



Temporal and spatial variation of light, nutrients and phytoplankton production in Lake Bonney,
Antarctica

by Thomas Robert Sharp

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in
Biological Sciences

Montana State University

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Abstract:

Lake Bonney, Antarctica is characterized by a permanent 4 m thick ice cap, a dichothermic temperature profile and strong vertical conductivity, oxygen and nutrient gradients. The ice cap reduces under-ice irradiance to less than $50 \mu\text{E m}^{-2} \text{s}^{-1}$ and, together with the chemical stratification, create a non-turbulent environment. Hypothetically, phytoplankton communities can be separated along resource gradients, because of the non-turbulent environment. Photosynthesis, growth and nutrient concentrations within these stratified phytoplankton communities were routinely measured over the 1989-1990 and 1990-1991 austral spring and summer and during the winter spring transition of 1991, to determine how these parameters vary during the phytoplankton growing season. Nutrient enrichment bioassays were used to test for nutrient deficiency of phytoplankton photosynthesis. A light-dependent phytoplankton growth model was developed. The results of this study indicate that 1) photosynthesis in the surface phytoplankton populations may intermittently be enhanced by N and P enrichments 2) maximum phytoplankton growth rates occur in December and January and 3) the efficiency of light utilization by the phytoplankton is high in comparison to other marine or freshwater phytoplankton. Net chlorophyll specific growth rates range from -0.071 to 0.151 d^{-1} . Model results indicate that gross chlorophyll specific growth rates range between 0.002 and 0.017 d^{-1} . The significance of the research is most applicable to other pelagic polar ecosystems and deep chlorophyll maxima in general.

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A thesis submitted in partial fulfillment
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ABSTRACT

Lake Bonney, Antarctica is characterized by a permanent 4 m thick ice cap, a dichothermic temperature profile and strong vertical conductivity, oxygen and nutrient gradients. The ice cap reduces under-ice irradiance to less than $50 \mu\text{E m}^{-2} \text{s}^{-1}$ and, together with the chemical stratification, create a non-turbulent environment. Hypothetically, phytoplankton communities can be separated along resource gradients, because of the non-turbulent environment. Photosynthesis, growth and nutrient concentrations within these stratified phytoplankton communities were routinely measured over the 1989-1990 and 1990-1991 austral spring and summer and during the winter spring transition of 1991, to determine how these parameters vary during the phytoplankton growing season. Nutrient enrichment bioassays were used to test for nutrient deficiency of phytoplankton photosynthesis. A light-dependent phytoplankton growth model was developed. The results of this study indicate that 1) photosynthesis in the surface phytoplankton populations may intermittently be enhanced by N and P enrichments 2) maximum phytoplankton growth rates occur in December and January and 3) the efficiency of light utilization by the phytoplankton is high in comparison to other marine or freshwater phytoplankton. Net chlorophyll specific growth rates range from -0.071 to 0.151 d^{-1} . Model results indicate that gross chlorophyll specific growth rates range between 0.002 and 0.017 d^{-1} . The significance of the research is most applicable to other pelagic polar ecosystems and deep chlorophyll maxima in general.

INTRODUCTION

The permanently ice-covered lakes of the dry valleys region of Antarctica have unusual physical, chemical and biological characteristics, making these lakes ideal systems for studying phytoplankton ecology, particularly the relationship between phytoplankton production and light. Photoautotrophic growth is restricted to the spring, summer and fall, because of the seasonal variation of light that these polar ecosystems receive.

Photosynthesis is the primary source of organic carbon in most ecosystems (Odum 1959; Whittaker et al. 1975). This is especially true for antarctic lake ecosystems where allochthonous organic carbon inputs are low (Aiken et al. 1990). Therefore, as the first step to gaining a better understanding of the flux of carbon and energy within these lake ecosystems, it is necessary to determine the temporal and spatial variation of photoautotrophic production and the environmental factors which govern it.

Attempts to predict phytoplankton production from incident light have long been one of the primary objectives of limnologists and oceanographers (reviewed by Cullen 1990). Inductive (Talling 1957) and deductive (Platt et al. 1988) methods have been used to derive mathematical formulations for the relationship between incident light and primary production. Random vertical displacement of

the phytoplankton from turbulence limits the ability of the light-dependent phytoplankton production models to make accurate predictions (Marra 1978, Harris 1986, Vincent 1991).

The underwater light field to which phytoplankton photosynthesis is coupled varies from first and second order effects. First order effects that influence light availability to phytoplankton include latitude, meteorological events, and seasonal and diurnal variation in irradiance (flux). Second order effects influencing light availability to phytoplankton are the vertical displacement of phytoplankton in the water column, which may result from either turbulent mixing or the migration of motile phytoplankton (Harris 1986).

Variations in light field experienced by phytoplankton are partially dependent on the physical structure of the water column. Turbulent mixing will occur, if the stress generated by the wind has sufficient force to overcome the potential energy of the density stratification of the water column. Phytoplankton will undergo random vertical displacement and experience a fluctuating light field when the water column is mixed (Spigel and Imberger 1987).

Phytoplankton communities growing below the mixed layer have been termed deep chlorophyll maxima and are common features of both freshwater and marine systems (Cullen 1982, Priscu and Goldman 1983). Other analogous

situations where algae are not subject to turbulent mixing and experience only first order variations in light are sea ice algae (Palmisano et al 1985, Lizotte and Sullivan 1991), snow algae (Thomas 1972, Mosser et al. 1977) and the phytoplankton communities of the dry valley lakes (Koob and Leister 1972, Vincent 1981, Priscu et al. 1987, 1988, Lizotte and Priscu 1992).

The constancy of the light field, experienced by these spatially stable algal communities (compared to phytoplankton in a turbulent environment), offers the opportunity for the phytoplankton to optimize photosynthesis by acclimating their photosynthetic apparatus to a specific light field. When the underwater light field varies at long time scales (months) a phytoplankton community responds by successional changes in community structure (Harris 1986). At short time scales (hours) phytoplankton respond by adjusting their photosynthetic apparatus (Perry et al 1981, Harding et al 1985, Sukenik et al 1990). Examples of short-term variations in photoacclimation resulting from varying underwater irradiance include changes in photosynthetic capacity (Marra 1978, Neale and Marra 1985) and the kinetics of photoinhibition (reviewed by Neale 1987). These short-term variations may significantly influence in situ phytoplankton production (Neale et al. 1991).

In the non-turbulent antarctic dry valley lakes, phytoplankton communities experience a light field that varies on daily and seasonal time scales only (Vincent 1981, Priscu et al. 1987). This constancy should eliminate the need for short-term variations in the photosynthetic response of phytoplankton. In this study, Lake Bonney (one of the lakes in the dry valleys) was examined over three field spring-summer seasons (September through January) to determine which environmental factors may control phytoplankton production and how phytoplankton production responds to the seasonal variation in irradiance and day length.

In many respects, because of the permanent ice cover, amixis, and simplified food webs, the dry valley lakes resemble experimental mesocosms (Goldman 1964). Vertical water movement in the water column of Lake Bonney is on the scale of molecular diffusion because the permanent ice cap prevents wind induced turbulence and strong density gradients over the water column increase stability (Spigel et al. 1990). Owing to its latitude, approximately 77° S, the phytoplankton experience continuous dark for four months and continuous light for four months separated by two months of twilight (Priscu 1989). Lake Bonney also lacks crustaceous zooplankton and fish, which may graze on the phytoplankton (Parker and Simmons 1985) and confound the determination of phytoplankton production and growth

(Welschmeyer and Lorenzen 1985). Lake Bonney is essentially a closed hydraulic system lacking a surface outlet and receiving intermittent stream inflow for only about two months during the summer. Additionally, the layered phytoplankton communities in Lake Bonney (Koob and Leister 1972) have been compared to a series of deep chlorophyll maxima (Lizotte and Priscu 1992). Finally, these communities are among the most shade adapted yet recorded for phytoplankton. Physiological studies have sought to reveal photosynthetic mechanisms which enable the phytoplankton to survive in this low light environment (Goldman 1964, Goldman et al. 1967, Parker et al 1977, Vincent 1981, Parker et al. 1982, Seaburg et al. 1983, Vincent and Vincent 1983, Priscu et al. 1987 and 1988, Neale and Priscu 1990, Priscu et al. 1990, Lizotte and Priscu 1992).

While most of the recent research on the phytoplankton of the dry valley lakes has examined the factors which influence photosynthesis, very little is known about the seasonal and vertical development of phytoplankton biomass and production (Priddle et al. 1986). Vincent (1981) suggested that the period of maximum growth for phytoplankton in the dry valley lakes occurs during the winter-spring transition after nutrients have accumulated from remineralization over the winter and irradiance rises above the compensation point for net photosynthesis.

However the data to test this hypothesis were not available to Vincent. Also with one exception (Priscu et al. 1987), no estimates of in situ specific growth rates have been reported.

Priscu et al. (1987) found that phytoplankton from two dry valley lakes had surprisingly high growth rates ($0.002-0.046 \text{ d}^{-1}$), despite the low irradiances. They speculated that the high growth rates resulted from the extreme hydraulic stability of the water column which allows the phytoplankton to acclimate to the environmental conditions, especially light, at a specific depth.

HYPOTHESES AND OBJECTIVES

In this study, the following hypotheses were tested:

- 1) Phytoplankton growth rates in Lake Bonney are greatest during the winter-spring transition when nutrient concentrations should be highest after remineralization over the winter and irradiance rises above the compensation irradiance for net photosynthesis;
- 2) The high degree of photoacclimation by Lake Bonney phytoplankton is reflected by a high efficiency of light utilization.

To test these hypotheses the following objectives were undertaken:

- 1) Describe the temporal and spatial distribution of nutrients, phytoplankton biomass and production in terms of the seasonal variation in light;
- 2) Use nutrient enrichment bioassays to test for temporal variation of nutrient deficiency of phytoplankton photosynthesis;
- 3) Develop a light-dependent phytoplankton growth model to predict gross specific growth rates.

DESCRIPTION OF STUDY SITE

Geography and Geology

Lake Bonney is located at the head of the Taylor Valley in the dry valleys region of Southern Victoria Land, Antarctica ($77^{\circ}10' - 77^{\circ}45' \text{ S}$, $160^{\circ}20' - 160^{\circ}00' \text{ E}$). The dry valleys region of Southern Victoria Land is an ice-free area of the antarctic continent covering about 3700 km². The Taylor Valley extends from McMurdo Sound to the terminus of the Taylor Glacier. Lakes Fryxell, Hoare, Chad, and Mummy Pond are also located in the Taylor Valley. The annual mean temperature is between -20 and -25°C and annual mean humidity is about 50% (Heywood 1984). The area receives about 10 cm of precipitation per year, making it the most arid region in Antarctica (Heywood 1984). Mummified seal carcasses have been radio-dated at between 300 and 1250 years old, indicating the area has been arid for at least 300 years (Olsen and Broecker 1961).

Bedrock consists of gneiss, marble, schist, and metagreywacke, which have been intruded by granite and covered by shales and sandstones (Clark 1965). Plutonic intrusions of dolerite are common and break up the tan color of the peri-glacial landscape.

Previous Limnological Studies on Lake Bonney

Scientific study of the dry valley lakes began in 1961 when the ice cover of Lakes Bonney and Vanda was first penetrated (Angino et al. 1963). Initial studies on the dry valley lakes were primarily geochemical in nature. Goldman (1964) conducted the first biological investigations in Lake Bonney in the austral summer of 1961-62 and concluded that the phytoplankton were highly shade-adapted. Koob and Leister (1972) made a more detailed study of the phytoplankton populations and production during 1964-65 austral summer. They discovered three distinct phytoplankton communities and primary productivity maxima. An extensive algal mat community was reported in the benthos on the eastern end of Lake Bonney (Parker et al. 1977).

METHODS

Routine Data Collection

Data collected from the center of the east lobe are presented in this thesis (station E30, see Spigel et al in press). Samples were collected over the austral spring and summer (October-January) during 1989-1990 and 1990-1991, and over the winter-spring (September-December) transition during 1991. To reduce confusion with the 1990-1991 season, I will refer to the 1991 winter-spring transition as the 1991-1992 sampling season, although no data were collected in 1992. The only data presented from the 1989-1990 season are nutrient concentrations of lake water and glacial stream samples and phytoplankton biovolume. The dates and routine sampling depths for chlorophyll a (CHL), primary production (PPR), NH_4^+ , $\text{NO}_2^- + \text{NO}_3^-$, and soluble reactive phosphorus (SRP) are listed in Table 1.

The ice of Lake Bonney was penetrated with a 25 cm or a 10 cm ice auger. When the 10 cm ice auger was used, the hole was enlarged by melting with a copper pipe through which heated glycol was circulated. The ice hole was allowed to cool before sampling. All depths are measured from the piezometric water level in the ice hole (usually about 25 cm below the ice surface). This avoids confusion caused by measuring depths from the top or bottom of the

Table 1. Inventory of depths analyzed for CHL, PPR, and nutrients.

Sampling Dates	CHL	PPR	NH ₄ ⁺	NO ₂ ⁻ + NO ₃ ⁻	SRP
24 Nov 1989	A	ND	A	A	A
14 Dec	A	ND	A	A	A
16 Jan 1990	A	ND	A	A	A
30 Oct	B	B	B,C	ND	B,C
6 Nov	B	B	B,C	ND	B,C
13 Nov	B,H	B	ND	ND	ND
20 Nov	B	B	B,C	ND	B,C
27 Nov	B,C	B	B,C	ND	B,C
4 Dec	B,C	B	ND	ND	ND
11 Dec	B,C	B	ND	ND	ND
20 Dec	B,C	B	B,C	ND	B,C
3 Jan 1991	B,C	B	ND	ND	ND
11 Jan	B,C	B	ND	ND	ND
22 Jan	B,C	ND	ND	ND	ND
9 Sep	C,D	E	C,D	C,D	C,D
14 Sep	C,D	E	C,D	C,D	C,D
19 Sep	C,D	E	C,D	C,D	C,D
24 Sep	C,D	E	C,D	C,D	C,D
29 Sep	C,D	D	C,D	C,D	C,D
3 Oct	C,D	E	C,D	C,D	C,D
10 Oct	C,D	E	C,D	ND	C,D
17 Oct	C,F	F	C,F	ND	C,F
24 Oct	C,F	F	C,F	C,F	C,F
31 Oct	C,F	F	C,F	ND	C,F
6 Nov	C,G	G	C,G	C,F	C,G
13 Nov	C,G	G	C,G	ND	C,G
19 Nov	C,G	G	C,G	C,F	C,G
25 Nov	C,G	G	C,G	ND	C,G
1 Dec	C,G	G	C,G	C,F	C,G

A = 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30, 32, 34, and 35 m

B = 4.5, 6, 8, 10, 13, 15, 16, 17, 18 and 20 m

C = 23, 26, 29, 32, and 35 m

D = 3.9, 4.5, 6, 8, 10, 13, 15, 16, 17, 18 and 20 m

E = 3.9, 4.5, 6, 8, 10, 13, 15, 16, 17, and 20 m

F = 3.9, 4.5, 6, 8, 10, 12, 13, 16, 17, 18 and 20 m

G = 3.9, 4.5, 6, 8, 10, 12, 13, 15, 16, 17, 18 and 20 m

H = 23 and 26 m

ND = not determined

ice as the ice thickness may change over the summer; however the depths were displaced when substantial run-off occurred in January of 1991.

Physical and Chemical Measurements

Water temperature was measured from under the ice to the bottom with a YSI model 57 temperature probe. Dissolved oxygen concentrations were determined by a modified (for supersaturation) Winkler titration method (APHA 1985).

During 1990-1991, surface irradiance was monitored with a Li-Cor 2π quantum sensor (400-700 nm) and logged onto a Campbell data logger, while under-ice irradiance was monitored at 10 m depth with a Li-Cor 4π quantum sensor and logged with a Li-Cor model Li-1000 data logger. In 1991-1992 surface and underwater irradiance were logged contemporaneously with a Li-Cor model LI-1000 data logger connected to both the 2π and 4π Li-Cor quantum sensors, respectively.

Water column transparency was determined at approximately weekly intervals from irradiance profiles (400-700nm) made with a 4π quantum sensor. Because light is attenuated exponentially in the water column, the data were log transformed and a linear regression model was applied over the depths where the relationship between log transformed data and depth appeared linear. This gave the

diffuse attenuation coefficient for photosynthetically available radiation (the intrinsic rate at which light is attenuated) over the water column (Wetzel 1983). The extinction coefficients were used to extrapolate from irradiance monitored at 10 m to other depths.

A 2.2 L Niskin bottle with a teflon coated spring was used to collect water from each of the routine sampling depths for measurement of nutrient concentrations, dissolved inorganic carbon (DIC), chlorophyll a (CHL) concentrations, phytoplankton numbers, biomass and photosynthesis. One liter high density polyethylene (HDPE) bottles were rinsed 3 times with sample, filled and placed in a cooler. The remainder of the sample in the Niskin bottle was used to measure photosynthesis in situ.

The cooler containing the samples was returned to a shoreside laboratory. One to three hundred mL of sample was vacuum filtered (< 0.3 atm) through 2.5 cm Whatman GF/F (1989-1990) or GF/C (1990-1991 and 1991-1992) filters. The filtered sample was used for chlorophyll a determinations. Filtrate was collected in acid washed 250 mL sidearm flasks. The filtrate was then transferred to acid washed 125 mL HDPE bottles and frozen until analysis for NH_4^+ , NO_2^- , NO_3^- , and soluble reactive phosphorus (SRP) at the Eklund Biology Center (EBC), McMurdo Station. Nutrient concentrations for each of the glacial meltwater streams flowing into Lake Bonney were analyzed once in 1989-1990.

The limit of detection (defined as three times the sample standard deviation plus the blank signal, see Miller and Miller 1988) of each method is listed in Table 2.

Ammonium concentrations were determined in 10 mL samples by the blue indophenol reaction between NH_4^+ , phenol and hypochlorite at high pH (Solorzano 1969). Water samples below 14 m in 1989-1990 and 1990-1991 and below 16 m in 1991-1992 were diluted 9:1 with deionized water (9 parts deionized water (18 Mohm) to 1 part sample), to prevent salt interference of the color forming reaction. A 1 cm pathlength cell in a Beckman DB-G spectrophotometer was used for all determinations.

Table 2. The average limit of detection for NH_4^+ , $\text{NO}_2^- + \text{NO}_3^-$, and SRP methods. L.O.D. = limit of detection.

Nutrient	Season	L.O.D. (μM)
NH_4^+	1989-1990	1.541
	1990-1991	0.850
	1991-1992	0.474
$\text{NO}_2^- + \text{NO}_3^-$	1989-1990	1.870
	1991-1992	0.805
SRP	1989-1990	0.112
	1990-1991	0.071
	1991-1992	0.040

The effect of freezing the sample on NH_4^+ concentrations was tested on samples representative of the upper freshwater layer (4.5 m), chemocline (17 m) and deep salt layer (35 m). Samples were refrigerated (4°C) or frozen (-80°C) for five days before analysis. There was no

significant difference between frozen and refrigerated samples (Table 3).

Table 3. Comparison of frozen and unfrozen samples analyzed for NH_4^+ (μM). S.D. = standard deviation.

Depth (m)	Refrigerated Average $\pm$ S.D.	Frozen Average $\pm$ S.D.
5	0.78 $\pm$ 0.03	0.72 $\pm$ 0.07
17	27.37 $\pm$ 0.34	27.77 $\pm$ 0.35
35	133.48 $\pm$ 5.327	128.44 $\pm$ 2.43

In 1989-1990, NO_3^- and NO_2^- concentrations were determined by reducing NO_3^- to NO_2^- by a cadmium-copper reduction column at pH = 8.3, with subsequent measurement of NO_2^- by diazotizing with sulfanilamide and coupling with NAD dihydrochloride. The method was followed as outlined in Standard Methods (APHA 1985), 20 mL of the ammonium chloride EDTA buffer was added to each 10 mL sample before the reduction step. In 1991-1992, $\text{NO}_2^- + \text{NO}_3^-$ was measured by reducing NO_3^- to NO_2^- with spongy cadmium (Jones, 1984) and measuring the resulting NO_2^- with the NED/sulfanilamide method. Samples from 1990-1991 were not analyzed for $\text{NO}_2^- + \text{NO}_3^-$ at the time of data analysis. A one cm cell pathlength in a Beckman DB-G was used in all determinations.

The ammonium molybdate/potassium antimonyl tartrate method was used for the determination of soluble reactive phosphorus (SRP). The method was followed as in Downes (1978) with the exception that the reduction step, used to

remove arsenate interference, was omitted. In 1989-1990 and 1990-1991, water samples from depths below 15 m were diluted 1:1 (1 part sample:1 part deionized water) and below 20 m were diluted 9:1 (deionized water to sample). A 1 cm pathlength cell was used in a Perkin-Elmer λ 4 Spectrophotometer for color determination. In 1991-1992 none of the water samples for SRP were diluted and a 10 cm pathlength cell in a Perkin-Elmer λ 4 Spectrophotometer was used.

Average recovery efficiencies for the three nutrient analyses were determined on samples collected from depths representing the upper freshwater layer (4.5 m), chemocline (17 m) and deep saline layer (35 m) (Table 4). Recovery efficiencies were not used to correct the sample concentrations.

Table 4. Average recovery efficiencies + coefficient of variation for NH_4^+ , NO_3^- , and SRP from 4.5, 17, and 35 m samples. The number of replicate groups tested for each assay are in parenthesis. ND = not determined.

Assay	Season	4.5 m	17 m	35 m
NH_4^+	1989-1990/	113 $\pm$ 9 (4)	122 $\pm$ 28 (4)	103 $\pm$ 33 (4)
	1990-1991/			
	1991-1992			
NO_3^-	1989-1990	110 (2)	116 $\pm$ 6 (3)	96 (2)
	1991-1992	133 (1)	100 (1)	105 (1)
SRP	1989-1990/	110 (2)	96 $\pm$ 2 (3)	100 (1)
	1990-1991			
	1991-1992	99 (1)	100 (1)	ND

Biological Data Collection

Chlorophyll a

Chlorophyll a (CHL) concentrations were determined from 100 to 300 mL of lake water filtered through 2.5 cm Whatman GF/C glass fiber filters. Samples were immediately frozen until analysis at the Eklund Biology Center (<2 months). Samples were not routinely duplicated until after 27 November 1991.

CHL was extracted from the frozen sample filters in 10 mL of 90% acetone in 20 mL glass scintillation vials. Samples were vortexed for 1 minute and then allowed to extract for 12-24 hours at 4° C in the dark. Tests showed that this extraction procedure was as efficient as extraction by homogenization (Lizotte and Priscu, unpublished data). Extracted CHL was measured fluorometrically in a Turner Design model 10 fluorometer calibrated with standard concentrations of purified CHL (Sigma Chemical). To correct for phaeopigment fluorescence, extracts were read before and after acidification with 0.2 mL of 1N HCl (Holm-Hansen et al. 1965).

Phytoplankton Biovolume

Samples for phytoplankton identification and enumeration were collected from the same water sample used

to measure photosynthesis, CHL, and nutrients. Table 5 lists the phytoplankton samples that were analyzed. Phytoplankton samples were preserved with acid-Lugol's solution (APHA 1985) immediately upon collection (final concentration = 1%). One hundred mL samples were settled for at least 5 days in Utermohl chambers and cells were identified (Seaburg et al. 1979) and enumerated using the inverted microscope technique (Lund et al. 1957).

The dimensions of the phytoplankton were measured and cell volumes were calculated using appropriate geometrical equations. The density of the cells was assumed to be the same as water, and cell volume was converted to biomass (g C) by the equation:

$$1) \quad \log_{10} C = 0.94 * (\log_{10} \text{biovolume}) - 0.60$$

(Smayda 1978), where C is grams carbon and biovolume is cell volume (μm^3).

Table 5. Inventory of phytoplankton samples analyzed.

Sampling Date	4.5	6	8	10	13	15	16	17	18	20
24 Nov 1989	X	X	X	X	X	X		X	X	X
14 Dec	X	X	X	X	X	X	X	X	X	
16 Jan 1990	X	X	X	X	X	X	X	X	X	
30 Oct	X	X		X		X	X		X	
13 Nov	X	X	X	X	X	X		X		
27 Nov	X	X	X	X		X	X		X	X
11 Dec	X	X		X		X			X	
20 Dec	X	X	X	X	X			X		
3 Jan 1991	X	X		X	X		X	X	X	
22 Jan		X		X		X				

Phytoplankton Productivity: Measurement and Verification

Photosynthesis was measured in situ by the ^{14}C method. Two clear and one opaque acid washed 145 mL Pyrex glass screw-top bottles were rinsed 3 times with sample, filled gently, and placed in a darkened box until all the samples were collected. The entire sampling procedure was done under a tent and took about an hour.

An ampulated working solution of $^{14}\text{C}-\text{CO}_3^{-2}$ (120 $\mu\text{Ci/mL}$, 1990-1991; 121 $\mu\text{Ci/mL}$, 1991-92) was added to the samples as a tracer to measure photosynthesis. The tracer was injected into the samples with a Gilson P1000 Pipetman. In 1990-1991, 26.4 μCi and 84.0 μCi of ^{14}C -carbonate were added to samples from 4.5 to 10 m and 13 to 20 m, respectively. In 1991-1992, 26.6 μCi and 69.0 μCi of tracer were added to samples from 3.9 to 10 m and 13 to 20 m, respectively. On 9 September 1991, 53.2 μCi and 157.3 μCi were added to samples from 3.9 to 10 m and 13 to 20 m, respectively. To samples from 12 m, 42.4 μCi was added, during both 1990-1991 and 1991-1992. A bubble was left in the bottle to help mix the tracer into the sample especially at deeper depths where the difference in density between the ^{14}C solution and sample was greatest.

After all the samples were inoculated, samples were taken from the tent in the darkened box to the ice hole and resuspended from a nylon cord at the depth of collection for 24 hours. The nylon cord was checked twice during the

1990-1991 season and at the start of the 1991-1992 season for stretching or shrinkage; neither occurred. The ice hole was covered by a dark blanket to reduce the direct transmittance of surface light through the ice hole to where the samples were suspended. Incubations were usually started between 0600-0800 h local time when nearby mountains obstructed direct sunlight.

After the incubation, samples were again placed in the darkened box and taken to the Lake Bonney field laboratory. Samples were filtered through Whatman GF/C glass fiber filters under low vacuum (<10 mm Hg). Filtering all the samples took less than 2 hours and was done in a dark room. Filters, filtration funnels and incubation bottles were not rinsed with deionized water (to remove unassimilated ^{14}C) to avoid rupturing cells from the depths of high salinity. Instead, filters were placed in 20 mL glass scintillation vials and 0.5 mL 3 N HCl was added to volatilize unassimilated inorganic ^{14}C . Samples were then dried on a hot plate (50°C). Care was taken that the filters were completely immersed in the acid to ensure that the inorganic label would be converted to CO_2 .

Dissolved inorganic carbon (DIC) in water samples was measured by infrared absorption. Samples were injected into a glass chamber filled with 6N H_2SO_4 and sparged with ultra high purity N_2 gas, which passed through an ascarite pre-column to remove any CO_2 contamination. The instrument

was calibrated with a freshly prepared standard of NaHCO_3 . Infrared absorbance as an output voltage was monitored on a chart recorder. Peak areas were later integrated on a Jandel digitizing board and converted to mg L^{-1} by means of a standard curve.

The radioactivity of the seston on the filters was measured at the EBC in McMurdo Station by liquid scintillation spectrometry. Ten mL of CytoScint ES (ICN Pharmacueticals) 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. A quench curve was prepared with standard amounts of ^{14}C -toluene using acetone as a quenching agent.

Disintegrations per minute (dpm) were converted to photosynthetic rate by the following equation:

$$2) \quad \text{mg C m}^{-3} \text{ day}^{-1} = (\text{DIC}) * (\text{light dpm} - \text{dark dpm}) * \\ (\mu\text{Ci} * (2.2 * 10^6 \text{ dpm})^{-1}) * 1.06 * \\ (\mu\text{Ci added})^{-1} * (\text{day})^{-1}$$

where DIC is the concentration of dissolved inorganic carbon (mg L^{-1}), and 1.06 is the isotope discrimination factor.

Presumably, the 24 hour incubations measure daily net primary productivity. For instance, long incubation periods (> 4 hours) in eutrophic systems may underestimate primary production because the nutrient pool becomes depleted when phytoplankton are confined within a bottle

(Peterson 1980). On 20 November 1990, the depth integrated (trapezoidal) daily primary production of a single 24 hour incubation was compared to the sum of three 8 hour incubations. Primary production was measured at the usual depths for the 24 h incubation and at 4.5, 6, 10, 16 and 17 m for each of the 8 h incubations. Integrated daily primary production was virtually identical between the two methods (Table 6). In an arctic lake, Kalff and Welch (1974) also found no significant difference between daily primary production measured in a single 24 hr incubation and 5-6 hr incubations made over the same period.

Table 6. A comparison of a 24 hour incubation versus 3-8 hour incubations to measure daily integrated (4.5-20 m) primary production (PPR) on 20 November and 21 November 1991.

Time Period	mg C m ⁻² incubation period ⁻¹
0620-1419	9.6
1420-2232	6.4
2235-0620	1.1
sum = 17.1 mg C m ⁻² d ⁻¹	
PPR measured in one 24 hour incubation = 17.7 mg C m ⁻² d ⁻¹	

Experiments to determine the effects of rinsing the filters with deionized water were conducted on 28 November and 16 December 1989. Three clear 145 mL Pyrex glass bottles filled with lake water samples from 17 m (the depth of highest salinity where a PPR maximum occurred) were incubated in situ for at least 8 hours with ¹⁴C. Following incubation, samples were split in half and filtered through 2.5 cm Whatman GF/F filters. The duplicate filters were

then rinsed with 20 mL of either deionized water or filtered 17 m lake water. While the radioactivity of the seston on filters rinsed with deionized water did not differ significantly from the filters rinsed with 17 m lake water, the radioactivity of the rinsed seston was always lower on average (Table 7).

Table 7. Comparison of the effects of rinsing with deionized water or filtered 17 m lake water on the retention of ^{14}C by filtered 17 m phytoplankton. p is the probability of making a Type I error, two-sided t -test. H_0 : DIW rinse = 17 m rinse. DIW = deionized water. S.D. = standard deviation.

Date	Type of Rinse	Average $\pm$ S.D.	$p >$
28 Nov 1989	DIW	8333 $\pm$ 1183	0.4
	17 m	8815 $\pm$ 384	
16 Dec	DIW	227 $\pm$ 22	0.05
	17 m	286 $\pm$ 30	

Previous investigators (Parker et al. 1977) reported that an extremely high percentage ($\geq 90\%$) of the photoassimilated C was excreted during the incubation period. I determined the percentage of photoassimilated ^{14}C that was excreted to test Parker et al's claim. On 16 December 1989, water was collected from 4.5 m and distributed into two clear 145 mL Pyrex glass bottles. The bottles were then inoculated with $^{14}\text{C}-\text{CO}_3^{2-}$ (final activity = $0.67 \mu\text{Ci/mL}$). One of the bottles was immediately vacuum filtered ($< 10 \text{ mm Hg}$) through a Whatman GF/F filter. The filtrate was collected 20 mL at a time in 20 mL glass

scintillation vials. Both the filter and the filtrate were acidified with 1 mL of 3N HCl and dried on a hot plate. The other bottle was placed in an incubator ($15 \mu\text{E m}^{-2} \text{ s}^{-1}$, 1°C) for 12 h. After incubation, the sample was filtered and the filtrate collected and dried as described above. The radioactivity of the filter and filtrate from the bottle that was filtered initially were subtracted from the activity of the filter and filtrate of the sample, which was incubated, as shown below:

$$3) \quad \% \text{C excreted} = \frac{(\text{filtrate dpm}) * 100}{(\text{filter dpm} + \text{filtrate dpm})}.$$

On 18 December 1990, vacuum filtration was compared with gravity filtration to determine its effect on the release of assimilated ^{14}C in samples from 4.5, 10 and 13 m. In this test, samples were placed into 145 mL bottles and inoculated with $^{14}\text{C-CO}_3^{2-}$ (4.5 m to a final activity of $0.56 \mu\text{Ci mL}^{-1}$; 10 m to a final activity of $0.8 \mu\text{Ci mL}^{-1}$; 13 m to a final activity of $1.2 \mu\text{Ci mL}^{-1}$). The samples were then incubated in situ for 23 h. Following incubation, samples were split in half. One subsample was vacuum filtered through a 2.5 cm Whatman GF/C filter, while the other was filtered by gravity through a 4.7 cm Whatman GF/C filter. The filter and filtrate were collected, acidified and dried. If 20 mL of the filtrate from 10 or 13 m samples was dried, the salt and carbonate residue left in the scintillation vial quenched the samples beyond the limits

of the quench curve. To avoid this problem only 15 and 7 mL of the filtrate, from 10 and 13 m samples, respectively, was collected in each 20 mL glass scintillation vial. The radioactivity of dried filtrate minus 40 dpm (background activity registered for a blank scintillation vial containing 10 mL of scintillation cocktail) were summed for each depth to estimate the total radioactivity of the filtrate.

Table 8. Measurements of the percentage excretion of ^{14}C assimilated during an incubation period.

Date	Depth (m)	Filtration Method	% C excreted
16 Dec 1989	4.5	vacuum	24
18 Dec 1990	4.5	vacuum	12
	4.5	gravity	6
	10	vacuum	15
	10	gravity	22
	13	vacuum	27
	13	gravity	30

The results (Table 8) show that the fraction of fixed ^{14}C passing through the filter (excreted) was well within the range traditionally reported (5-35%) for phytoplankton (Fogg 1966); however, excretion rates greater than 5% may be methodological artifacts (see Sharp 1977). Only for the 4.5 m sample did gravity filtration yield a lower percentage of excreted ^{14}C . Phytoplankton from 10 and 13 m may excrete more of the total ^{14}C assimilated than those from 4.5 m. A paired t-test (2-sided) was used to check for a significant difference between the radioactivity of

the filtrate collected by gravity and vacuum filtration at each depth. There was no significant difference ($p > 0.05$) between the radioactivity collected by the two filtration methods.

Displacement Experiments

Two separate displacement experiments were conducted between 26 and 29 September 1991 to examine the photosynthetic viability of the phytoplankton at 18 m, during late winter. In the first experiment, a water sample from 18 m was collected, placed in a 1 L polyethylene collapsible container (cubitainer) and incubated at 11 m. Eleven m was chosen as the displacement because of similar temperatures (4.6°C at 11 m and 5.9°C at 18 m) and increased mean daily irradiance at 11 m. The mean daily irradiance at 11 m during these experiments was about $1.2 \mu\text{E m}^{-2} \text{s}^{-1}$, which unfortunately is lower than the irradiance later estimated for the initiation of net daily production (e.g. Fig 21). The sample was allowed to pre-incubate at 11 m for 24 hours. On 25 and 27 September, the sample was subsampled to measure the photosynthetic rate. Briefly, subsamples were placed in 2 clear and 1 opaque 145 mL Pyrex glass screw top bottles, inoculated with $^{14}\text{C-CO}_3^{-2}$ and incubated at 11 m for 24 hours. In the second experiment conducted on 29 September 1991, a sample was collected from 18 m and treated as above to measure the

photosynthetic rate, except that one set of bottles (2 clear and 1 opaque) was incubated at 11 m and a second set at 18 m.

CHL was detectable at 23 m (see Appendix Table 29). To determine whether this CHL was photosynthetically viable, light and dark bottles were inoculated with $^{14}\text{C}-\text{CO}_3^{2-}$ and incubated in the lake at 15 m and 23 m for 25 hours, on 15 November 1990. The samples were collected and treated as described above.

Nutrient Bioassays

Nutrient enrichment bioassays were used to examine possible phytoplankton nutrient deficiencies. Lake water samples from 4.5, 10 and 17 m were collected using either a 2.2 L or a 10 L Niskin bottle and were transferred to a 20 L HDPE carboy. Samples were pre-incubated with nutrients for about 24 hours (see Tables 9 and 10 for nutrient amendments and incubation periods) in 1 L polycarbonate bottles (1989-1990) or in 1 L polyethylene cubitainers (1990-1991 and 1991-1992) before photosynthesis was measured. The dates over which the bioassays were conducted and the protocols for each experiment are detailed in Tables 9, 10 and 11.

