LIGHT UTILIZATION AND EXCRETION OF ORGANIC MATTER BY ANTARCTIC LAKE PHYTOPLANKTON

by

Mark Kaspar

Thesis submitted to the Faculty of the

Virginia Polytechnic Institute and State University

in partial fulfillment of the requirement for the degree of

MASTER OF SCIENCE

in

Botany

APPROVED:

B. C. Parker, Chairman

S. G. Hornor

J. C. Servaites

G. M. Simmons, Jr.

December, 1986

Blacksburg, Virginia

LIGHT UTILIZATION AND EXCRETION OF ORGANIC MATTER BY ANTARCTIC LAKE PHYTOPLANKTON

by

Mark Kaspar

Committee Chairman: Bruce C. Parker

Biology

(ABSTRACT)

Quantum yields (Φ) were determined for the phytoplankton of four perennially ice-covered lakes of southern Victoria Land, Antarctica. The phytoplankton communities of these oligiotrophic lakes are dominated by cryptophytes, unicellular chrysophytes and flagellated chlorophytes. Quantum yields were calculated using a suggested value for the spectral extinction coefficient of chlorophyll a (k_C) = 0.016 and an empirical estimation of k_C = 0.0328. Quantum yields ranged from 0.0045 to 0.156 using k_C = 0.016, while Φ were lower when calculated using k_C = 0.0328, ranging from 0.0022 to 0.076. Values of Φ were comparable to values reported for phytoplankton elsewhere. Light utilization efficiencies (ε) ranged from 0.006 to 1.46% and are among the lowest values yet reported from aquatic ecosystems. The estimations of Φ indicate that the phytoplankton were efficient at trapping the low levels of photosynthetically active radiation present in these dimly lit lakes, while ε indicate that environmental conditions of these lakes are limiting their respective phytoplankton communities.

Percent extracellular release (PER) of organic matter was great-

est in the shallow depths studied in comparison to the mid-depths sampled. The shallower waters of these lakes were supersaturated with oxygen, brighter and probably nutrient limited. Photosynthesis in Chlamydomonas subcaudata Wille was 2.5 to 3.5 x less at supersaturated oxygen in comparison to saturated oxygen. The higher amount of PER in the shallow depths and the inhibition of photosynthesis in C. subcaudata by supersaturated oxygen indicates that the reduction of photosynthesis due to photorespiration might be limiting the development of the phytoplankton communities of these lakes.

ACKNOWLEDGEMENTS

I would like to thank the faculty and staff of the Department of Biology for their help. I am also grateful to Dale Anderson, Ian Farrance, Gordon Love, Arpad Vass, Tony Watkinson and Dr. Robert Wharton for their assistance in the collection and processing of samples during the 1980-1981 field season in Antarctica and for the preparation of the samples for their return to Virginia.

I am thankful to Lawson Bailey, Kurt Buckwalter, Lawrence Heiskell, Richard Jack, Lisa Marchlik, Hung Phun, Berry Seaver and William Thompson for their help in the laboratory at Virginia Tech. I am grateful to Richard and Sandra Siakel at McIntosh Visuals and Marie Kaspar for their help in the preparation of the figures used in this thesis. I would like to thank Virginia Kaspar, Pearl Samocki and Ileen Neal for their help in typing several drafts of this thesis.

I am also thankful for the help and advice of Dr. Kenneth Seaburg and Dr. Alfred Mikell. I'm especially grateful to the members of my advisory committee, Dr. George Simmons, Jr., Dr. Jerome Servaites and Dr. Sally Hornor for their assistance and guidance.

I am most thankful to Dr. Bruce Parker who gave me the opportunity to study with him at Virginia Tech and for his support, guidance and understanding as my major professor.

Mark Kaspar

Table of Contents

Table of Contents, continued

List of Tables

List of Tables, continued

List of Tables, continued

List of Figures

INTRODUCTION

The lakes and ponds of southern Victoria Land, Antarctica have been the site of numerous limnological investigations since the first study by Armitage and House (1962). This initial study addressed the chemical and thermal stratification of the waters of Lakes Bonney and Vanda and prompted many subsequent studies which sought to determine the origin and chemical composition of these lakes and explain their unusual thermal properties. Such studies included Angino et al. (1962, 1964), Wilson and Wellman (1962), Ragotzkie and Likens (1964), Hoare et al. (1965), Boswell et al. (1967 a,b), Jones and Faure (1967, 1968), Goldman et al. (1967), Hoare (1968), Torii et al. (1975), Bydder and Holdsworth (1977), Hendy et al. (1977), Wilson (1979) and Matsubaya et al. (1979).

Studies of the plankton communities of these lakes included Benoit et al. (1971), Lane (1977), Cathey et al. (1981, 1982), Vincent et al. (1981) and Mikell et al. (1984). Those dealing primarily with the planktonic algae of some of the southern Victoria Land lakes at first documented the paucity of the phytoplankton communities (Armitage and House 1962; Bell 1967; Goldman et al. 1967; Koob and Leister 1972; Parker et al. 1977) and the low rates of primary production (Goldman 1964; Goldman et al. 1967; Koob and Leister 1972; Parker et al. 1977). The low temperature of the lake waters and the low amount of light penetrating the ice cover of these lakes were thought to be the major reasons for the sparse phytoplankton communities (Goldman 1964; Goldman et al. 1967). Later studies of the phytoplankton communities investigated the

distribution and taxonomic composition of the phytoplankton (Seaburg et al. 1979), the occurrence of nitrogen fixation in these lakes (Allnutt et al. 1981), temperature adaptation of the algae (Seaburg et al. 1981), the ecological physiology of the phytoplankton of Lake Fryxell (Vincent 1981), the comparative ecology of the phytoplankton (Parker et al. 1982a) and phosphorus limitation in several of the lakes (Seaburg et al. in press).

Noteworthy is Parker et al. (1977) who reported an abundant benthic community in comparison to the sparse plankton community of Lake Bonney. Subsequent studies of the benthic communities of these southern Victoria Land lakes include Simmons et al. (1979, 1983), Cathey et al. (1981, 1982), Parker et al. (1981, 1982b), Allnutt et al. (1981), Parker and Simmons (1981), Wharton et al. (1982, 1983), Love et al. (1982) and Parker and Wharton (in press). These studies of the southern Victoria Land lakes described the unusual features of these aquatic environments. The perennial ice cover of the lakes severely restricts the amount of light reaching the waters (Goldman et al. 1967; Vincent 1981; Parker et al. 1982a). The ice cover also perpetuates the chemical and physical stratification of the lake waters, contrary to most other aquatic ecosystems where the water is well mixed due to wind generated turbulence. Goldman et al. (1967) hypothesized that the biota of Lakes Bonney and Vanda might be associated with pycnoclines. Subsequently, Koob and Leister (1972) discovered distinct phytoplankton communities which are vertically distributed within the waters of Lake Bonney, and Vincent (1981) reported the vertical occurrence of three distinct algal populations within the euphotic zone of Lake Fryxell.

The planktonic algae of the southern Victoria Land lakes are predominately flagellates (Parker et al. 1977; Seaburg et al. 1979; Vincent 1981; Parker et al. 1982a) and they are able to actively control their position in the water column (Vincent 1981) in contrast to the algae of most other aquatic ecosystems which are subjected to constantly changing light levels due to the vertical mixing of their environment. Wright (1964) found that during winter, the phytoplankton of ice-covered Beaver Pond were distributed along the light gradient based upon their specific preference for light. Some investigators reported that maximal adaptation by phytoplankton to ambient light levels occurred only under conditions of strong thermal stratification of the aquatic environment (Tilzer and Schwartz 1976; Tilzer and Goldman 1978; Harris 1980).

The low light and stability of the environment of these lakes provides an unique opportunity to study the efficiency at which the phytoplankton communities of several southern Victoria Land lakes are able to convert photosynthetically active radiation (PAR) into photosynthate. Bannister (1974) proposed the use of quantum yields as defined in Kok (1960) as a means of comparing the efficiency of phytoplankton at utilizing light. Tyler (1975), Morel (1978) and Dubinsky and Berman (1976, 1981) reported quantum yields from several aquatic ecosystems. Another concept used to study the ability of algae to utilize PAR is light utilization efficiency (Dubinsky and Berman 1976, 1981).

Another consequence of the perennial ice cover of these lakes is that very little exchange of gasses occurs between the atmosphere and the lake waters, resulting in the supersaturation of the water with

oxygen formed as a result of photosynthesis (Koob and Leister 1972; Parker et al. 1980, 1981, 1982a; Vincent 1981). The shallower waters of the lakes receive more light, have lower concentrations of nutrients (Torii et al. 1975; Hoehn et al. 1977; Vincent 1981; Vincent et al. 1981) and higher concentrations of oxygen. Bright light, high concentrations of oxygen and low nutrient levels favor a greater percentage of extracellular release of organic matter by algae due to photorespiration (Tolbert 1974; Harris 1980). Parker et al. (1977) reported high percentages of extracellular release by the phytoplankton of Lake Bonney and Parker et al. (1980) reported similar findings in Lake Hoare. Parker et al. (1977, 1980) stated that environmental conditions in the lakes might favor the occurrence of photorespiration. Later, Parker et al. (1981a) reported that photorespiration might be a common occurrence in the southern Victoria Land lakes and that the supersaturated oxygen conditions in the euphotic zone could be limiting the phytoplankton communities.

Two of the main objectives of this thesis are the determination of quantum yields and light utilization efficiencies for the phytoplankton of the southern Victoria Land lakes for the purpose of comparing these values with values calculated for phytoplankton elsewhere (Tyler 1975; Morel 1978; Dubinsky and Berman 1976, 1981), as well as comparing the concepts of quantum yield and light utilization efficiency for the phytoplankton of some of the southern Victoria Land lakes. As the rates of primary production are important in the determinations of quantum yields and light utilization efficiencies, the percent of extracellular release of organic matter by the algae was measured in

several of the lakes to obtain more accurate values for primary productivity; while at the same time further investigation of the possible significance of photorespiration in these highly oxygenated environments was carried out.

LITERATURE REVIEW

Four areas of previous research are especially important to the central objectives of this thesis. They are (1) primary productivity studies of antarctic lake phytoplankton; (2) determinations of quantum yields and light utilization efficiencies in aquatic ecosystems; (3) measurements of the excretion of organic matter by phytoplankton, including antarctic lake phytoplankton; and (4) the occurrence of photorespiration in algae.

Primary Productivity Studies of Antarctic Lake Phytoplankton

Many investigators have conducted studies on the primary productivity of antarctic lake phytoplankton. The lakes studied include Heywood Lake (Light 1977; Light et al. 1981) and Knob Lake (Fogg and Horne 1970) on Signey Island (60° 43'S, 45° 38'W), lakes near Anvers Island (64° 46'S, 60° 05'W) (Samsel and Parker 1971, 1972), lakes of Enderby Land (67° 40'S; 45° 51'E) (MacNamara 1970), Deep Lake situated in the Vestfold Hills (68° 34'S, 78° 11'E) (Campbell 1978) and several lakes of the Ongul Islands (69° 01'S, 39° 35'E) (Tominaga 1977). Other investigators have conducted studies on the lakes of Ross Island and southern Victoria Land (77° 00'S, 162° 52'E) (Armitage and House 1962; Goldman et al. 1963; Goldman 1964; Goldman et al. 1967; Koob and Leister 1972; Parker et al. 1977, 1982a; Vincent 1981; Vincent et al. 1981). These studies focused on a comparison of a number of lakes (Tominaga 1977; Parker et al. 1982) or only a few lakes within a region (Goldman et al. 1967; Samsel and Parker 1971, 1972; Campbell 1978).

