 10, 12, 13, 15, 16, 17, 18, 20, 23, 26, 29, 32, 35 m.

C= 4, 5, 6, 8, 10, 12, 13, 15, 16, 17, 18, 20, 22, 25, 30, 32, 35 m.

D= 4, 6, 8, 10, 12, 13, 15, 18, 20, 22 m.

E= 4, 6, 8, 10, 12, 13, 15, 18, 20, 22, 25, 30, 35, 38 m.

Table 1 , cont. Dates and depths of collection for various parameters.
WEST LOBE

Sampling Dates	CHL	PPR	SRP	DIN	PC/PN
26 Nov 1992	B	A	B	B	B
6 Dec	B	A	B	B	B
26 Dec	B	A	B	B	B
6 Jan 1993	B	A	B	B	B
7 Jan	B	NA	B	B	B
29 Oct	D	C	D	D	D
12 Nov	D	C	D	D	D
26 Nov	D	C	D	D	D
9 Dec	D	C	D	D	D
23 Dec	D	C	D	D	D

A= 4, 5, 6, 8, 10, 12, 13, 14, 15, 17 m.

B= 4, 5, 6, 8, 10, 12, 13, 14, 15, 17, 20, 22, 25, 30, 35 m.

C= 4, 6, 8, 10, 12, 13, 14, 15, 17, 20 m.

D= 4, 6, 8, 10, 12, 13, 14, 15, 17, 20, 22, 25, 30, 35, 38 m.

RESULTS

Nutrients

Profiles of NH_4^+, NO_3^-, NO_2^-, and SRP from 1993 routine data collections in each lobe are summarized in Figure 1. Concentrations of all nutrients are low above the first chemocline, and nutrient gradients are generally strong within and directly beneath the chemocline. SRP concentrations in each lobe and NO_2^- concentrations in the west lobe rarely exceed 1 μM.

Primary Productivity and Chlorophyll a

Primary productivity and CHL (Figure 2) were closely correlated in upper 20 m of each lobe. Below 20 m, productivity was undetectable despite the presence of chlorophyll.

In the east lobe, CHL typically reached its maximum concentration just below the ice (4-6 m). There was often another, less prominent, chlorophyll a peak within the first chemocline (10-13 m). Primary productivity followed the same general pattern, except that primary productivity peaks within the first chemocline were more prominent than the productivity peaks from 4-6 m. CHL concentrations in the upper 20 m of the west lobe consistently exceeded concentrations of the east lobe.

Particulate Carbon and Nitrogen

Representative profiles of PC:PN ratios are illustrated in Figure 3. PC:PN is always greater than the Redfield ratio of 6.6 (by atoms),

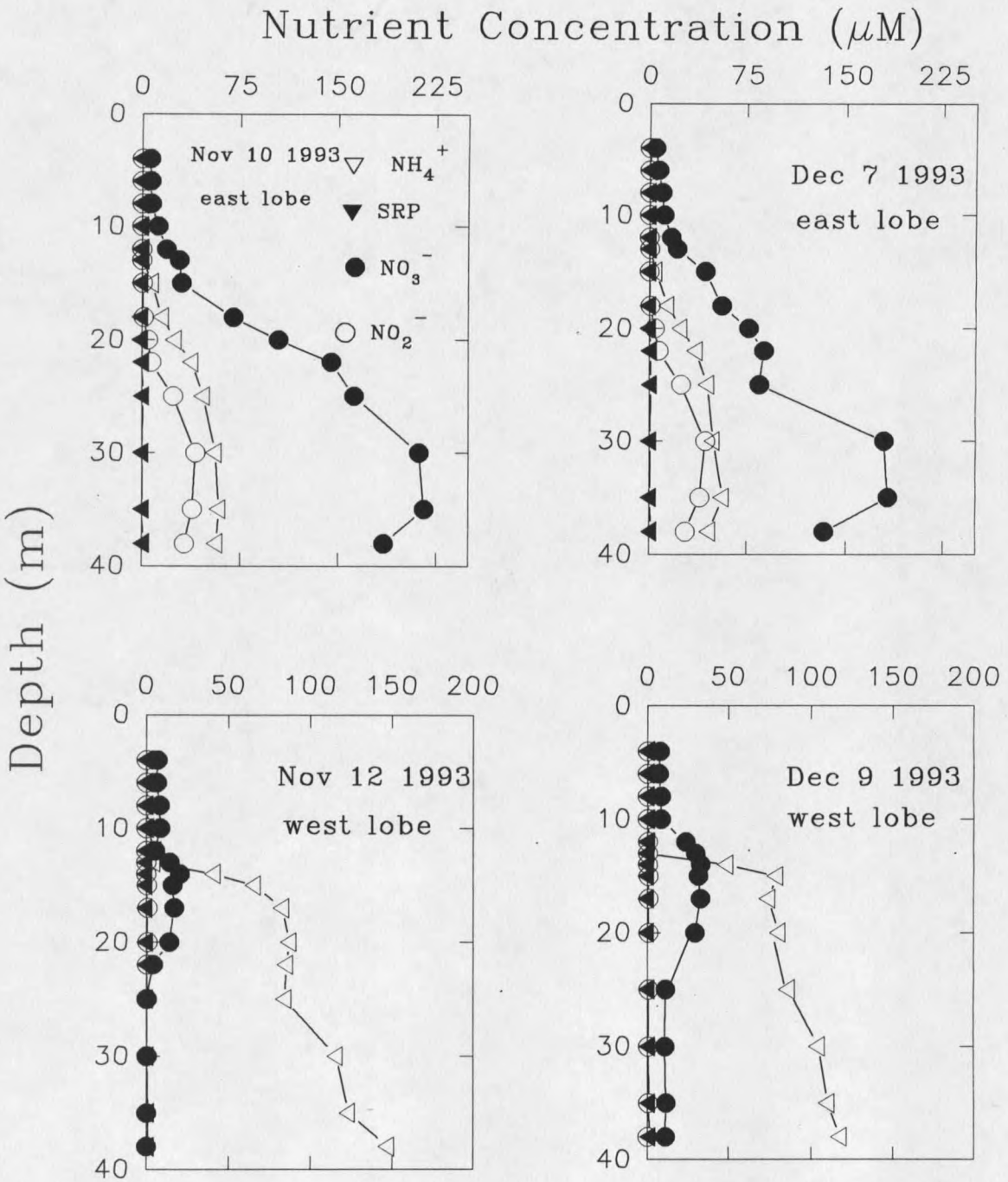

Figure 1. NH_4^+, NO_2^-, NO_3^-, and SRP concentrations (μM) in east and west lobes of Lake Bonney, 1993.