Following the pre-incubation period during 1989-1990, four subsamples were transferred from the single treatment bottle to three clear and one opaque 145 mL Pyrex glass

bottles. Treatments were duplicated or triplicated in 1990-1991, but were not replicated in 1989-1990 and 1991-1992. In the experiments conducted during 1990-1991, two clear and one opaque 60 mL glass stoppered Wheaton bottles were filled with subsamples from each treatment container, following the pre-incubation period, and inoculated with $^{14}\text{C-HCO}_3^-$ to measure photosynthesis (see Tables 10 and 11 for incubation period length and location). Following the incubation, samples were filtered through Whatman GF/F (1989-1990) or GF/C (1990-1991 and 1991-1992) filters. The amount of radiolabel incorporated by the phytoplankton was determined by liquid scintillation spectrometry at the EBC. The radioactivity of the dark bottle was subtracted from the average radioactivity of the light bottle subsamples to determine the amount of tracer that was assimilated in the light.

Table 9. Nutrient amendments (μM) for the various nutrient bioassays that were conducted.

Date	Control	NH_4^+	PO_4^{3-}	$\text{NH}_4^+ + \text{PO}_4^{3-}$
15-19 Nov 1989	--	50	10	50 + 10
29 Nov-2 Dec	--	50	10	50 + 10
5-7 Jan 1990	--	50	10	50 + 10
3-8 Nov	--	20	2	20 + 2
24-25 Nov	--	20	2	20 + 2
7-8 Jan 1991	--	20	2	20 + 2
9 Oct	--	20	2	20 + 2

Table 10. Incubation type, temperature ($^{\circ}\text{C}$) and irradiance ($\mu\text{E m}^{-2} \text{s}^{-1}$) the nutrient bioassay experiments. When samples were incubated in situ, temperature remained constant but light fluctuated according to the ambient field.

Date	Incubation Type	Incubator Temperature	Incubator Irradiance
15 Nov 1989	<u>in situ</u>	--	--
29 Nov	<u>in situ</u>	--	--
5 Jan 1990	incubator	0-4	4
3 Nov	ice bath/incubator*	0-4	5(max)/50
24 Nov	<u>in situ</u>	--	--
29 Nov	<u>in situ</u>	--	--
7 Jan 1991	<u>in situ</u> /moat*	--/1	--/10
9 Oct	<u>in situ</u>	--	--

* - Photosynthetic rate was measured in an incubator or in the lake moat, where the samples were protected from inhibitory irradiances with appropriate layers of window screening.

Table 11. Length (hours) of incubation period with nutrients and incubation period over which photosynthesis was measured.

Date	Length of pre-incubation with nutrients	Length of incubation with $^{14}\text{C-HCO}_3^-$
15 Nov 1989	24.3, [24]	6.8, [8.6]
29 Nov	17, [20]	7.0, [7.6]
5 Jan 1990	15.5, [22]	10.5, [8.7]
3 Nov	44, (44)	10.5, (10.5)
24 Nov	24	8
29 Nov	22.3	8.5
7 Jan 1991	19	7
9 Oct	21.1	8

[] - 17 m bioassay

() - 10 m bioassay

For the 1989-1990 and 1991-1992 experiments, a two-sided Student's t-test was used to determine whether the photosynthetic rate of nutrient enriched treatments was significantly different from that of the control. A one-way analysis of variance (ANOVA) was used to test for significant differences between the mean photosynthetic

rates of the treatments for the 1990-1991 nutrient bioassays. Tukey's method of multiple comparisons was used to assess the significance of differences between treatments. I followed statistical procedures as described in Neter, Wasserman and Kutner (1985) and results were only considered significant at p values of less than or equal to 0.05.

Phytoplankton Growth and Loss Rates

A trapezoidal integration routine was used to integrate CHL and PPR over each of the phytoplankton layers (see RESULTS, Phytoplankton Biovolume as Biomass). The limits of integration for the surface, middle and deep phytoplankton layers were from 4.5 (1990-1991) or 3.9 (1991-1992) to 8 m, 8 to 16 m, and 16 to 20 m, respectively. CHL specific net growth rates ($\mu_{n,i,t}$, d^{-1}) were determined from changes in CHL integrated over each of the phytoplankton layers within the trophogenic zone by

$$4) \quad \mu_{n,i,t} = \frac{(CHL_{i,t+1} - CHL_{i,t})}{(\Delta t * 0.5 * (CHL_{i,t} + CHL_{i,t+1}))}^{-1}$$

where $CHL_{i,t}$ and $CHL_{i,t+1}$ are the integrated CHL concentrations over layer i at time t and t+1 and Δt is the time (days) between t and t+1. Equation 4 implicitly assumes that the rate remains constant and linear between t and t+1.

CHL specific loss rates ($\lambda_{i,t}^*$, d^{-1}) for each phytoplankton layer were calculated according to

$$5) \lambda_{i,t}^* = ((PPR_{i,t} * (C:CHL_i)^{-1} + CHL_{i,t}) - CHL_{i,t+1}) / (\Delta t * 0.5 * (CHL_{i,t} + CHL_{i,t+1}))^{-1}$$

where C:CHL_i is the phytoplankton carbon to CHL ratio for layer i. The definitions of all the symbols used in equations 3 and 4 are described in Table 12.

This method is similar to one presented by Jassby and Goldman (1974), except that loss rates are determined from the difference in the observed CHL at each time step and the amount of CHL predicted to be synthesized within a layer. Jassby and Goldman's method is carbon specific while mine is CHL specific. Primary productivity (g C m⁻² d⁻¹) was converted to a daily rate of change for integrated CHL by using an average C:CHL ratio determined for each phytoplankton assemblage. The average C:CHL (g:g) was approximated from measured CHL and phytoplankton carbon estimates based on cell counts and is assumed not to vary seasonally. Specific loss rates (d⁻¹) are determined by dividing daily loss rates by the average integrated CHL concentration over that time interval.

Model of Light-Dependent Phytoplankton Production

A one dimensional model of phytoplankton production was developed assuming that phytoplankton growth is consistently light-dependent and nutrients do not limit growth. The use of the one dimensional model is justified in Lake Bonney which receives little advective inflow and lacks a surface outlet. This model is similar to one used

to predict growth rates for phytoplankton in the Southern Ocean in relation the mixed layer depth (Mitchell and Holm-Hansen 1991, Mitchell et al. 1991). Because of low under-ice irradiance, the photosynthetic rate of Lake Bonney phytoplankton is always light-limited (Lizotte and Priscu, 1992). This allows for the exclusion of the parameter for the light-saturated rate of photosynthesis from the model; model predictions rely on only one photosynthetic parameter, the initial slope of the photosynthesis-irradiance relationship, α . The model predicts gross chlorophyll specific growth rates for integrated CHL over each of the stratified phytoplankton layers within the trophogenic zone. These phytoplankton layers are (1) a surface layer from under the ice to 8 m; (2) a middle layer from 8 to 16 m; and (3) a deep layer from 16 to 20 m. These divisions correspond to the vertical distribution of the phytoplankton taxonomic groups in Lake Bonney (see RESULTS, Phytoplankton Biovolume as Biomass). Definitions of symbols and parameters used in the model are summarized in Table 12. In the light dependent-phytoplankton growth model, α_i , $C:CHL_i$, D_i , ϵ_i , EXC_i , $I_{i,t}$, Δt , z_i , and the initial integrated CHL concentration are all independent variables in the model. These parameters were empirically determined with the exception of day length, which was taken from a Nautical Almanac Office publication.

Table 12. Definition of abbreviations and model parameters.

α_i	Initial slope of photosynthesis-irradiance relationship within layer i, $\text{mg C (mg CHL)}^{-1} \text{h}^{-1} [\mu\text{E m}^{-2} \text{s}^{-1}]^{-1}$
C:CHL _i	Ratio of carbon to CHL of phytoplankton within layer i (g:g); 60.29 for the surface layer, 78.68 for the middle layer, 81.54 for the deep layer
CHL	Chlorophyll <u>a</u> , mg m^{-3}
CHL _{i,t}	Integrated CHL over layer i at time t, mg CHL m^{-2}
$\Delta\text{CHL}_{i,t}$	Daily rate of change of CHL integrated over layer i at time t, $\text{mg CHL m}^{-2} \text{d}^{-1}$
Δt	Time between irradiance measurements (routine primary productivity measurements), d
d	Deep phytoplankton layer, 16-20 m
D _t	Day length at time t, h
ϵ_t	Vertical extinction coefficient for PAR over the trophogenic zone at time t, m^{-1}
EXC _i	Percent of photoassimilated carbon excreted by the phytoplankton during an incubation period within layer i, unitless
I _{i,t}	Mean daytime irradiance (400-700 nm) at top of layer i at time t, $\mu\text{E m}^{-2} \text{s}^{-1}$
I _{li,t}	Mean daytime irradiance (400-700 nm) within layer i at time t, $\mu\text{E m}^{-2} \text{s}^{-1}$
$\lambda_{i,t}$	Specific loss rate for integrated CHL from phytoplankton layer i, at time t, as the difference between μ_g and μ_n
$\lambda_{i,t}^*$	Specific loss rate for integrated CHL from phytoplankton layer i at time t, as determined by the modified method of Jassby and Goldman (1974), d^{-1}
m	Middle phytoplankton layer, 8-16 m

Table 12 (continued).

$\mu_{g,i,t}$	Gross specific growth rate for phytoplankton within layer i at time t , d^{-1}
$\mu_{n,i,t}$	Net specific growth rate within phytoplankton layer i at time t , d^{-1}
ψ_i	Light utilization index for layer i , $g\ C\ (g\ CHL)^{-1}\ m^2\ (E)^{-1}$
PPR	Primary productivity, $mg\ C\ m^{-3}\ d^{-1}$
$PPR_{i,t}$	Integrated daily primary production over layer i at time t , $mg\ C\ m^{-2}\ d^{-1}$
s	Surface phytoplankton layer, 3.9 or 4.5-8 m
z_i	Depth of layer i , m

Values for α of Lake Bonney phytoplankton (Lizotte and Priscu 1992, Lizotte unpublished) have been determined by photosynthesis-irradiance experiments and are summarized in Table 13. The α values reported in Lizotte and Priscu (1992) were multiplied by a correction factor to normalize the incubator's light spectra to the in situ light spectra. This correction factor is the ratio of the spectrally-weighted CHL-specific absorption coefficients for phytoplankton in situ versus the incubator. The ratio was computed from phytoplankton absorption spectra and spectral irradiance measured during the 1990-1991 season and was applied to α values measured during the 1989-1990 season from similar depths.

Table 13. Measured photosynthetic efficiencies (α , mg C (mg CHL)⁻¹ h⁻¹ [μ E m⁻² s⁻¹]⁻¹) from Lake Bonney phytoplankton during the 1989-1990 and 1990-1991 seasons. Averages are for specific assemblages (4.5-6 m, 10-12 m, and 17 m). S.D. = standard deviation. Data from Dr. M.P. Lizotte.

Date	Depth (m)	α	Average $\pm$ S.D.
13 Nov 1989	5	0.0056	0.0032 $\pm$ 0.0017
28 Nov	5	0.0028	
28 Nov	6	0.0021	
5 Dec	5	0.0050	
5 Dec	6	0.0052	
25 Nov 1990	4.5	0.0017	
25 Nov	6	0.0015	0.0105 $\pm$ 0.0063
10 Dec	4.5	0.0014	
10 Dec	6	0.0014	
4 Jan 1991	4.5	0.0044	
4 Jan	6	0.0037	
13 Nov 1989	10	0.0194	0.0197 $\pm$ 0.0115
28 Nov	10	0.0150	
5 Dec	10	0.0163	
25 Nov 1990	10	0.0048	
10 Dec	10	0.0035	
4 Jan 1991	10	0.0069	
4 Jan	12	0.0075	0.0108
28 Nov 1989	17	0.0972	
7 Dec 1990	17	0.0337	
4 Jan 1991	17	0.0108	

The correction factor was usually around 2 for samples from each phytoplankton layer and decreased in January to around 1.4. The decreased correction factor results from spectral changes in the underwater light field during January 1991 when glacial flour is washed into the lake by meltstreams (Lizotte, personal communication). Alpha values from 1990-1991 were already corrected for the in situ light field. The empirically determined α values from within each phytoplankton layer were averaged and used in

the model. I assume that α does not vary seasonally or within each phytoplankton layer. Photosynthetic efficiency (α) has been shown not to vary with temperature for Lake Bonney phytoplankton (Lizotte and Priscu 1992), consequently, temperature effects on α are not included in the phytoplankton growth model.

The mean daytime irradiance integrated over each phytoplankton layer at time t , $I_{li,t}$ is defined as

$$6) \quad I_{li,t} = [I_{i,t} * (\epsilon_i * z_i)^{-1}] * [1 - \exp(-\epsilon_i * z_i)]$$

where $I_{i,t}$ is the average daytime irradiance at the top of layer i at time t , ϵ_i is the extinction coefficient for the trophogenic zone at time t and z_i is the depth of layer i .

The rate of primary production integrated over layer i at time t is determined by

$$7) \quad PPR_{i,t} = D_t * CHL_{i,t} * \alpha_i * I_{li,t} - D_t * CHL_{i,t} * \alpha_i * I_{li,t} * EXC_i,$$

where D_t is day length at time t , $CHL_{i,t}$ is integrated CHL over layer i at time t , α is the initial slope of the photosynthesis-irradiance relationship within layer i , $I_{li,t}$ is the mean daytime irradiance integrated over layer i at time t and EXC_i is an estimate for the daily percentage of photosynthetically reduced carbon that is excreted by phytoplankton within layer i . I assume EXC_i does not vary seasonally. The daily rate of integrated primary productivity of layer i at time t is converted to the daily increase of CHL within layer i at time t ($\Delta CHL_{i,t}$) by

dividing by the average carbon to CHL ratio within that layer

$$8) \quad \Delta \text{CHL}_{i,t} = \text{PPR}_{i,t} * (\text{C:CHL}_i)^{-1}.$$

The C:CHL_i is assumed not to vary seasonally. The gross specific growth rate (μ_g) can then be derived according to

$$9) \quad \mu_{g,i,t} (d^{-1}) = \ln\{(\text{CHL}_{i,t} + \Delta \text{CHL}_{i,t}) * (\text{CHL}_{i,0})^{-1}\}$$

The resultant CHL integrated over layer i at the next time step ($\text{CHL}_{i,t+1}$) is then computed by

$$10) \quad \text{CHL}_{i,t+1} = \text{CHL}_{i,t} * e^{\mu_{g,i,t} * \Delta t}.$$

For simplicity, I assume that μ is constant from t to t+1. Since my model predicts light-dependent gross CHL specific growth rates (i.e. independent of losses) in Lake Bonney, specific loss rates ($\lambda_{i,t}$, d^{-1}) can be determined by subtracting the observed (net) specific growth rate from the predicted growth rates. This specific loss rate would be the sum of all loss processes (including respiration, physiological death, decomposition, sinking and grazing). Excretion, another loss process, is accounted for in the model.

RESULTS

Physical and Chemical Limnology

Lake Bonney is divided into two lobes (east and west) connected by a narrow, shallow (12 m) channel. Both lobes combined are approximately 7 km long and each is about 1 km wide. Maximum depth recorded in the east and west lobes was about 38 m. Morphometric data was presented in Angino et al. (1964); however it is believed that the level of the lake has been rising throughout this century. This may be the result of a changing climate (Wharton et al. 1989). The west end of the west lobe abuts the Taylor Glacier. Glacial meltwater streams flow into the lake from the Taylor, Calkin, Hughes, Sollas, LaCroix, Matterhorn and Rhone glaciers during December and January. The catchment area for Lake Bonney is 370 km² (Heywood 1984). Lake Bonney has no surface outlet.

Lake Bonney was covered by 3.7-4.0 m of ice during the study. The permanent ice cover on lakes in the dry valleys reduces PAR to 1-4% of surface values and irradiances are typically less than 50 $\mu\text{E m}^{-2} \text{ s}^{-1}$ (Palmisano and Simmons 1987, Lizotte and Priscu 1992, Priscu in press). The ice cover becomes less transparent as the ice temperature rises usually during early December (Priscu in press). Diffuse

attenuation coefficients were about 0.1 m^{-1} over the trophogenic zone (3.9 to 20 m) (Table 14).

Table 14. Vertical extinction coefficients in the trophogenic zone.

Date	Depth Range	Extinction Coefficient (m^{-1})
7 Nov 1990	6-20 m	0.089
14 Nov	6-20 m	0.117
21 Nov	6-20 m	0.107
29 Nov	6-20 m	0.136
6 Dec	6-20 m	0.107
10 Dec	6-20 m	0.109
21 Dec	6-20 m	0.116
3 Jan 1991	6-20 m	0.141
11 Jan	6-20 m	0.157
6 Sep	6-20 m	0.086
11 Sep	6-20 m	0.121
14 Sep	4-20 m	0.106
20 Sep	4-20 m	0.144
22 Sep	5-20 m	0.117
29 Sep	5-20 m	0.086
5 Oct	6-20 m	0.085
10 Oct	6-20 m	0.087
18 Oct	5-20 m	0.089
25 Oct	5-20 m	0.083
1 Nov	5.5-20 m	0.098
7 Nov	5-10 m	0.126
14 Nov	5-20 m	0.093
20 Nov	5-20 m	0.094
25 Nov	5-20 m	0.091
2 Dec	5-20 m	0.104

Lake Bonney is chemically stratified (Angino and Armitage 1963, Goldman et al. 1967) with conductivities ranging from those typical of freshwater to approximately 10 times that of seawater. Over the upper relatively freshwater layer, extending from under the ice to 10 m, conductivities increased from 0 to 1 S m^{-1} . In the chemocline, from 10 to 20 m, conductivity increased from 1

to 11 S m^{-1} . Below 20 m, conductivities initially increased slightly to 12 S m^{-1} at 23 m and then decreased slightly to the bottom, perhaps because of decreasing water temperature rather than a decrease in the concentration of ionic species (Spigel et al. 1990).

Lake Bonney is dichothermic (Parker et al. 1982). In the east lobe temperature increased from 0° C under the ice to a peak of around $5.5\text{--}7^{\circ} \text{ C}$ at 16 m, then decreased to -2.5° C at 37 m (Fig. 1). Dissolved oxygen concentrations ranged from 0.2 to greater than $40 \text{ mg O}_2 \text{ L}^{-1}$ (Fig. 1). Waters above 17 m were supersaturated with oxygen. The oxycline extended from 17 to 23 m. Concentrations decreased below 23 m but were still detectable. Below 31 m dissolved oxygen concentrations apparently increased to 1 mg L^{-1} using both O_2 electrodes and Winkler oxygen methodology.

Profiles of dissolved inorganic carbon (DIC) and pH (Fig. 2) were similar to those reported previously (Koob and Liester 1972) except that the depths of maximum DIC and minimum pH were about 5 m deeper in this study, another indication that lake level has risen. DIC concentrations increased over the trophogenic zone to a maximum at 20 m. Concentrations increased most rapidly over the chemocline. Below 20 m, DIC concentrations decreased to 29 m, then remained constant to the bottom. The pH was highest above the chemocline and decreased over the chemocline to a

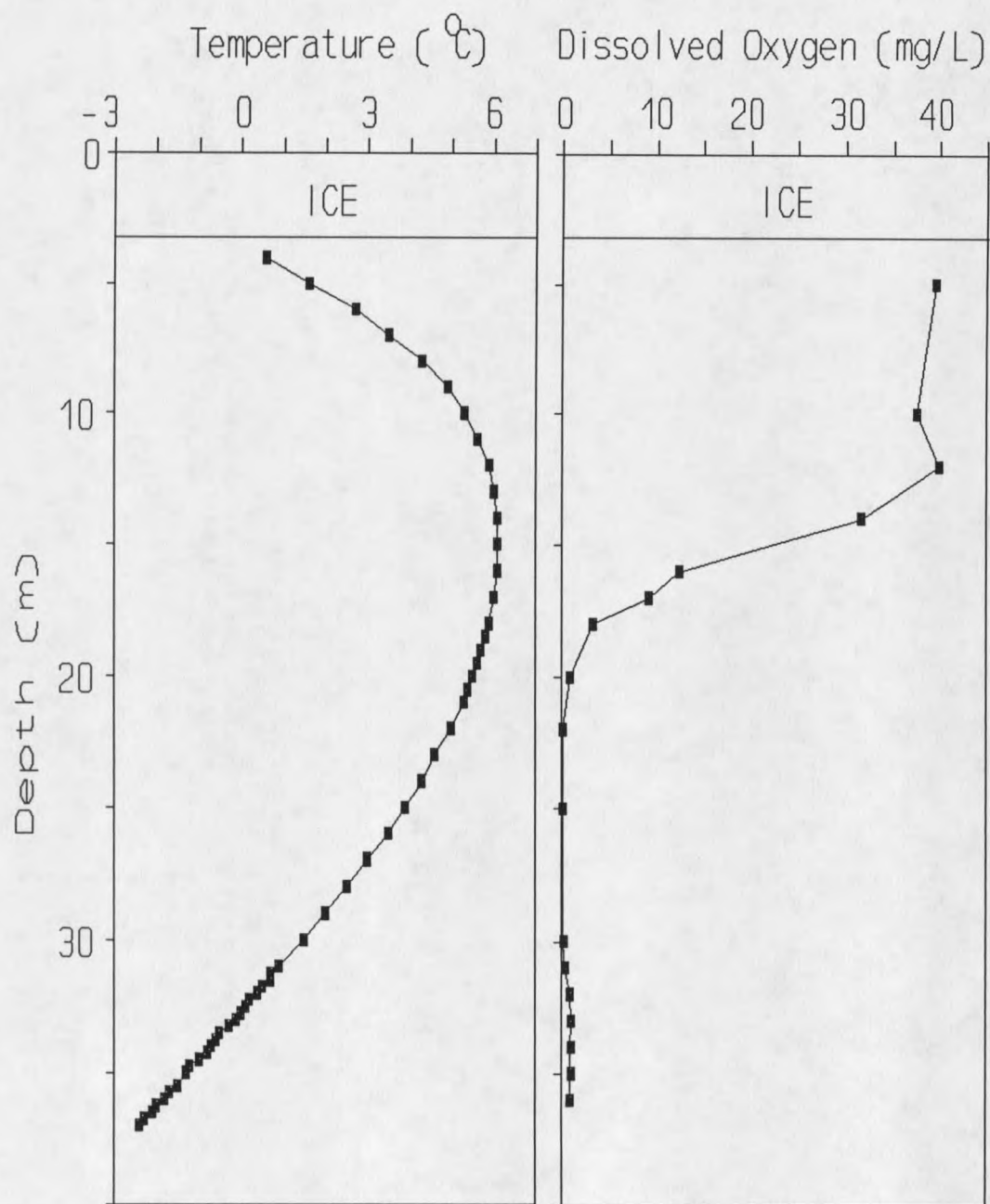


Figure 1. Vertical profiles of temperature (5 Dec 1990) and dissolved oxygen (5-25 m, 12 Nov 1990; 30-35 m, 15 Dec 1990).

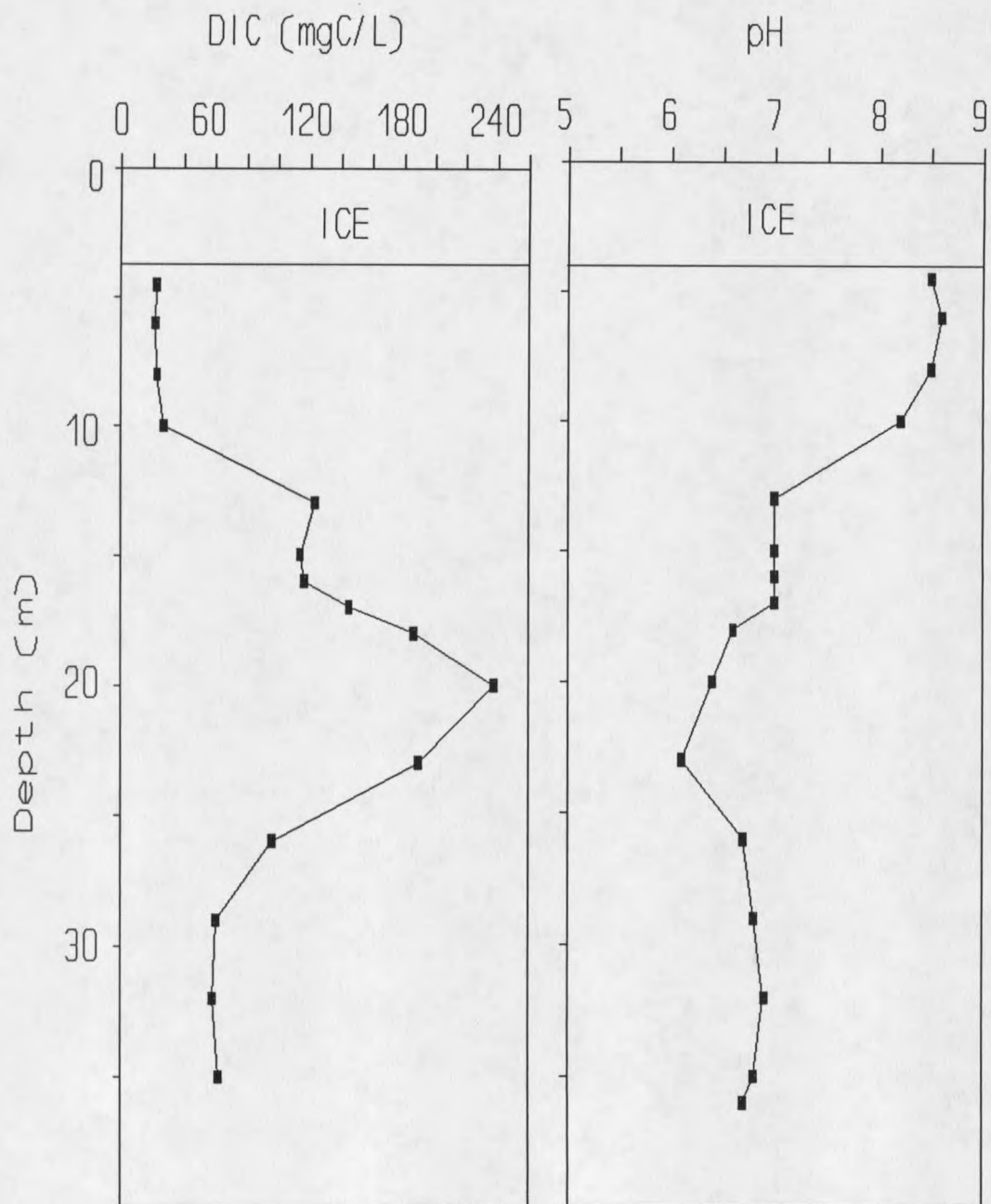


Figure 2. Vertical profiles of dissolved inorganic carbon (DIC) and pH on 6 November 1990.

minimum at 23 m. pH increased below 23 m and was relatively constant to the bottom.

The average NH_4^+ , $\text{NO}_2^- + \text{NO}_3^-$ and SRP concentrations ($\pm$ their standard deviations for the routine sampling depths) and the number of samples assayed are listed in Tables 15, 16 and 17, respectively. Profiles of NH_4^+ from three sampling seasons (Fig. 3) resembled the conductivity profile. NH_4^+ concentrations were lowest above the chemocline with higher concentrations just below the ice cover. NH_4^+ concentrations increased from $1.9 \mu\text{M}$ at 10 m to $152 \mu\text{M}$ at 32 m with the steepest gradient from 17 to 32 m.

Profiles of $\text{NO}_2^- + \text{NO}_3^-$ concentrations also resemble the conductivity profile (Fig. 4). Water samples from immediately below the ice had the lowest concentrations of $\text{NO}_2^- + \text{NO}_3^-$. Concentrations increased slowly from below the ice until 15 m with the steepest gradient from 15 to 29 m where concentrations increased on average from 26 to $217 \mu\text{M}$ $\text{NO}_2^- + \text{NO}_3^-$. Concentrations of $\text{NO}_2^- + \text{NO}_3^-$ were higher at all depths in the 1989-1990 season with the highest concentrations measured on 16 January 1990.

Water column profiles of SRP concentrations were relatively homogenous above 15 m (Fig. 5). Often SRP concentrations within the mixolimnion were near the limit of detection (see Table 2). SRP concentrations are greater from 15 to 18 m, than at shallower depths. Samples

analyzed during the 1989-1990 field season did not show this zone of elevated SRP concentrations as clearly as profiles from two following seasons (Fig. 5). Minimum SRP levels occurred at 20 m whereas maximum levels occurred at 23 m. The SRP concentrations below the chemocline during 1989-1990 and 1990-1991 were on average higher than samples analyzed during the 1991-1992 season. This difference may result from not diluting the samples during the 1991-1992 season. Perhaps the high salinity of the monomolimnetic water samples interfered with the color forming reaction during the assay. However, the ascorbic acid method is reportedly not subject to salt interference in Lake Bonney (Fortner et al 1976).

Nutrient data collected during the 1989-1990 and 1990-1991 seasons do not show any clear seasonal variation in concentration (with the possible exception of SRP concentrations, which decrease over part of 1990-1991). However, the nutrient data collected during the 1991-1992 season is of special interest because it was collected during the winter-spring transition when the highest phytoplankton growth rates are hypothesized to occur (Vincent 1981).

Table 15. Average NH_4^+ concentrations $\pm$ standard deviation for all samples measured.

Depth (m)	$\mu\text{M NH}_4^+$	Number of samples
3.9	3.29 ± 1.83	15
4.5	2.84 ± 1.74	23
6	1.86 ± 1.87	23
8	1.37 ± 1.56	23
10	1.90 ± 1.86	23
12	4.06 ± 1.74	11
13	4.94 ± 2.05	20
14	10.99 ± 1.92	3
15	13.97 ± 15.48	17
16	16.54 ± 13.20	23
17	24.85 ± 15.14	20
18	43.99 ± 15.60	23
20	73.81 ± 14.31	23
22	121.38 ± 11.51	3
23	108.41 ± 14.06	18
24	133.59 ± 30.14	3
26	134.14 ± 17.61	22
28	167.57 ± 22.98	3
29	144.51 ± 14.51	19
30	173.50 ± 23.20	3
32	152.59 ± 19.17	22
34	170.66 ± 25.90	3
35	145.99 ± 18.26	22

Table 16. Average $\text{NO}_2^- + \text{NO}_3^-$ concentrations $\pm$ standard deviation for all samples measured.

Depth (m)	$\mu\text{M NO}_2^- + \text{NO}_3^-$	Number of samples
3.9	5.57 ± 1.17	10
4.5	6.02 ± 1.75	13
6	7.53 ± 1.99	13
8	11.32 ± 1.28	12
10	13.76 ± 1.75	13
12	22.45 ± 7.25	7
13	25.31 ± 9.49	10
14	34.39 ± 4.83	3
15	25.98 ± 7.14	8
16	43.05 ± 16.94	13
17	46.94 ± 7.93	10
18	70.12 ± 17.76	13
20	110.14 ± 25.49	13
22	174.47 ± 9.83	3
23	145.95 ± 19.68	10
24	190.12 ± 16.16	3
26	180.54 ± 25.03	13
28	242.94 ± 11.16	3
29	217.13 ± 12.21	10
30	250.53 ± 3.38	3
32	231.94 ± 14.16	13
34	251.84 ± 8.02	3
35	227.53 ± 10.48	12

Table 17. Average SRP concentrations $\pm$ standard deviation for all samples measured.

Depth (m)	μM SRP	Number of samples
3.9	0.10 ± 0.04	15
4.5	0.10 ± 0.04	23
6	0.10 ± 0.05	23
8	0.08 ± 0.04	23
10	0.09 ± 0.05	23
12	0.07 ± 0.05	11
13	0.12 ± 0.10	20
14	0.19 ± 0.04	3
15	0.18 ± 0.28	17
16	0.19 ± 0.18	23
17	0.20 ± 0.23	20
18	0.15 ± 0.19	23
20	0.12 ± 0.14	23
22	1.09 ± 1.32	3
23	0.87 ± 0.57	19
24	0.74 ± 0.37	3
26	0.67 ± 0.52	22
28	0.64 ± 0.52	3
29	0.62 ± 0.36	19
30	0.66 ± 0.29	3
32	0.63 ± 0.44	22
34	0.61 ± 0.65	3
35	0.57 ± 0.50	22

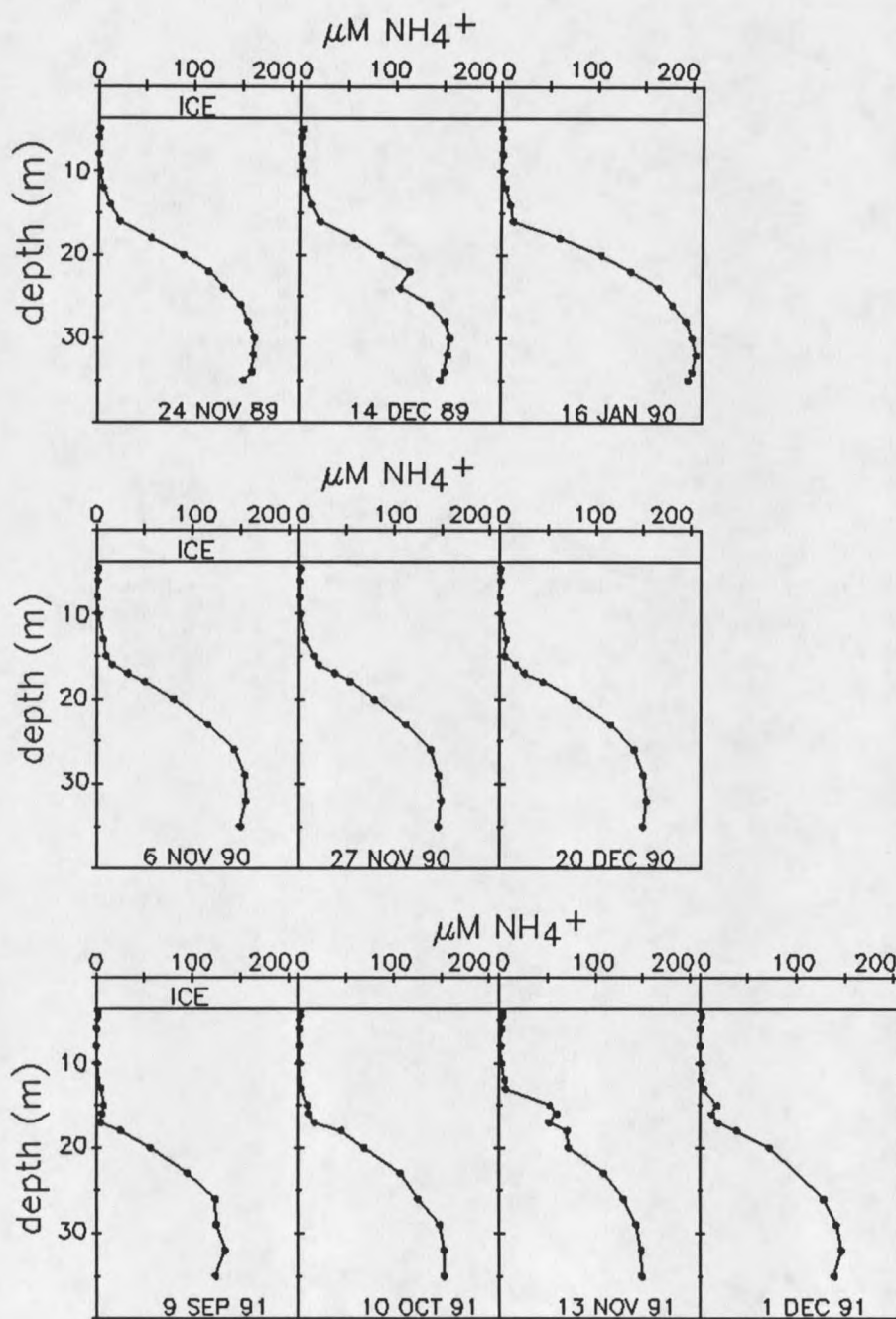


Figure 3. Selected vertical profiles of NH_4^+ concentrations from the 1989-1990, 1990-1991, and 1991-1992 seasons.