Several of the lakes were studied for a period of several months (Parker et al. 1977; Vincent 1981), while Heywood Lake was studied continuously over a period of approximately three years. (Light 1977; Light et al. 1981). This only year-round study of Heywood lake showed that during the winter (May to September), rates of carbon fixation dropped below levels of detection and chlorophyll a (Chl a) concentrations and algal biovolumes were at their lowest yearly levels. During spring, carbon (C) fixation increased to 0.12 to 0.5 g $C/m^2/d$ and algal biovolume increased as Chl a concentrations reached their maximum levels. During summer (December to March), Heywood Lake was completely ice-free and the annual maximum rates of C-fixation of 3 to 5 g $C/m^2/d$ coincided with maximal algal cell volumes. Chlorophyll a levels were approximately one-quarter to one-third of the highest values recorded during the spring. Carbon fixation, Chl a concentrations and algal biovolumes decreased during the fall to winter levels (Light 1977; Light et al. 1981). Heywood Lake was moderately eutrophic (Light et al. 1981), while Deep Lake was considered one of the least productive lakes ever studied with an estimated phytoplankton production no greater than 10 g $C/m^2/y$ (Campbell 1978). Deep Lake, which is ice-free year-round due to its hypersaline waters, was low in productivity apparently due to nutrient limitation, hypersalinity, low temperature of its waters and annual extremes in light levels (Kerry et al. 1977; Campbell 1978).

Samsel and Parker (1971, 1972) found that two lakes located near Anvers Island were markedly different in their primary productivities. Humble Lake was far more productive than the other due to the greater

influx of nutrients contained in the waste products from large nearby populations of terrestrial fauna associated within the lake basin. This fauna consisted of antarctic terns, giant petrels and skuas. Another source of nutrients to Humble Lake was ammonia gas evolved from a nearby Adelie penguin rookery (Samsel and Parker 1971, 1972; Wodehouse and Parker 1981).

Early studies conducted on the lakes of southern Victoria Land, more specifically Lakes Bonney and Vanda, demonstrated the low primary productivity of these lakes (Goldman 1964; Goldman et al. 1967; Koob and Leister 1971). Parker et al. (1977) reported primary productivity values for Lake Bonney based upon $NaH^{14}CO_3$ particulate fixation that were comparable to values obtained in these earlier studies. When the amount of ^{14}C-labelled organic matter contained in the filtrate was included, the amount of primary production was higher and at certain depths in Lake Bonney it was several orders of magnitude greater (Parker et al. 1977). In a comparative study of several southern Victoria Land lakes, Parker et al. (1982a) found that all of the lakes were oligotrophic. Primary productivity values reported for Lakes Vanda, Bonney, Joyce and Fryxell were 1.86, 18.33, 11.46 and 27.84 mg $C/m^2/d$, respectively. Low light, low concentrations of nutrients, grazing by protozoans and the hypersalinity of the waters of some of the lakes were proposed for explaining the oligotrophic state of these lakes (Parker et al. 1982a).

In conjunction with previous data from studies of Lakes Bonney and Vanda, Vincent (1981) concluded that the reduced irradiance present was more important than the low temperature of the lake's water in controll-

ing the amount of primary production in Lake Fryxell as well as certain other southern Victoria Land lakes. While the annual regime and the reduced irradiance present in ice-covered antarctic lakes limit primary productivity, the high light intensities present during the austral summer inhibited photosynthesis in two lakes located on Ross Island (Goldman et al. 1963). Phytoplankton from Alga Lake exposed to 5 minutes of surface light intensities exhibited a 17 to 21% decrease in their rate of photosynthesis. Phytoplankton from Skua Lake showed a 30 to 32% decrease in their rate of photosynthesis under the same conditions. The greater inhibition of the phytoplankton of Skua Lake resulted from less adaptation to high light levels (Goldman et al. 1963). The waters of Skua Lake were more turbid than the more transparent waters of Algal Lake, resulting in the algae of Skua Lake being acclimated to lower light levels. The amount of time required for recovery of photosynthetic rates to pre-exposure values was directly proportional to the duration of exposure to inhibitory light levels (Goldman et al. 1963). Algae acclimated to higher levels of light recovered quicker than algae from a low light environment (Goldman et al. 1963).

Light Utilization Efficiencies and Quantum Yields

Two concepts used to study the ability of plants to utilize light energy are light utilization efficiency and quantum yield. Light utilization efficiency (ε) is the percentage of light energy assimilated by photosynthesis compared to the total amount of avaliable light energy. In aquatic ecosystems ε has been calculated as above (Talling et al. 1973; Tilzer et al. 1975; Morel 1978) or as the ratio of light

energy absorbed by a specific volume of water (Dubinsky and Berman 1976, 1981).

Values for ε ranged from 0.0 to ca. 13% in Lake Kinneret, Israel (Dubinsky and Berman 1976, 1981). In marine ecosystems ε ranged from 0.01 to ca. 8% (Morel 1978). Light utilization efficiencies were lower in the oligotrophic waters of the Sargasso and Caribbean seas in comparison for ε determined for the more productive waters of the East Central Atlantic Ocean (Morel 1978). Light utilization efficiencies increased with decreasing light levels (Dubinsky and Berman 1976, 1981; Morel 1978).

Several studies have reported values of areal light utilization efficiencies ($\overline{\varepsilon}$) (Talling et al. 1973; Tilzer et al. 1975; Morel 1978; Dubinsky and Berman 1981). Areal light utilization efficiency is defined as the percentage of the light energy utilized in photosynthesis per unit area compared to the amount of light energy at the water's surface. Values for $\overline{\varepsilon}$ in two eutrophic lakes of Ethiopia ranged from 0.51 to 3.34% (Talling et al. 1973). Morel (1978) reported values for $\overline{\varepsilon}$ ranging from 0.02 to 1.66% for marine ecosystems. Higher values of $\overline{\varepsilon}$ occurred at sites which had the higher measurements of biomass (Morel 1978). Values for $\overline{\varepsilon}$ ranged from 0.34 to 4.01% for the waters of Lake Kinneret (Dubinsky and Berman 1981). Higher values of $\overline{\varepsilon}$ also occurred when biomass measurements were at their higher values (Dubinsky and Berman 1981). Annual mean values for $\overline{\varepsilon}$ in eight lakes of differing trophic states ranged from 0.035 to 1.76% (Tilzer et al. 1975). Here again the highest mean annual efficiency occurred in the lakes with the greatest biomass (Tilzer et al. 1975).

Quantum yield (Φ)(Kok 1960) is a measure of the moles of photosynthetically-fixed carbon or oxygen evolved divided by the moles of PAR absorbed by a plant. A theoretical maximum value of 0.125 has been estimated for Φ (Rabinowitch and Govindjee 1969). When the rate of photosynthesis is plotted versus light absorption by the photosynthetic organism, Φ is the slope of the lined formed. Based upon theoretical considerations, Φ increases with decreasing light absorption approaching a constant at low light levels. Bannister (1974) proposed an average value of 0.06 for Φ at light intensities below those required to saturate photosynthesis. This value was proposed for natural populations to take into account any asynchrony in metabolism and differences in the light trapping ability of different algal species (Bannister 1974). Determinations of Φ for 6 different algal species for exponentially growing cells was not significantly different under similar assay conditions (Welschmeyer and Lorenzen 1981). Quantum yields were different between cultures of Thalassiosira pseudonana Hasle & Heimdal exhibiting exponential growth in comparison to stationary phase cultures (Welschmeyer and Lorenzen 1981).

Tyler (1975) reported values for Φ of 0.0 to 0.08 for areas of the Carribean and Sargasso Seas. Quantum yields ranged from 0.00144 to about 0.15 in Lake Kinneret (Dubinsky and Berman 1976, 1981). The majority of values of Φ reported by Morel (1978) were less than 0.10 for the Sargasso Sea, Carribbean Sea and the East Central Atlantic Ocean. Overall, average higher values for Φ occurred in the more productive waters sampled (Morel 1978). In all studies, Φ decreased with decreasing light levels at greater depth (Tyler 1975; Dubinsky

and Berman 1976, 1981; Morel 1978). Values approaching 0.125 have been reported from the bottom of the photic zone in several studies of Φ in aquatic ecosystems (Morel 1978; Dubinsky and Berman 1981).

Excretion of Organic Matter by Phytoplankton

A fraction of the organic compounds formed by metabolism in algae is released into the surrounding environment. A wide variety of compounds are excreted by algae. These include carbohydrates, organic acids, amino acids, peptides, proteins and lipids (Hellebust 1974). These excreted compounds serve as carbon and energy sources for other microorganisms, growth factors, vitamins, antibiotics, toxins and chelators for certain ions such as trace metals (Fogg and Westlake 1953; Fogg 1971; Hellebust 1974).

The amount of organic material released into the environment is usually expressed as percent extracellular release (PER). Percent extracellular release is determined by dividing the rates of organic carbon excreted into the environment by the total amount of carbon assimilated by photosynthesis. Values of PER can be significant, ranging from 20 to 90% in several studies of freshwater (Fogg et al. 1965; Watt 1966; Nalewajko and Marin 1969; Allen 1973; Watanabe 1980) and marine (Ignatiades 1973) ecosystems. Other investigators have reported overall values for PER of usually less than 20% for freshwater (Berman 1976; Nalewajko and Schindler 1976; Lee and Nalewajko 1978; Tilzer and Horne 1979) and marine (Hellebust 1965; Anderson and Zeutschel 1970; Thomas 1971; Williams and Yentsch 1976) ecosystems. In the case of antarctic lakes, Fogg and Horne (1970) reported that PER

by the phytoplankton of Signey Island lakes ranged from 23 to 40% and in the case of Heywood Lake the range of PER was from 10 to 30% (Light et al. 1981). Reported values of PER in Taylor Valley lakes were greater than 50% in Lake Hoare (Parker et al. 1980) and up to 90% in Lake Bonney (Parker et al. 1977).

Higher values of PER occur in oligotrophic waters in comparison to more productive waters (Watt 1966; Anderson and Zeutschel 1970; Thomas 1971; Nalewajko and Schindler 1976). The amount of organic matter excreted is usually proportional to the rate of primary production (Watt 1966; Anderson and Zeutschel 1970; Thomas 1971; Nalewajko and Schindler 1976). The mean value of PER for the entire euphotic zone was significantly correlated with PER at the depth of maximum primary productivity (Watt 1966; Berman 1976). Watt (1966) and Berman (1976) found that PER is inversely proportional to algal biomass as measured by Chl a or other algal pigments.

Greater values for PER were reported from nutrient-limited or declining phytoplankton populations (Ignatiades and Fogg 1973; Hellebust 1965). In laboratory studies PER increased in nutrient-limited cultures (Ignatiades and Fogg 1973; Watanabe 1980). Rates of photosynthesis as well as the rate of extracellular release of organic compounds increased with increasing growth rates of the algal cultures (Nalewajko and Marin 1966; Nalewajko and Lean 1972; Williams and Yentsch 1976). Percent extracellular release was generally low (less than 5%) in most logarithmically growing cultures (Nalewajko and Marin 1966; Huntsman 1972; Nalewajko and Lean 1972; Williams and Yentsch 1976). Percent extracellular release is sometimes greater in

stationary phase in comparison to exponentially growing cultures of the same algae (Hellebust 1965; Huntsman 1972). Sharp (1977) has hypothesized that actively dividing phytoplankton release no more than 5% of their photoassimilated carbon based upon his review of the literature pertaining to determinations of PER in aquatic ecosystems and for algal cultures.

Values for PER were greatest at shallower depths in many studies (Fogg et al. 1965; Watt 1966; Thomas 1971; Allen 1973; Watanabe 1980), but Tilzer and Horne (1979) reported no increase in PER towards the lake's surface. Several studies showed an increase in PER at light intensities that are inhibitory to photosynthesis. These studies attributed the increase in PER due mostly to a decrease in particulate fixation retained within the algal cell even though there was a small increase in the range of extracellular release of organic compounds (Nalewajko 1966; Watt 1966; Watanabe 1980). Fogg et al. (1965) reported an increase in PER at inhibiting light intensities but observed no increase in the range of release of organic compounds by algae. Percent extracellular release was nearly constant at light levels where photosynthesis was saturated (Fogg et al. 1965; Watt 1966; Watanabe 1980).