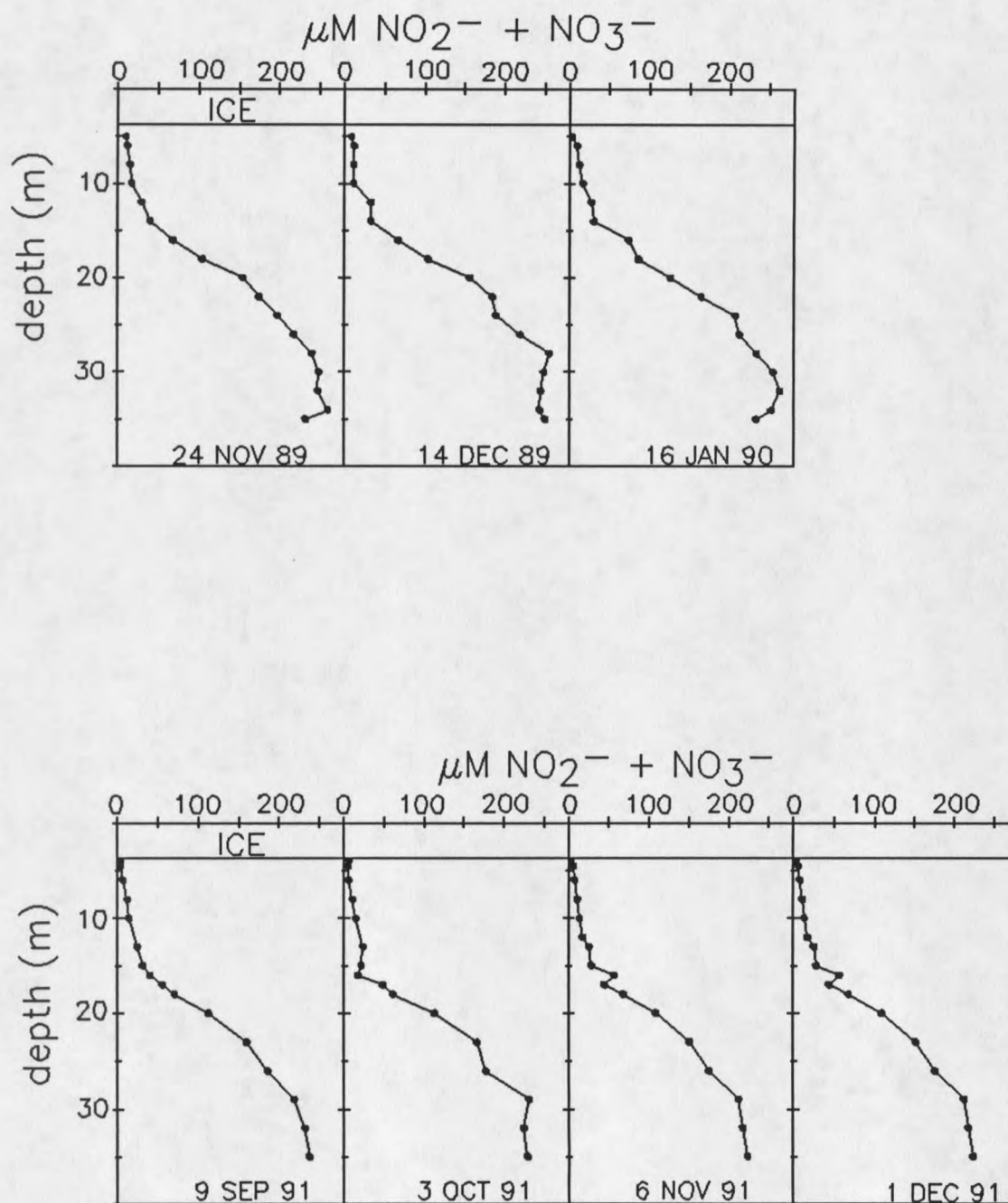


Figure 4. Selected vertical profiles of $\text{NO}_2^- + \text{NO}_3^-$ concentrations from the 1989-1990 and 1991-1992 seasons.

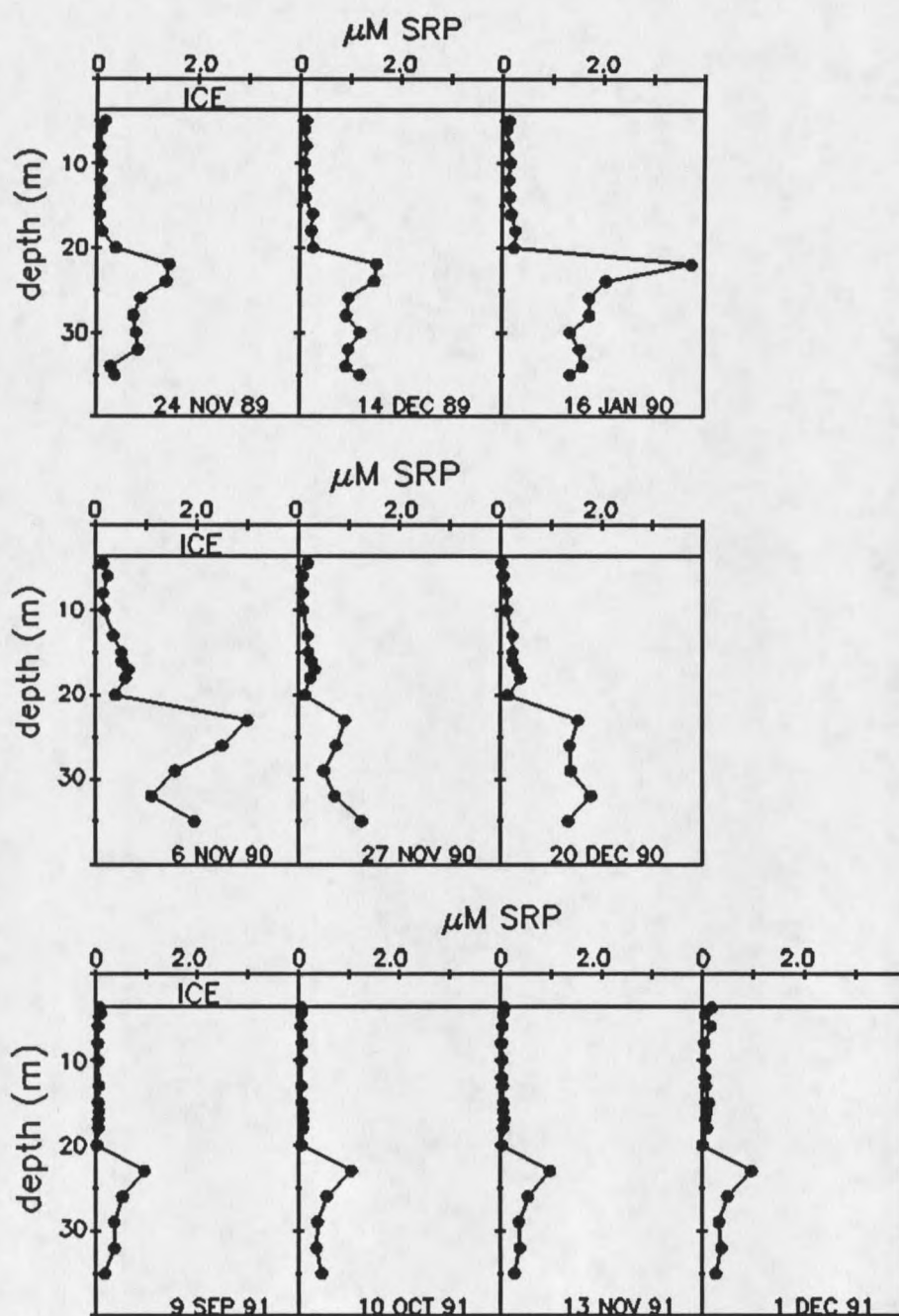


Figure 5. Selected vertical profiles of soluble reactive phosphorus (SRP) concentrations in the 1989-1990, 1990-1991, and 1991-1992 seasons.

Figure 6 shows the seasonal variation in $\text{NO}_2^- + \text{NO}_3^-$ and SRP concentrations for depths representative of the three phytoplankton layers present within the trophogenic zone (under the ice to 20 m): the surface (4.5 m), middle (10 m) and deep (17 m) layers. Neither $\text{NO}_2^- + \text{NO}_3^-$ nor SRP showed a clear seasonal trend in concentrations. Concentrations remained constant as in the case of $\text{NO}_2^- + \text{NO}_3^-$ at 4.5 and 10 m or fluctuated as in the case of $\text{NO}_2^- + \text{NO}_3^-$ at 17 m and SRP concentrations at all three depths.

NH_4^+ concentration increased over the winter-spring transition of 1991 at 4.5, 10 and 17 m (Fig. 7). Concentrations at all three depths increased until 6 November (day 310) and then decreased or showed no directional change. Concentrations at 16 and 18 m are plotted on the graph to illustrate that the trend is not restricted to 17 m. The increase at 17 m is the most dynamic with concentrations increasing about 7 fold from 5 to 37 μM over this period.

Dissolved inorganic N (NH_4^+ and $\text{NO}_2^- + \text{NO}_3^-$, DIN) concentrations of the glacial meltwater streams were generally lower than concentrations immediately below the ice, while meltwater SRP concentrations were higher than surface waters (Table 18).

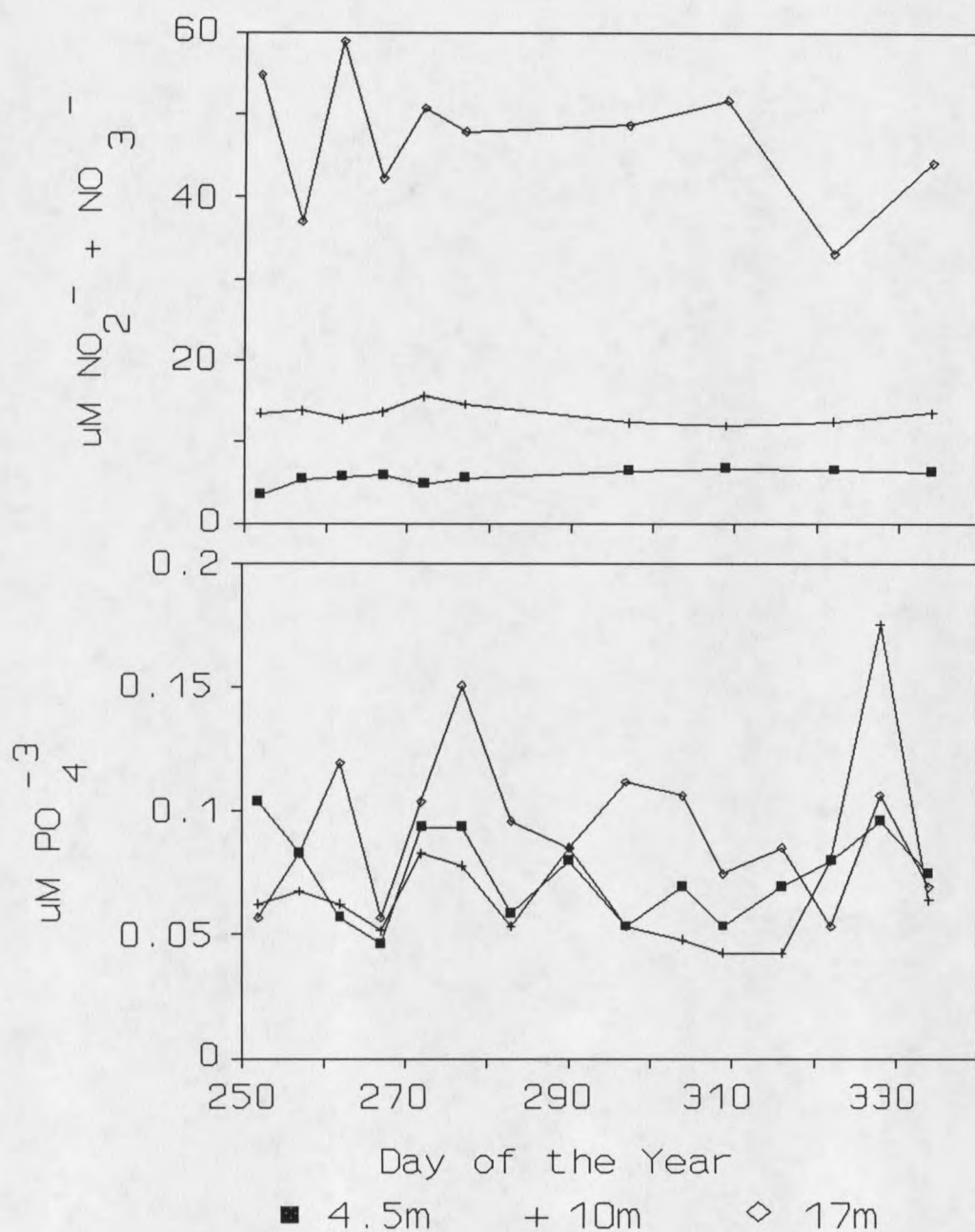


Figure 6. Temporal variation of $\text{NO}_2^- + \text{NO}_3^-$ and SRP concentrations from depths representative of the surface (4.5 m), middle (10 m), and deep (17 m) phytoplankton layers during the 1991-1992 season.

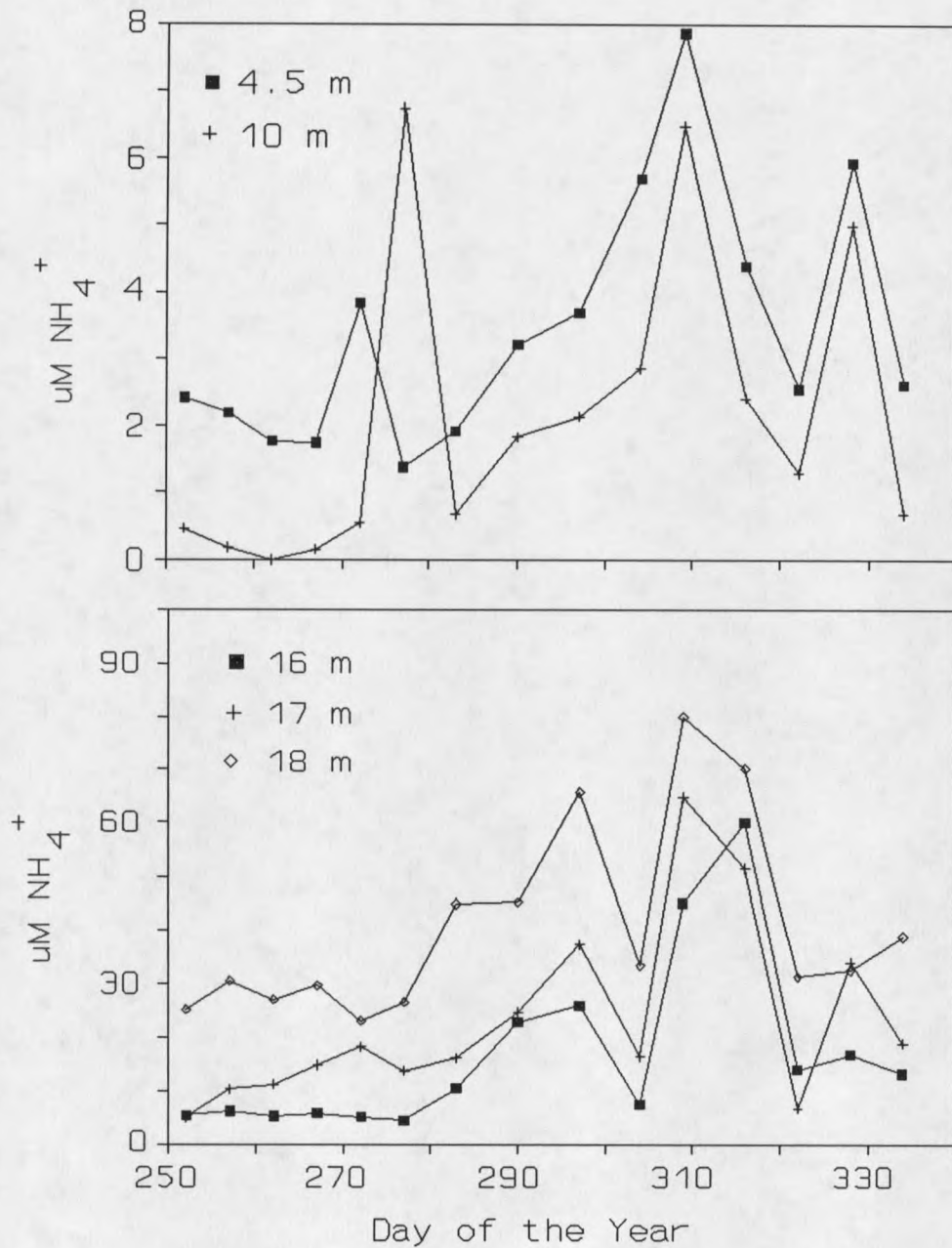


Figure 7. Temporal variation of NH_4^+ concentrations from depths representative of the surface (4.5 m), middle (10 m), and deep (17 m) phytoplankton layers during 1991-1992.

Table 18. Glacial meltwater nutrient concentrations collected on 7 January 1990. NA = not available.

Stream	$\mu\text{M NH}_4^+$	$\mu\text{M NO}_2^- + \text{NO}_3^-$	$\mu\text{M SRP}$
Eastern Inflow	0.219	2.477	0.551
Taylor	1.596	21.730	0.499
Hughes	1.940	0.247	0.765
Matterhorn	0.822	NA	0.840
Rhone	0.047	9.799	0.191
Calkin	0.133	1.235	0.442

Biological Limnology

Three assemblages of phytoplankton exist within the trophogenic zone in the east lobe of Lake Bonney which extends from below the ice to 20 m (these assemblages are described in the next section). In this section, I examine the seasonal trends in phytoplankton biomass and production in the trophogenic zone. A model is presented which predicts gross specific growth rates of each phytoplankton assemblage from empirical photosynthetic parameters, incident light, the extinction coefficient of the trophogenic zone and chlorophyll concentrations.

Phytoplankton Biovolume as Biomass

Microscopic examination of lake water samples revealed two unique features of the water column in Lake Bonney. First was the absence of zooplankton and the second was the layered phytoplankton communities (Fig. 8 and 9). Only phytoplankton samples collected during the 1989-1990 and

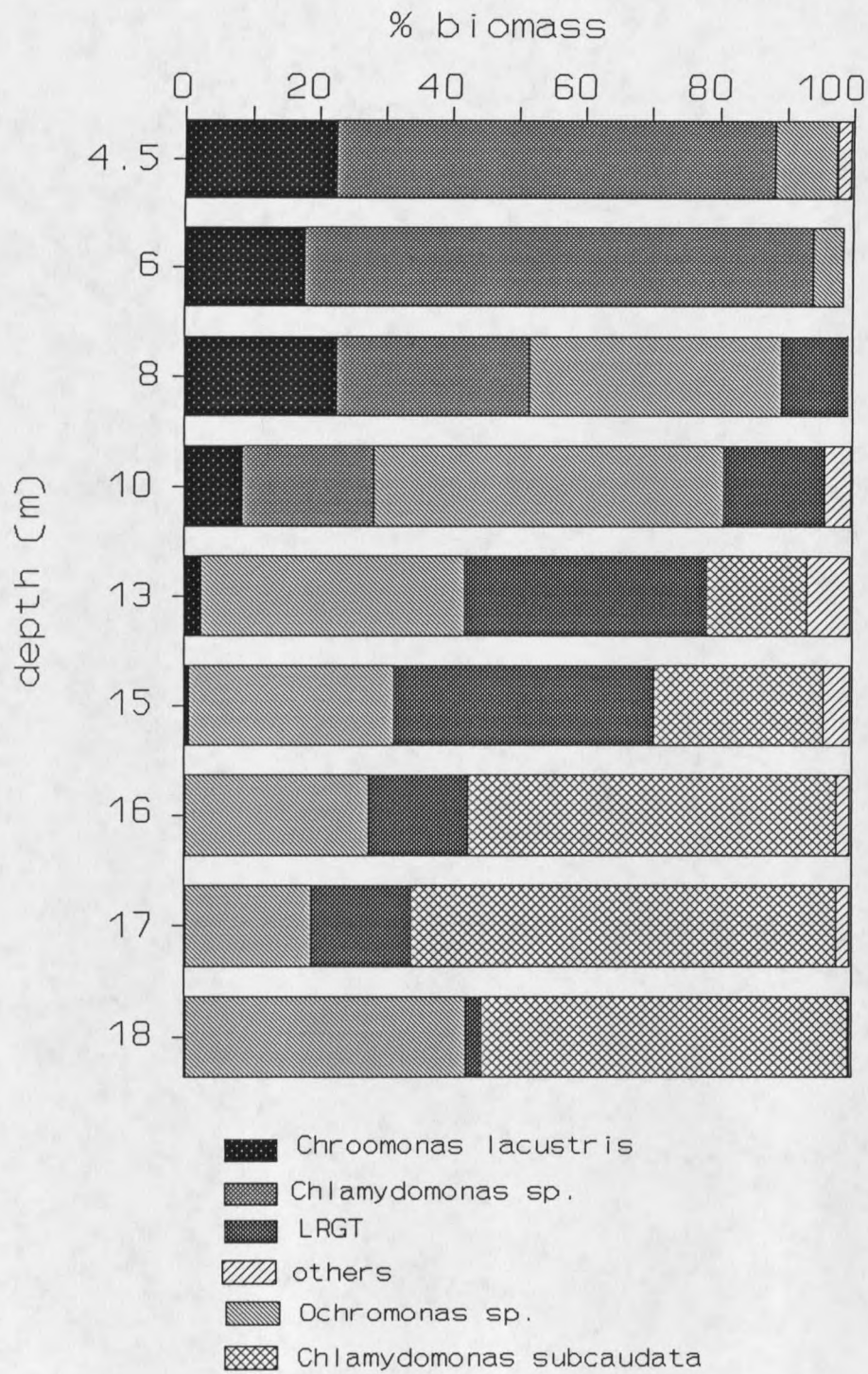


Figure 8. Vertical distribution of phytoplankton taxa expressed as a percentage of the total biomass averaged over the 1989-1990 season.

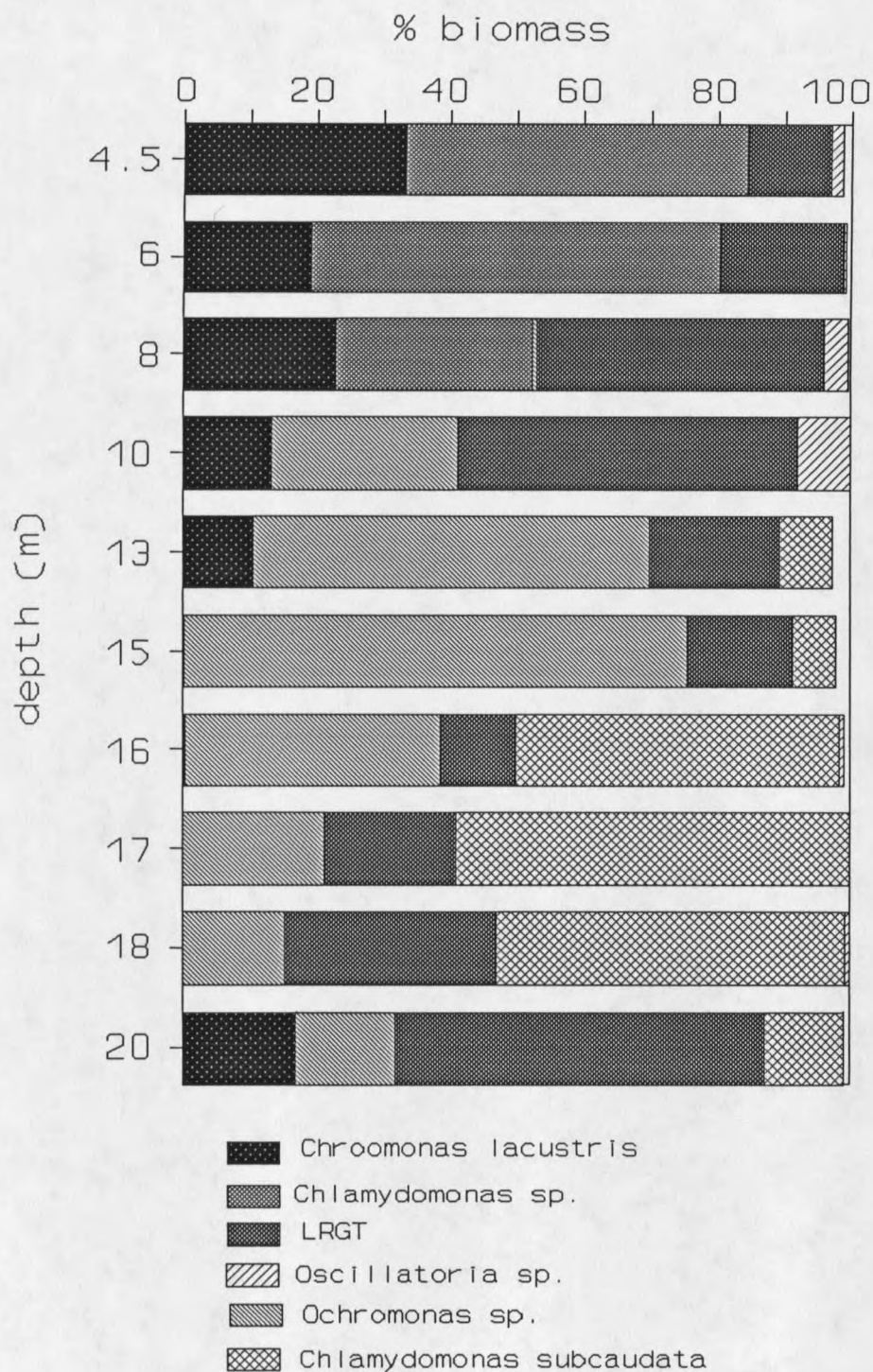


Figure 9. Vertical distribution of phytoplankton taxa expressed as a percentage of the total biomass averaged over the 1990-1991 season.

1990-1991 seasons were examined. The percentage biomass contributed by each phytoplankton member changed gradually with depth; the different layers were not monospecific, with one phytoplankton member completely excluding the others. Despite the gradual change of phytoplankton members with depth, the trophogenic zone was divided into three functional layers based on the dominant taxa.

A surface layer from under the ice to 8 m was composed of Chroomonas lacustris Pasher and Ruttner and a species of Chlamydomonas. The latter may be C. subcaudata Wille but the cells differ morphometrically from the more typical C. subcaudata found in deeper populations; the cells lacked the large clear posterior area. Zygospores and zoospores were also observed and presumed to be Chlamydomonas sp. for the purpose of assessing phytoplankton biomass. The remainder of phytoplankton biomass within this layer was contributed by unidentifiable flagellated or non-flagellated coccoid phytoplankton ($< 4 \mu\text{m}$ diameter), referred to as little round green things (LRGT) and occasionally a filament belonging to the Oscillatoriaceae, referred to as Oscillatoria sp. There was no clear evidence of seasonal succession within this layer from samples collected during 1989-1990 and 1990-1991.

A middle phytoplankton layer extended from 8 to 16 m. This layer can be split into two subzones: 1) a region

where conductivity increased gradually, from 8 to 10 m, LRGT dominated while an Ochromonas sp. and Chroomonas lacustris accounted for the remainder of the biomass and 2) from 10 to 16 m, where conductivity gradient was steeper, Ochromonas sp. dominated, and LRGT and Chlamydomonas subcaudata contributed the remaining biomass. Over both seasons, the amount of biomass contributed by C. subcaudata within in this zone (8-16 m) increased.

From 16 to 20 m, the phytoplankton assemblage was composed of Ochromonas sp., C. subcaudata and LRGT. Seasonal succession occurred within this phytoplankton layer, as follows. In mid-spring (early November), the percentage biomass contributed by each phytoplankton member was similar to phytoplankton samples collected from 13 and 15 m with Ochromonas sp. being the dominate phytoplankter. However, by the end of November, C. subcaudata became the dominate phytoplankter (Fig. 10).

Total cell numbers and biomass generally increased, at all depths within the trophogenic zone, over the spring and summer for 1989-1990 and 1990-1991 season. Because of the small changes in cell numbers and biomass over time relative to the error of counting samples (ca. $\pm$ 50%, see Lund et al. 1958), growth rates were not determined from cell counts. Another problem with interpreting these data is apparent on examination of the ratio of C:CHL (g:g).

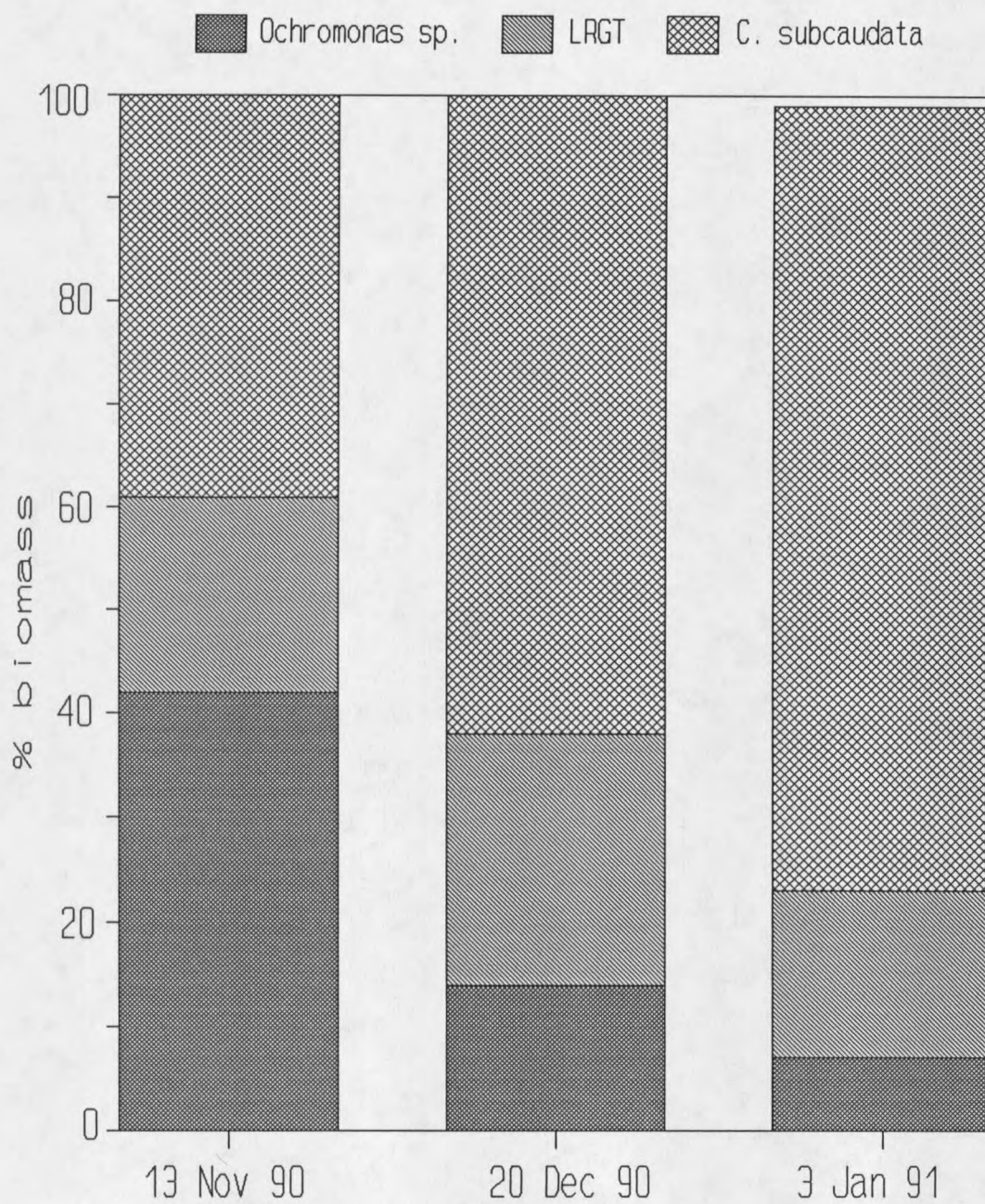


Figure 10. Temporal changes in the percentage of total biomass contributed by the various phytoplankton taxa at 17 m.

The average C:CHL_i ratios for samples collected from the surface, middle and deep phytoplankton layers, were 60.29, 78.68 and 81.54 g C (g CHL)⁻¹, respectively. These ratios were higher than the C:CHL ratios reported for phytoplankton in the Southern Ocean, which are about 50 (Holm-Hansen and Mitchell 1991). It is possible that some portion of the phytoplankton biomass, as detected by microscopic counts of settled phytoplankton samples, is non-viable; the C:CHL of one sample from 20 m was 471.72. Samples from 20 m were not included in the average C:CHL for the deep phytoplankton layers.

Chlorophyll a as Phytoplankton Biomass

Chlorophyll a (CHL) concentrations were measured over the entire water column, from under the ice to 35 m (see Appendix B, Table 30). CHL concentrations exceeding 1 $\mu\text{g L}^{-1}$ were measured at some depths below 20 m. As the primary objective for my study was to describe the factors influencing seasonal trends in phytoplankton biomass and production, I will not discuss further chlorophyll below 20 m and will only consider biological processes occurring within the trophogenic zone.

Two previous studies on ice-covered lakes reported that flagellated phytoplankton migrated to either optimal light levels (Wright 1964) or migrated during the day to optimal light levels and to deeper nutrient rich water at night (Vincent 1981). On 22 September 1991, water samples

were taken at 1200 and 2300 hours from 4, 5, 6, 7, and 8 m to examine if the near surface phytoplankton migrated in response to the diurnal variation in irradiance. On this date, there was approximately 13 h daylight and 11 h night. Deeper samples were not collected because CHL concentrations below 8 m were very low on this date (Fig. 11). From each water sample, triplicate CHL samples were collected. The data (Table 19) implied that the phytoplankton did not migrate diurnally at this time. This agreed with a previous study of Lake Bonney phytoplankton where no diel trend in either photosynthesis or CHL distribution was noted over the austral summer (November-January) (Priscu et al 1990).

Table 19. Diel variation in CHL distribution from under the ice to 8 m. Samples were collected on 22 September 1991. Results from a two-sided t-test of the null hypothesis, H_0 : average CHL concentration at 11:20 is equal to the average CHL concentration at 23:00. p is the probability of accepting a false H_0 .