Photorespiration in Algae

Photorespiration is the light-dependent uptake of oxygen and release of carbon dioxide that occurs in aerobic photosynthetic organisms (Tolbert 1974). High concentrations of O_2 and low concentrations of CO_2 tend to favor the occurrence of photorespiration, resulting in a

decrease in the rate of photosynthesis (Tolbert 1974). Under conditions favorable to photorespiration, the enzyme ribulose bisphosphate carboxylase functions as an oxygenase and catalyzes the oxygenation of ribulose bisphophate to yield phosphoglyceric acid and phosphoglycolate (Tolbert 1974; Harris 1980). A fraction of the glycolate formed is thought to be one of the major compounds excreted into the environment by algae (Hellebust 1974; Tolbert 1974; Harris 1980), while the remaining fraction of the glycolate is utilized to form glyoxylate, glycine, serine and CO_2 (Tolbert 1974).

The occurrence of photorespiration in algae has been verified in experiments showing an increase in the CO_2 compensation point with increasing O_2 tensions and increasing temperature (Coleman and Colman 1980; Birmingham et al. 1982) and the inhibition of photosynthesis at increasing O_2 concentrations (Bunt 1971; Beardall and Morris 1975; Pope 1975; Black et al. 1976; Burris 1977). Other investigators have demonstrated the presence of photorespiration in algae by detecting the release of CO_2 in light (Cheng and Colman 1974) and observing an increase in the release of CO_2 under increasing O_2 tensions (Birmingham et al. 1982; Findenegg and Fischer 1978). The relative extent of photorespiration in algae is not as well documented.

Several investigators have not detected any photorespiration in algae (Bidwell 1977; Lloyd et al. 1977). Lloyd et al. (1977) concluded that photorespiration doesn't occur in algae grown under normal CO_2 and O_2 concentrations and Birmingham et al. (1982) found that photorespiration would occur in algae at CO_2 levels that would be less than those required to saturate photosynthesis. Other investigators showed

that bluegreen algae exhibited a lower rate of photorespiration than the green algae studied (Cheng and Colman 1974; Coleman and Colman 1980). Out of 7 algal species investigated, only 2 green algae exhibited any O_2 inhibition of photosynthesis at low levels of CO_2 (Bunt 1971). Oxygen inhibition of photosynthesis in some algae could be overcome by increasing concentrations of CO_2 (Beardall and Morris 1975; Pope 1975).

An increase in the rate of excretion of glycolate under conditions that favor photorespiration or in the presence of inhibitors of the glycolate pathway was observed (Tolbert 1974; Harris 1980). This indicates that the occurrence of photorespiration in algae could affect the release of organic matter by algae. Percent extracellular release was higher under higher concentrations of O_2, while the amount of organic matter released was variable depending upon the algae (Burris 1977). The amount of organic matter released was nearly constant over a range of CO_2 concentrations (Smith and Wiebe 1976), while PER increased at lower concentrations of CO_2 (Nalewajko 1966; Smith and Wiebe 1976). Percent extracellular release ranged from 1 to 5% for most algae (Pope 1975; Burris 1977) and the highest value of PER was less than 10% (Nalewajko 1966) under conditions that might be favorable to photorespiration. Pope (1975) concluded that the inhibition of photosynthesis due to photorespiration couldn't be explained by a dramatic increase in the amount of organic matter released, because PER was relatively constant and low.

MATERIALS AND METHODS

Site Description

Four previously studied lakes within a 40 x 40 km area were selected for this investigation: Lakes Bonney (77° 43'S, 162° 23'E), Hoare (77° 38'S, 162° 53'E), Fryxell (77° 37'S, 162° 07'E) in Taylor Valley and Lake Vanda (77° 32'S, 161° 33'E) in adjacent Wright Valley (Figure 1). Lake Fryxell has a surface area of ca. 5.4 km^2, while the surface areas of Lakes Vanda, Bonney and Hoare are ca. 5.0, 3.8 and 1.1 km^2 (Cathey et al. 1981). Lake Vanda is the deepest of the lakes having a maximum depth of 70 m (Cathey et al. 1981). Maximum depths for Lakes Bonney, Hoare and Fryxell are 34, 31 and 19 m (Cathey et al. 1981).

All four lakes have perennial ice covers which ranged in thickness from ca. 3.0 to 4.7 m during this study. Melting of the margins of the ice covers does occur during the austral summer, but the persistence of the perennial ice perpetuates the physical, chemical and biological stratification of these lakes and preserves their amictic condition. The water temperature profile of Lake Vanda is inversely stratified with the range of <u>in situ</u> temperatures being ca. 0.0 to 25.0°C (Ragotzkie and Likens 1964). The range of water temperatures in Lakes Fryxell, Hoare and Bonney are 0.75 to 3.1°C (Angino et al. 1962; Parker et al. 1982a), 0.0 to 1.0°C (Parker et al. 1982a) and -4.0 to 7.0°C (Angino et al. 1964). The maximum water temperatures in the Taylor Valley lakes occur at intermediate depths (Parker et al. 1982a). The waters of all of these lakes are chemically stratified. Lakes

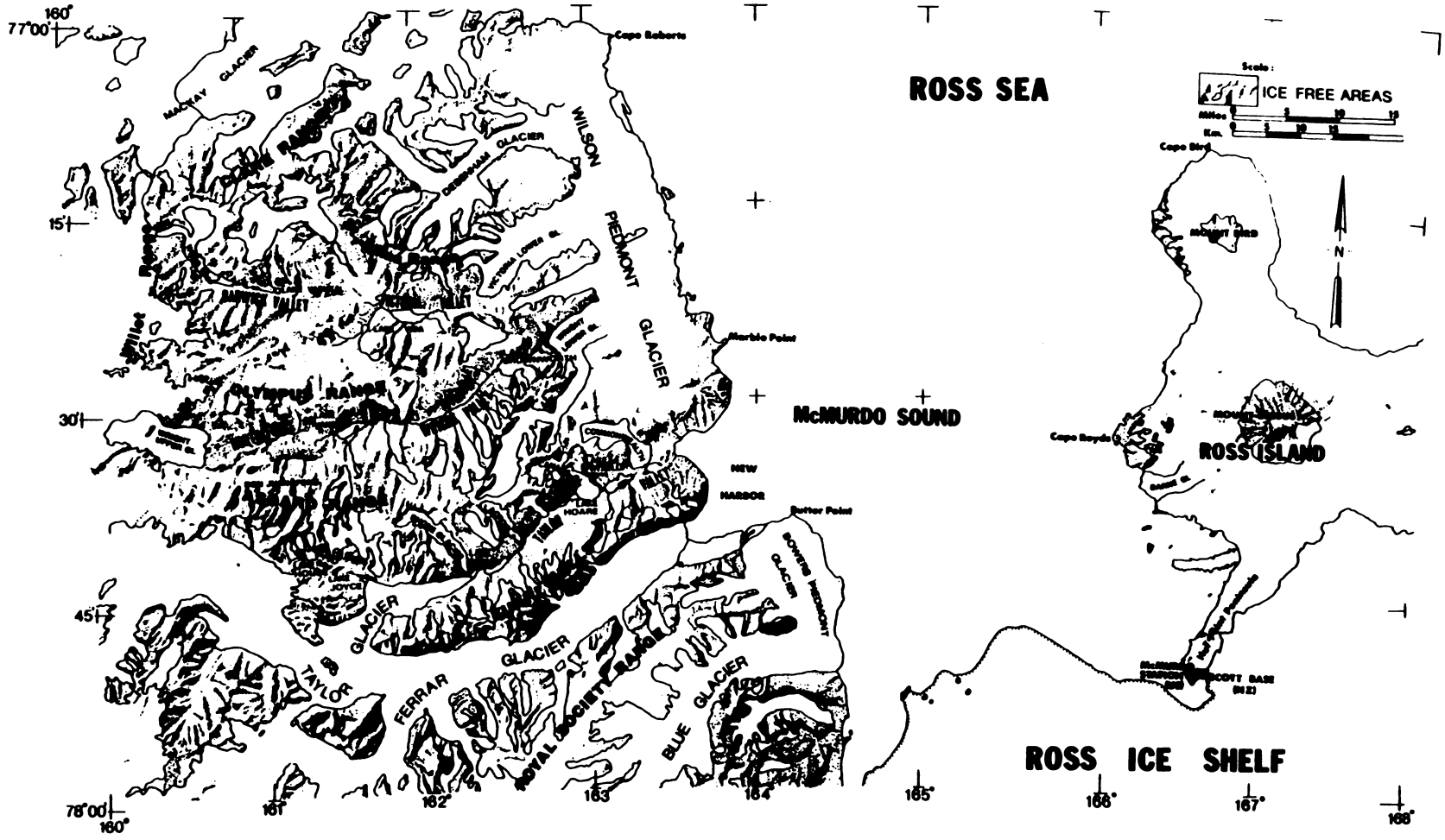

Figure 1. Map showing Taylor and Wright Valleys, southern Victoria Land, Antarctica.

Fryxell, Bonney and Vanda possessed deeper layers with pronounced differences in specific conductance in comparison to their fresher overlaying waters. The maximum specific conductance reported in the deepest layers are 10,700 μmhos/cm for Lake Fryxell (Torii et al. 1975), 212,765 μmhos/cm for Lake Bonney (Angino et al. 1964) and 125,000 μmhos/cm for Lake Vanda (Torii et al. 1975). The specific conductance of the fresher waters of Lake Hoare ranged from 500 to 800 μmhos/cm (Parker et al. 1982a). The only input of water into these lakes was from ephemeral glacial meltstreams originating from nearby glaciers and sparce precipitation. Outflows were entirely lacking.

In Situ Measurements and Sample Collection

Primary productivity was measured by the $NaH^{14}CO_3$ method (Saunders et al. 1962) and on some sampling dates, the amount of labelled excreted dissolved matter was determined. Pyrex screw cap test tubes containing 55 ml of lake water collected at specific depths were inoculated with 1.0 ml of $NaH^{14}CO_3$, 10 to 20 μCi, (ICN Pharmaceuticals, Inc., sp. act. 8.4 Ci/M) at a pH of 9.5. All inoculations of samples took place inside a tent. Quadruplicate light, dark and fixed (ca. 1% neutralized formaldehyde) test tubes were incubated in situ for 4 to 6 hrs. At the end of the incubation, samples were retrieved and the unfixed ones were promptly fixed with 1 ml of neutralized formaldehyde. Each sample was vacuum ($\leq$ 10 cm Hg) filtered through a 0.45 μm porosity Millipore HA filter (47 mm diam.) The filters were placed in open scintillation vials within a desiccator containing a beaker of conc. HCl. After 2

to 4 hrs., the vials were removed and 10 ml of Aquasol (New England Nuclear) was added, recapped and stored in the dark for 24 to 48 hrs. The samples were counted on a Beckman 100 C liquid scintillation counter (LSC). The filtrates were collected and acidified with 1 N HCl to a pH of 3.5 and bubbled with CO_2 for 1 hr to remove any residual $NaH^{14}CO_3$. Five to 10 ml aliquots of each sample filtrate were dispensed into scintillation vials, frozen at -20°C and lyophilized to dryness (McKinley et al. 1977). This process was repeated until $\geq$25% of each filtrate volume was lyophilized. One ml of distilled water, then 10 ml of Aquasol was added to each vial and the radioactivity determined by LSC. The sum of the filter (particulate) and filtrate (PER) activities was taken to represent total primary productivity (Saunders et al. 1962).