Depth (m)	Time	Average CHL ($\mu\text{g L}^{-1}$)	$p >$
4	11:20	3.94 ± 0.12	0.2
4	23:00	3.77 ± 0.19	
5	11:20	3.02 ± 0.09	0.4
5	23:00	3.09 ± 0.18	
6	11:20	1.94 ± 0.00	0.2
6	23:00	2.13 ± 0.23	
7	11:20	1.18 ± 0.12	0.2
7	23:00	1.29 ± 0.00	
8	11:20	0.89 ± 0.16	0.2
8	23:00	0.99 ± 0.01	

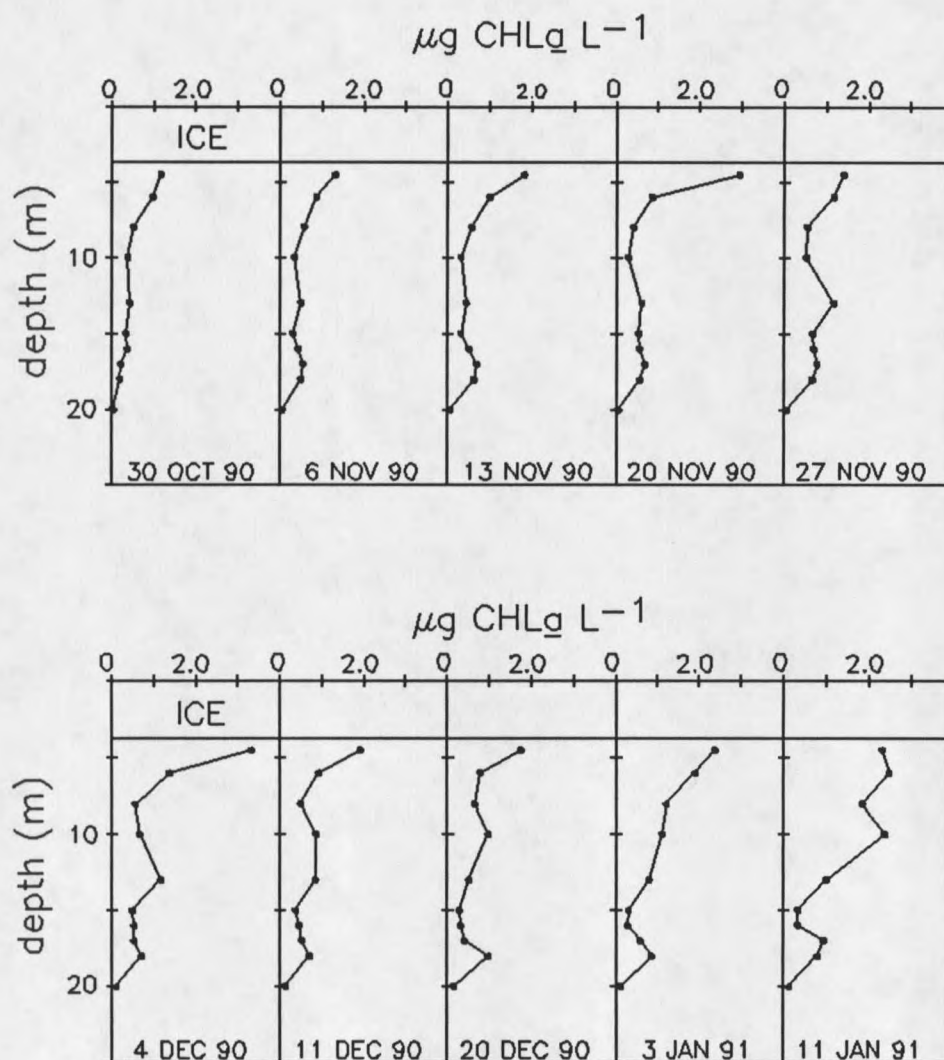


Figure 11. Vertical profiles of CHL concentrations (pheophytin corrected) over the 1990-1991 and 1991-1992 seasons.

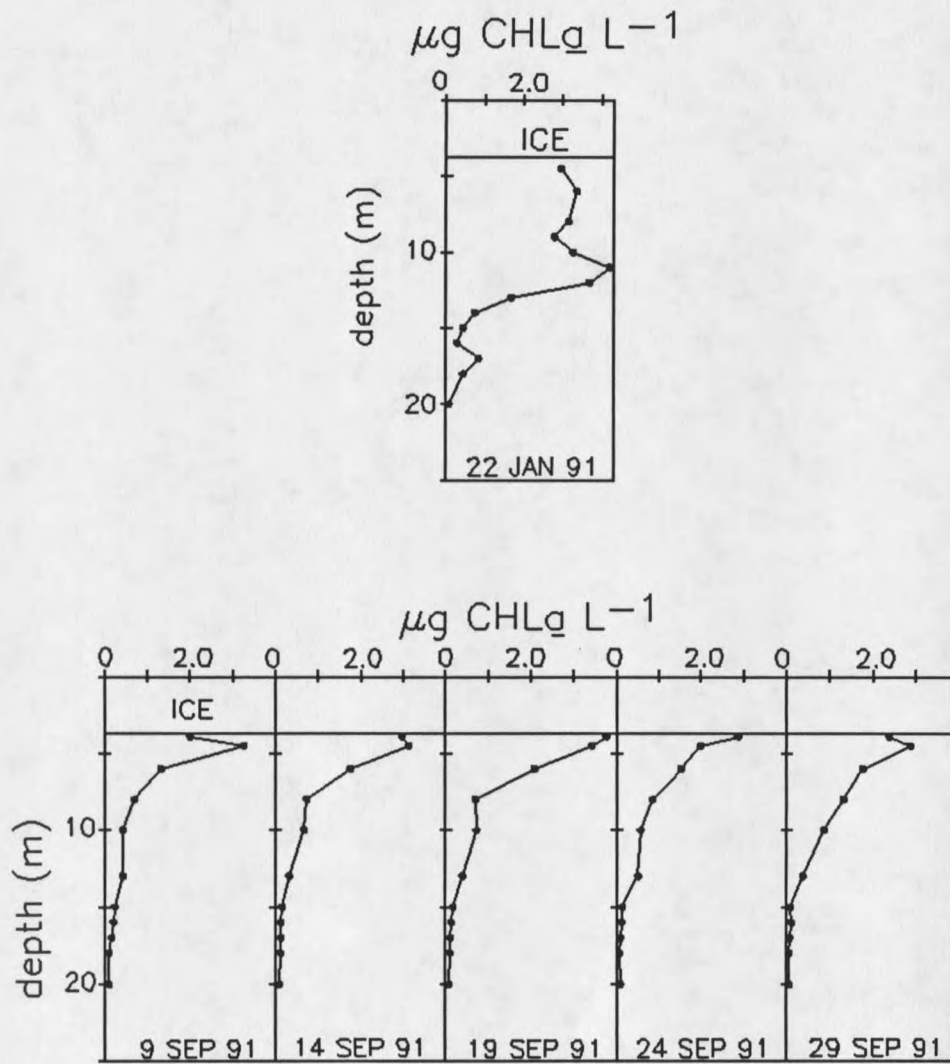


Figure 11. Continued.

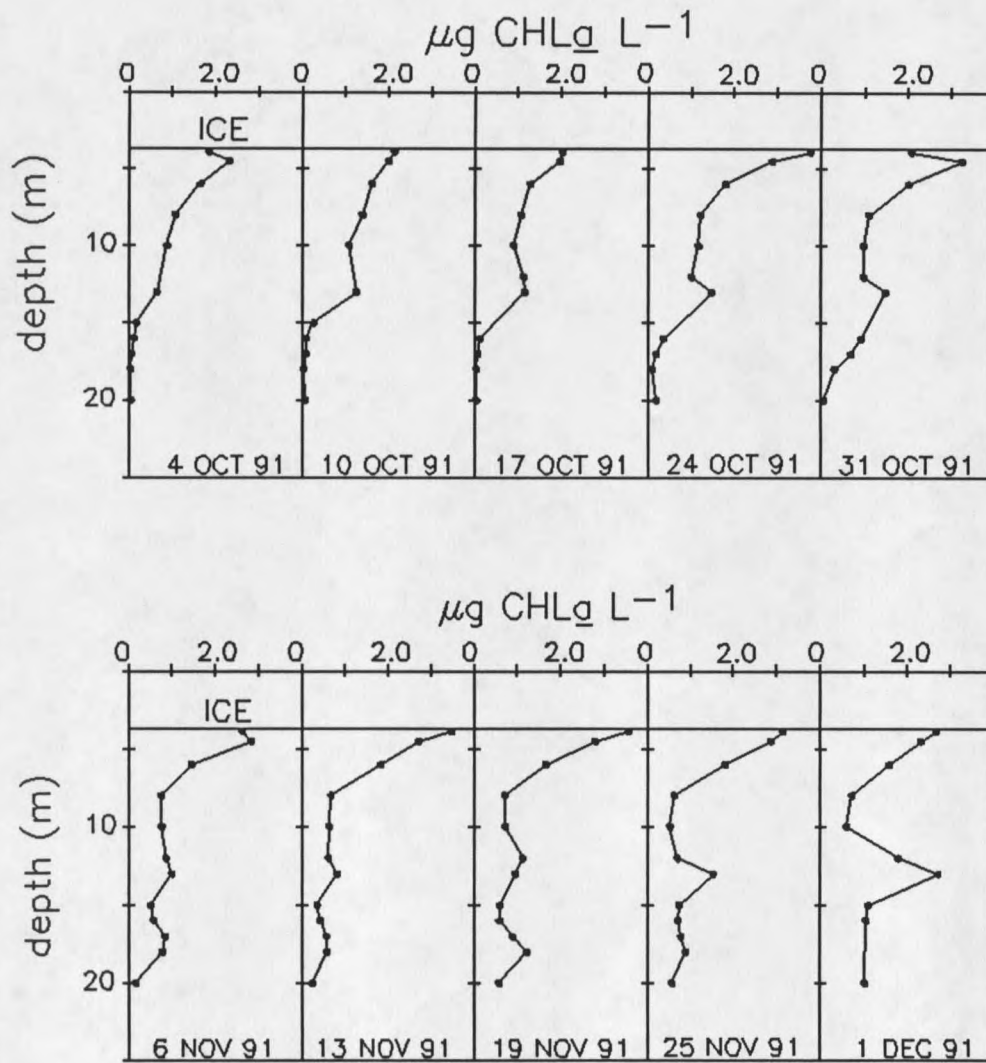


Figure 11. Continued.

CHL profiles show the seasonal development of the three distinct maxima (Fig. 11). For both 1990-1991 and 1991-1992, CHL concentrations were higher in the surface layer than in the two deeper layers until mid-January. The CHL concentrations in the surface layer were always greater at 3.9, 4.5 and 6 m than 8 m. CHL ranged from 0.42 (at 8 m on 20 November 1990), to 3.36 $\mu\text{g L}^{-1}$ (at 6 m on 22 January 1991), in 1990-91. During 1991-92, concentrations ranged from 0.62 (at 8 m on 25 November 1991) to 3.76 $\mu\text{g L}^{-1}$ (at 3.9 m on 24 October 1991).

Chlorophyll concentrations within the middle phytoplankton layer (8-16 m) generally increased over both sampling seasons. During the spring and summer of 1990-1991, the minimum and maximum concentrations measured within this layer were 0.28 (at 10 m on 20 November 1990) and 3.25 $\mu\text{g L}^{-1}$ (at 10 m on 22 January 1991), respectively. During the winter-spring transition of 1991, the minimum and maximum concentrations measured were 0.10 (at 15 m on 29 September 1991) and 2.71 $\mu\text{g L}^{-1}$ (at 13 m on 1 December 1991), respectively.

Chlorophyll concentrations within the deep phytoplankton layer (16-20 m) in the spring and summer of 1990-91 ranged from 0.35 (at 20 m on 30 October 1990) to 0.973 $\mu\text{g L}^{-1}$ (at 18 m on 20 December 1990). In 1991-1992, chlorophyll concentrations varied from 0.03 (at 20 m on 17 October 1991) to 1.21 $\mu\text{g L}^{-1}$ (at 18 m on 19 November 1991).

CHL integrated over the surface layer (CHL_s) remained relatively constant until 20 December 1990 (day 354), after which CHL_s increased until the last sampling date (22 January 1991), in 1990-1991 (Fig 12). CHL_s contributed 32 to 43% to total integrated CHL (4.5 to 20 m, CHL_{tot}), during 1990-1991. CHL_s fluctuated, in 1991-1992, but in general neither increased nor decreased (Fig. 13). Initially in 1991-1992, CHL_s contributed over 60% of CHL_{tot} , but as of the last sampling date (1 Dec 1991), CHL_s contributed only 30% to CHL_{tot} .

Three phases of change can be identified over 1990-1991 (Fig. 12) when CHL is integrated over the middle phytoplankton layer (8-16 m, CHL_m). CHL_m remained relatively constant from 30 October to 20 November (day 303-324), fluctuated or decreased slightly from 20 November (day 324) to 20 December (day 354), and then increased until 22 January 1991 (day 22). CHL_m accounted for approximately 50% of CHL_{tot} , during 1990-1991. In 1991-1992, CHL_m initially accounted for about 35% of CHL_{tot} and increased to 50% by the end of the sampling season.

CHL integrated over the deep phytoplankton layer (16-20 m, CHL_d) increased initially from 30 October 1990 (day 303) to 13 November (day 317), and then remained relatively constant until 22 January 1991 (day 22), during the 1990-1991 season (Fig. 12). The percentage CHL_d contributed to CHL_{tot} was usually less than 20%, in 1990-1991.

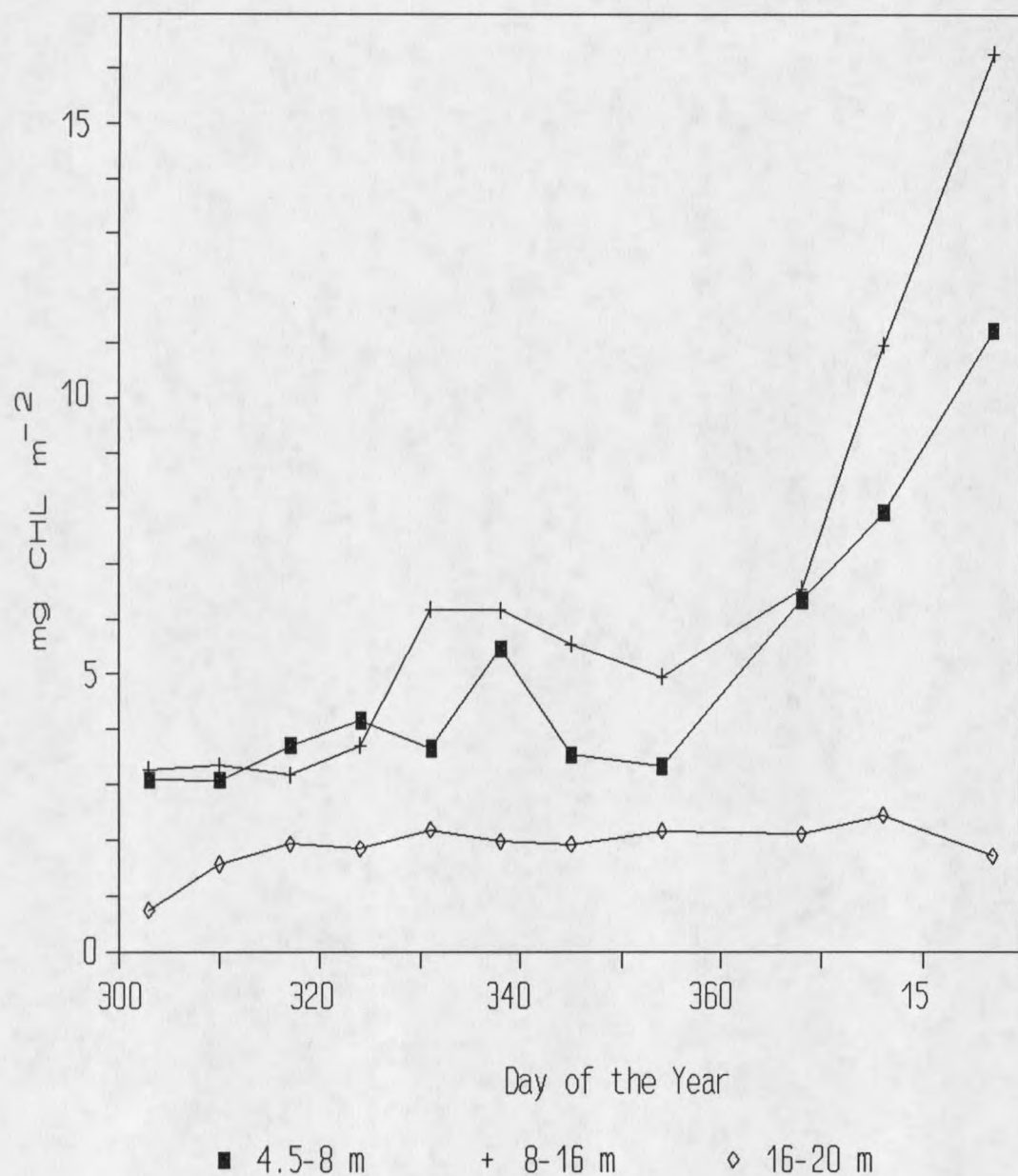


Figure 12. Temporal variation of CHL integrated over the surface, middle and deep phytoplankton layers during the 1990-1991 season.

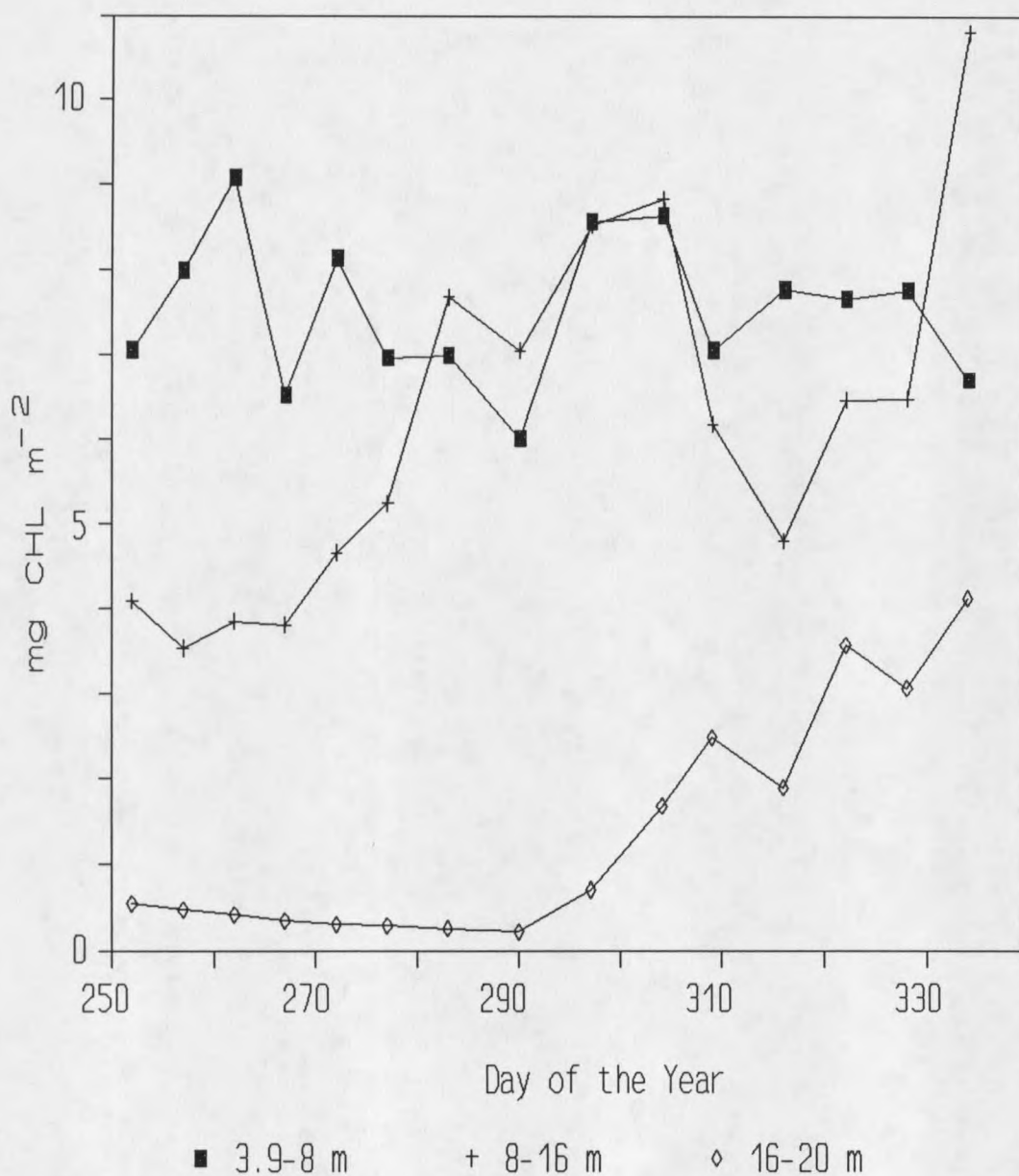


Figure 13. Temporal variation of CHL integrated over the surface, middle and deep phytoplankton layers during the 1991-1992 season.

From 9 September 1991 (day 252) until 17 October 1991 (day 290), CHL_d responded more dynamically, during the 1991-1992 season (Fig. 13). CHL_d decreased from 4.7% to 1.6% of CHL_{tot} . CHL_d increased over the remainder of the season and eventually contributed 20% of CHL_{tot} .

Phytoplankton Productivity

Several primary production maxima were observed in the water column during both the 1990-1991 and 1991-1992 seasons (Fig. 14). Profiles of primary production (PPR) at the same times from different sampling seasons are similar. Therefore, the following section describes the seasonal development of the distinct production maxima for both seasons.

On the earliest sampling date (9 September 1991), net production occurred only immediately below the ice. Production was measurable from below the ice to 15 m, decreasing exponentially with depth by the end of September. The middle production maximum developed during October. Photosynthetic rates within this layer were always highest at the 13 m sampling depth at this time. By mid-October, the middle production maxima contributed more than half of the total integrated (3.9-20 m) daily primary production (PPR_{tot}) and PPR was initiated within the deep layer. All 3 production maxima were evident in November. After 24 October, the photosynthetic rates measured within the surface phytoplankton layer did not continue to

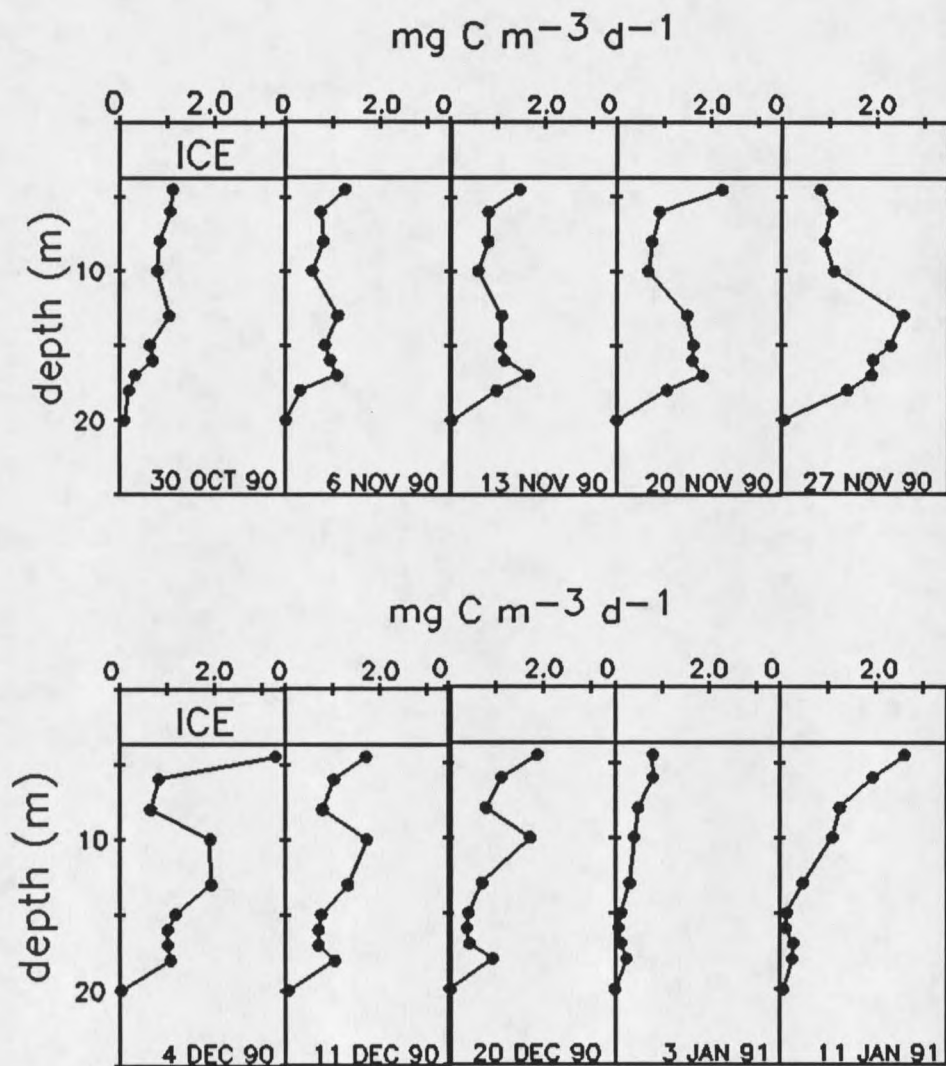


Figure 14. Vertical profiles of primary productivity over the 1990-1991 and 1991-1992 seasons.

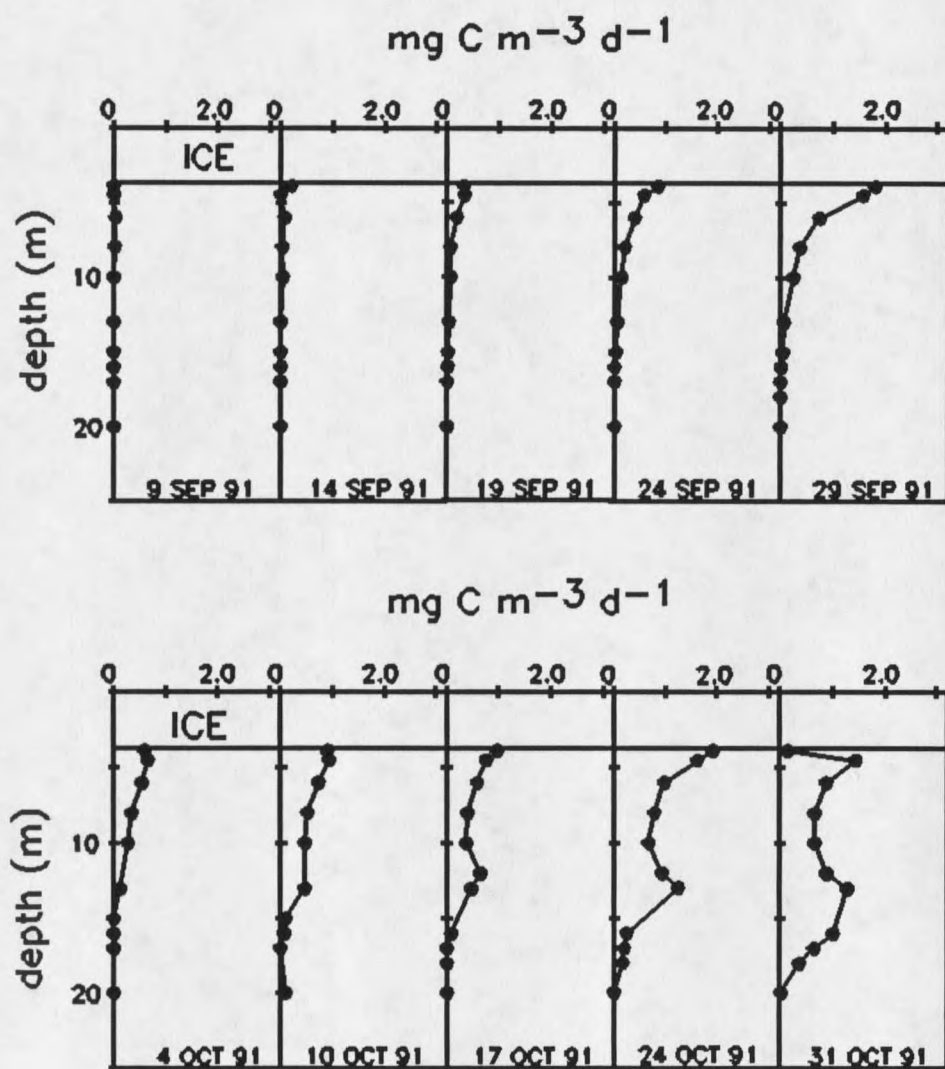


Figure 14. Continued.

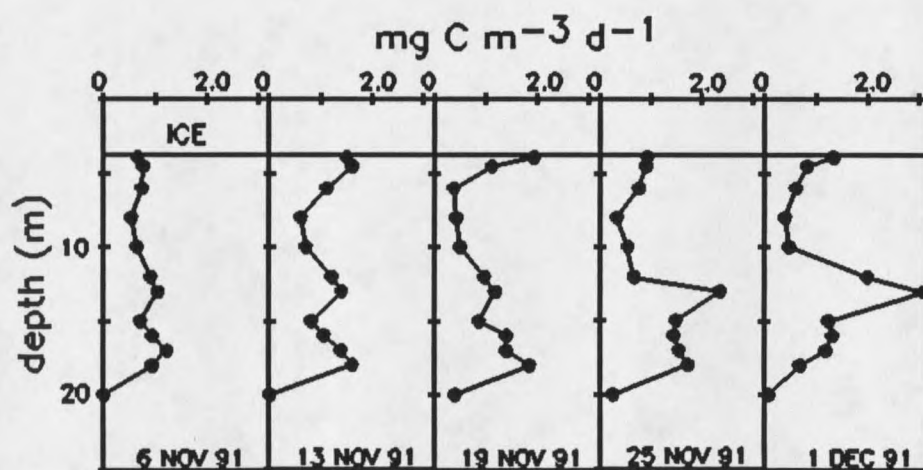


Figure 14. Continued.

increase despite increasing irradiance. PPR_s contributed less than 30% of PPR_{tot} , while the PPR_m and PPR_d contributed approximately 50% and 25%, respectively, during November. PPR profiles from December were similar to those in November. In January, the distinctive boundary between the surface and middle production maximum was lost, but the deep production maxima was still discrete (Fig. 14). PPR_s , as a percentage of PPR_{tot} , increased from 30% to 45 to 51%, while PPR_m and PPR_d decreased from 55% to 45% and from 15% to 6%, from December to mid-January.

Another way to examine the seasonal trend in primary production is to plot PPR_{tot} (3.9 or 4.5 to 20 m) and daily under-ice irradiance (4.5 m for 1990-1991 or 3.9 m for 1991-1992) for all measurements of primary production made during both 1990-1991 and 1991-1992 (Fig. 15). Irradiance increased until mid-December and declined thereafter. PPR_{tot} followed the general trend in under-ice irradiance. A linear regression model was used to quantify the relationship between primary production and under-ice irradiance. The relationship was fairly well described by the linear regression; however, at low irradiances the relationship may be non-linear (Fig 16). The y-intercept was unrealistically positive (photosynthesis in the dark) but did not differ significantly from zero ($p < 0.05$).

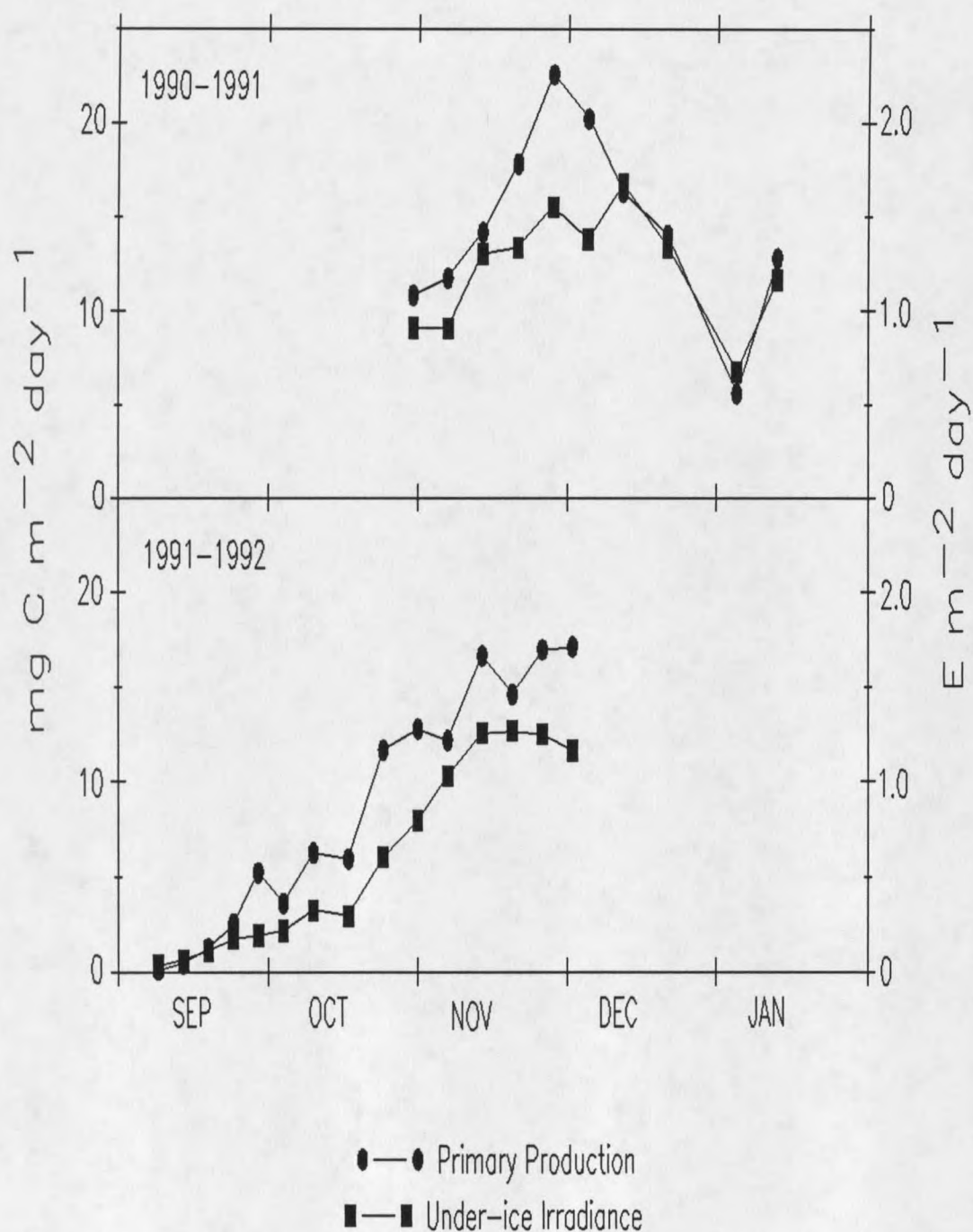


Figure 15. Temporal variation of total integrated (3.9 or 4.5-20 m) primary productivity and under-ice irradiance during the 1990-1991 and 1991-1992 seasons.

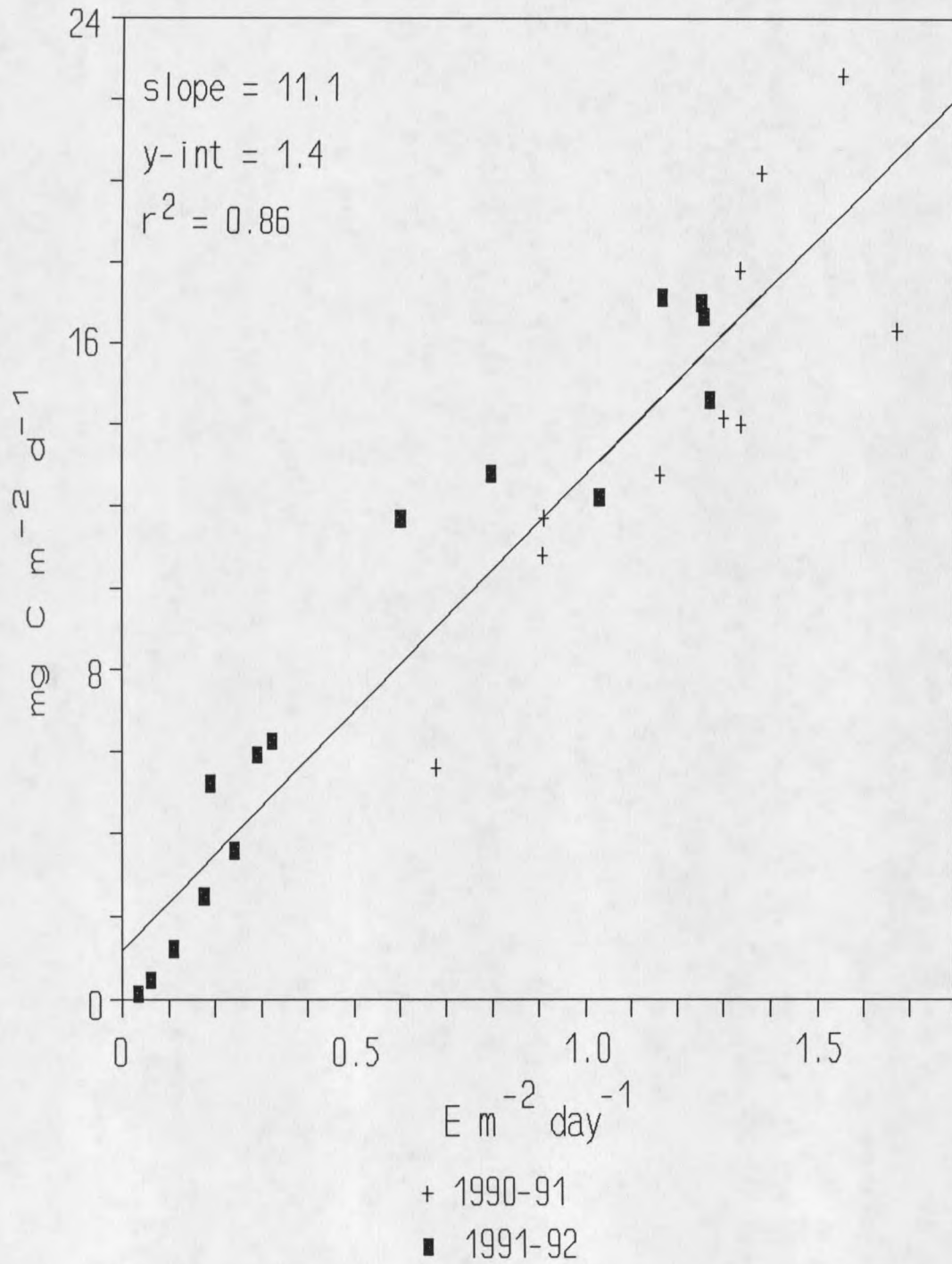


Figure 16. Relationship between total integrated (3.9 or 4.5-20 m) primary productivity and under-ice irradiance in the 1990-1991 and 1991-1992 seasons.