Available inorganic carbon (AIC) was estimated from *in situ* alkalinity which was measured by titration of the water sample with 0.02 N H_2SO_4 to a pH of 4.3 using methyl purple indicator (A.P.H.A. 1976). Temperature was measured with a Yellow Spring Instrument (SCT Meter Model 33) and pH with a Corning pH meter, (Model 610 A). Carbon dioxide was measured by titration of the water sample with 0.02 N NaOH using phenolphthalein indicator (A.P.H.A. 1976). Dissolved oxygen (DO) was measured by the azide modification of the Winkler method (A.P.H.A. 1976). Photosynthetically active radiation (400 to 700 nm wavelength) was measured with a LiCor Model 185 A quantum light meter equipped with a remote submersible probe.

Chlorophyll a was measured by filtering 200 to 500 ml of lake water through Whatman GFC filters under a vacuum pressure of $\leq$ 10 cm

Hg. The filter was placed in a scintillation vial and 5 ml of spectral grade dimethyl sulfoxide (DMSO) was added and allowed to sit for 2 to 4 hrs. at 25°C to extract the Chl a (Shoaf and Lium 1976). After extraction, 5 ml of spectral grade 90% (v/v) aqueous acetone solution was added and the fluorescence of the solution was read on a Turner designs 10-005 R fluorometer. Chlorophyll a fluorescence was corrected for any fluorescence due to phaeophytin by adding a few drops of 6 N HCl and rereading the sample (Yentsch and Menzel 1963). Chlorophyll a concentrations were calculated from a standard curve of pure Chl a (Sigma Chemical Company) treated in the same way.

One liter water samples were collected and fixed with 8 ml of 10% (v/v) Acid Lugol's solution for the enumeration and determination of phytoplankton bivolume (Utermohl 1958). These samples were returned to Blacksburg, Virginia where the samples were concentrated by settling chambers before being examined and counted using a Wild Model M-40 inverted microscope (Seaburg et al. 1979). Standard references [Bourrelly (1966, 1968, 1970), Ettl (1976) and Seaburg et al. (1979)] were used in the identification of the algal taxa. Phytoplankton biovolume was calculated by the method of Nauwerck (1973).

Total organic carbon (TOC) and dissolved organic carbon (DOC) samples were collected in duplicate. Samples were prepared for shipment back to Blacksburg, Virginia according to the procedures of Menzel and Vaccaro (1964) as outlined in Wetzel and Likens (1979). The TOC and DOC samples were processed on a Lira Infrared Analyzer Model 303 and the values for organic carbon were calculated from standard curves using acidified Na_2CO_3.

Methodology Involved in Calculating Quantum Yields and Light Utilization Efficiencies

Data necessary for calculating quantum yield include the rate of primary production, amount of Chl a, mean spectral extinction coefficient of Chl a (k_c) and the extinction coefficient of PAR (E_{PAR}). Measurements of PAR were taken 2 to 3 times during the course of the incubation to correct for any changes in levels of PAR and then compared to the change in total continuous surface solar energy as measured by a Belfort Instrument Company Recording Pyreheliometer Model 5-3850 so that an accurate measurement of PAR absorption could be made. The absorbance of PAR at any given depth was represented by the equation:

$$E_{PAR} = k_c \text{ (Chl a)} + k_w \text{ (C)}$$

where

E_{PAR} = amount of PAR absorbed at that depth;
Chl a = concentration of Chl a as the measure of viable plant pigment;
k_c = mean spectral extinction coefficient of viable plant pigments;
C = concentration of all compounds and particles that absorb PAR except for viable plant pigments;
k_w = spectral extinction coefficient of all PAR absorbing components of the water except for viable plant pigments.

The percentage of PAR absorbed by viable plant pigments is given by the factor k_c (Chl a) when it is assumed that the amount of PAR

absorbed at a given depth equals 100% (Tyler 1975). The amount of PAR absorbed by viable plant pigments was then estimated by multiplying the amount of PAR absorbed at that depth by the product of (k_c) and the amount of Chl a at that depth.

Two values of k_c were used in the determination of Φ because Φ is very dependent upon the value of k_c. A value of 0.016 for k_c was used in the first case (Bannister 1974; Atlas and Bannister 1980). The second value of k_c was estimated by plotting E_{PAR} against Chl a concentrations (Tyler 1975). The value for k_c was the slope of the line formed by the linear regression of the lowest lying points on the graph. The lowest lying points were used because at these points it was assumed that the absorption of light at these depths was due mostly to viable plant pigments as measured by Chl a (Tyler 1975).

Light utilization efficiencies were calculated by dividing the energy equivalents of primary productivity by the energy equivalents of PAR absorbed at the sampled depth. It was assumed that 1 mg of C = 9.33 cal and 1 Einstein of visible light equals 52,000 cal (Dubinsky and Berman 1976). Energy equivalent quantum yield is equal to 2.2 (Φ) (Dubinsky and Berman 1976).

Isolation and Purification of a Clonal Culture of Chlamydomonas subcaudata Wille

A clonal culture of Chlamydomonas subcaudata Wille was isolated from a water sample collected on December 28, 1980 from 5 m in Lake Fryxell by K.G. Seaburg. This culture was maintained at 4°C in Guillard's Woods Hole MBL medium (Nichols 1973) prior to any attempts

to remove any bacterial contamination.

An axenic culture was obtained by repeating washing and centrifugation. Following this treatment, a dilution series for the algae was made. Aliquots of this dilution series were streaked on 10% (v/v) Guillard's Woods Hole MBL medium pH = 8.0 in 1.5% (w/v) agar and incubated at 12°C. This procedure was repeated until an axenic culture was obtained. The culture was determined to be axenic by observing no bacterial or fungal contamination at 1000X under phase microscopy and no bacterial or fungal growth in enriched media incubated at 12°C and 25°C for two weeks in the dark. The media employed included 0.5% (w/v) tryptone and 0.02% (w/v) yeast extract, 0.8% (w/v) nutrient broth, 1.0% (w/v) glucose and tryptone enriched with 0.5% (w/v) yeast extract and Woods Hole MBL medium containing 1 mg of glycolic acid, sodium acetate, glucose and yeast extract per liter. These media were employed as broth and with 1.5% agar. Other media included 3.0% (w/v) thioglycolate in 0.2% (w/v) agar, 0.2% (w/v) proteose peptone medium in 1.5% (w/v) agar and peptone-yeast extract-soil medium which contained 0.1% (w/v) peptone, 0.2% (w/v) yeast extract and 200 ml of soil extract in 1 liter of distilled water with 1.5% (w/v) agar.

Effect of Purging and Lyophilization on the Recoverery of Glycolate and Glucose

Triplicate 2.5 μCi aliquots of [^{14}C-U]-glycolic acid (ICN Pharmaceuticals, Inc., sp. act. 50 Ci/M) and [^{14}C-U]-glucose (Amersham, sp. act. 274 Ci/M) were added to 6, 125 ml Nalgene plastic bottles containing 90 ml of Woods Hole MBL medium. The pH of these solutions were

adjusted to 3.5. One ml from each replicate was added to a scintillation vial containing 10 ml of Aquasol to determine the initial activity of the solutions. The samples were then purged with air at a flow rate of 1200 ml/min. One ml aliquots from each bottle were withdrawn after 5, 10, 15, 30 and 60 min of purging. Following addition of 10 ml of Aquasol to each sample, the vials were counted on a Beckman LS-3150T LSC.

Three ml (0.15 mCi) of [^{14}C-U]-glycolic acid (ICN Pharmaceuticals, Inc., sp. act. 50 Ci/M) was added to 27 ml of distilled water. The pH of each of these solutions was adjusted with 1 N HCl or 1 N NaOH so that there was one solution each with a pH of 1.25, 2.0, 3.0, 3.5, 4.0, 4.5, 5.0 and 6.0 as measured with an Orion Research Model 601 Digital Ionalyzer. Ten ml were dispensed into scintillation vials, frozen at -20°C and then freeze-dried with a FTS FD-6-84 freeze dryer. The vials received 1 ml of distilled water and 10 ml of Aquasol before counting by LSC. This procedure was repeated using [^{14}C-U]-glucose (0.3 mCi) (Amersham, sp. act. 274 Ci/M).

Using a $NaH^{14}CO_3$ solution (pH = 9.0) containing 0.2 mCi of ^{14}C (ICN Pharmaceuticals, Inc., sp. act. 55 Ci/M), 1.0 ml was added to scintillation vials containing a Reeve Angel 984 H glass fiber filter. Vials containing filters and $NaH^{14}CO_3$ were then placed in an evacuated desiccator containing a beaker of conc. HCl. At 2, 4, 8, 12, 24, 48 and 96 hrs, 3 vials were removed. Ten ml of Aquasol was added to each vial before counting by LSC. The background radioactivity of the $NaH^{14}CO_3$ stock solution was determined by acidifying a portion of the stock solution to a pH of 3.5 and bubbling with air for 2 hrs. One ml

of this solution was then counted.

Effect of Oxygen on Photosynthesis of Chlamydomonas subcaudata Wille

An axenic culture of Chlamydomonas subcaudata Wille was grown in 2 l Fernbach flasks at 4°C and ca. 70 μEin/m^2/sec cool white light in a Sherer Model CEL-34-F growth chamber. The medium used for culturing was 10% (v/v) Guillard's Woods Hole MBL (Nichols 1973). The available AIC level of the media was ca. 1.8 mg/l and in equilibrium with air. The pH of the media was 8.0. Cells were harvested by centrifugation at 3000 g for 20 min at 4°C by a Damon IEC B-20 A centrifuge. The stock cultures were in log phase growth and at a concentration of approximately 14,000 cells/ml. Cells were dispensed into 51, 150 ml serum bottles containing 80 ml of 10% (v/v) Guillard's Woods Hole MBL medium to which filter-sterilized bicarbonate solution had been added to yield a final concentration of AIC of ca. 1.8, 18 and 90 mg/l. Cells were then allowed to stand for 1 hr at the growth conditions previously mentioned. Five replicate bottles of each carbon concentration were pressurized with pure oxygen to a partial pressure of oxygen that would yield a concentration of DO of ca. 40 mg/l. Cultures were then allowed to acclimate for 24 hr at their respective environmental conditions.

The next day five bottles from each AIC concentration were fixed with 1 ml of neutralized formaldehyde. Two bottles from each oxygen concentration (saturation levels and supersaturated DO of ca. 40 mg/l) and each AIC concentration were used to determine AIC and Chl a at the start of the experiment. Triplicate bottles were used to determine the DO concentration of the pressurized and unpressurized bottles by the

azide modification of the Winkler method (A.P.H.A. 1976). The light and formalin fixed bottles were then inoculated with $NaH^{14}CO_3$ (ICN Pharmaceuticals, Inc., sp. act. 55 Ci/M). The samples containing ca. 1.8 mg/l AIC received 10 μCi of $NaH^{14}CO_3$, the samples containing ca. 18 mg/l AIC; 30 μCi of $NaH^{14}CO_3$ and the samples containing ca. 90 mg/l AIC; 100 μCi of $NaH^{14}CO_3$. Prior to inoculation the ^{14}C-bicarbonate stock solution had been purified according to the method of Wiebe and Smith (1977). After 6 hrs, the experiment was terminated by immediate filtration of the samples onto 0.5 μm Reeve Angel 984 H glass fiber filters under a vaccuum pressure of $\leq$ 5 cm Hg. The filters were rinsed with 10 ml of acidic (pH = 4.0) MBL media and then placed in scintillation vials inside a desiccator in the presence of conc. HCl for 4 hr. The filtrates were acidified to a pH of 3.5 and purged with air at a flow rate of 1200 ml/min for 1 hr. The flow rate was measured with a Lab Crest Mark III Flowmeter. Fifteen ml aliquots of the filtrate were dispensed into scintillation vials and frozen at -20°C. The filtrates were lyophilized (McKinley et al. 1977) to dryness on a FTS System FD-6-84 freeze dryer. This process was repeated until 2/3 of the filtrate was freeze dried. One ml of distilled water was added to the filters and filtrates and then 10 ml of Aquasol prior to counting on a Beckman LS-3150T LSC. Available inorganic carbon was measured on a Lira Infrared Analyzer Model 303 connected to a Fischer Recordall Series 5000 recorder (Menzel and Vaccaro 1964). Chlorophyll a was determined by fluorescence (Yentsch and Menzel 1963) after filtration of the sample onto Reeve Angel 984 H filters and extracted with DMSO (Shoaf and Lium 1976) as outlined in the first part of this section.

RESULTS

Measurements of Photosynthetically Active Radiation

Table 1 shows the dates and the maximum depths for sampling in the four lakes. Also shown is the range of measured surface PAR values, approximate ice cover thickness, percent transmission of surface PAR and E_{PAR}. The lowest surface PAR measured was 350 $\mu Ein/m^2/$ sec on one date at Lake Hoare and the highest was 1700 $\mu Ein/m^2/sec$ at Lake Fryxell. Lake Vanda had the thinnest ice cover and Lakes Hoare and Fryxell had the thickest. As would be expected, the greatest percentage of PAR transmitted through ice occurred in the lake with the thinnest ice cover. Up to 16 to 18% of surface PAR passed through the 3.1 to 3.7 m thick ice cover of Lake Vanda, while only 0.29 to 1.11% of surface PAR passed through the 4.6 m thick ice cover of Lake Hoare. Lake Vanda water had the lowest extinction coeficient for PAR of 0.55 and Lake Fryxell had the highest value of E_{PAR} of 0.733 for the lakes studied.

Figure 2 shows the percentage of PAR transmitted through the waters of the southern Victoria Land lakes. PAR was quickly attenuated in Lake Fryxell water with no detectable PAR below 10 m. Lake Hoare water received very low levels of PAR with less than 0.1% reaching depths greater than 10-12 m and ca. 0.02% at 23 m. In Lake Bonney 1.11% of surface PAR reached 16 m, while in the clearer waters of Lake Vanda 1.26% of surface PAR reached the maximum depth of 57 m sampled.

Table 1. Maximum depth sampled, surface PAR, approximate ice cover thickness, percent transmission of PAR through the ice cover and the average extinction coefficient of PAR throughout the depths sampled on the dates shown for the lakes studied.

Lake	Dates Sampled	Maximum Depth Studied	Surface PAR $\mu Ein/m^2/sec$ [1.]			Approximate Ice Cover Thickness	% Transmission of Surface PAR	E_{PAR}
Hoare	11-04-1980	23 m	350	(360)	370	4.5 m	0.29	0.179
Hoare	11-19-1980	23 m	940	(1293)	1500	4.5 m	0.56	0.192
Bonney	12-05-1980	16 m	920	(1118)	1250	3.7 m	7.00	0.157
Vanda	12-15-1980	20 m	730	(876)	1140	3.1 m	18.00	0.055
Vanda	12-16-1980	57 m	510	(683)	980	3.7 m	16.00	0.063
Fryxell	1-08-1981	19 m	730	(1212)	1700	4.6 m	1.31	0.733
Hoare	1-15-1981	23 m	1000	(1147)	1500	4.6 m	1.11	0.185

1. Ranges of surface PAR during the times that the lakes were sampled; the average surface PAR is shown in parenthesis.

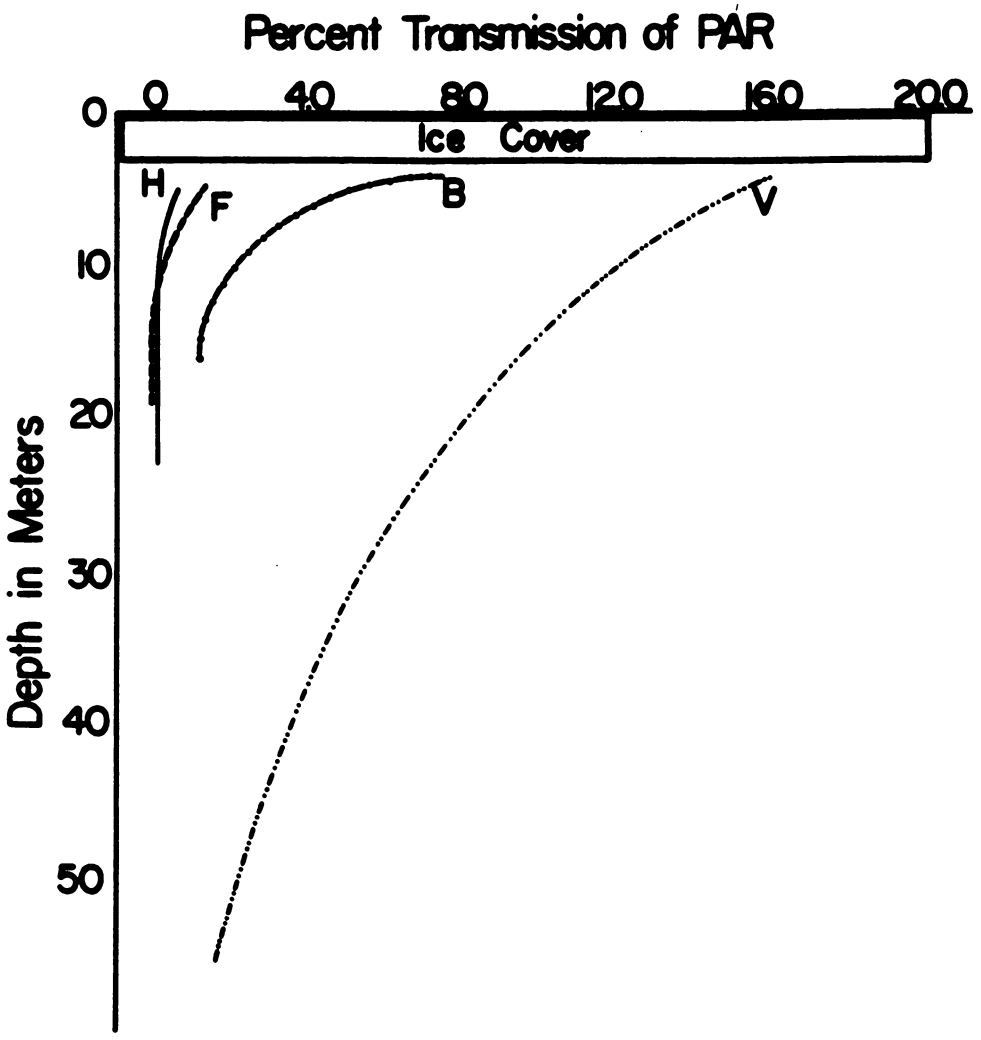

Figure 2. Percent transmission of photosynthetically active radiation (PAR) through the ice covers of Lake Hoare (H), Lake Fryxell (F), Lake Bonney (B) and Lake Vanda (V).

Depth Profiles of Oxygen, Carbon Dioxide, pH and Chlorophyll a

Figures 3-8 show carbon dioxide concentrations, dissolved oxygen concentrations, pH and Chl a levels in the southern Victoria Land lakes. In all of the lakes CO_2 concentrations increased with depth. Levels ranged from 0.0 at 4 m in Lake Bonney (Figure 5) to 240 mg/l at 15 m in Lake Fryxell (Figure 7). Parker et al. (1982a) reported that AIC also increased with depth in these lakes.

Dissolved oxygen levels in the lakes represented up to ca. 3 times normal saturation. Dissolved oxygen conditions in these lakes ranged from anaerobic at mid-depth and below in Lake Fryxell (Figure 7) to the supersaturation of DO throughout the water column of Lake Hoare (Figure 3, 4 and 8) and the upper 20 m of Lake Vanda (Figure 6). The highest value for DO was 45 mg/l at 9 m in Lake Bonney (Figure 5) and at 6 m in Lake Hoare (Figure 8). In Lakes Hoare, Vanda, to mid-depth in Lake Bonney and the shallower waters of Lake Fryxell DO concentrations exceeded CO_2 concentrations.

In Lakes Hoare, Vanda and Bonney, pH decreased with depth, while in the case of Lake Fryxell (Figure 7) no such trend was present. The lowest pH was 5.8 at 16 m in Lake Bonney (Figure 5), while the highest was 8.58 at 6 m for Lake Hoare in January (Figure 8).

On January 1, 1981 for Lake Fryxell, CO_2 levels were 17.2, 92.2 and 101.2 mg/l, DO levels were 27.2, 6.8 and 2.1 mg/l and the pH was 7.42, 7.30 and 7.45 for 5, 8.5 and 9m, respectively.

Chlorophyll a levels decreased with depth in Lake Hoare in early November and January (Figure 3 and 8), overall in Lake Bonney (Figure

5) and in the upper 20 m of Lake Vanda (Figure 6). On November 11, 1980 in Lake Hoare (Figure 4), maximum Chl a values occurred at mid-depth being 2.32 µg/l at 9 m and 2.23 µg/l at 12 m. A maximum value of 11.88 µg/l occurred at 8 m in Lake Fryxell (Figure 7). Lake Vanda (Figure 6) had the lowest levels of Chl a in comparison to the other lakes.

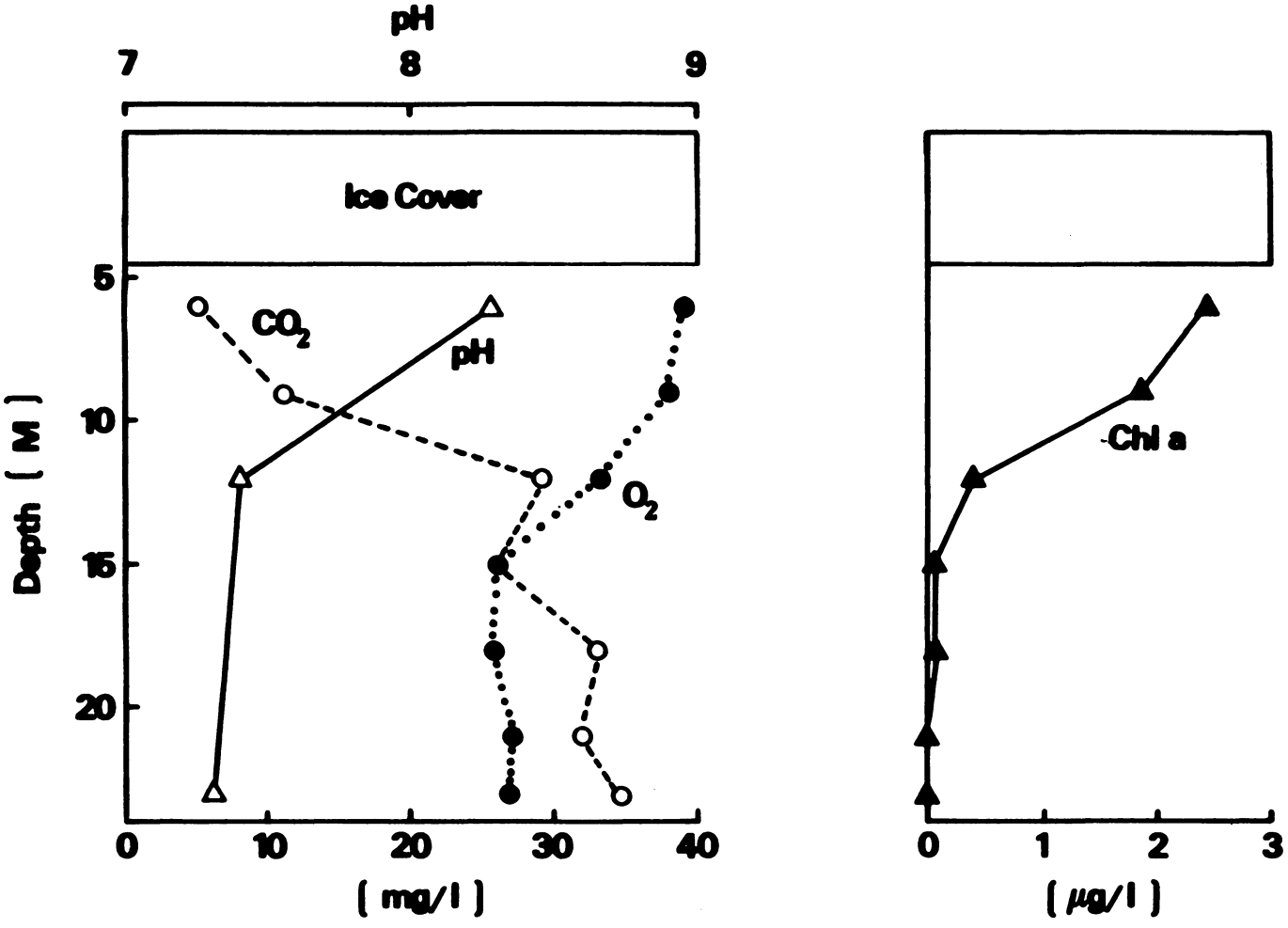

Figure 3. Depth profiles of carbon dioxide, dissolved oxygen, pH and chlorophyll a for Lake Hoare on 11-04-1980.