The relationship between PPR and irradiance for each of the 3 phytoplankton layers (3.9 to 8 m, 8 to 16 m, 16 to 20 m) was also analyzed with regression statistics to determine if the different layers responded differently to increasing irradiance.

Because photosynthesis was not measured at 3.9 m during the 1990-1991 season, PPR_s , from 1990-1991 was multiplied by a factor of 1.21 to correct for the different integration limits. This correction factor was derived using the production data collected during the 1991-1992 season. It is the ratio between integrated PPR from 3.9 to 8 m and that from 4.5 and 8 m.

PPR_s increased linearly with irradiance until irradiances exceeded $0.5 \text{ E m}^2 \text{ d}^{-1}$, after which PPR_s asymptotized (Fig. 17). Only PPR_s measurements made on days with the 10 lowest mean daily irradiances were included in the regression, and the measurements made on days with the 15 highest mean daily irradiances were averaged (Fig. 17), so that the initial slope of the relationship could be compared to those from the other phytoplankton layers. The y-intercept was positive but not significantly different from zero ($p > 0.05$).

The relationship between irradiance at 8 m and PPR_m was essentially linear except at the lowest daily irradiances (Fig. 18). The slope was not significantly different from the slope of the surface layer ($p > 0.05$),

and the y-intercept was not significantly different from zero ($p > 0.05$).

In the deep (16-20 m) phytoplankton layer, only the last 9 data points were used to determine the PPR-irradiance relationship (Fig. 19) because the rates could not be detected by the ^{14}C light-dark bottle method previous to this period. The slope of this relationship did not differ significantly ($p > 0.05$) from slopes of PPR_m or PPR_{tot} versus irradiance, however, the slope was significantly greater than that of the surface phytoplankton layer ($p < 0.05$). The y-intercept was not significantly different from zero ($p > 0.05$). The y-intercept, despite its statistical insignificance, implies a compensation irradiance for the initiation of photosynthesis of $0.17 \text{ E m}^2 \text{ d}^{-1}$ or a mean daily flux of $1.9 \mu\text{E m}^2 \text{ s}^{-1}$ which would occur at this depth near 17 October.

In Figs. 20, 21 and 22 integrated PPR_i is normalized to CHL_i for each of the phytoplankton layer and plotted versus daily irradiance at the top of the layer. PPR normalized to CHL for the middle and deep phytoplankton layers responded to the irradiance at the top of the layer in a similar fashion to integrated PPR alone versus irradiance at the top of the layer. However PPR_s normalized to CHL_s responded more strongly to irradiance in 1990-1991 than 1991-1992.

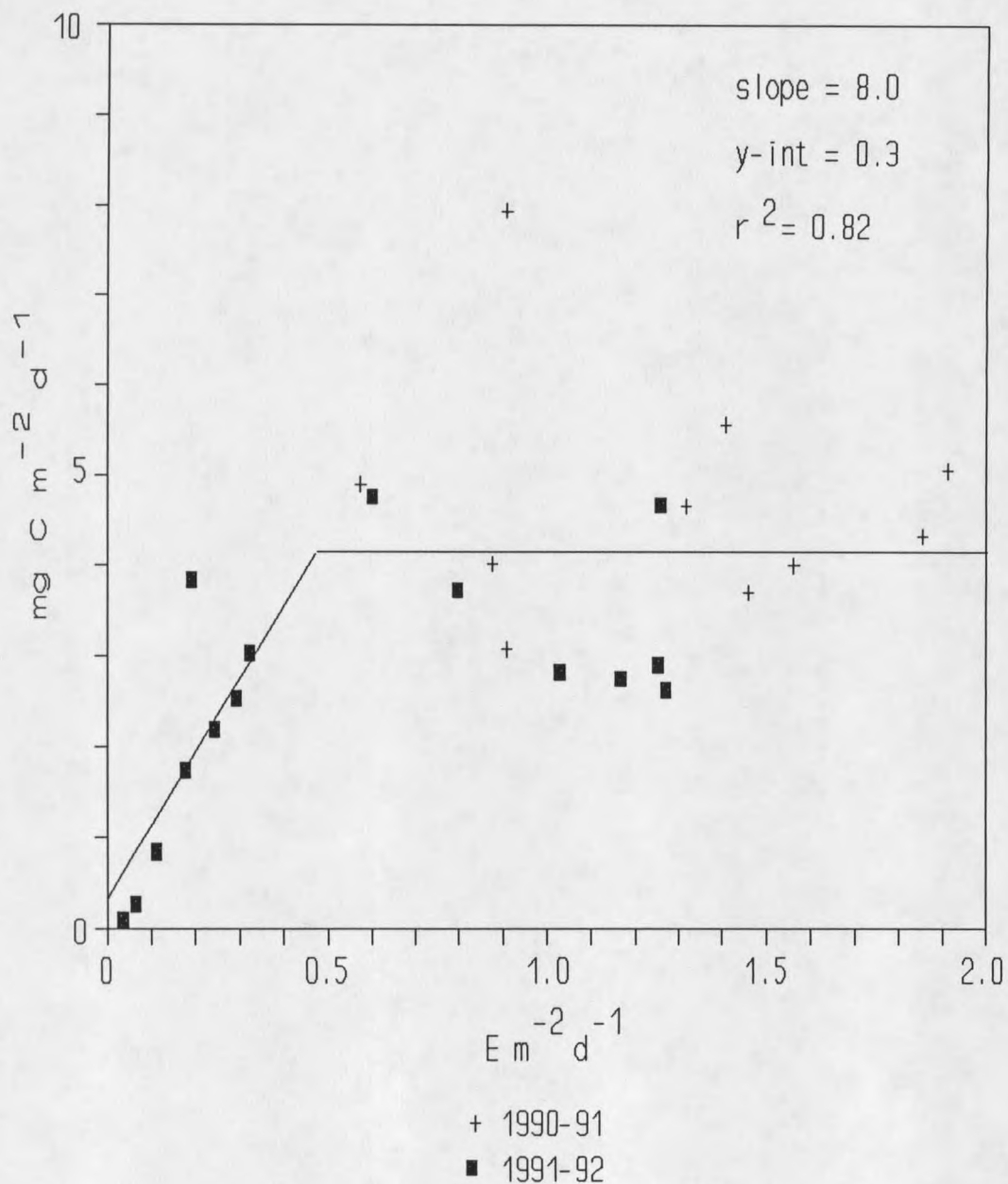


Figure 17. Relationship between integrated photosynthesis over the surface phytoplankton layer (3.9-8 m) and under-ice irradiance in the 1990-1991 and 1991-1992 seasons.

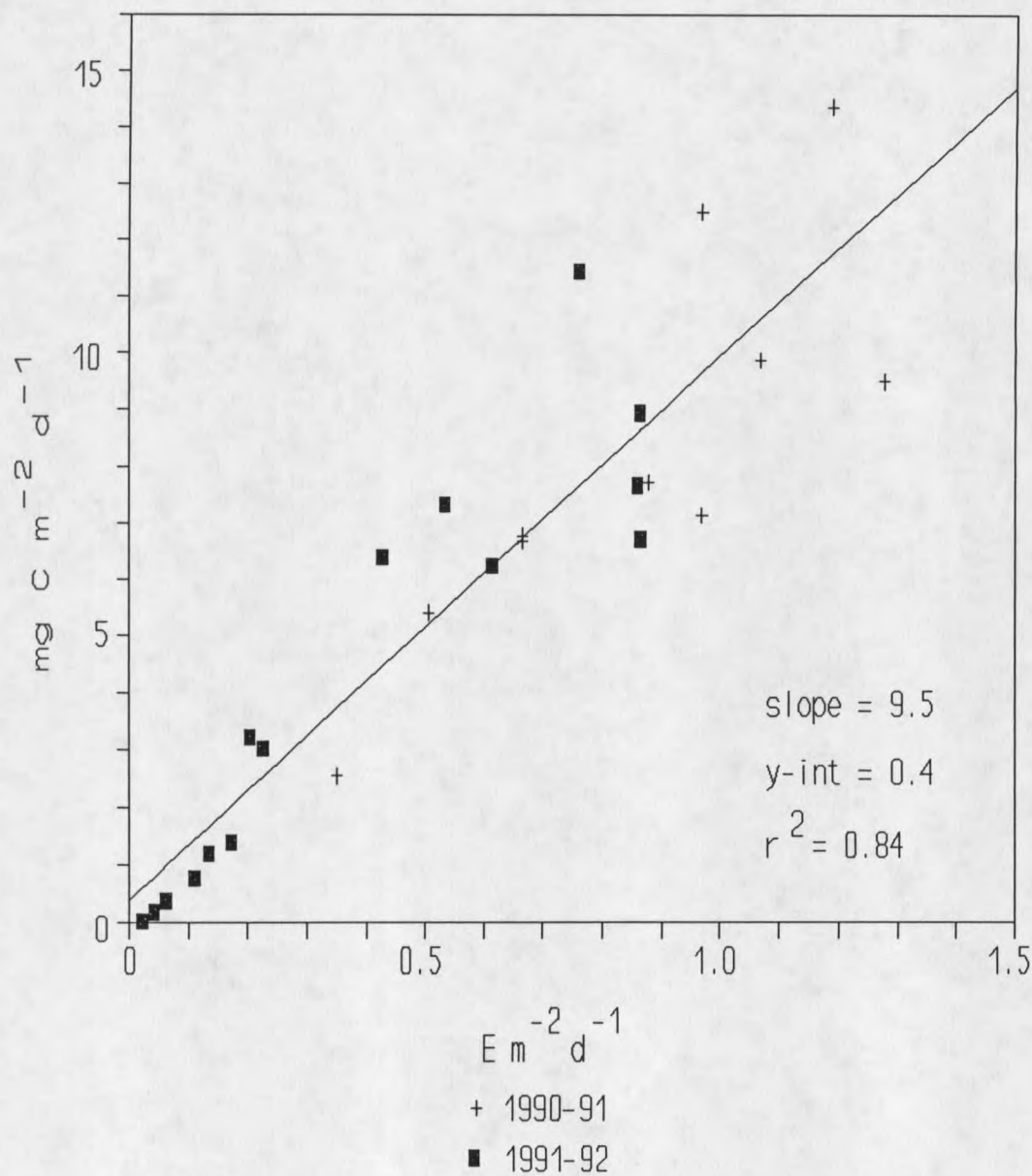


Figure 18. Relationship between photosynthesis integrated over the middle phytoplankton layer (8-16 m) and irradiance at 8 m in the 1990-1991 and 1991-1992 season.

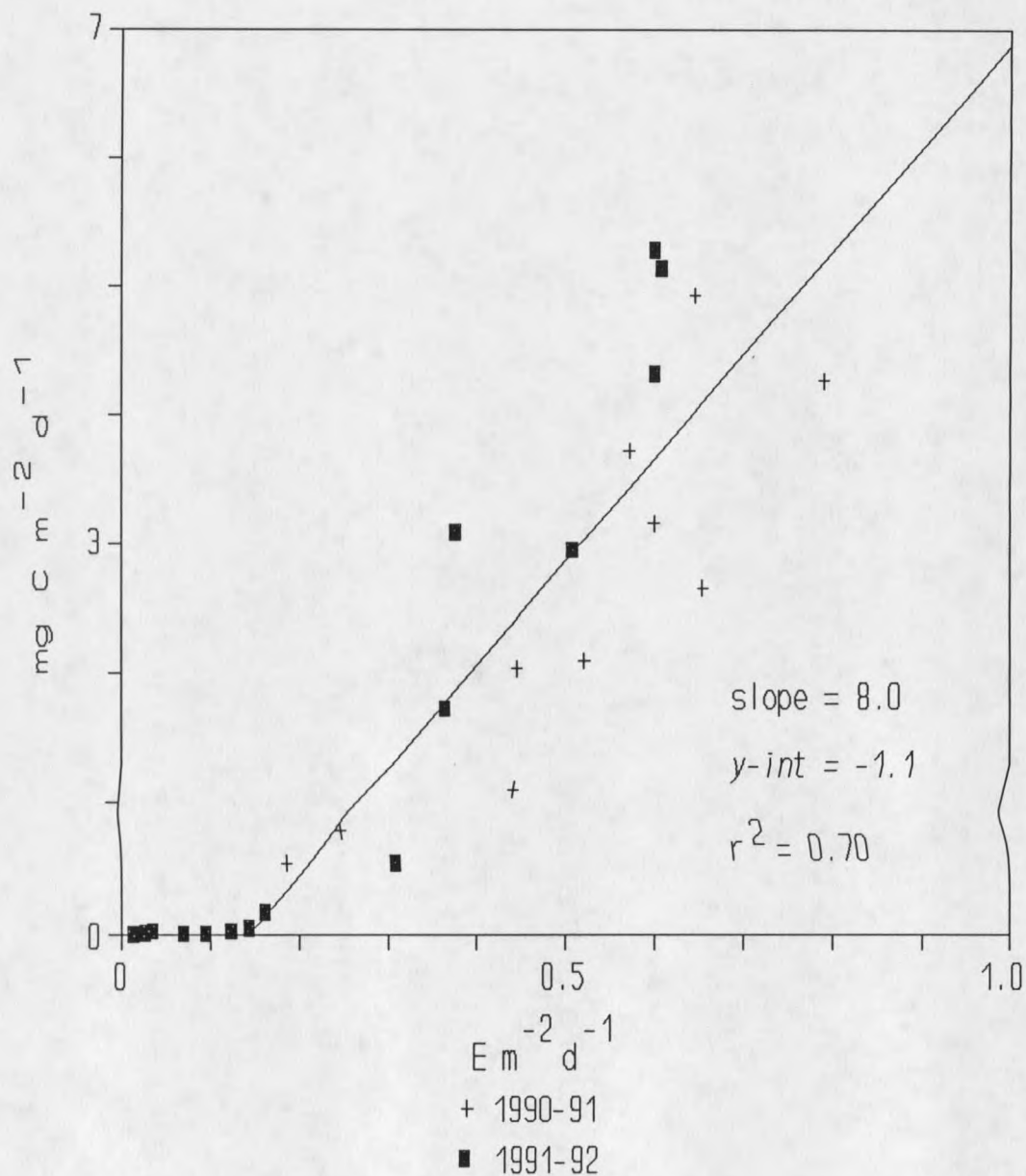


Figure 19. Relationship between photosynthesis integrated over the deep phytoplankton layer (16-20 m) and irradiance at 16 m in the 1990-1991 and 1991-1992 seasons.

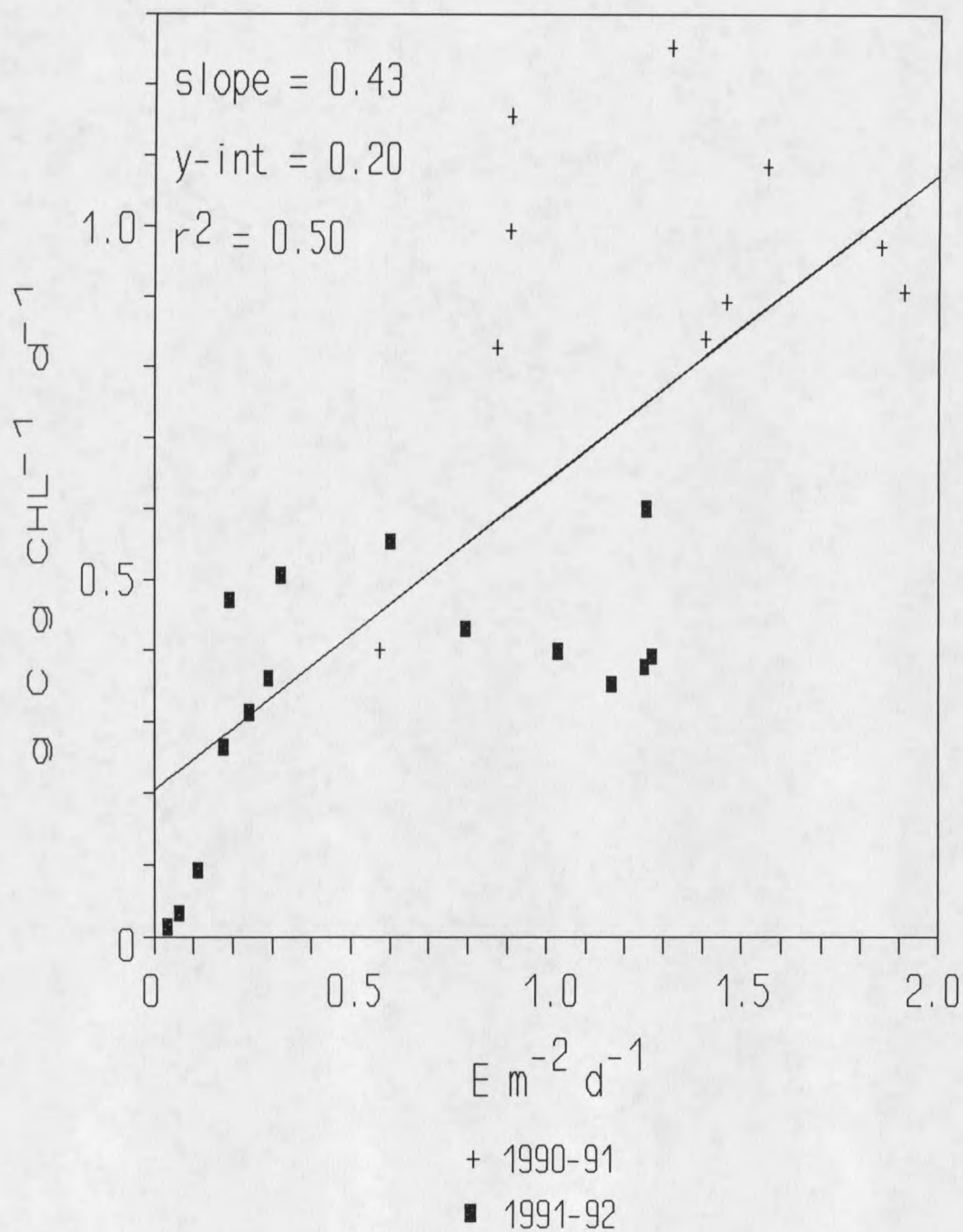


Figure 20. Relationship between integrated photosynthesis normalized to integrated CHL in the surface phytoplankton layer (3.9 or 4.5-8 m) and under-ice irradiance in the 1990-1991 and 1991-1992 seasons.

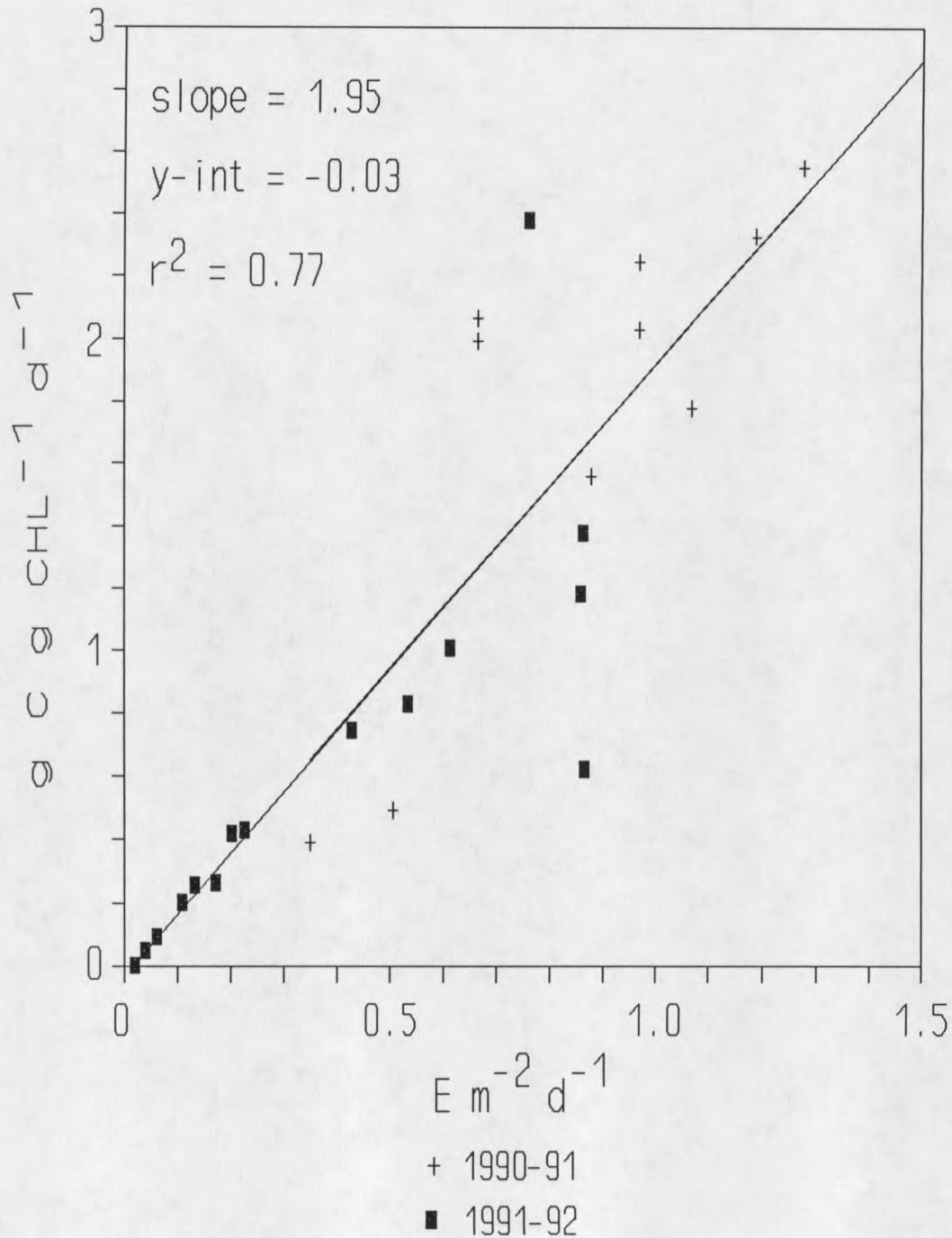


Figure 21. Relationship between integrated photosynthesis normalized to integrated CHL in the middle phytoplankton layer (8-16 m) and irradiance at 8 m in the 1990-1991 and 1991-1992 seasons.

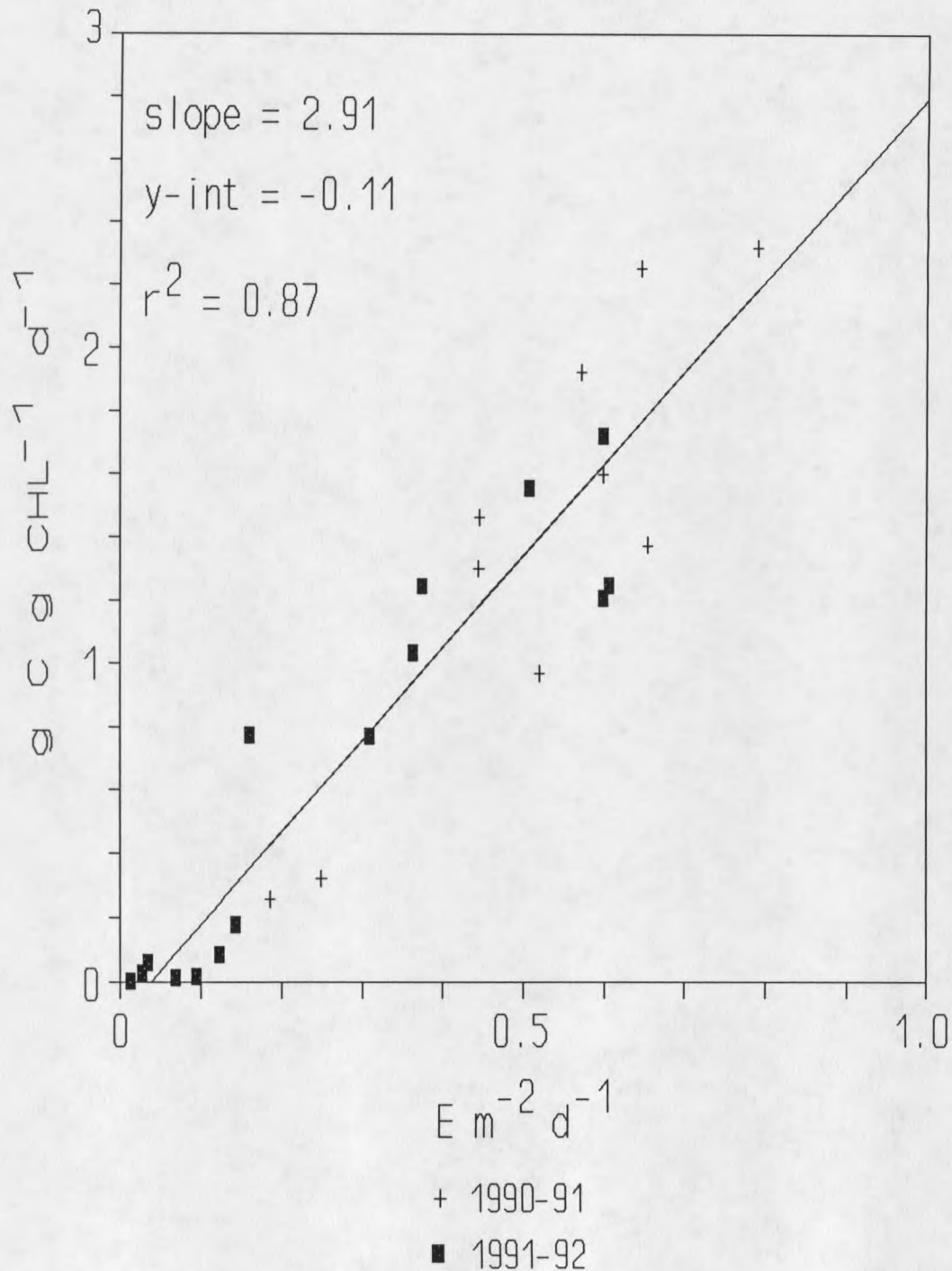


Figure 22. Relationship between integrated photosynthesis normalized to integrated CHL in the deep phytoplankton layer (16-20 m) and irradiance at 16 m in the 1990-1991 and 1991-1992 seasons.

While primary production was a linear function of light, for at least part of the season in each of the production maxima, it did not reveal seasonal trends in the photosynthetic response of the phytoplankton (see Figs. 17 to 22). To determine if the photoresponse of the phytoplankton changed over the season, PPR_i was divided by CHL_i and daily irradiance at the top of the layer (Figs. 23, 24 and 25). This parameter, the ecological photosynthetic efficiency or light utilization index (ψ), has units of $g\ C\ (g\ CHL)^{-1}\ m^2\ (E)^{-1}$. Data from both sampling seasons, combined for each layer, showed distinct seasonal trends in this parameter. (This points to one of the weaknesses of the light-dependent phytoplankton growth model in its present form.)

In the 1990-1991 season, the surface layer light utilization index (ψ_s) decreased over November (day 304 to 334) and then increased during December (day 335 to 354) (Fig. 23). ψ_s increased initially during September (day 252 through 273) and then decreased over the remainder of the 1991-1992 season (Fig. 23). The range in magnitude of ψ_s was similar for data from both seasons. The decline of ψ_s in 1991-1992 coincided with the leveling of PPR_s as irradiance increased (Fig. 17).

In general, the middle layer ψ (ψ_m) values were greater during the 1990-1991 season than the 1991-1992 season (Fig 24). ψ_m decreased over the 1990-1991 season.

During the 1991-1992 season, ψ_m increased initially (day 252 through 283) (Fig. 24). After mid-October (day 283), ψ_m gradually decreased over the remainder of the 1991-1992 season, with the exception of one measurement.

The deep layer ψ (ψ_d) values were similar during part of both sampling seasons (Fig. 25). In 1990-1991, ψ_d remained fairly constant in November (day 304 to 334) and then decreased over the rest of the sampling season. In the 1991-1992 sampling season, data collected before 27 September 1991 (day 270) probably does not reflect a physiological change of phytoplankton within this layer, but rather the uncertainties in measuring photosynthesis with the ^{14}C method; at these depths low irradiances and high DIC concentrations increase variability in ^{14}C measurements. ψ_d increased after 27 September (day 273) until the end of October (day 304) and then showed no clear trend afterwards.

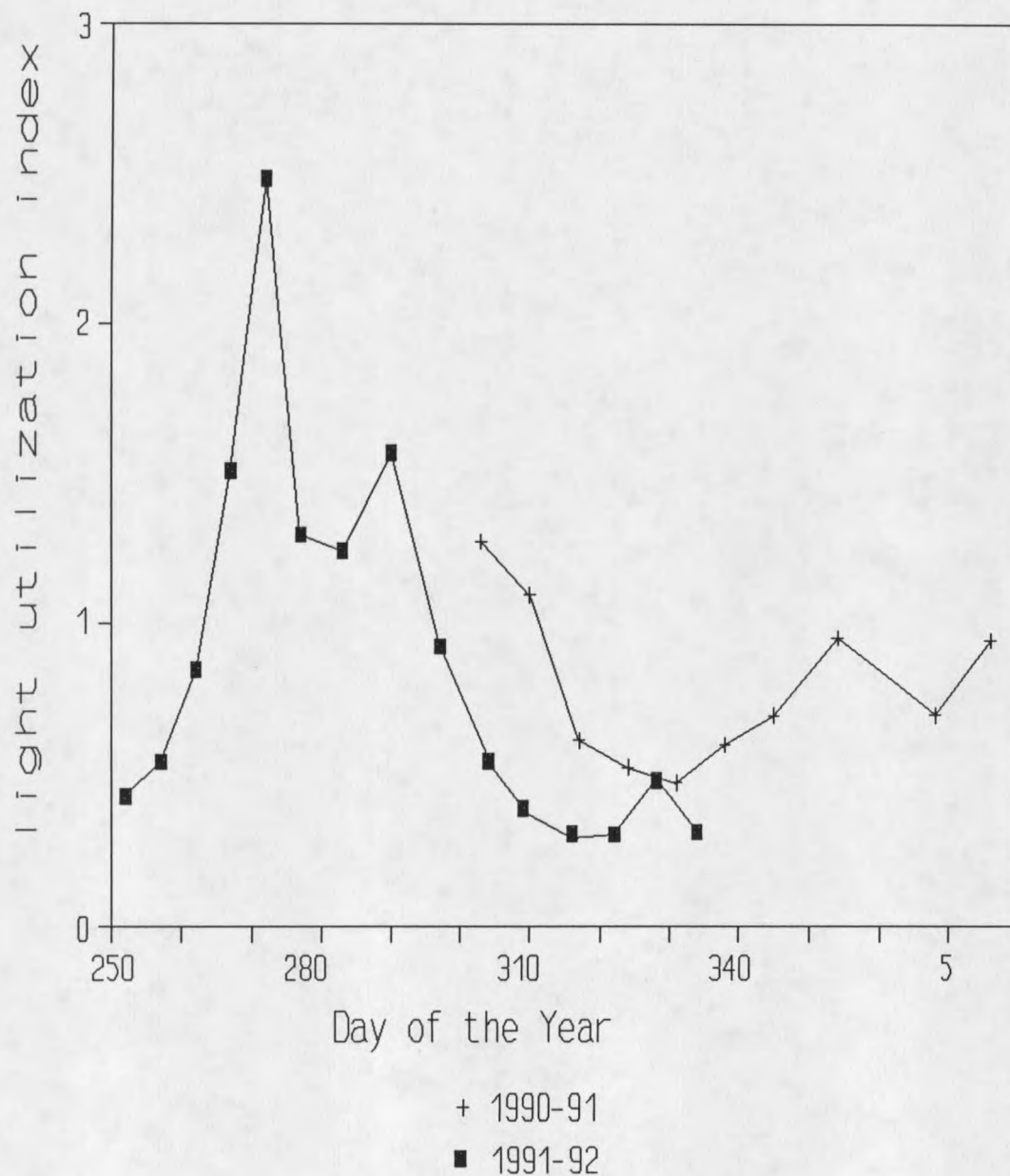


Figure 23. Temporal variation of the light utilization index (ψ , $\text{g C (g CHL)}^{-1} \text{ m}^2 (\text{E})^{-1}$) in the surface phytoplankton layer during the 1990-1991 and 1991-1992 seasons.

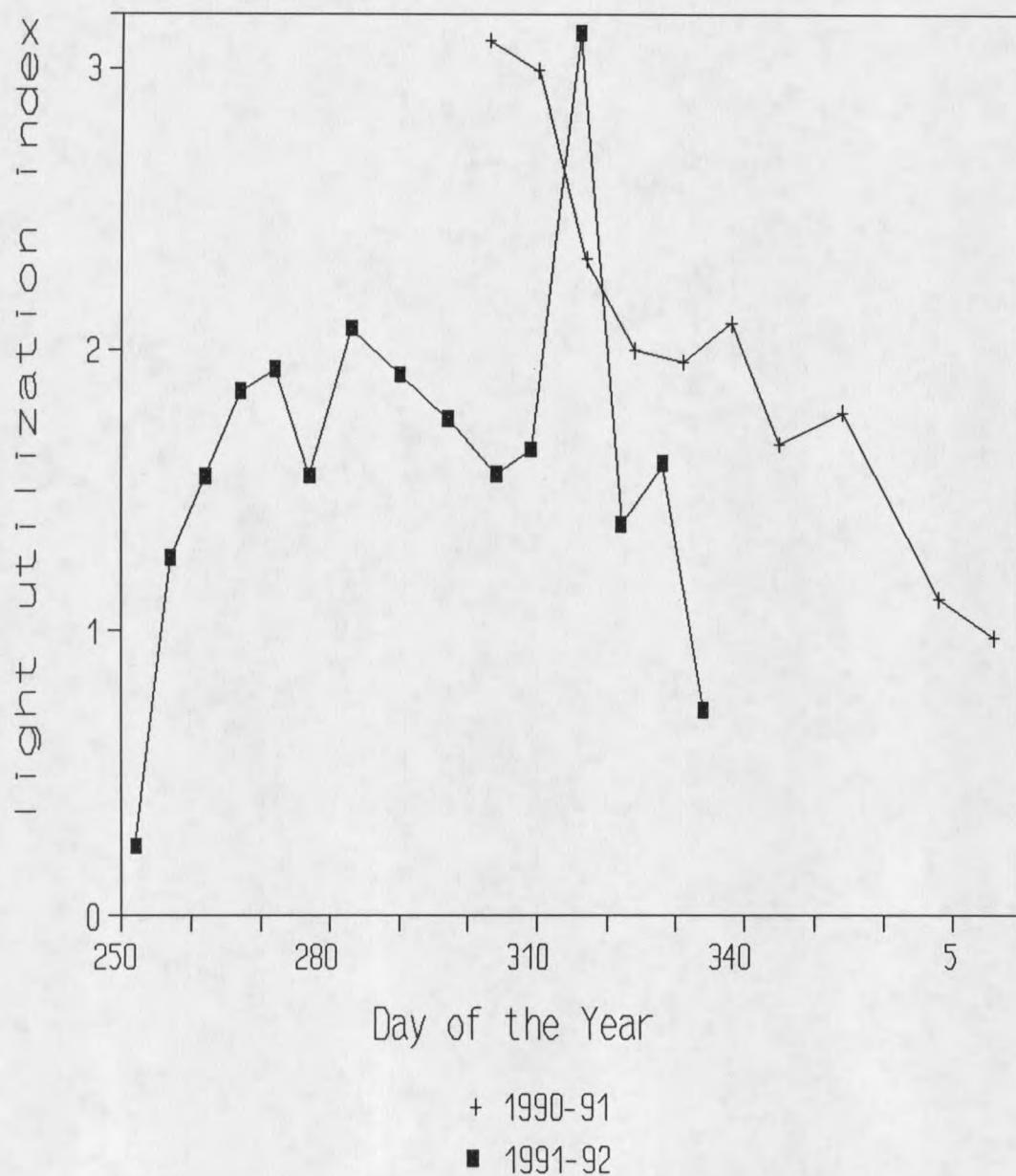


Figure 24. Temporal variation of the light utilization index (ψ , $\text{g C (g CHL)}^{-1} \text{ m}^2 (\text{E})^{-1}$) in the middle phytoplankton layer during the 1990-1991 and 1991-1992 seasons.

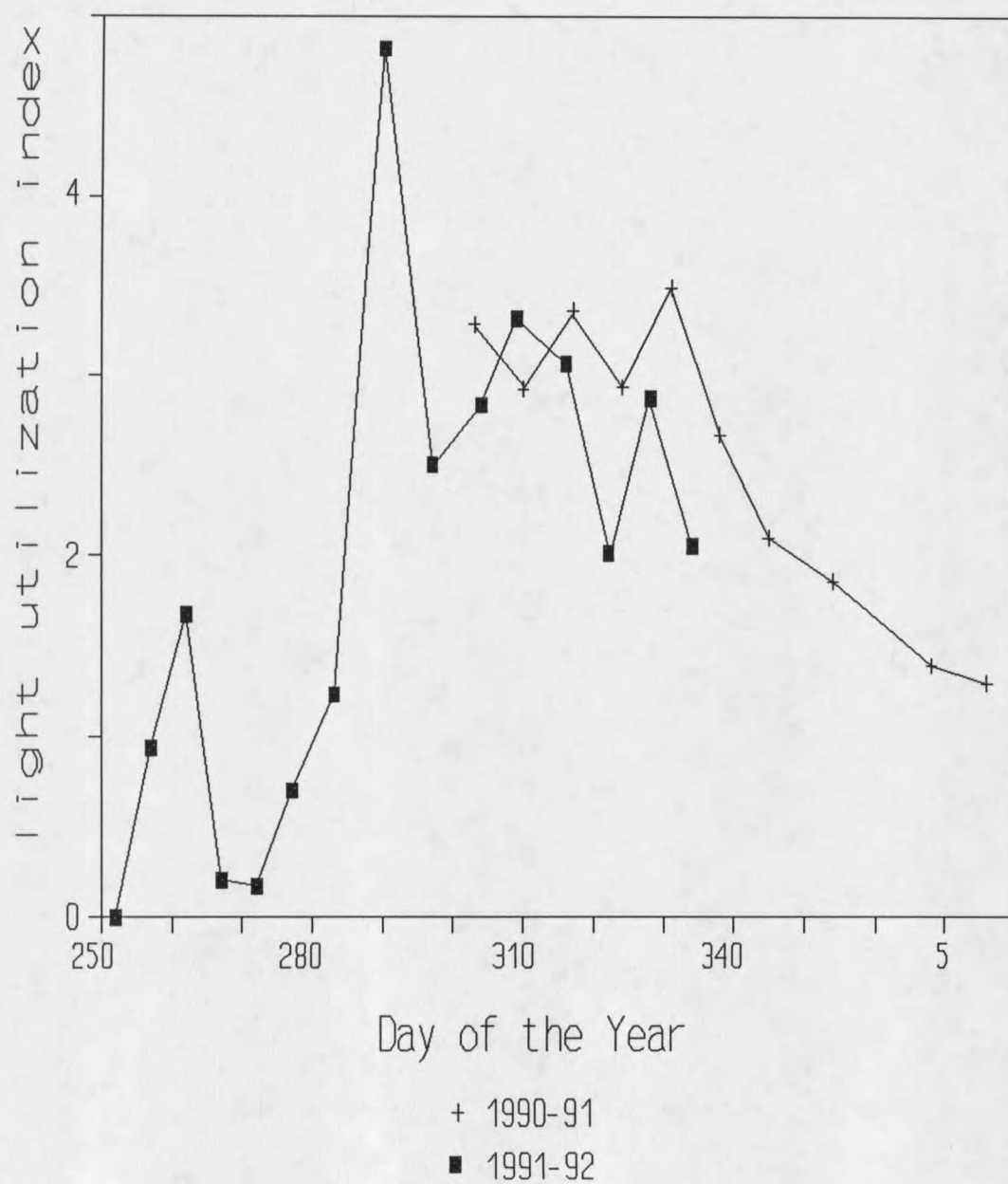


Figure 25. Temporal variation of the light utilization index (ψ , g C (g CHL)⁻¹ m² (E)⁻¹) in the deep phytoplankton layer during the 1990-1991 and 1991-1992 seasons.

Displacement Experiments

Photosynthesis was not initiated in 18 m samples at either depth during the displacement experiments conducted in 1991-1992 (Table 20). The results of the 23 m displacement experiment conducted in 1990-1991 indicate that CHL from this depth was not associated with viable phytoplankton (Table 21).

Table 20. Results of 18 m displacement experiment. Light DPM is the average of both light bottles.

Date	Depth (m)	Light DPM	Dark DPM
26 Sep 1991	11	1359	1610
28 Sep	11	1004	1995
29 Sep	11	690	707
29 Sep	18	686	562

Table 21. Results from the 23 m displacement experiment on 15 Nov 1990. DPM = distegrations per minute.

Depth (m)	Bottle type	Average DPM
15	light	108
15	dark	80
23	light	75
23	dark	75

Nutrient Bioassays

Results of nutrient bioassays conducted in 1989-1990 and 1991-1992 indicate that the photoassimilation of ^{14}C - HCO_3^- was stimulated by NH_4^+ on 30 November 1989 and by NH_4^+ + PO_4^{3-} on 15 November 1989, in a 4.5 m sample (Table 22). NH_4^+ alone apparently stimulated ^{14}C uptake on 15 November, but this cannot be stated with strong statistical

confidence because of insufficient (pseudo)replication. Nutrient enrichment of 17 m water never significantly enhanced photosynthesis. All the results from this set of experiments are pseudoreplicates, i.e. the averages and standard deviations are from subsamples obtained from a single nutrient enrichment (see METHODS, Nutrient Bioassays).

In 1990-1991, experiments were designed with replicate (3) treatments such that significant differences between nutrient treatments could be determined using a one-way analysis of variance (ANOVA). Significant differences between treatment means occurred in only two of the experiments (Table 23). P enrichment enhanced the photosynthetic rate significantly more than the control and N enriched treatment in the 25 November 1990 bioassay; the control and N enriched treatments were not significantly different from each other. P and N + P enriched treatments had significantly lower photosynthetic rates than the control and the N enriched treatments in the 7 January 1991 experiment. Again, the photosynthetic rate of the control and N enriched treatments did not differ significantly (Table 24).

Table 22. Results of 1989-1990 and 1991-1992 nutrient bioassays (treatments not replicated). ** - indicates that the photosynthetic response of the nutrient enriched treatment was significantly ($p < 0.05$, Student's t-test, two-tailed) greater than that of the control.

Date	Depth (m)	Treatment	Average DPM $\pm$ S.D.	n
15 Nov 1989	4.5	Control	2495 $\pm$ 123	3
		N	3898 $\pm$ 173	2
		P	1975 $\pm$ 443	3
		N + P	3620 $\pm$ 465	3 **
18 Nov	17	Control	228 $\pm$ 48	3
		N	292 $\pm$ 112	3
		P	249 $\pm$ 47	3
		N + P	241 $\pm$ 31	3
30 Nov	4.5	Control	1036 $\pm$ 210	3
		N	1664 $\pm$ 220	3 **
		P	1312 $\pm$ 107	3
		N + P	1217 $\pm$ 378	3
1 Dec	17	Control	555 $\pm$ 67	3
		N	543 $\pm$ 31	3
		P	523 $\pm$ 51	3
		N + P	564 $\pm$ 221	3
5 Jan 1990	4.5	Control	4349 $\pm$ 2938	3
		N	6467 $\pm$ 3329	3
		P	2985 $\pm$ 2011	3
		N + P	4363 $\pm$ 2703	3
7 Jan	17	Control	1904 $\pm$ 261	3
		N	1444 $\pm$ 763	3
		P	1549 $\pm$ 81	3
		N + P	1382 $\pm$ 256	3
9 Oct 1991	4.5	Control	6294 $\pm$ 1600	3
		N	5064 $\pm$ 1792	3
		P	6413 $\pm$ 2047	3
		N + P	5637 $\pm$ 2838	3

Table 23. The effect of nutrient additions on the photosynthetic rate of Lake Bonney phytoplankton in 1990-1991. A multiple sample hypothesis of equal means was rejected at $p \leq 0.05$, by one-way ANOVA. Unless indicated, all samples for the bioassays were taken from 4.5 m. d.f. = degrees freedom. * = ($p < 0.05$).

Date	Depth (m)	Source of Variance	d.f.	Sum of Squares	Mean Squares	F Value
5 Nov	4.5	Treatment	3	1.7×10^5	5.5×10^4	0.4
		Error	8	1.1×10^6	1.3×10^5	
5 Nov	10	Treatment	3	6.0×10^3	2.0×10^3	0.5
		Error	7	3.1×10^4	4.5×10^3	
25 Nov	4.5	Treatment	2	1.9×10^6	6.3×10^5	4.3*
		Error	6	8.9×10^5	1.5×10^5	
30 Nov	4.5	Treatment	3	3.0×10^5	9.9×10^4	1.1
		Error	8	7.5×10^5	9.4×10^4	
7 Jan	4.5	Treatment	3	2.4×10^8	8.1×10^7	7.2*
		Error	7	8.0×10^7	1.1×10^7	

Table 24. Results from Tukey's method of multiple comparisons between treatment means for bioassays showing significant differences in Table 23. Treatment means are arranged in order of increasing activity. Treatment means that are underlined are not significantly different from each other.

Date	Treatment (mean dpm)			
25 Nov 90	Control	N	P	
	<u>2946</u>	<u>3572</u>	<u>4070</u>	
7 Jan 91	P	N+P	Control	N
	<u>29853</u>	<u>31050</u>	<u>37114</u>	<u>41092</u>

Phytoplankton Growth and Loss Rates

A model of light-dependent growth (see Methods eqns. 6-10) was used to predict the accumulation of biomass within each phytoplankton layer in the trophogenic zone. The model was run using several C:CHL ratios (30, 40, and

50) in addition to C:CHL determined for each layer using microscopic counts to compute cell carbon and CHL analysis. Because specific loss rates were not included in the model, predicted biomass should always exceed observed biomass at each time step.

Observed CHL_s initially increased faster than model results using the measured C:CHL ratio during both seasons (Fig. 26). In 1990-1991, observed CHL_m was always less than the predicted CHL_m for all the C:CHL ratios used in the model projections, except for one measurement of CHL_m (Fig. 27). Between day 270 and 310 of the 1991-1992 season, observed CHL_m increased quicker than predicted CHL_m , for all C:CHL ratios tested. Predicted CHL_d was generally less than predicted CHL_d , in 1990-1991 (Fig. 28). Observed CHL_d did not increase until after day 290; before then it decreased during 1991-1992. Predicted CHL_d was much less than the actual CHL_d , in 1991-1992. A C:CHL ratio of about 10 would be needed to match the model projection with the observed increases in CHL_d .

Gross specific growth rates for each phytoplankton layer ($\mu_{g,i,t}$) were estimated from increases in predicted CHL concentrations for each time interval according to eqn. 3, using the C:CHL derived from phytoplankton counts (Fig. 29). $\mu_{g,i}$ followed the seasonal increase in irradiance with the difference in the amplitude of the response between layers resulting from their different values of α . μ_g for

each phytoplankton layer showed the greatest increase from mid-October to mid-November (day 290-325), remained fairly constant through late November to mid-December (day 325-350), and then decreased through late December and early January.

Net specific growth rates (determined by equation 4) in the surface phytoplankton layer showed no clear seasonal trend and tended to fluctuate around zero (Fig. 30). Net growth rates in the middle phytoplankton layer were positive during the winter-spring transition (September to mid-October) and decreased to negative values in late October and early November (day 300). The rate increased again in late November (day 320), remained near zero during December, and increased in January (day 1). The net growth rates of the 16 to 20 meter phytoplankton layer showed the most dynamic seasonal variation with negative values until mid-October (day 290) followed by a rapid increase and decrease by early December (day 330); the rates fluctuated around zero after day 330.

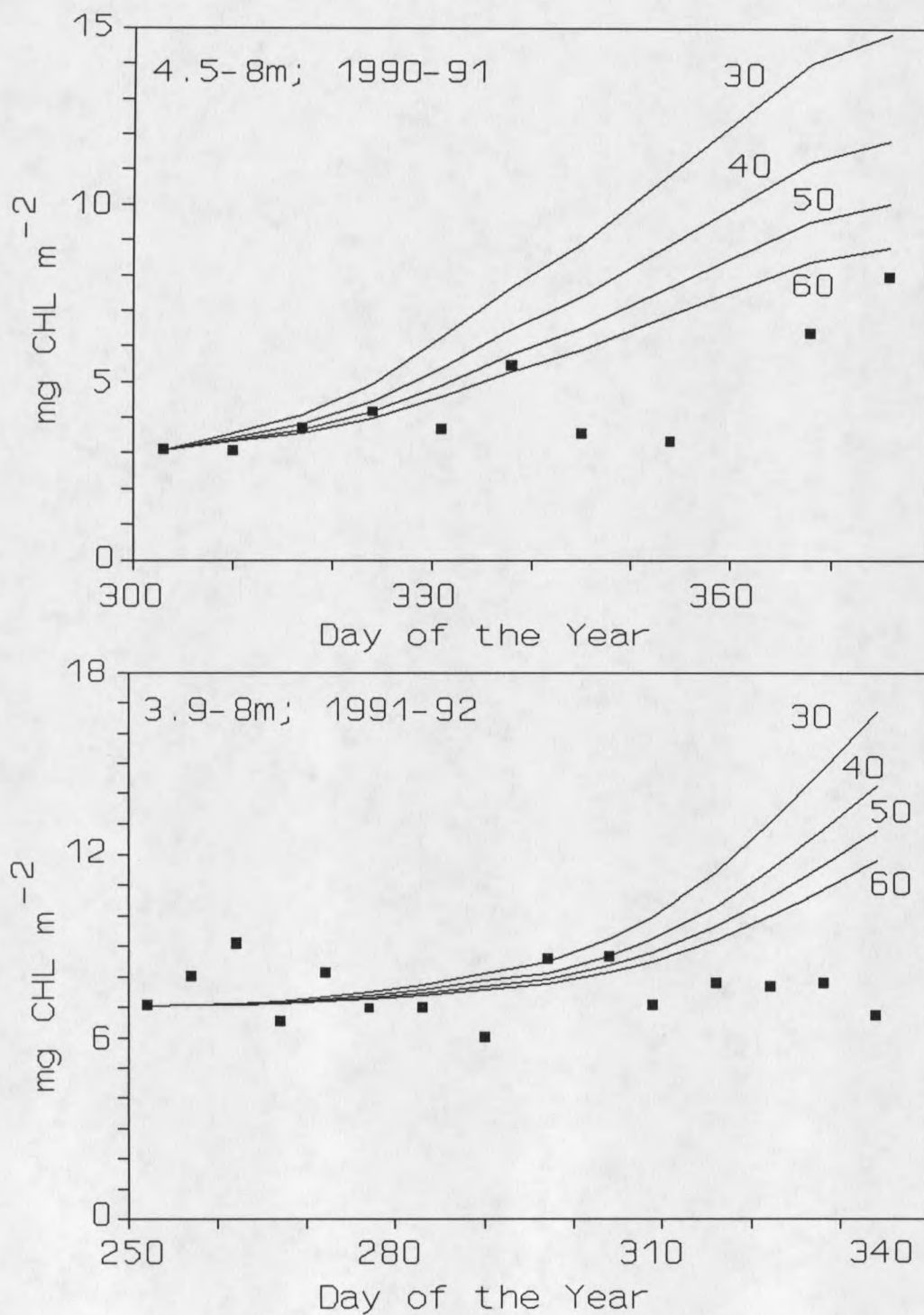


Figure 26. Observed (■) and predicted (-) biomass accumulation within the surface phytoplankton layer during the 1990-1991 and 1991-1992 seasons, for various C:CHL ratios.

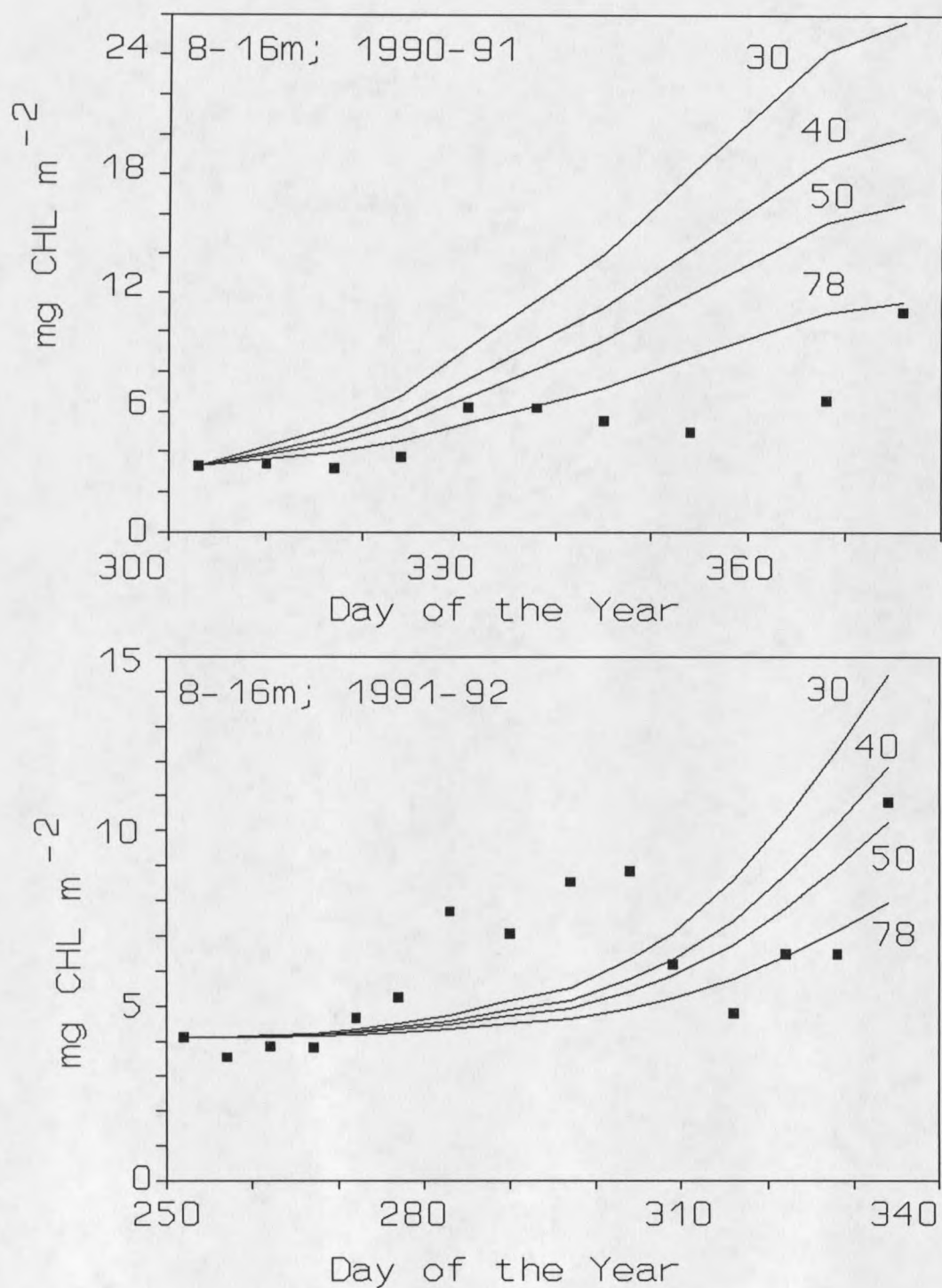


Figure 27. Observed (■) and predicted (-) biomass accumulation within the middle phytoplankton layer during the 1990-1991 and 1991-1992 seasons, for various C:CHL ratios.

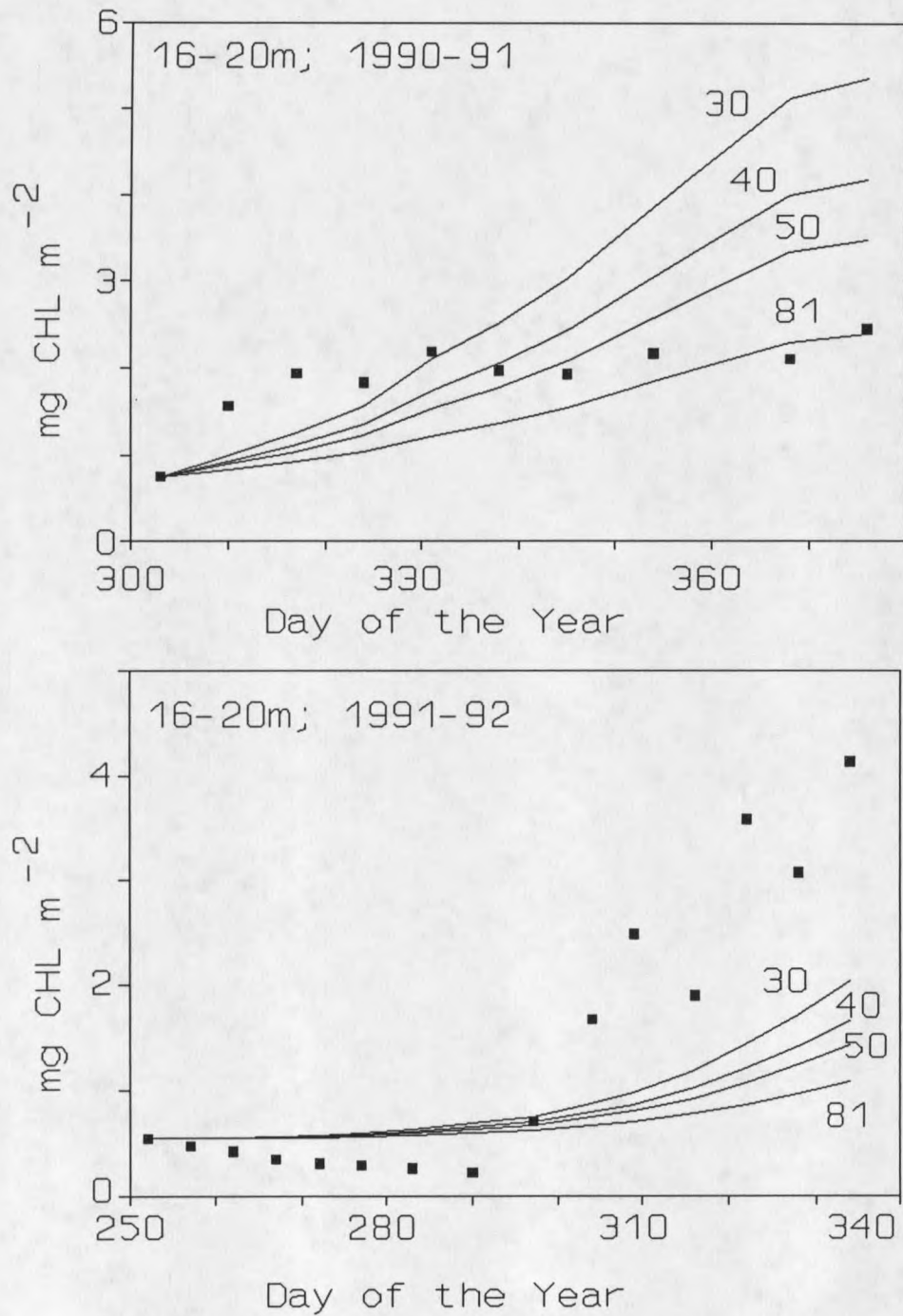


Figure 28. Observed (■) and predicted (-) biomass accumulation within the deep phytoplankton layer during the 1990-1991 and 1991-1992 seasons, for various C:CHL ratios.

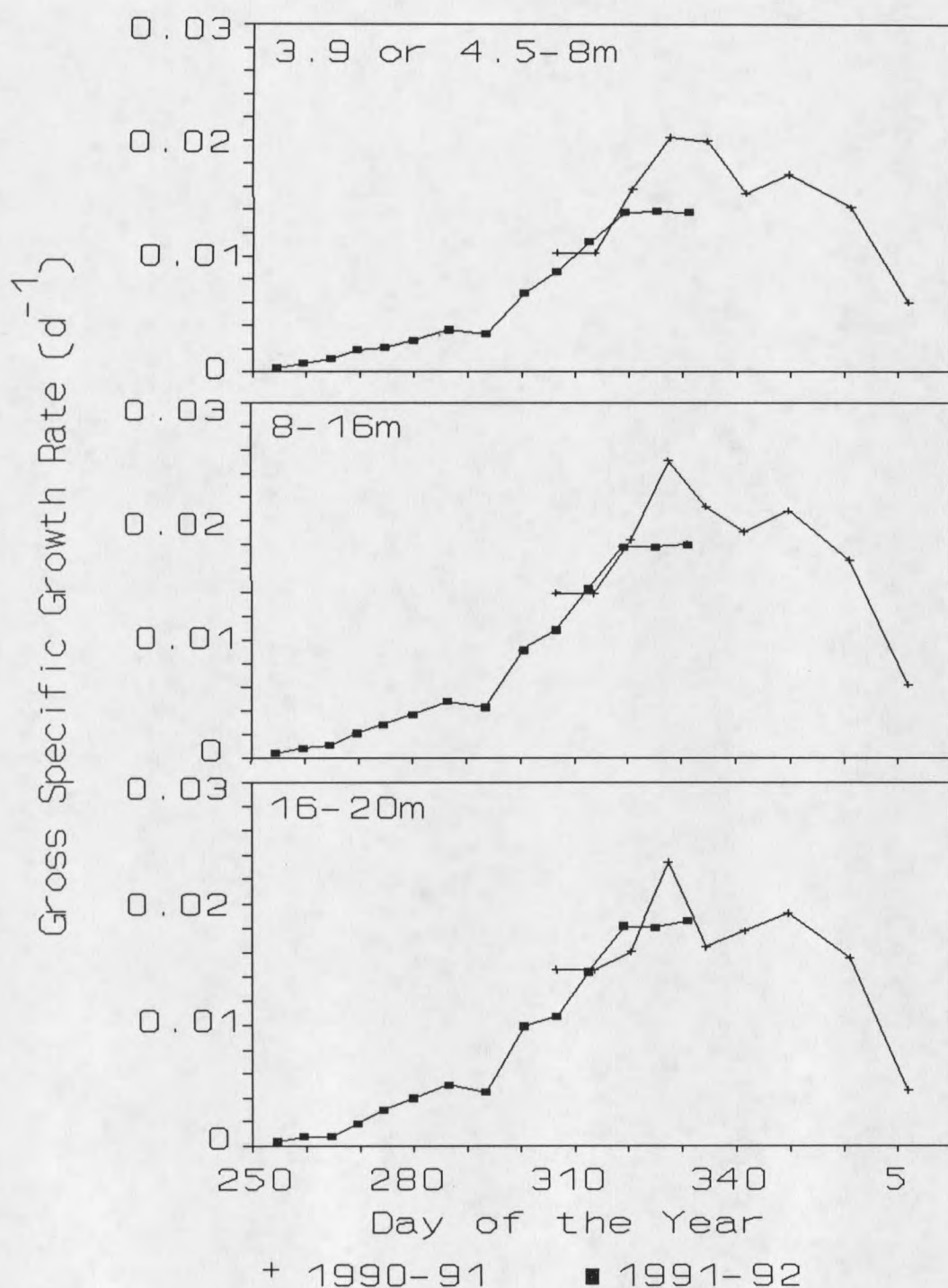


Figure 29. Gross specific growth rates for CHL integrated over the surface, middle, and deep phytoplankton layers predicted by the light-dependent phytoplankton growth model.

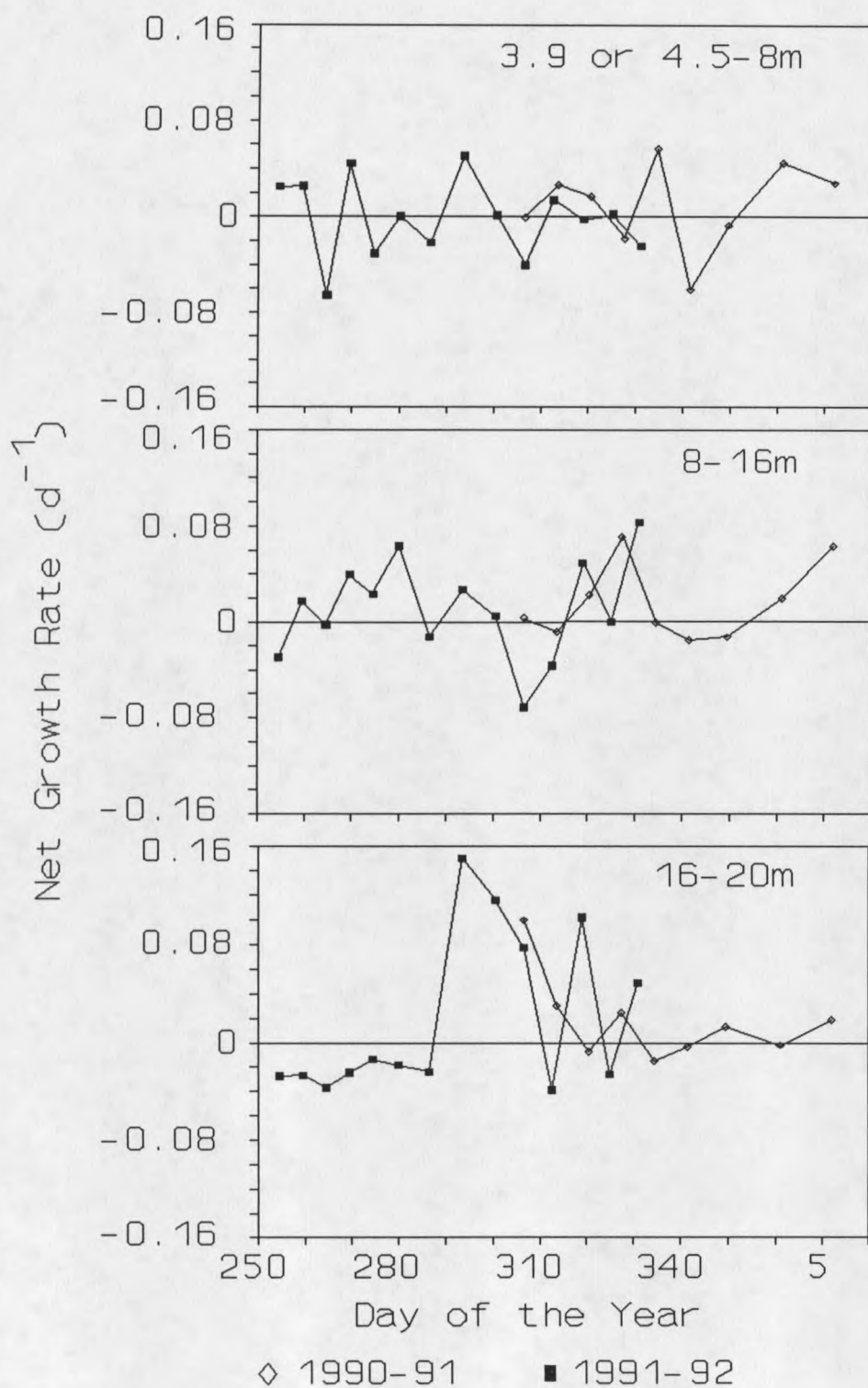


Figure 30. Net specific growth rates for CHL integrated over the surface, middle, and deep phytoplankton layers.

Specific loss rates for each phytoplankton layer ($\lambda_{i,t}$) were defined as the difference between gross (predicted) and net (observed) specific growth rates (Fig. 31). This approach to determining $\lambda_{i,t}$ is not independent of the modified Jassby and Goldman (1974) method of determining specific loss rates ($\lambda_{i,t}^*$, Fig. 32). The difference between the two is that the Jassby and Goldman method uses the PPR measured in situ to predict gross production; whereas my method relies on the light-dependent growth model to predict gross production. In other words, both methods as I use them are dependent on observed $CHL_{i,t}$. When net specific growth rates exceeded gross specific growth rates, the result is a negative specific loss rate, indicating that over the sampling interval, CHL accumulated faster than would be predicted from observed photosynthesis and $C:CHL$ ratios within that layer. The two methods give nearly identical results (compare Figs. 31 and 32). Specific loss rates of phytoplankton biomass integrated over each of the three phytoplankton assemblages were always less than $0.10\ d^{-1}$ in both seasons. Specific loss rates showed no clear seasonal trend in any of the phytoplankton layers, except in deep phytoplankton layer where they were relatively constant up to 17 October 1991 (day 290).

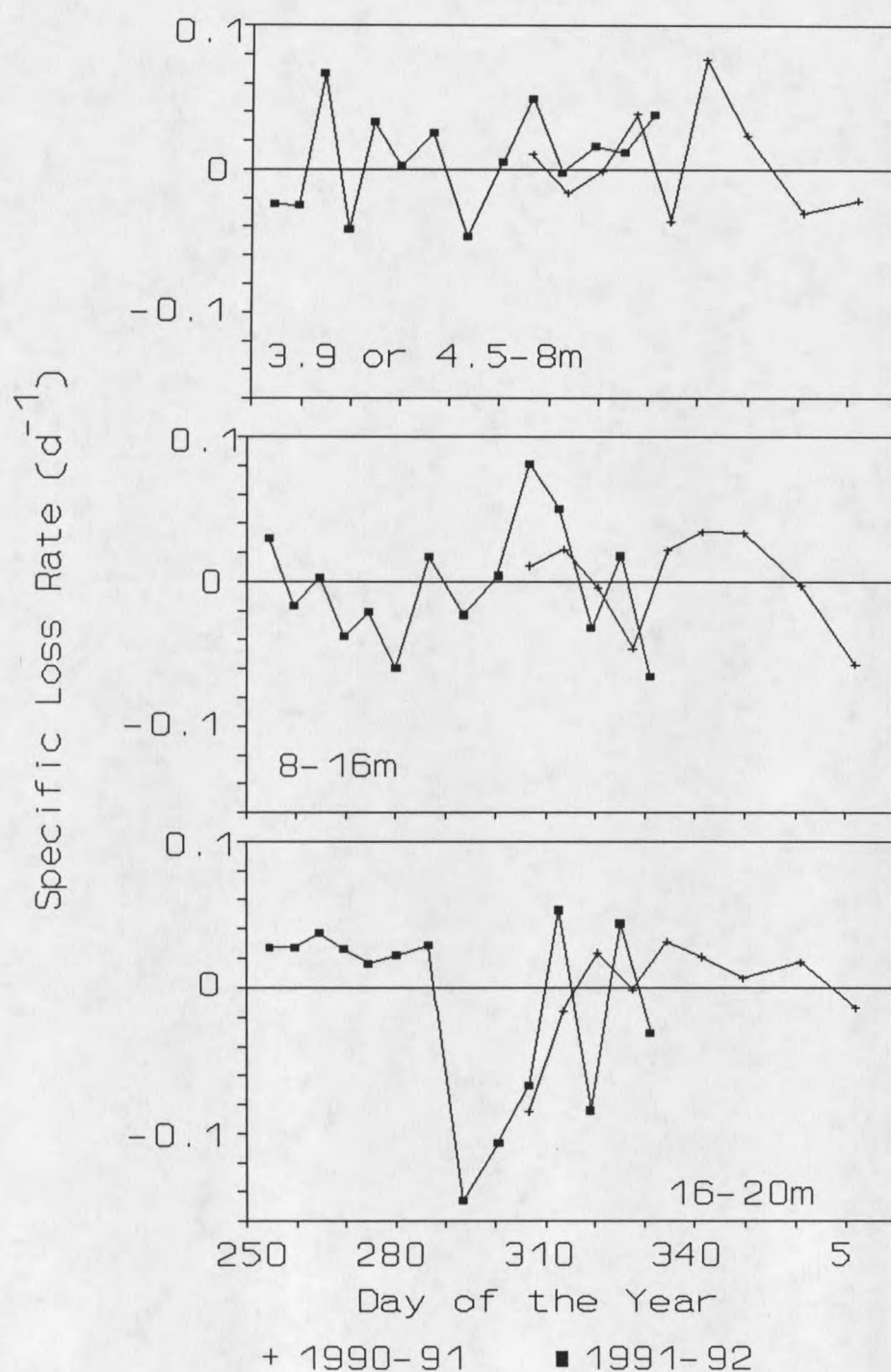


Figure 31. Specific loss rates for CHL integrated over the surface, middle, and deep phytoplankton layers, determined as the difference between predicted gross specific growth rates and net specific growth rates.