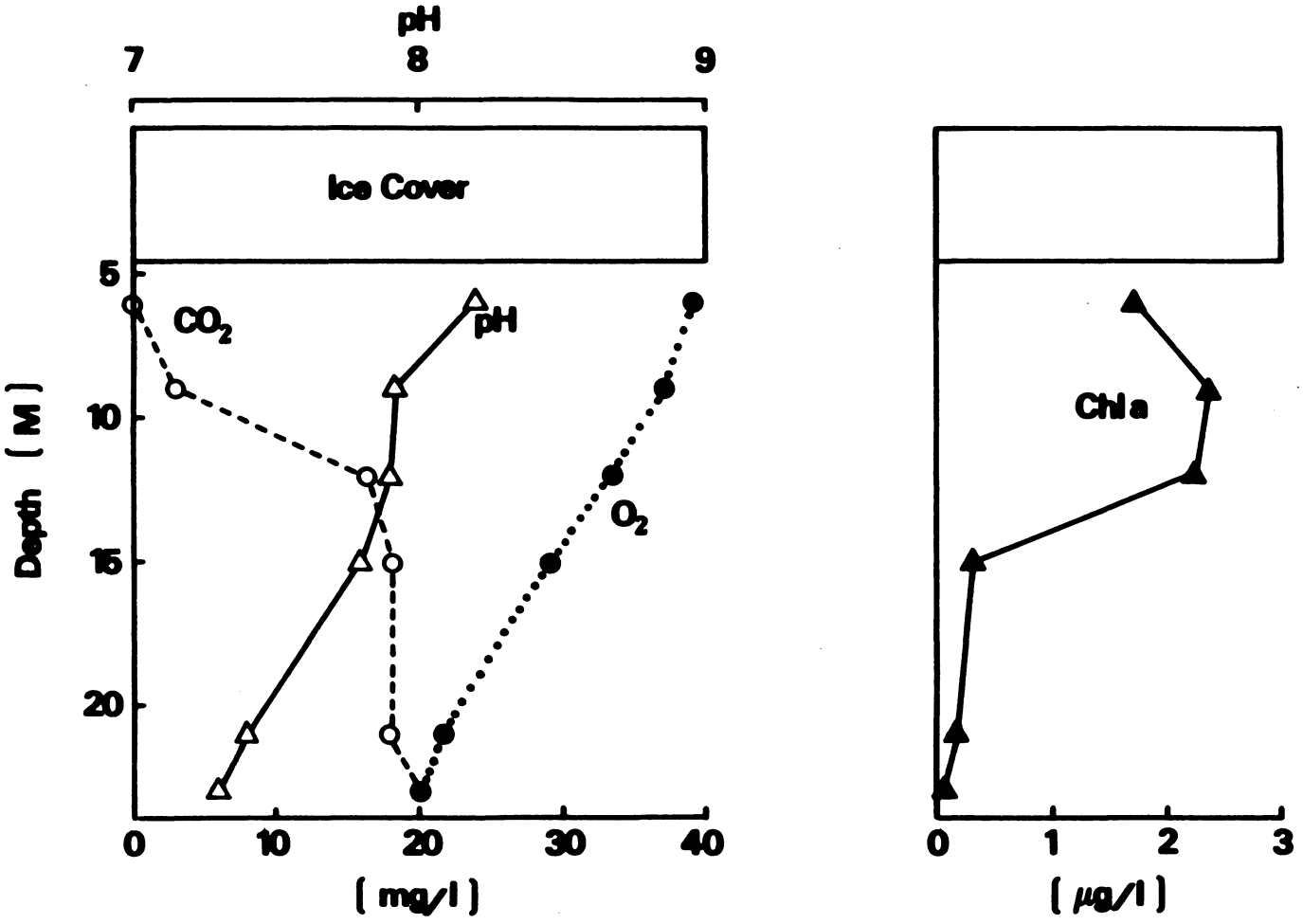

Figure 4. Depth profiles of carbon dioxide, dissolved oxygen, pH and chlorophyll a for Lake Hoare on 11-19-1980.

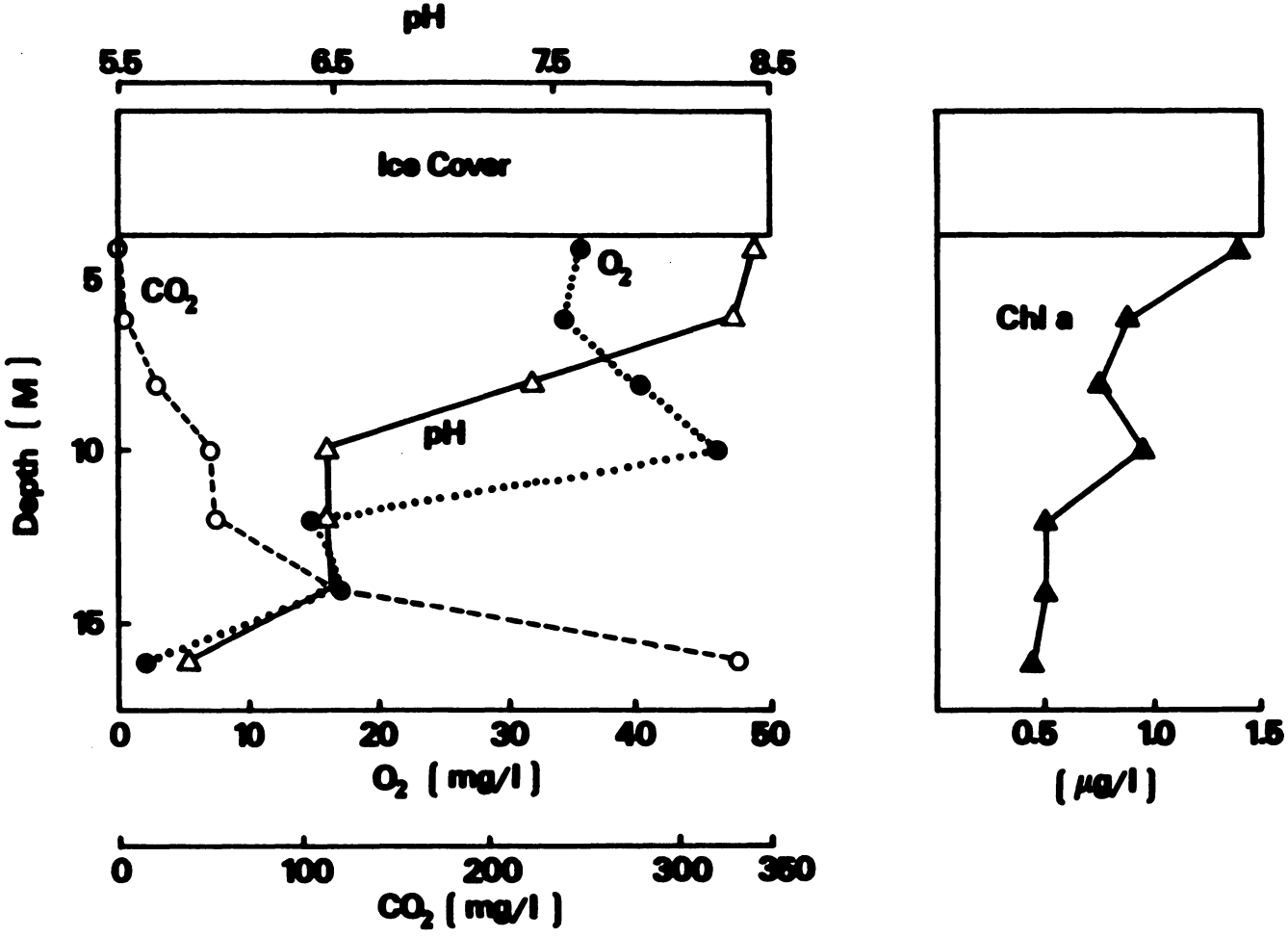

Figure 5. Depth profiles of carbon dioxide, dissolved oxygen, pH and chlorophyll a for Lake Bonney on 12-05-1980.

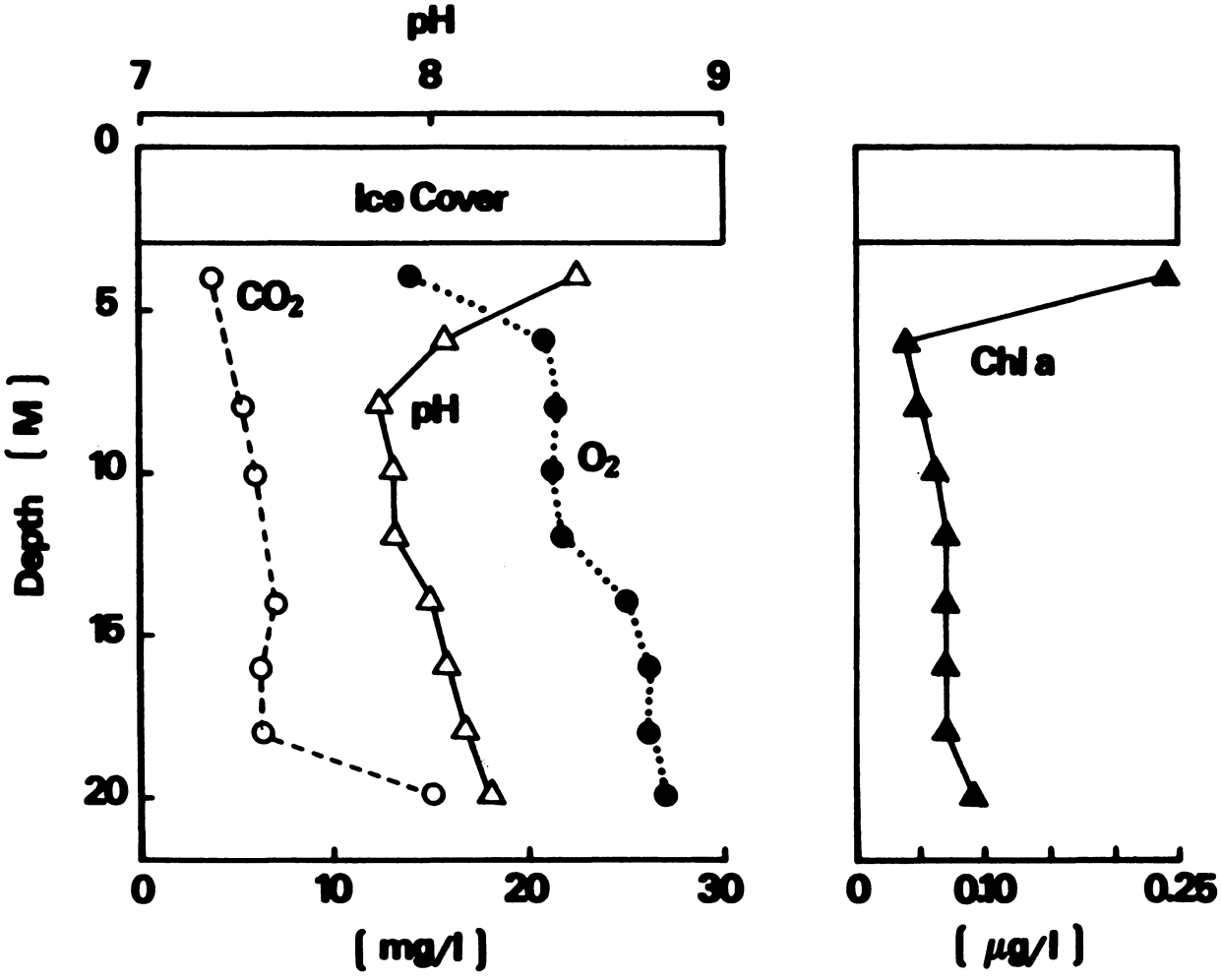

Figure 6. Depth profiles of carbon dioxide, dissolved oxygen, pH and chlorophyll a for Lake Vanda on 12-15-1980.

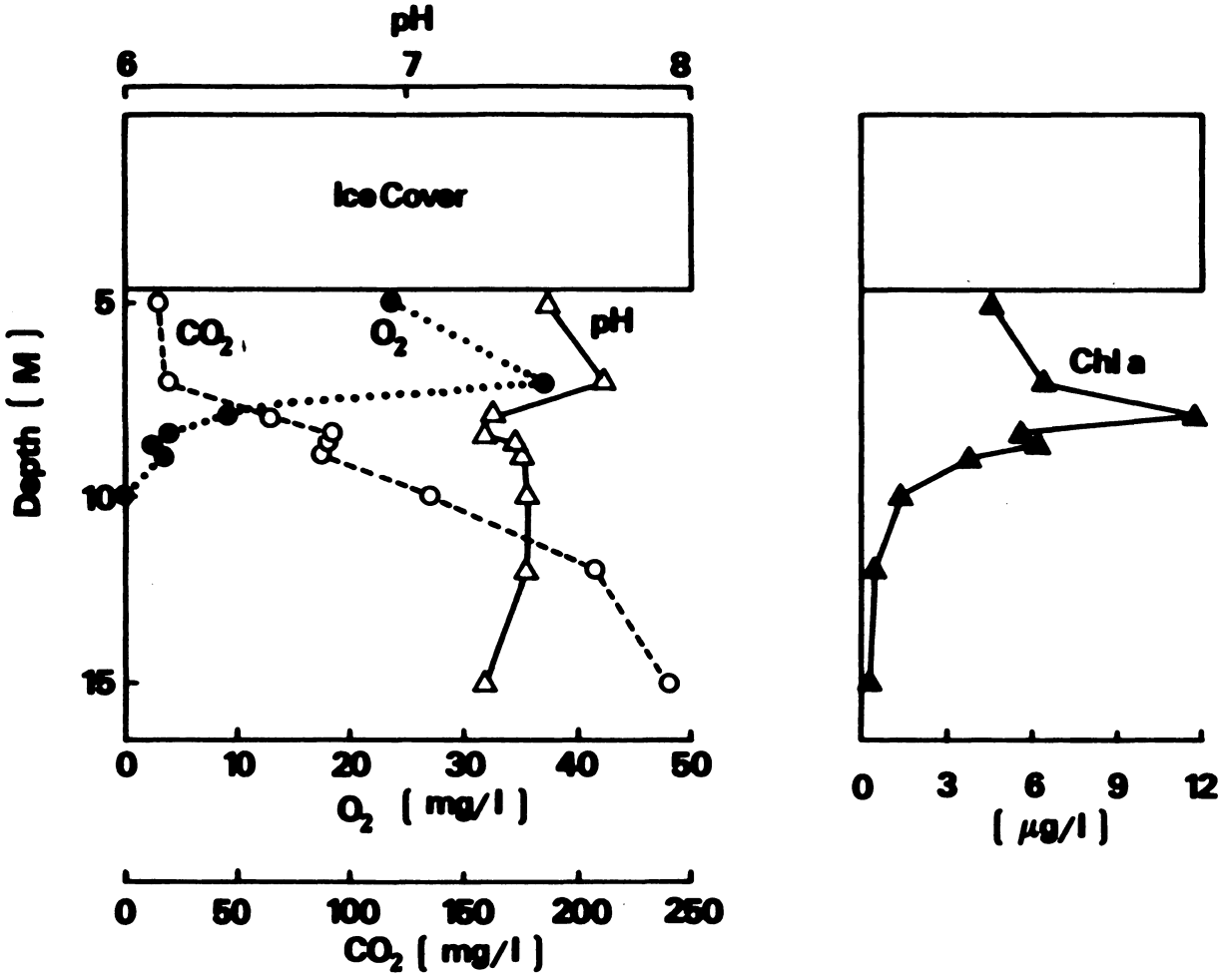

Figure 7. Depth profiles of carbon dioxide, dissolved oxygen, pH and chlorophyll a for Lake Fryxell on 12-28-1980.

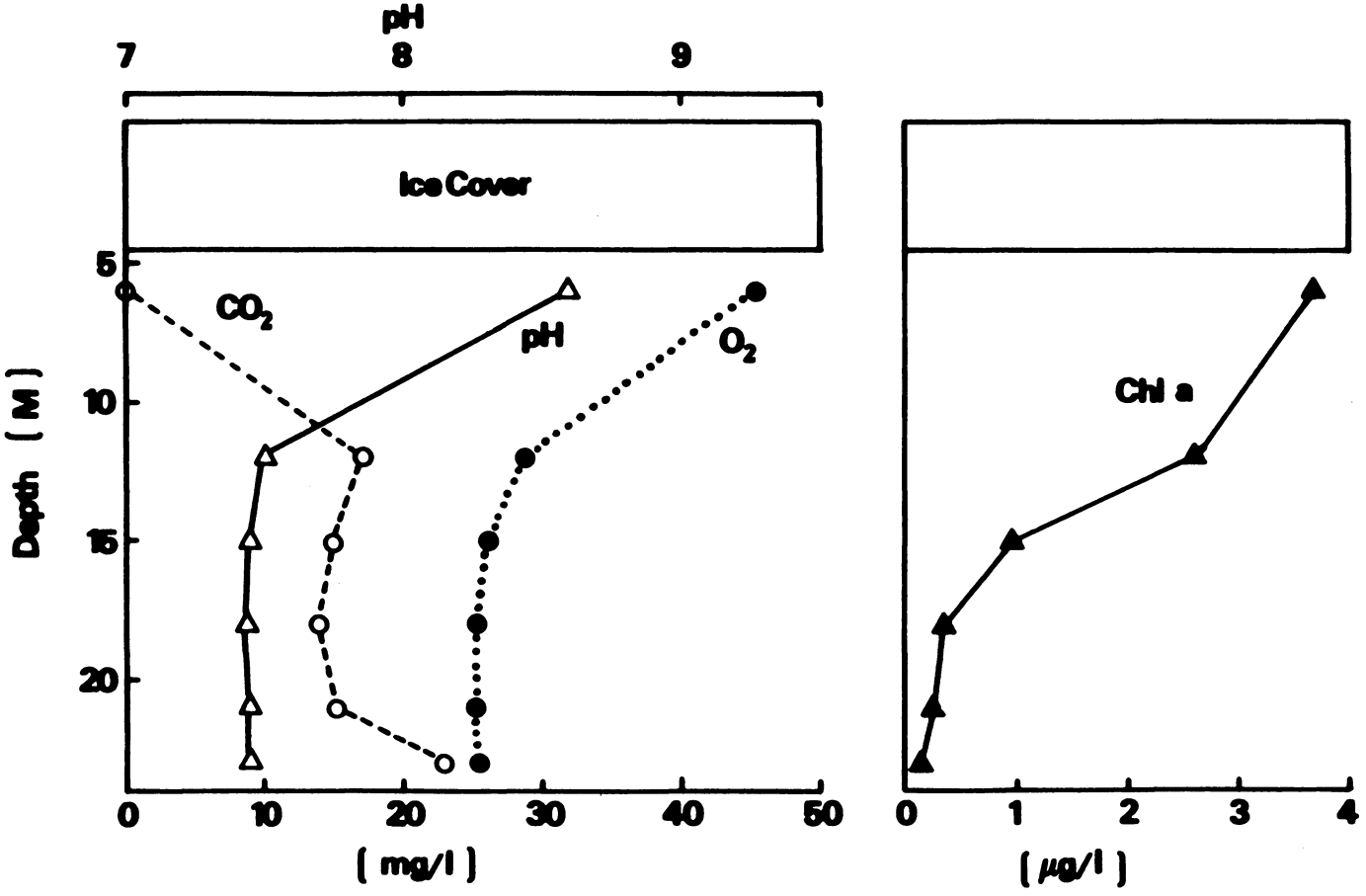

Figure 8. Depth profiles of carbon dioxide, dissolved oxygen, pH and chlorophyll a for Lake Hoare on 1-15-1981.

Phytoplankton Numbers and Biovolumes, PAR Absorption, Primary Productivity and Quantum Yields

Figure 9 shows a plot of E_{PAR} vs Chl a used to estimate k_C by the method of Tyler (1975); k_C was determined to be 0.0328. Tables 2 to 7 shows Chl a, phytoplankton numbers and biovolumes, PAR absorption at the given depth, PAR absorption by the phytoplankton using the value for k_C = 0.16 (A) (Bannister 1974) and the empirically estimated value of k_C = 0.0328 (B). Particulate carbon fixation and for some dates moles (M) of carbon (C) excreted and total M of C fixed for each depth sampled is also shown. Quantum yields (Φ_A and Φ_B) calculated using either 0.016 or 0.0328 as values for k_C are also shown. The highest phytoplankton density both in terms of number and biovolumes occurred in Lake Fryxell (Table 6) and the least in Lake Vanda (Table 5). Not included in any of the tables are the phytoplankton numbers and biovolumes on December 28, 1980 in Lake Fryxell. Phytoplankton numbers were 5585, 5072 and 701 algal units/ml and 13,460, 12,943 and 0.769 x 10^6 μm^3/ml for 5, 8.5 and 9 m, respectively. Total PAR absorbed was greatest at 5 m in Lake Fryxell (Table 6) and the least at 23 m in Lake Hoare (Table 2). The amount of PAR absorbed by the phytoplankton decreased with depth in all of the lakes. No PAR absorption occurred at 23 m in Lake Hoare on November 4, 1980 (Table 2) due to no detectable Chl a and at 9 m in Lake Fryxell (Table 6). The greatest PAR absorption by the phytoplankton occurred at 5 m in Lake Fryxell (Table 6).

Primary production was greatest in Lake Fryxell (Table 6) and the

least in Lake Vanda (Table 5). In Lake Vanda PER was over 90% of the total C fixation (Table 5). In Lakes Fryxell (Table 6) and Hoare (Table 7) the greatest PER occurred at the shallower depths just under the ice cover. No net primary productivity was detected in Lake Hoare on November 4, (Table 2), at 9 m in Lake Fryxell (Table 6) and at 10 m in Lake Bonney (Table 4). Values for quantum yields were the greatest at the greatest depth in which C fixation was detected. Values for ϕ_A and Φ_B were the greatest at 20 m in Lake Vanda (Table 5).