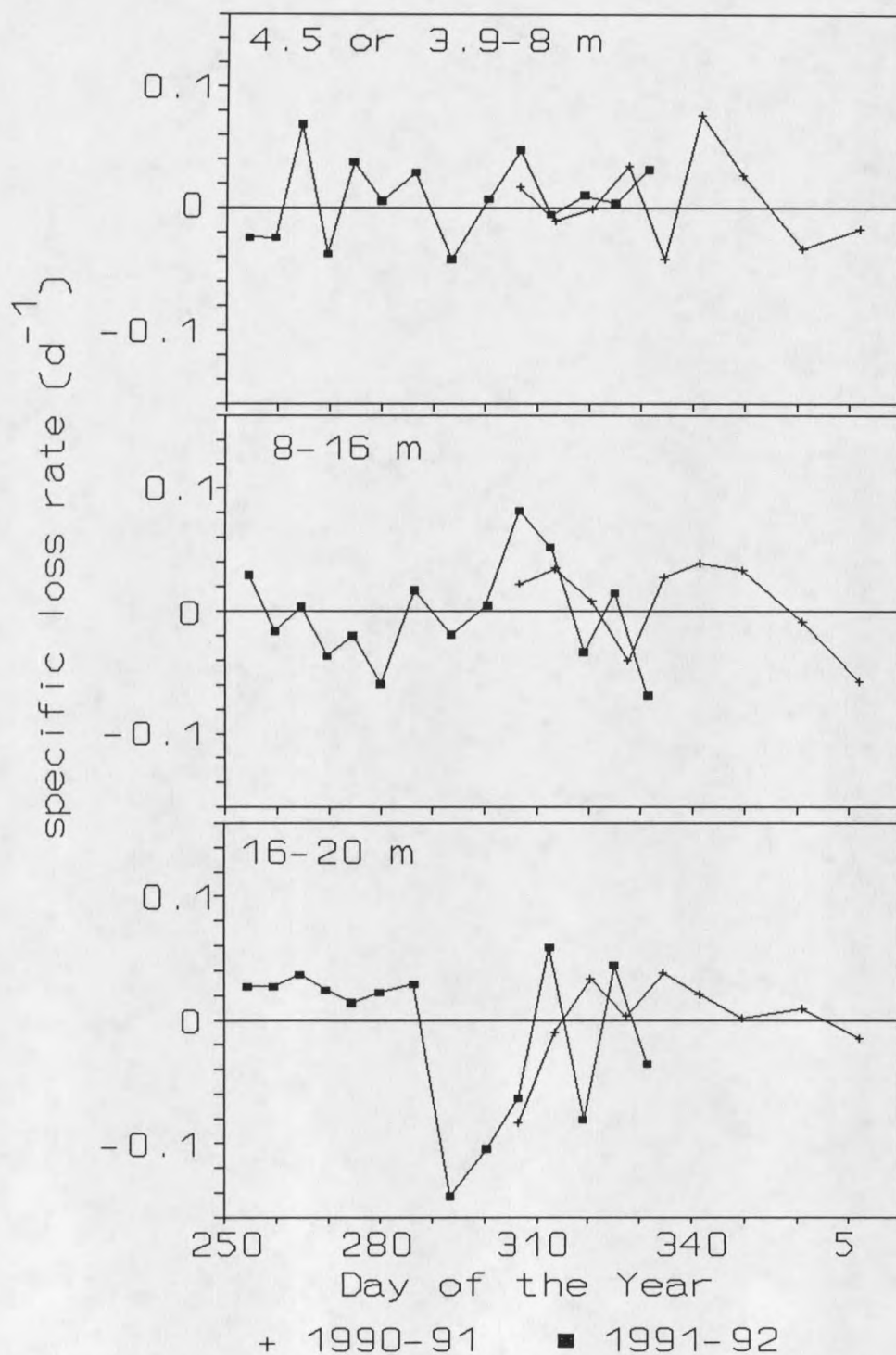


Figure 32. Specific loss rates for CHL integrated over the surface, middle, and deep phytoplankton layers, determined by the modified method of Jassby and Goldman (1974).

Specific net and gross growth rates and specific loss rates were averaged (time weighted) over 1990-1991 (day 303 to 11). The rates from 1991-1992 were averaged over two periods; from day 252 to 290 when there was a light:dark period and from 290 to 334 when the sun was continually above the horizon (Table 25).

μ_g , averaged over 1990-1991, was greatest in the middle layer. From day 252 until day 290 in 1991, μ_g was greater in the middle and deep phytoplankton layers than in the surface layer. In the latter part of the 1991-92 season, μ_g was greater in the middle and deep phytoplankton layers than in the surface layer.

The surface layer had the lowest μ_n averaged over 1990-1991 and the latter part of 1991-1992. μ_n was similar in all three layers averaged over 1990-1991. The average $\mu_{n,s}$ and $\mu_{n,d}$ were negative from day 252 to 290 in 1991-1992 (Table 25) indicating that biomass declined within these two layers. The middle (8-16 meters) layer had the highest average μ_n from day 252-290 in 1991-1992. The lowest and highest μ_n of the three layers occurred in the deep (16-20 meters) layer for the time intervals from day 252 to 290 and from day 290-334, respectively, in 1991-1992.

The surface phytoplankton layer had the greatest specific loss rate, averaged over the 1990-1991 season as determined by either method (Table 25). Averaged over day 252 to 290 in the 1991-1992 season, specific loss rates

were highest in the deep phytoplankton and lowest in the middle phytoplankton layer. Specific loss rates averaged over the latter part of 1991-1992 (day 290 to 334) were lowest in the deep phytoplankton layer, while the highest average rate occurred either in the surface layer (as determined by model results) or in the middle layer (as determined by the modified method of Jassby and Goldman). Aside from this difference loss rates determined by both methods were generally in good agreement.

Table 25. Average daily gross and net specific growth rates and specific loss rates determined by the difference between gross and net specific growth rates (λ) and the modified method of Jassby and Goldman (λ^*) for each phytoplankton layer.

Phytoplankton Layer	μ_g	μ_{net}	λ	λ^*
Surface				
1990-1991				
Day 303-11	0.0143	0.0126	0.0017	0.0049
1991-1992				
Day 252-290	0.0019	-0.0042	0.0062	0.0087
Day 290-334	0.0100	0.0024	0.0076	0.0003
Middle				
1990-1991				
Day 303-11	0.0172	0.0162	0.0009	0.0007
1991-1992				
Day 252-290	0.0024	0.0142	-0.0112	-0.0112
Day 290-334	0.0130	0.0095	0.0035	0.0109
Deep				
1990-1991				
Day 303-11	0.0157	0.0157	0.0001	0.0015
1991-1992				
Day 252-290	0.0024	-0.0241	0.0265	0.0260
Day 290-334	0.0133	0.0623	-0.0490	-0.0481

CHL_{tot} (3.9 or 4.5 to 20 m) increased in both sampling seasons (Fig. 33). The rate at which CHL_{tot} increased was determined by using a linear regression model with time (days) as the independent variable and natural log transformed areal CHL concentrations as the dependent variable. During 1990-1991, there were two distinct periods when integrated chlorophyll increased: (1) from 30 October to 4 December 1990 (days 303-338) when CHL_{tot} doubled once every 35 days ($\mu_{n,tot} = 0.02$) and (2) from 11 December 1990 to 22 January 1991 (days 345-22) when CHL_{tot} doubled once every 22 days ($\mu_{n,tot} = 0.03$). The doubling time for CHL_{tot} , from 9 September to 1 December (day 252-335) 1991, was 166 days ($\mu_{n,tot} = 0.004$). Doubling rates were determined by dividing μ by the natural log of 2.

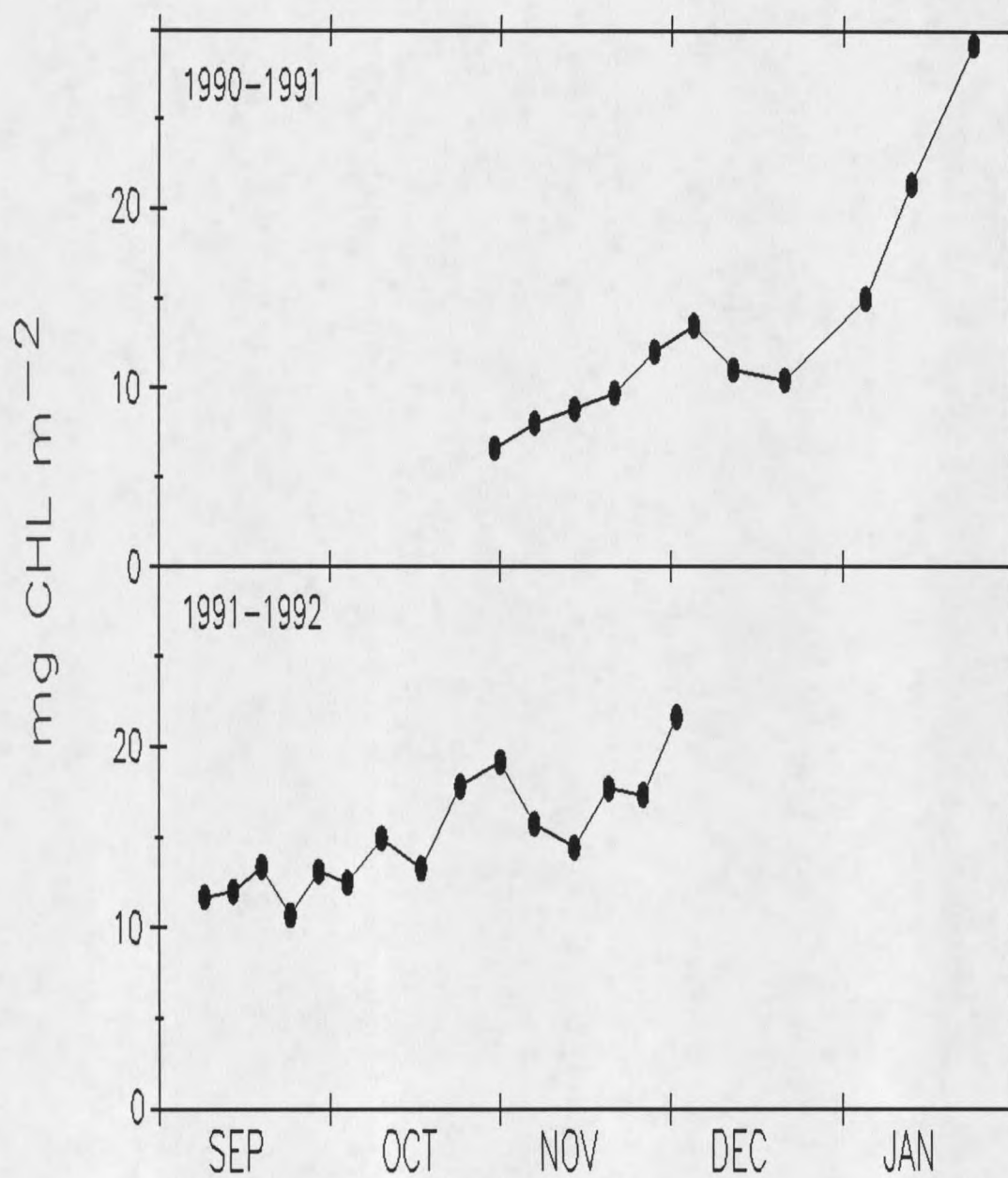


Figure 33. Temporal variation of total integrated (3.9 or 4.5-20 m) CHL during the 1990-1991 and 1991-1992 seasons.

DISCUSSION

The Physical and Chemical Environment

The water column of Lake Bonney has strong vertical gradients of conductivity, temperature, oxygen and nutrients. In combination, these environmental factors structure distinct habitats for the phytoplankton populations. In this section, I will discuss possible explanations for the vertical distribution of these factors and how they may influence phytoplankton production.

The unusual temperature profile is considered to result from solar heating and not from geothermal sources (Heywood 1984), despite considerable controversy in the past (e.g. Armitage and House 1962, Angino et al. 1964, Goldman et al. 1967). Water column stability is maintained despite the increasing temperature with depth from under the ice to 15 m by the increase in salinity (Spigel et al. 1990). This dichothermic temperature profile may allow the middle phytoplankton layer to maintain higher growth rates than the surface phytoplankton layer despite the lower irradiances (Lizotte and Priscu 1992). Conversely, the lower temperatures immediately below the ice may decrease decomposition and respiration within the surface layer.

Oxygen supersaturation in the mixolimnion may result from oxygen dissolved in glacial meltwater (which flows

into the lake under the ice cover) being exuded when the meltwater freezes during the winter (Craig et al. 1992). For nearby Lake Hoare, Craig et al. (1992) calculated that 89% of the dissolved oxygen was derived from meltwater, while only 11% is derived from in situ photosynthesis.

It was suggested previously (Parker et al. 1977) that the supersaturation of oxygen in the trophic zone may increase photorespiration thereby increasing the amount of photoassimilated carbon which is excreted by the phytoplankton. Since my measurements of excretion of photosynthetically fixed carbon were within the range traditionally reported for phytoplankton (see METHODS: Phytoplankton Productivity; Measurement and Verification), I reject the earlier contention of Parker et al. However, further study may reveal a physiological adaptation that these phytoplankton may have to compensate for increased ratio of O_2 :DIC.

Nutrient concentrations determined by our research team over three field seasons differed from previous measurements (Angino et al. 1964, Goldman 1964, Matsumoto et al. 1982), except for agreement with one of the previous reports on SRP concentrations (Fortner et al. 1976, Weand et al. 1977).

NH_4^+ concentrations reported by Fortner et al. (1976) and Weand et al. (1977) were much higher for both samples from the mixolimnion (55.7 and 16.7 $\mu M NH_4^+$ at 8 m) and

monolimnion (122.8 and 539.28 $\mu\text{M NH}_4^+$ at 25 m) than NH_4^+ concentrations reported in this study. Concentrations reported by Matsumoto et al. (1982) were much lower, $< 1 \mu\text{M NH}_4^+$ for epilimnetic samples and $< 4 \mu\text{M NH}_4^+$ for monolimnetic samples. All of these researchers used the phenol hypochlorite method for NH_4^+ analysis similar to what I used; however, it is not clear whether Matsumoto et al. (1982) diluted their samples to avoid salt interference. One possible explanation for why higher values reported by Fortner et al. (1976) and Weand et al. (1977) is that their samples were analyzed within 24 hr of collection, while the samples I analyzed were frozen for up to 2 months. Freezing water samples before analysis may change NH_4^+ concentrations. However, this problem was tested in this study (Table 3) and freezing did not reduce NH_4^+ concentrations.

Concentrations of $\text{NO}_2^- + \text{NO}_3^-$ are within the same order of magnitude reported by Fortner et al. (1976) and Weand et al. (1977). Differences in concentrations may simply result from different sampling locations. Their sampling station was located on the east end of the east lobe, an area that receives glacial meltwater during late summer; these streams were enriched in NO_3^- relative to the lake water (see Table 6). NO_3^- concentrations measured by Goldman (1964) and Matsumoto et al. (1982) are much lower than all data reported by Fortner et al. (1976) and Weand

et al. (1977); Angino et al. (1964) did not detect NO_3^- . Again this may be a result of not diluting samples from the chemocline and monomolimnion but the methods used in these previous investigations are not clear.

SRP concentrations reported here are within the same order of magnitude as Fortner et al. (1976) and Weand et al. (1977) while concentrations measured by Angino et al. (1964) and Goldman (1964) are at least an order of magnitude greater than I measured. Matsumoto et al. (1982) did not detect SRP; their limit of detection was $0.003 \mu\text{M}$ SRP.

The shape of the NH_4^+ and oxidized N profiles are very similar to the conductivity profile. Conversely, profiles of SRP do not resemble the conductivity profile. Above and within the chemocline, SRP concentrations were low, often near the limits of detection of the method (ca. $0.07 \mu\text{M}$). The maximum SRP concentrations consistently occurred around 23 m, which is also the oxygen minimum zone for the water column. While the redox potential was not measured, it would be expected to decrease with depth because of declining oxygen concentrations. This may allow for SRP adsorbed to particles to mobilize and appear in the water column (Hutchinson 1957). It is possible that PO_4^{3-} absorbs to settling particles in the oxic portion of the water column, settle to the chemocline where in the anoxic water the PO_4^{3-} is released. SRP concentrations do not continue

to increase below the chemocline because of the increasing density of the water which decreases the settling velocity. I contend that the rate at which PO_4^{3-} is released from particles at 20 m is greater than the velocity at which they settle.

Seasonal variation (or its absence) in the concentrations of NH_4^+ , $\text{NO}_2^- + \text{NO}_3^-$ and SRP is particularly interesting in terms of the seasonal trends of phytoplankton production. Based on studies of Lakes Fryxell, Vanda and Signey Island lakes (Vincent 1981, Vincent and Vincent 1982, Priddle et al. 1986), Vincent hypothesized that phytoplankton growth rates may be highest in the early spring when irradiance rises above the compensation point for net phytoplankton photosynthesis and nutrient concentrations are maximal after remineralization during the winter without uptake by phytoplankton. After the initiation of phytoplankton production, it was assumed that the phytoplankton depleted nutrients until production became nutrient limited. The data presented here (Figs. 6 and 7) clearly demonstrate that NH_4^+ , oxidized N and SRP concentrations are not depleted over this period. In the case of NH_4^+ , concentrations actually increase. This implies that the regeneration of NH_4^+ may be stimulated by the initiation of phytoplankton production. However, some other process may be responsible for the increase because the increase in NH_4^+ extends below the trophogenic zone

(see Appendix A, Table 26), where there are not any viable phytoplankton. Bacterial remineralization of N may respond to the seasonal increase in irradiance. An abiotic process such as diffusion may cause the increasing NH_4^+ concentrations. These possibilities warrant further study and demonstrate the complexities of these "simple ecosystems".

Temporal Trends in Phytoplankton Production

Primary production in Lake Bonney is strongly correlated with light for most of the austral spring and summer in all three of the phytoplankton layers (Figs. 16 through 21). In this section, I will discuss and at times speculate (due to the imprecise nature of nutrient bioassays) on seasonal trends in the relationship between primary production and light, the influence of environmental factors on this relationship and finally the relevance of this research to other aquatic ecosystems.

For the surface phytoplankton layer, PPR was correlated only with light early in the 1991-1992 season and then failed to increase as irradiance increased (Fig. 17). Since photosynthesis within this assemblage would not be saturated at in situ irradiances (Lizotte and Priscu 1992), some other environmental factor may control production within the surface layer. In the middle and deep phytoplankton layers, production was strongly

correlated with irradiance over the entire season.

Comparing the environment of the surface to the middle and deep phytoplankton layers (Figs. 3, 4 and 5), the lower nutrient concentrations within the surface layer would suggest that the ambient nutrient regime may influence the photoresponse of the surface layer.

The higher concentrations of dissolved nutrients in the middle and deep phytoplankton layers as compared to the surface layer may imply that the failure of photosynthesis in the surface layer to increase with increasing irradiance results from nutrient deficiency. Phytoplankton in both Lakes Vanda and Fryxell have shown increased photochemical capacity on enrichment with P or N, respectively (Vincent and Vincent 1982, Vincent 1981).

Nutrient enrichment bioassays in Lake Bonney did show significantly different photosynthetic rates between treatments on a few occasions. However, the results of these experiments show no clear temporal trends. On 16 November and 30 November 1989, NH_4^+ additions increased the photosynthetic rate, but the statistical power of this experiment was weakened by the pseudoreplication of the treatments. The design of the nutrient enrichment bioassays in 1990-1991 was statistically more stringent. In this set of experiments, the photosynthetic rate of the treatment amended with NH_4^+ was never significantly different from the control (Tables 23 and 24).

In two of the 1990-1991 experiments, treatments enriched with PO_4^{3-} had significantly different photosynthetic rates than the control; on 25 November 1990, the photosynthetic rate of the PO_4^{3-} treatment was significantly greater than the control and on 7 January 1991, the photosynthetic rate of treatments enriched with PO_4^{3-} was significantly less than the control. Despite the contradictory photosynthetic response of the phytoplankton community at 4.5 m to the PO_4^{3-} addition, both may indicate P deficiency. This is possible because when P deficient phytoplankton are exposed to increased PO_4^{3-} concentrations, PO_4^{3-} may be taken up at the expense of CO_2 fixation (Lean and Pick 1981). Because of the extremely low under-ice irradiance in Lake Bonney, energy needed to transport PO_4^{3-} into a cell may become limiting, thus increasing the length of the period during which rate of CO_2 fixation would be depressed. Maybe if the 19 h pre-incubation of the 7 January 1991 bioassay had been longer, the photosynthetic rate of the PO_4^{3-} treatment may have increased after the phytoplankton had become P replete. Perhaps increased irradiance during the 25 November 1990 bioassay allowed for uptake of PO_4^{3-} to be completed earlier in the experiment than in the 7 January 1991 bioassay.

Another possibility is that these nutrient bioassay results may indicate intermittent N deficiency during 1989-1990 and intermittent P deficiency, during 1990-1991.

Pulses of regenerated nutrients from the decomposition of detritus could stimulate primary production within the surface layer. In nearby Lake Fryxell, where phytoplankton production is nitrogen-limited (Vincent 1981), biological production was supported to a large extent by regenerated nitrogen (Priscu et al. 1989). It is plausible that, in Lake Bonney, production may at times be supported by available new or regenerated N and P while at other times N and P demand by the phytoplankton may exceed the rate at which it is supplied. Considering recent reviews (Elser et al. 1990, Dodds and Priscu 1990) of N and P limitation of phytoplankton growth, the results may be interpreted as an indication that phytoplankton production in Lake Bonney may suffer from N and P co-deficiency.

The nutrient bioassay results are too variable to clearly demonstrate a trend in nutrient deficiency in the surface phytoplankton layer. Given the low growth rates of phytoplankton in Lake Bonney, my short-term bioassays only examined changes in the photosynthetic rate rather than in the growth rate of the phytoplankton. Long-term nutrient enrichment bioassays (> 5 days) (Hecky and Kilham 1988, Dodds and Priscu 1990) or more sensitive physiological assays (Vincent et al. 1984) would be more insightful indicators of nutrient deficiency.

Nutrient concentrations within the surface layer did not decrease from the initial sampling date (9 September

1991) to 24 October when the photosynthetic rate failed to increase despite the increasing irradiances (Figs 6 and 17). The inability of the nutrient bioassays, or changes in nutrient concentrations within the surface layer, to demonstrate clearly nutrient deficiency over the winter-spring transition leads me to speculate that the unrealized photosynthetic potential of surface phytoplankton assemblage may result from something other than nutrient deficiency.

Interestingly, the date at which the photosynthetic rate of the surface phytoplankton assemblage leveled off coincided with the onset of 24 hours of daylight (around 17 October). The physiology of the dominant surface phytoplankton species (Chroomaonas lacustris) may require a dark period to achieve optimal rates. This decrease in photosynthesis did not occur in the middle and deep phytoplankton layers. The difference in the seasonal photosynthetic trends may reflect the differing physiologies of taxa comprising each layer. A similar decrease in growth rate has been observed in cultures of temperate phytoplankton when placed under continuous light (Paasche 1968, Zevenboom and Mur 1984); however, the growth rate of a polar marine Chrysophyte (Bacillariophyceae) did not decrease when grown under continuous illumination (Sakshuag and Andresen 1986).

The increase in day length may have affected the light utilization index (ψ_i) in the three phytoplankton layers in Lake Bonney. In all three phytoplankton layers, ψ initially increased (Figs. 23, 24 and 25) over the winter-spring transition. Ryther (1956) first suggested that day length would influence modeled relationships between integrated production normalized to biomass (CHL) and irradiance on an annual scale. Cullen (1990) manipulated the model of Sakshaug (1989) to generate a model of integrated production normalized to integrated biomass versus irradiance as a function of day length. In this model, integrated production normalized to biomass increases with day length for a specific average daily irradiance. Simply, on long days there is more time during which photosynthesis occurs compared to short days. After the initial increase, ψ decreased in each of phytoplankton layers.

The decrease in ψ occurred earliest in the surface and middle phytoplankton layers and coincided with the start of the 24 hr photoperiod, on 17 October (day 290). In the deep phytoplankton layer, ψ decreased after 27 November (day 331). If the photosynthetic rate of phytoplankton in the surface layer was depressed under continuous light, as I have suggested above, ψ_s would have decreased during a 24 hour photoperiod. Unfortunately, I have no way of separating the concurrent effects of increasing photoperiod

and irradiance on photosynthesis. Further study on cultures of Lake Bonney phytoplankton may clarify how the photosynthetic response varies as a function of photoperiod and irradiance.

Another way that ψ can decrease is when photosynthesis is light saturated. If this occurred, integrated production normalized to biomass would have remained constant as irradiance increased, thereby lowering the ratio of the two. It is doubtful that this happened because it was demonstrated that photosynthesis in the phytoplankton populations in Lake Bonney is virtually always light-limited (Lizotte and Priscu 1992). However, it is possible that the photosynthetic parameters derived from the photosynthesis versus irradiance (PI) curve do not accurately portray the photosynthetic behavior of phytoplankton in situ because photosynthesis was measured over short incubation periods (4 hr) under non-fluctuating irradiances (Cullen 1990).

In summary, the average ψ_s may be lower than the two deeper populations for several reasons. The greater ψ of the deeper populations may reflect greater shade-adaptation of these populations whereas nutrient deficiency within the surface layer may cause the lower ψ . Taxonomic differences have been suggested for variations in ψ (Campbell and O'Reilly 1988); however seasonal succession of the phytoplankton taxa was not observed in the surface layer of

Lake Bonney. Finally, the lower ψ of the surface population may result from a fraction of the CHL present in this layer being non-viable during the first part of 1991-1992.

The possibility that some of the CHL immediately beneath the ice is non-viable becomes apparent when CHL normalized PPR_s is plotted versus integrated daily irradiance (Fig. 20). Data collected during the 1990-1991 season reveals PPR_s normalized to CHL is higher at similar irradiances than data collected during the 1991-1992 season. In contrast, PPR_s for both seasons responded equivalently to similar irradiance (Fig. 17), suggesting that some of the CHL present during the 1991-1992 season was not photosynthetically viable. This trend is similar to laboratory experiments conducted with phytoplankton from Lake Tahoe, where it was observed that the photosynthetic potential of the phytoplankton when left in complete darkness decreased more rapidly than did CHL concentrations (Tilzer et al. 1977). Apparently over the winter of 1991, the phytoplankton within the surface layer lost their photosynthetic viability faster than their CHL decomposed. With the exception of the surface phytoplankton layer, ψ was higher than those previously reported for marine phytoplankton (Platt et al. 1988). Integrated production normalized to biomass was highly correlated to incident irradiance and ranged from 0.29 to 0.52 g C (g chl)⁻¹ m² (E)⁻¹.

¹ (Platt et al 1988). ψ for the surface, middle and deep phytoplankton layers, as determined by a linear regression of integrated production normalized to biomass on incident daily irradiance, were 0.43, 1.95 and 2.91 g C (g CHL)⁻¹ m² (E)⁻¹, respectively. The average values ($\pm$ standard deviation) of α (Table 13) when converted to the units of ψ , for the surface, middle and deep phytoplankton layers, are 0.89 ± 0.47 , 2.71 ± 1.75 , and 5.47 ± 3.19 , respectively. It is not surprising that these two estimates of photosynthetic efficiencies differ, considering the different methods by which they were determined. The higher photosynthetic efficiencies measured in a incubator could result from the inclusion of excreted photoassimilated C in the determination of the photosynthetic rate as well as the lack of photosynthesis versus irradiance measurements from the winter-spring transition, when ψ was lowest.

Phytoplankton Growth

Gross specific growth rates predicted by the light-dependent model are about 75% lower than experimental measurements of carbon specific growth rates of Lake Fryxell phytoplankton, at 0.9 to 3.0° C (Priscu et al. 1987) and are about 1% of the maximum growth rates of dry valley lake phytoplankton under optimal conditions (at 10-20° C and 75 $\mu\text{E m}^{-2} \text{ s}^{-1}$; Seaburg et al. 1981). The increased

gross specific growth rates determined for phytoplankton from Lake Fryxell may reflect the difference in nutrient concentrations between the two lakes. The average μ_g for Lake Bonney phytoplankton are at least an order of magnitude lower, in comparison to a wide variety of other lake phytoplankton (Forsberg 1985). Sea-ice microalgal communities also grow in a non-fluctuating low light environment similar to that experienced by Lake Bonney phytoplankton, however, sea-ice microalgal daily growth rates were approximately an order of magnitude greater than those of Lake Bonney phytoplankton (0.28 d^{-1} ; Palmisano and Sullivan 1982).

The low μ_g may reflect the extreme low light and temperature environment of Lake Bonney. Because of low photosynthetic efficiency (α or ψ) of the surface phytoplankton layer, $\mu_{g,s}$ is lowest within this layer, despite receiving the highest irradiance in the water column. The deep phytoplankton layer may have a higher photosynthetic efficiency than the middle phytoplankton layer but this physiological capability does not quite overcome the difference in average daily irradiance between the middle and deep phytoplankton layers; thus, $\mu_{g,m}$ is the greatest (Table 25).

Similarly, $\mu_{n,m}$ was greater than $\mu_{n,s}$ or $\mu_{n,d}$ during 1990-1991. Again the greater growth rate of the deep populations could have resulted from increased growth

efficiency despite lower light because of the compensating effect of higher temperature and nutrient concentrations with depth. The highest rates (both in the two deeper layers) may be illusory, resulting not from primary production but from the settling of biomass from above. While microscopic observation of phytoplankton genera numbers is prone to high errors, it did not support this contention that the high growth rates resulted from the settling of cells from the overlying layer.

The average net specific growth rates for Lake Bonney phytoplankton are about 4-times lower than those previously reported for other lake phytoplankton (Forsberg 1985) and are lower than those for phytoplankton in antarctic Lakes Fryxell and Vanda (mean growth rates of 0.072 and 2.16 d⁻¹ were estimated from the data of Priscu et al. 1987). This may suggest that Lake Bonney phytoplankton are among the slowest growing phytoplankton yet reported. However, the rates reported by Priscu et al. (1987) are based on carbon incorporation into protein which do not include losses other than respiration.

In comparison (Figs. 31 and 32), specific loss rates as determined by the difference of gross and net specific growth rates and from Jassby and Goldman's method (Jassby and Goldman 1974) are quite similar. Unfortunately, the methods are not independent because the observed change in CHL_i is a variable in both. However, the near agreement of

rates determined by both methods would indicate that the light-dependent phytoplankton growth model gives a good approximation of gross specific growth rates.

In comparison to a wide variety of lake phytoplankton, specific loss rates are at least two orders of magnitude lower for Lake Bonney phytoplankton (Forsberg 1985). There are several possible reasons for these low specific loss rates. Firstly, losses of biomass from settling may be reduced because a majority of the cells are flagellated or may have some other adaptation to regulate their buoyancy. Secondly, the low water temperatures (0-7° C) of Lake Bonney may reduce respiratory losses (Priscu and Goldman 1984, Tilzer and Dubinsky 1987). Also, when there is continuous daylight during the summer, respiratory losses could decrease (Tilzer and Dubinsky 1987). Finally, grazing losses are probably insignificant because of the lack of protozoans and zooplankton in the pelagos of Lake Bonney. Excretion is not included in this summation of loss rates because it was accounted for in the light-dependent production model and not measured in routine monitoring of PPR.

Specific loss rates were greatest in the surface layer. Several possible explanations exist for this. Experimental measurements of bacterial decomposition rates indicate that rates are greatest in the surface layer (Priscu, unpublished data). The average specific loss rate

of phytoplankton biomass due to bacterial decomposition was 0.0008 d^{-1} , indicating that losses for respiration, settling and possible grazing range from -0.0005 to 0.0079 d^{-1} on average. Another possible explanation is that biomass may accumulate in the deeper layers from the settling of phytoplankton from shallower depths, thereby decreasing apparent specific loss rates that are determined solely by changes in CHL_i . Also, heterotrophic or phagotrophic growth within the middle or deep phytoplankton layers would decrease specific loss rates determined by assuming growth is only photoautotrophic. The middle layer is composed mainly of a Ochromonas sp.; members of this genus have been shown to grow mixotrophically (Sanders and Porter 1987). Metalimnetic phytoplankton maxima in low light environments may be composed of mixotrophic phytoplankton that depend more on consumed prey than on photosynthesis for growth (Bird and Kalff 1989).

Additionally, the greater than expected C:CHL ratio in the deeper phytoplankton layers, if incorrect, would decrease specific loss rates. Above I pointed out that C:CHL ratios increase with depth and suggested that this may result in erroneous estimates of phytoplankton biomass by including dead phytoplankton cells in the counts. If the estimates of the C:CHL ratios for the middle and deep phytoplankton layers were too high, the rate at which photoassimilated C is converted to CHL would be lower than

actual rates. This error would cause the specific loss rates to be lower. In addition to potential inaccuracies in estimates of the C:CHL ratio, I have also assumed that the ratio does not vary seasonally. C:CHL can vary as a function of nutrient limitation, irradiance (Bannister and Laws 1980) and temperature (Eppley 1972). The C:CHL ratio would be expected to decrease as average daily irradiance increases over the season. Also, considering the succession of species that occurs within the deep phytoplankton layer, it is possible that the C:CHL ratio changes over the season.

Finally, the large negative specific loss rates that occurred during the period when production began in the deep phytoplankton layer may not necessarily reflect an increase in biomass resulting from primary production. I believe there are two possible explanations for this. Previously, it was mentioned that the negative rates may result from CHL settling from the surface and middle phytoplankton layers. However, considering that before mid October (day 290, Figs. 31 and 32), specific loss rates are positive and fairly constant then dramatically decrease, it seems unreasonable to assume that the contribution from the settling of biomass from shallower depths would start all at once. Perhaps, the phytoplankton may control the rate at which they settle and adjust this rate in response to the increasing depth at which the compensation irradiance

occurs. Once the compensation depth reaches the deep phytoplankton layer, the phytoplankton may decrease their sinking rate because of the elevated nutrient concentrations (particularly SRP) within this layer. Similar hypotheses have been postulated to explain the formation of deep CHL maximums in other systems (Cullen 1982, Prisco and Goldman 1983). Alternatively, the increase in CHL within this layer may result from a physiological response of the phytoplankton. It is probable that the onset of the 24 hour photoperiod may trigger vegetation of resting stage cells (cysts, zygotes or spores) and the synthesis of CHL.

In summary, phytoplankton growth and loss rates in Lake Bonney are apparently low in comparison to a wide variety of lake phytoplankton (Forsberg 1985). These rates vary in each of the layers. Growth rates tend generally to be maximal in December and January, coinciding with highest irradiances. The variation of growth rates between layers most likely reflects the differences between temperature and nutrient regime, the life histories of the phytoplankton and the seasonal descent of the compensation irradiance during the winter-spring transition.

CONCLUSIONS AND FUTURE RESEARCH

Two main conclusions may be drawn from this study:

- 1) Maximum phytoplankton growth rates in Lake Bonney occurred after the onset of continuous daylight (around 17 October), similar to what Tilzer and Dubinsky (1987) hypothesized for phytoplankton in the Southern Ocean.
- 2) The high ψ of Lake Bonney phytoplankton implies that the phytoplankton are highly acclimated to their light environment. I speculate that the general decline of ψ over the summer, which occurs in all of phytoplankton layers, is caused by nutrient deficiency in the surface layer or, as in the case of the middle and deep phytoplankton layers, a reduction in photosynthetically utilizable radiation. This decrease in photosynthetically utilizable radiation is effected by accumulation of phytoplankton biomass in the surface phytoplankton layer and turbidity from glacial runoff.

Future research on phytoplankton ecology in Lake Bonney should continue to focus on the environmental factors influencing primary production and biogeochemical cycling within the lake. The possible existence of a crossover point between light and nutrient limitation (sensu Priscu 1989) of phytoplankton growth should be examined. Also, the effects of irradiance and day length on phytoplankton growth should be determined.

Finally, if the lakes are to be used as indicators of environmental change (e.g. global warming, see Wharton et al. 1989), a more complete knowledge of the interannual variability of primary production is needed. In addition, there are areas of the microbial ecology which remain completely uninvestigated, for example the existence of microbial foodweb loop. Attempting to utilize the dry valley lakes as indicators of climatic change, without a more complete understanding of the processes governing biogeochemical cycles and the time scales upon which these processes act, would be premature.

This study of a dry valley lake, as in a previous study (Vincent 1981), concludes that it is deceiving to suggest that these lakes are simple or model ecosystems. Further study should reveal more of subtle complexities of how these organisms interact with their environment.

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APPENDICES

APPENDIX A
NUTRIENT CONCENTRATIONS

Table 26. Nutrient concentrations from routine primary productivity measurements in the east lobe of Lake Bonney.

Date	Depth (m)	NH ₄ ⁺ (μM)	ox. N (μM)	NO ₂ ⁻ (μM)	SRP (μM)
11 Nov 1989	4.2	1.51	7.93		0.28
	6.2	0.56	9.79		0.18
	8.2	0.22	6.26		0.18
	10	1.17	14.92		0.18
	12	4.00	22.19		0.25
	14	9.42	3.99		0.30
	16	11.66	5.26		0.46
	19	81.33	10.60		0.61
	21	114.87	14.36		2.59
21 Nov 1989	5	1.94	9.32		0.11
	6	1.42	9.30		0.06
	8	1.68	13.34		0.11
	10	1.25	17.63		0.11
	13	9.25	34.45		0.10
	15	10.80	26.88		0.16
	17	50.36	63.38		0.17
	19	95.95	126.02		0.07
	20	120.03	161.90		0.44
	21	132.08	159.79		1.47
24 Nov 1989	5	1.82	9.54		0.17
	6	1.03	11.18		0.09
	8	0.90	14.91		0.05
	10	2.34	16.89		0.09
	12	5.29	28.87		0.08
	14	12.93	39.78		0.07
	16	22.75	67.21		0.07
	18	55.48	103.91		0.10
	20	88.87	154.27		0.38
	22	115.06	174.39		1.43
	24	131.43	197.46		1.38
	26	149.11	217.57		0.88
	28	156.31	239.57		0.74
	30	163.51	248.63		0.79
	32	162.20	247.39		0.83
	34	160.89	259.80		0.28
	35	151.73	232.12		0.37
14 Dec 1989	5	2.60	8.72	0.08	0.12
	6	0.90	11.60	-0.01	0.10
	8	1.49	11.22	0.08	0.12
	10	2.08	11.18	0.08	0.10
	12	5.16	32.85	0.08	0.15
	14	10.96	32.93	-1.14	0.11

Table 26. continued.

Date	Depth (m)	NH ₄ ⁺ (μM)	ox. N (μM)	NO ₂ ⁻ (μM)	SRP (μM)
14 Dec 1989	16	20.78	66.36	-0.08	0.26
	18	56.14	103.90	2.87	0.22
	20	84.29	156.71	8.77	0.27
	22	114.41	184.34	12.99	1.52
	24	104.59	189.29	28.60	1.47
	26	136.01	219.39	42.31	0.97
	28	152.38	255.40	42.31	0.92
	30	156.97	248.53	40.20	1.20
	32	155.00	244.79	40.62	0.97
	34	151.07	243.76	38.72	0.92
	35	147.14	250.21	34.50	1.20
16 Jan 1990	5	0.74	3.28	0.03	0.14
	6	1.17	9.39	0.09	0.10
	8	1.25	12.46	0.09	0.12
	10	0.74	16.63	0.03	0.16
	12	4.52	27.32	0.17	0.14
	14	9.08	30.47	0.23	0.15
	16	12.52	73.29	0.73	0.18
	18	60.68	85.64	2.12	0.27
	20	103.69	125.99	8.96	0.24
	22	134.66	164.69	7.93	3.76
	24	164.76	206.68	26.58	2.06
	26	179.38	212.45	37.98	1.72
	28	194.01	233.85	43.16	1.72
	30	200.03	254.44	41.09	1.35
	32	204.33	262.67	39.64	1.54
	34	200.03	251.97	39.43	1.58
	35	195.73	233.03	37.36	1.35
30 Oct 1990	5	1.82			0.21
	6	1.70			0.21
	8	0.91			0.19
	10	2.36			0.19
	13	7.02			0.34
	15	8.82			1.17
	16	10.33			0.72
	17	30.30			0.78
	18	40.88			0.69
	20	78.39			0.36
6 Nov 1990	5	1.91			0.15
	6	1.31			0.24
	8	1.03			0.15
	10	1.40			0.19
	13	7.02			0.36
	15	9.73			0.52
	16	15.78			0.53

Table 26. continued.

Date	Depth (m)	NH ₄ ⁺ (μM)	ox. N (μM)	NO ₂ ⁻ (μM)	SRP (μM)
	17	32.41			0.66
	18	49.96			0.60
	20	80.20			0.40
	23	115.59			3.00
	26	142.81			2.51
	29	154.00			1.58
	32	154.91			1.58
	35	155.82			1.96
	36	149.16			1.70
20 Nov 1990	4.5	2.91			0.09
	6	1.21			0.11
	8	0.94			0.18
	10	1.37			0.21
	13	8.11			0.29
	15	5.49			0.46
	16	13.66			0.49
	17	27.57			0.65
	18	46.93			0.56
	20	78.99			0.35
	23	112.56			2.49
	26	137.37			1.27
	29	150.67			0.82
	32	149.46			1.39
	35	145.23			0.82
	36	139.79			1.07
27 Nov 1990	4.5	1.37			0.18
	6	0.76			0.08
	8	0.64			0.08
	10	1.15			0.09
	13	5.84			0.18
	15	15.17			0.20
	16	20.32			0.25
	17	37.25			0.32
	18	53.59			0.23
	20	78.69			0.13
	23	112.26			0.92
	26	137.97			0.74
	29	146.74			0.50
	32	149.16			0.72
	35	145.83			1.25
	36	131.92			0.64
20 Dec 1990	4.5	1.00			0.03
	6	0.88			0.06
	8	0.64			0.12

Table 26. continued.

Date	Depth (m)	NH ₄ ⁺ (μM)	ox. N (μM)	NO ₂ ⁻ (μM)	SRP (μM)
20 Dec 1991	10	0.91			0.12
	13	6.84			0.24
	15	5.49			0.24
	16	16.69			0.24
	17	25.46			0.34
	18	44.51			0.40
	20	76.57			0.15
	23	115.29			1.52
	26	140.09			1.37
	29	150.07			1.39
	32	153.40			1.78
	35	149.16			1.33
9 Sep 1991	3.9	1.80	3.58		0.09
	4.5	2.42	3.47		0.10
	6	0.44	6.61		0.06
	8	-0.19	11.58		0.05
	10	0.47	13.43		0.06
	13	5.04	24.38		0.07
	15	7.85	30.80		0.06
	16	5.46	39.71		0.07
	17	4.94	54.85		0.06
	18	25.10	70.18		0.06
	20	56.32	111.70		0.03
	23	94.36	159.45		0.97
	26	123.87	185.29		0.53
	29	124.73	218.26		0.37
	32	133.81	231.62		0.38
	35	124.16	237.33		0.19
	36	131.82	214.16		0.10
14 Sep 1991	3.9	2.20	5.88		0.08
	4.5	2.20	5.40		0.08
	6	0.84	5.90		0.07
	8	0.32	10.46		0.08
	10	0.18	13.84		0.07
	13	4.04	26.34		0.09
	15	7.19	31.51		0.10
	16	6.23	37.21		0.08
	17	10.34	37.03		0.08
	18	30.49	43.63		0.10
	20	59.44	71.25		0.03
	23	93.79	117.94		0.94
	26	116.78	137.54		0.51
	29	129.27	192.42		0.31
	32	130.97	227.35		0.35
	35	127.85	218.97		0.22

Table 26. continued.

Date	Depth (m)	NH ₄ ⁺ (μM)	ox. N (μM)	NO ₂ ⁻ (μM)	SRP (μM)
19 Sep 1991	3.9	1.80	5.18		0.08
	4.5	1.77	5.66		0.06
	6	0.41	6.41		0.08
	8	-0.24	11.10		0.06
	10	-0.04	12.81		0.06
	13	3.42	19.04		0.07
	15	7.68	32.04		0.10
	16	5.26	41.84		0.10
	17	11.19	58.95		0.12
	18	27.08	68.22		0.11
	20	56.89	112.23		0.05
	23	95.49	163.73		0.93
	26	115.08	187.25		0.03
	29	130.40	225.74		0.33
	32	134.94	241.07		0.38
	35	128.98	229.31		0.25
24 Sep 1991	3.9	2.71	6.04		0.07
	4.5	1.74	5.91		0.05
	6	0.69	7.48		0.05
	8	0.24	11.21		0.08
	10	0.15	13.68		0.05
	13	4.30	20.64		0.04
	15	8.27	NA		0.05
	16	5.77	31.33		0.05
	17	14.88	42.20		0.06
	18	29.64	53.07		0.07
	20	58.87	69.64		0.00
	23	94.07	107.06		1.03
	26	119.62	149.83		0.55
	29	135.80	220.40		0.42
	32	134.94	238.75		0.44
	35	125.29	226.10		0.30
29 Sep 1991	3.9	2.88	5.97		0.10
	4.5	3.84	4.84		0.09
	6	4.33	5.47		0.07
	8	0.89	10.28		0.07
	10	0.55	15.61		0.08
	13	3.08	20.28		0.09
	15	7.90	25.45		0.10
	16	5.04	35.96		0.10
	17	18.29	50.75		0.10
	18	23.11	62.52		0.13
	20	60.29	102.97		0.05
	23	98.04	157.14		0.99
	26	111.67	185.47		0.59

Table 26. continued.

Date	Depth (m)	NH ₄ ⁺ (μM)	ox. N (μM)	NO ₂ ⁻ (μM)	SRP (μM)
29 Sep 1991	29	140.05	234.65		0.38
	32	127.00	222.54		0.44
	35	127.28	224.67		0.34
3 Oct 1991	3.9	2.03	6.06		0.13
	4.5	1.37	5.52		0.09
	6	0.24	5.93		0.09
	8	-0.19	10.62		0.09
	10	6.74	14.59		0.08
	13	0.52	23.49		0.10
	15	3.36	21.53		0.11
	16	4.55	17.25		0.11
	17	13.74	47.90		0.15
	18	26.52	60.56		0.11
	20	57.17	112.59		0.04
	23	91.52	166.23		0.97
	26	110.25	177.63		0.66
	29	124.16	231.45		0.43
	32	129.27	225.03		0.41
	35	135.23	229.49		0.31
10 Oct 1991	3.9	1.86			0.06
	4.5	1.92			0.06
	6	1.14			0.04
	8	0.71			0.07
	10	0.68			0.05
	13	2.49			0.06
	15	9.24			0.06
	16	10.45			0.09
	17	16.18			0.10
	18	44.86			0.09
	20	69.00			0.06
	23	107.03			1.04
	26	125.74			0.55
	29	148.38			0.37
17 Oct 1991	32	152.61			0.35
	35	152.61			0.45
	3.9	3.64			0.13
	4.5	3.22			0.08
	6	2.86			0.07
	8	2.10			0.07
	10	1.83			0.09
	12	2.58			0.05
	13	4.64			0.10
	16	22.82			0.09

Table 26. continued.

Date	Depth (m)	NH ₄ ⁺ (μM)	ox. N (μM)	NO ₂ ⁻ (μM)	SRP (μM)
17 Oct 1991	17	24.63			0.09
	18	45.16			0.12
	20	72.62			0.04
	23	116.09			0.95
	26	148.08			0.50
	29	151.40			0.31
	32	160.76			0.37
	35	153.81			0.26
24 Oct 1991	3.9	3.94	6.63		0.07
	4.5	3.70	6.41		0.05
	6	2.25	6.67		0.06
	8	1.29	10.39		0.05
	10	2.13	12.34		0.05
	12	2.58	14.79		0.07
	13	5.90	51.99		0.08
	16	25.84	28.76		0.08
	17	37.31	48.69		0.11
	18	65.68	62.98		0.11
	20	75.04	99.08		0.07
	23	116.99	139.11		0.90
	26	135.40	165.63		0.55
	29	151.40	214.92		0.35
	32	154.42	216.02		0.39
	35	149.59	214.13		0.28
31 Oct 1991	3.9	3.79			0.06
	4.5	5.69			0.07
	6	2.95			0.11
	8	2.61			0.11
	10	2.86			0.05
	12	3.34			0.02
	13	6.24			0.05
	16	7.43			0.04
	17	16.48			0.11
	18	33.39			0.09
	20	103.41			0.02
	23	134.20			0.94
	26	151.70			0.54
	29	177.96			0.43
	32	186.41			0.46
	35	188.83			0.29
6 Nov 1991	3.9	7.96	6.49		0.06
	4.5	7.87	6.72		0.05
	6	8.23	6.11		0.06
	8	6.66	10.65		0.04

Table 26. continued.

Date	Depth (m)	NH ₄ ⁺ (μM)	ox. N (μM)	NO ₂ ⁻ (μM)	SRP (μM)
6 Nov 1991	10	6.48	11.95		0.04
	12	7.23	14.95		0.06
	13	7.41	16.05		0.05
	15	55.42	27.66		0.05
	16	44.86	36.45		0.06
	17	64.78	51.68		0.07
	18	79.87	64.08		0.07
	20	93.75	104.57		0.01
	23	142.34	143.19		0.92
	26	167.70	159.82		0.55
	29	174.34	207.54		0.34
	32	180.98	216.02		0.35
	35	157.44	211.31		0.25
13 Nov 1991	3.9	4.21			0.09
	4.5	4.40			0.07
	6	2.89			0.04
	8	2.19			0.03
	10	2.40			0.04
	12	6.12			0.04
	13	6.48			0.05
	15	52.40			0.06
	16	59.95			0.06
	17	51.50			0.09
	18	70.21			0.06
	20	72.02			0.04
	23	108.84			0.97
	26	129.97			0.54
	29	143.55			0.37
19 Nov 1991	32	148.99			0.39
	35	149.59			0.28
	3.9	3.28	6.52		0.18
	4.5	2.55	6.53		0.08
	6	1.65	7.51		0.18
	8	1.47	NA		0.06
	10	1.29	12.44		0.08
	12	3.10	20.91		0.02
	13	4.97	25.46		0.03
	15	10.75	10.55		0.04
	16	14.07	33.94		0.05
	17	6.83	33.15		0.05
	18	31.27	65.65		0.03
	20	58.74	102.69		0.01
	23	100.09	154.17		1.06
	26	124.24	173.01		0.65
	29	138.42	213.66		0.31

Table 26. continued.

Date	Depth (m)	NH ₄ ⁺ (μ M)	ox. N (μ M)	NO ₂ ⁻ (μ M)	SRP (μ M)
19 Nov 1991	32	162.87	224.18		0.34
	35	139.33			0.36
25 Nov 1991	3.9	6.27			0.15
	4.5	5.93			0.10
	6	4.88			0.07
	8	4.76			0.05
	10	5.00			0.18
	12	3.34			0.05
	13	1.50			0.06
	15	4.41			0.04
	16	16.79			0.05
	17	33.99			0.11
	18	32.48			0.04
	20	61.76			0.00
	23	102.81			0.96
	26	120.61			0.57
	29	133.59			0.49
	32	141.74			0.45
	35	129.06			0.21
1 Dec 1991	3.9	1.11	3.41		0.19
	4.5	2.61			0.07
	6	0.77			0.17
	8	0.41			0.05
	10	0.68			0.06
	12	1.44			0.06
	13	4.03			0.07
	15	18.30			0.13
	16	13.16			0.10
	17	18.90			0.07
	18	38.82			0.10
	20	72.62			0.01
	23	NA			0.97
	26	127.56			0.51
	29	140.53			0.33
	32	145.67			0.38
	35	138.72			0.27

Table 27. Nutrient concentrations in the west lobe of Lake Bonney.

DATE	DEPTH (m)	NH ₄ ⁺ (μM)	ox. N (μM)	NO ₂ ⁻ (μM)	SRP (μM)
28 Nov 1989	5	NA	9.04	0.03	0.07
	6	0.90	9.03	0.08	0.09
	8	1.23	10.06	0.03	0.08
	10	1.69	12.64	0.12	0.11
	12	43.59	30.85	0.03	0.37
	14	177.92	26.51	0.49	0.48
	16	191.01	25.39	0.49	0.67
	18	192.32	25.91	0.41	0.65
	20	208.03	18.47	0.36	0.67
	24	252.56	1.96	0.62	0.63
	28	297.08	1.55	0.36	0.25
	30	300.35	1.91	0.49	0.52
	35	321.30	-1.11	0.03	0.64
	12	72.73			0.53
	24	279.38	0.69		
	28	342.82	0.71		
	30	355.15	0.57		
	35	367.49	1.23		

Table 28. Nutrient concentrations from 1989-1990 experiments in the east lobe of Lake Bonney.

Date	Experiment	NH ₄ ⁺ (μ M)	ox. N (μ M)	SRP (μ M)
16 Nov 1989	NB5mt=0	1.94	9.27	0.08
17 Nov	CONT	1.60	9.84	0.08
	P	0.85	7.67	0.05
	N	40.90	9.21	8.85
	N+P	46.92	9.08	8.97
	TAXIS	1.10	7.00	0.18
18 Nov	NB19mt=0	32.30	5.93	0.53
19 Nov	CONT	33.16	6.97	0.50
	P	33.16	6.94	0.47
	N	91.65	6.61	9.18
	N+P	89.93	6.18	9.25
29 Nov	NB5Mt=0	2.46	9.26	0.25
30 Nov	CONT	1.25	9.17	0.07
	P	1.08	9.00	0.07
	N	43.48	9.44	8.45
	N+P	45.20	9.37	8.10
1 Dec	NB17mt=0	43.66	82.38	0.31
2 Dec	CONT	37.49	82.15	0.27
	N	96.52	77.20	0.29
	P	36.61	74.84	8.96
	N+P	100.04	67.85	9.08
15 Dec	15NH4t=0	1.99	10.39	0.23
16 Dec	15NO3t=0	1.29	9.69	0.16
18 Dec	15NH4TCt=0	2.08	9.60	0.18
5 Jan 1990	NB3t=0	1.85	4.63	0.18
6 Jan	CONT	2.11	3.54	0.13
	N	1.60	6.39	0.11
	P	46.06	5.60	8.60
	N+P	46.92	5.43	8.64
	NB31t=0	38.32	74.93	0.26
7 Jan	CONT	40.90	88.11	0.31
	N	40.04	79.87	0.22
	P	105.41	38.70	5.25
	N+P	106.27	75.76	6.86
17 Jan	15NH4UPt=0	39.18	73.29	0.08

APPENDIX B
PHYTOPLANKTON BIOMASS AND PRODUCTIVITY

Table 29. Phytoplankton biomass and productivity in the east lobe of Lake Bonney in 1989-1990.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ h}^{-1}$)
14 Nov 1989	1700	5	1.56	
		6	1.00	
		8	0.75	
		10	0.72	
		12	0.54	
		13	0.37	
		15	0.40	
		16	0.36	
		17	0.57	
		18	0.84	
		19	0.99	
		20	1.06	
		21	0.18	
21 Nov	1145	5	1.20	0.048
		6	1.04	0.053
		8	0.54	0.048
		10	0.57	0.068
		13	0.46	0.063
		15	0.36	0.054
		17	0.89	0.109
		19	0.24	0.009
		20	0.04	0.010
		21	0.28	0.000
21 Nov	1843	5	1.16	0.005
		6	0.70	0.005
		8	0.42	0.003
		10	0.35	0.006
		13	0.36	0.007
		15	0.24	0.012
		17	0.63	0.014
		19	0.29	0.000
		20	0.11	0.000
		21	0.31	NA
22 Nov	0155	5	2.19	0.057
		6	0.84	0.039
		8	0.39	0.031
		10	0.35	0.046
		13	0.31	0.028
		15	0.35	0.044
		17	0.56	0.041
		19	0.16	0.003
		20	0.10	0.001

Table 29. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ h}^{-1}$)
22 Nov	1100	5	1.20	0.060
		6	0.89	0.065
		8	0.48	0.065
		10	0.37	0.090
22 Nov 1989	1100	13	0.28	0.063
		15	0.37	0.081
		17	0.65	0.089
		19	0.17	0.008
		20	0.04	0.007
12 Dec	0530	4.5	1.37	0.154
		6	1.04	0.118
		8	0.87	0.100
		10	1.07	0.143
		13	0.35	0.079
		15	0.26	0.026
		16	0.43	0.035
		17	0.72	0.055
		18	1.37	0.071
		20	0.15	0.000
12 Dec	1330	4.5	1.59	0.084
		6	1.46	0.057
		8	0.98	0.042
		10	1.26	0.063
		13	0.22	0.028
		15	0.37	0.015
		16	0.85	0.029
		17	1.15	0.031
		18	0.28	0.005
		20	0.15	0.002
12 Dec	2200	4.5	1.85	0.091
		6	0.80	0.033
		8	0.85	0.029
		10	0.87	0.041
		13	0.37	0.024
		15	0.24	0.012
		16	0.41	0.009
		17	0.85	0.025
		18	1.33	0.032
		20	0.13	0.000
14 Dec		4.5	0.91	
		6	0.77	
		8	0.78	
		10	0.84	

Table 29. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ h}^{-1}$)
14 Dec 1989		12	0.69	
		14	0.18	
		16	0.32	
		18	0.90	
		20	0.14	
		22	0.44	
		24	0.69	
3 Jan 1990	0520	5	1.68	0.238
		6	0.96	0.130
		8	0.96	0.096
		10	1.19	0.132
		13	0.37	0.108
		15	0.16	0.019
		16	0.26	0.020
		17	0.57	0.043
		18	1.06	0.059
		20	0.12	0.003
3 Jan	1412	5	1.58	0.056
		6	0.82	0.040
		8	0.90	0.032
		10	1.58	0.057
		13	0.47	0.029
		15	0.26	0.005
		16	0.23	0.005
		17	0.54	0.011
		18	0.90	0.022
		20	0.16	0.001
3 Jan	2204	5	2.00	0.018
		6	1.11	0.012
		8	0.89	0.009
		10	1.50	0.029
		13	0.40	0.010
		15	0.14	0.000
		16	0.32	0.002
		17	0.52	0.000
		18	1.25	0.005
		20	0.16	0.001
13 Jan		5	1.48	
		6	1.11	
		8	1.49	
		10	0.20	
		12	0.51	
		14	0.35	

Table 29. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ h}^{-1}$)
13 Jan 90		16	0.88	
		18	1.31	
		20	0.18	

Table 30. Phytoplankton biomass and productivity in the east lobe of Lake Bonney in 1990-1991 and 1991-1992.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)
30 Oct 1990	1115	5	1.12	0.046
		6	0.98	0.045
		8	0.53	0.036
		10	0.39	0.033
		13	0.43	0.044
		15	0.35	0.027
		16	0.37	0.029
		17	0.22	0.014
		18	0.21	0.009
		20	0.04	0.005
6 Nov	0700	5	1.31	0.053
		6	0.87	0.031
		8	0.57	0.033
		10	0.34	0.024
		13	0.50	0.046
		15	0.30	0.035
		16	0.44	0.039
		17	0.54	0.045
		18	0.50	0.013
		20	0.06	0.000
13 Nov	0800	4.5	1.81	0.061
		6	1.01	0.034
		8	0.58	0.033
		10	0.31	0.025
		13	0.44	0.045
		15	0.31	0.044
		16	0.50	0.048
		17	0.69	0.069
		18	0.62	0.041
		20	0.07	0.001
20 Nov	0612	23	0.50	
		26	0.77	
		4.5	2.99	0.094
		6	0.86	0.038
		8	0.42	0.032
		10	0.28	0.028
		13	0.60	0.063
		15	0.54	0.068
		16	0.55	0.068
		17	0.68	0.076
		18	0.56	0.045
		20	0.05	0.000

Table 30. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)
20 Nov	0612	4.5		0.142
		6		0.063
		10		0.057
		16		0.158
		17		0.167
20 Nov	1420	4.5	1.38	0.087
		6	0.63	0.047
		10	0.31	0.034
		16	0.62	0.106
		17	0.68	0.090
20 Nov	2235	4.5	2.92	0.027
		6	0.86	0.010
		10	0.29	0.006
		16	0.73	0.018
		17	0.95	0.022
27 Nov	0612	4.5	1.41	0.034
		6	1.17	0.043
		8	0.55	0.038
		10	0.53	0.046
		13	1.17	0.106
		15	0.68	0.095
		16	0.70	0.080
		17	0.78	0.078
		18	0.67	0.057
		20	0.06	0.002
		23	0.46	
		26	0.77	
		29	0.75	
		32	0.35	
4 Dec	0622	35	0.14	
		36.5	0.11	
		4.5	3.32	0.137
		6	1.38	0.035
		8	0.56	0.027
		10	0.67	0.079
		13	1.17	0.080
		15	0.49	0.049
		16	0.53	0.042
		17	0.53	0.042
		18	0.72	0.045
		20	0.10	0.001

Table 30. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)
4 Dec 1990		23	0.50	
		26	0.81	
		29	0.74	
		32	0.48	
		35	0.16	
11 Dec 1990	0545	4.5	1.91	0.071
		6	0.93	0.043
		8	0.49	0.032
		10	0.86	0.072
		13	0.84	0.055
		15	0.37	0.032
		16	0.46	0.029
		17	0.52	0.029
		18	0.71	0.043
		20	0.12	0.002
		23	0.13	
		26	0.52	
		29	0.94	
		32	0.81	
		35	0.44	
		36.5	0.16	
20 Dec	0620	4.5	1.75	0.078
		6	0.78	0.047
		8	0.66	0.033
		10	0.97	0.072
		11	1.85	
		12	2.01	
		13	0.52	0.030
		14	0.32	
		15	0.29	0.018
		16	0.31	0.017
		17	0.41	0.019
		18	0.97	0.039
		20	0.15	0.002
		23	0.45	
		26	0.74	
		29	0.74	
		32	0.40	
		35	0.15	
3 Jan 1991	0610	4.5	2.38	0.034
		6	1.91	0.034
		7	1.17	
		8	1.21	0.021
		9	1.28	

Table 30. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)
3 Jan 1991	0610	10	1.11	0.017
		11	2.32	0.051
		12	2.15	0.038
		13	0.79	0.013
		14	0.57	
		15	0.30	0.006
		16	0.28	0.003
		17	0.58	0.005
		18	0.85	0.010
		19	0.31	
		20	0.11	0.000
		21	0.09	
		23	0.45	
		26	0.74	
		29	0.77	
		32	0.56	
		35	0.15	
11 Jan	0633	4.5	2.32	0.108
		6	2.48	0.080
		8	1.85	0.052
		9	1.61	
		10	2.38	0.045
		11	3.32	0.105
		12	3.09	0.077
		13	1.00	0.020
		14	0.43	
		15	0.34	0.006
		16	0.33	0.005
		17	0.94	0.011
		18	0.81	0.011
		19	0.23	
		20	0.13	0.003
		23	0.42	
		26	0.69	
		29	0.75	
		32	0.69	
		35	0.19	
22 Jan	1400	4.5	2.95	
		6	3.36	
		8	3.15	
		9	2.79	
		10	3.25	
		11	4.20	
		12	3.68	
		13	1.68	

Table 30. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)
22 Jan	1400	14	0.74	
		15	0.44	
		16	0.29	
		17	0.83	
		18	0.44	
		20	0.08	
		23	0.41	
		26	0.71	
		29	0.73	
		32	0.70	
		35	0.21	
6 Sep 1991		3.9	3.09	
		4.5	3.26	
		6	0.71	
		10	0.54	
		15	0.20	
		17	0.16	
		20	0.11	
9 Sep	0900	3.9	2.01	0.000
		4.5	3.26	0.001
		6	1.34	0.002
		8	0.70	0.001
		10	0.74	0.000
		13	0.43	0.000
		15	0.24	0.000
		16	0.21	0.000
		17	0.17	0.000
		18	0.11	
		20	0.11	0.000
		23	0.32	
		26	0.82	
		29	0.85	
		32	0.63	
		35	0.23	
		36.5	0.16	
14 Sep	0700	3.9	2.97	0.008
		4.5	3.13	0.000
		6	1.75	0.004
		8	0.74	0.002
		10	0.67	0.002
		13	0.32	0.000
		15	0.16	0.000
		16	0.14	0.000
		17	0.14	0.000

Table 30. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)
14 Sep 1991	0700	18	0.12	
		20	0.09	0.000
		23	0.27	
		26	0.74	
		29	0.71	
		32	0.58	
		35	0.19	
19 Sep	0620	3.9	3.76	0.013
		4.5	3.42	0.014
		6	2.09	0.008
		8	0.70	0.003
		10	0.73	0.003
		13	0.40	0.002
		15	0.14	0.001
19 Sep 1991	0620	16	0.14	0.000
		17	0.12	0.000
		18	0.10	
		20	0.08	0.001
		23	0.31	
		26	0.65	
		29	0.94	
		32	0.74	
24 Sep	0600	35	0.31	
		3.9	2.88	0.035
		4.5	2.00	0.024
		6	1.55	0.016
		8	0.83	0.008
		10	0.57	0.006
		13	0.51	0.003
		15	0.14	0.001
		16	0.12	0.000
		17	0.09	0.000
		18	0.07	
		20	0.09	0.000
		23	0.32	
		26	0.74	
		29	0.78	
29 Sep	0600	32	0.70	
		35	0.23	
		3.9	2.38	0.075
		4.5	2.88	0.065
		6	1.76	0.031
		8	1.31	0.015

Table 30. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)
29 Sep	0600	10	0.87	0.010
		13	0.38	0.002
		15	0.10	0.002
		16	0.12	0.000
		17	0.08	0.000
		18	0.07	0.004
		20	0.07	0.000
		23	0.30	
		26	0.67	
		29	0.77	
		32	0.71	
		35	0.32	
3 Oct	0600	3.9	1.85	0.025
		4.5	2.32	0.027
		6	1.67	0.023
		8	1.07	0.015
		10	0.89	0.012
		13	0.65	0.005
		15	0.18	0.000
		16	0.12	0.000
		17	0.07	0.000
		18	0.05	
		20	0.09	0.000
		23	0.29	
		26	0.73	
		29	0.85	
		32	0.73	
		35	0.24	
10 Oct	0530	3.9	2.13	0.037
		4.5	2.01	0.039
		6	1.63	0.030
		8	1.39	0.022
		10	1.09	0.020
		13	1.25	0.019
		15	0.26	0.004
		16	0.09	0.003
		17	0.09	0.000
		18	0.04	
		20	0.08	0.000
		23	0.34	
		26	0.87	
		29	0.87	
		32	0.77	
		35	0.28	

Table 30. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)
17 Oct 1991	0630	3.9	2.02	0.040
		4.5	1.98	0.032
		6	1.29	0.025
		8	1.07	0.017
		10	0.90	0.016
		12	1.13	0.027
		13	1.15	0.020
		16	0.14	0.004
		17	0.07	0.000
		18	0.04	0.000
		20	0.03	0.004
		23	0.27	
		26	0.50	
		29	0.66	
		32	0.49	
		35	0.28	
24 Oct	0530	3.9	3.76	0.080
		4.5	2.88	0.067
		6	1.82	0.041
		8	1.23	0.032
		10	1.17	0.028
		12	1.01	0.039
		13	1.46	0.052
		16	0.35	0.010
		17	0.20	0.008
		18	0.10	0.007
		20	0.19	0.000
		23	0.30	
		26	0.71	
		29	0.87	
		32	0.81	
		35	0.25	
31 Oct 1991		3.9	2.07	0.006
		4.5	3.26	0.059
		6	2.01	0.036
		8	1.09	0.028
		10	0.97	0.027
		12	0.97	0.037
		13	1.48	0.053
		16	0.93	0.041
		17	0.69	0.027
		18	0.31	0.015
		20	0.06	0.001
		23	0.26	
		26	0.63	

Table 30. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)
31 Oct 1991	0530	29	0.85	
		32	0.71	
		35	0.30	
6 Nov	0530	3.9	2.63	0.027
		4.5	2.83	0.032
		6	1.46	0.031
		8	0.76	0.022
		10	0.77	0.027
		12	0.87	0.038
		13	1.00	0.044
		15	0.51	0.030
		16	0.59	0.039
		17	0.85	0.051
		18	0.78	0.039
		20	0.17	0.000
		23	0.34	
		26	0.74	
		29	0.81	
		32	0.74	
		35	0.26	
13 Nov	0530	3.9	3.48	0.062
		4.5	2.71	0.067
		6	1.82	0.046
		8	0.67	0.025
		10	0.62	0.029
		12	0.61	0.050
		13	0.81	0.058
		15	0.36	0.034
		16	0.43	0.044
		17	0.56	0.058
		18	0.59	0.066
		20	0.25	0.001
		23	0.29	
		26	0.74	
		29	0.83	
		32	0.67	
		35	0.29	
19 Nov		3.9	3.56	0.050
		4.5	2.79	0.047
		6	1.66	0.016
		8	0.71	0.018
		10	0.72	0.021
		12	1.13	0.041
		13	0.96	0.050

Table 30. continued.

Date	Time Sampled	Depth (m)	CHL ($\mu\text{g L}^{-1}$)	PPR ($\mu\text{g C L}^{-1} \text{ d}^{-1}$)
19 Nov 1991		15	0.60	0.036
		16	0.59	0.059
		17	0.89	0.059
		18	1.21	0.077
		20	0.58	0.017
		23	0.32	
		26	0.76	
		29	0.85	
		32	0.77	
		35	0.29	
25 Nov	0530	3.9	3.15	0.039
		4.5	2.87	0.038
		6	1.82	0.032
		8	0.62	0.014
		10	0.53	0.023
		12	0.70	0.028
		13	1.54	0.098
		15	0.73	0.062
		16	0.71	0.061
		17	0.78	0.065
		18	0.91	0.072
		20	0.58	0.010
		23	0.39	
		26	0.80	
		29	0.86	
		32	0.67	
		35	0.23	
1 Dec 1991	0530	3.9	2.67	0.055
		4.5	2.30	0.034
		6	1.58	0.026
		8	0.72	0.017
		10	0.60	0.020
		12	1.78	0.082
		13	2.71	0.128
		15	1.09	0.051
		16	1.05	0.054
		17		0.049
		18		0.029
		20	1.02	0.004
		23	0.42	
		26	0.34	
		29	0.83	
		32	0.67	
		35	0.26	

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Table 31. Phytoplankton biomass measurements in the west lobe of Lake Bonney.

Date	Depth (m)	CHL ($\mu\text{g L}^{-1}$)
14 Jan 1990	5	4.79
	6	5.54
	8	2.87
	10	2.38
	13	3.65
	15	0.34
	17	0.15
	20	0.14
	22	0.09
	25	0.09
28 Nov 1989	30	0.07

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