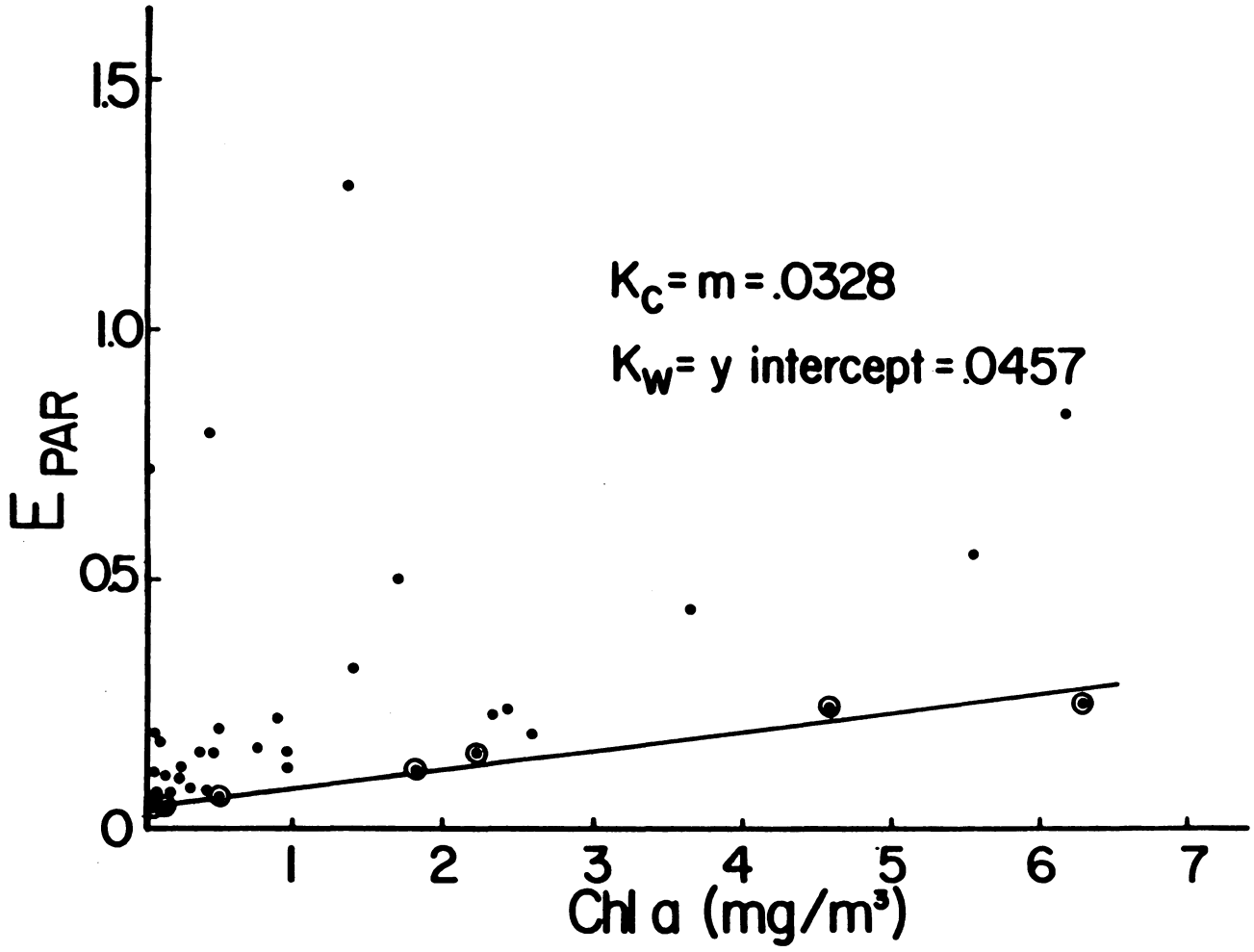

Figure 9. Plot of the extinction coefficient of photosynthetically active radiation (E_{PAR}) versus chlorophyll a (Chl a) used to estimate the mean spectral extinction coefficient of chlorophyll a (k_c). Also shown is the spectral extinction coefficient of all PAR absorbing components of the water except for viable plant pigments (k_w).

Table 2. Chlorophyll a concentrations, phytoplankton numbers and bivolumes, PAR absorption, primary productivity and quantum yields in Lake Hoare on 11-04-1980.

Depth	6 m	12 m	23 m
Chl a (mg/m^3)	2.44	0.42	0
Phytoplankton numbers (Algal units/ml)	2895	543	589
Phytoplankton biovolumes (10^6 μm^3/ml)	0.925	0.183	0.070
Total PAR absorbed [1] ($Ein/m^3/hr$)	0.68×10^{-3}	0.11×10^{-3}	0.72×10^{-4}
PAR absorbed by the phytoplankton [2] ($Ein/m^3/hr$)	2.65×10^{-5}	7.39×10^{-7}	0
PAR absorbed by the phytoplankton [3] ($Ein/m^3/hr$)	5.44×10^{-5}	1.52×10^{-6}	0
Particulate fixation (M of $C/m^3/hr$)	0	0	0
ECP fixation [4] (M of $C/m^3/hr$)	0	0	0
Total C fixation (M of $C/m^3/hr$)	0	0	0
Φ_A [2]	0	0	0
Φ_B [3]	0	0	0

1. Total PAR absorbed at that depth
2. Data calculated assuming $k_C = 0.016$
3. Data calculated assuming $k_C = 0.0328$
4. Extracellular product fixation

Table 3. Chlorophyll a concentrations, phytoplankton numbers and bivolumes, PAR absorption, primary productivity and quantum yields in Lake Hoare on 11-19-1980

Depth	6 m	12 m	23 m
Chl a (mg/m^3)	1.69	2.23	0.08
Phytoplankton numbers (Algal units/ml)	2128	694	N.D.[1]
Phytoplankton biovolumes (10^6 μm^3/ml)	0.739	0.253	N.D.
Total PAR absorbed[2] ($Ein/m^3/hr$)	7.30×10^{-3}	4.70×10^{-4}	1.73×10^{-4}
PAR absorbed by the phytoplankton[3] ($Ein/m^3/hr$)	1.97×10^{-4}	1.68×10^{-5}	2.21×10^{-7}
PAR absorbed by the phytoplankton[4] ($Ein/m^3/hr$)	4.05×10^{-4}	3.44×10^{-5}	4.54×10^{-7}
Particulate fixation (M of $C/m^3/hr$)	3.58×10^{-6}	1.63×10^{-6}	0
ECP fixation[5] (M of $C/m^3/hr$)	N.D.	N.D.	N.D.
Total C fixation (M of $C/m^3/hr$)	3.58×10^{-6}	1.63×10^{-6}	0
Φ_A.[3]	0.0180	0.107	0
Φ_B.[4]	0.0088	0.052	0

1. Not determined
2. Total PAR absorbed at that depth.
3. Data calculated assuming $k_c = 0.016$
4. Data calculated assuming $k_c = 0.0328$
5. Extracellular product fixation

Table 4. Chlorophyll a concentrations, phytoplankton numbers and bivolumes, PAR absorption, primary productivity and quantum yields in Lake Bonney on 12-05-1980.

Depth	4 m	10 m	14 m
Chl a (mg/m^3)	1.41	0.95	0.50
Phytoplankton numbers (Algal units/ml)	1868	363	566
Phytoplankton biovolumes (10^6 μm^3/ml)	0.912	0.142	0.233
Total PAR absorbed [1] ($Ein/m^3/hr$)	1.68×10^{-2}	1.31×10^{-2}	3.22×10^{-3}
PAR absorbed by the phytoplankton [2.] ($Ein/m^3/hr$)	3.71×10^{-4}	1.98×10^{-4}	2.58×10^{-5}
PAR absorbed by the phytoplankton [3.] ($Ein/m^3/hr$)	7.77×10^{-4}	4.07×10^{-4}	5.28×10^{-5}
Particulate fixation (M of $C/m^3/hr$)	3.47×10^{-6}	0	1.85×10^{-6}
ECP fixation [4.] (M of $C/m^3/hr$)	N.D.[5.]	N.D.	N.D.
Total C fixation (M of $C/m^3/hr$)	3.47×10^{-6}	0	1.85×10^{-6}
Φ_A. [2.]	0.0103	0	0.0718
Φ_B. [3.]	0.0050	0	0.0350

1. Total PAR absorbed at that depth
2. Data calculated assuming $k_C = 0.016$
3. Data calculated assuming $k_C = 0.0328$
4. Extracellular product fixation
5. Not determined

Table 5. Chlorophyll a concentrations, phytoplankton numbers and biovolumes, PAR absorption, primary productivity and quantum yields in Lake Vanda on 12-15-1980.

Depth	4 m	14 m	20 m
Chl a (mg/m^3)	0.24	0.07	0.09
Phytoplankton numbers (Algal units/ml)	411	801	882
Phytoplankton biovolumes (10^6 μm^3/ml)	0.016	0.027	0.037
Total PAR absorbed [1.] ($Ein/m^3/hr$)	7.40×10^{-2}	3.85×10^{-2}	1.03×10^{-2}
PAR absorbed by the phytoplankton [2.] ($Ein/m^3/hr$)	2.84×10^{-4}	4.31×10^{-5}	1.48×10^{-5}
PAR absorbed by the phytoplankton [3.] ($Ein/m^3/hr$)	5.82×10^{-4}	8.84×10^{-5}	3.04×10^{-5}
Particulate fixation (M of $C/m^3/hr$)	3.50×10^{-8}	1.16×10^{-7}	7.70×10^{-8}
ECP fixation [4.] (M of $C/m^3/hr$)	2.14×10^{-6}	1.00×10^{-6}	1.12×10^{-6}
Total C fixation (M of $C/m^3/hr$)	2.18×10^{-6}	1.12×10^{-6}	1.20×10^{-6}
Φ_A. [2.]	0.0076	0.0258	0.1560
Φ_B. [3.]	0.0037	0.0126	0.0760

1. Total PAR absorbed at that depth
2. Data calculated assuming $k_C = 0.016$
3. Data calculated assuming $k_C = 0.0328$
4. Extracellular product fixation

Table 6. Chlorophyll a concentrations, phytoplankton numbers and bivolumes, PAR absorption, primary productivity and quantum yields in Lake Fryxell on 1-08-1981.

Depth	5 m	8.5 m	9 m
Chl a (mg/m^3)	3.37	6.62	0.94
Phytoplankton numbers (Algal units/ml)	5398	3454	38
Phytoplankton biovolumes (10^6 μm^3/ml)	7.102	7.728	0.008
Total PAR absorbed [1.] ($Ein/m^3/hr$)	1.40×10^{-1}	1.40×10^{-2}	0
PAR absorbed by the phytoplankton [2.] ($Ein/m^3/hr$)	7.57×10^{-3}	1.48×10^{-3}	0
PAR absorbed by the phytoplankton [3.] ($Ein/m^3/hr$)	1.55×10^{-2}	3.03×10^{-3}	0
Particulate fixation (M of $C/m^3/hr$)	2.20×10^{-5}	8.22×10^{-5}	0
ECP fixation [4.] (M of $C/m^3/hr$)	1.24×10^{-5}	1.24×10^{-5}	0
Total C fixation (M of $C/m^3/hr$)	3.44×10^{-5}	9.46×10^{-5}	0
Φ_A. [2.]	0.0045	0.0636	0
Φ_B. [3.]	0.0022	0.0310	0

1. Total PAR absorbed at that depth
2. Data calculated assuming $k_c = 0.016$
3. Data calculated assuming $k_c = 0.0328$
4. Extracellular product fixation

Table 7. Chlorophyll a concentrations, phytoplankton numbers and bivolumes, PAR absorption, primary productivity and quantum yields in Lake Hoare on 1-15-1981.

Depth	6 m	12 m	23 m
Chl a (mg/m^3)	3.67	2.67	0.14
Phytoplankton numbers (Algal units/ml)	3716	1066	N.D. [1]
Phytoplankton biovolumes (10^6 μm^3/ml)	1.479	0.384	N.D.
Total PAR absorbed [2] ($Ein/m^3/hr$)	2.15×10^{-2}	3.22×10^{-3}	7.03×10^{-3}
PAR absorbed by the phytoplankton [3] ($Ein/m^3/hr$)	1.26×10^{-3}	1.34×10^{-4}	2.31×10^{-6}
PAR absorbed by the phytoplankton [4] ($Ein/m^3/hr$)	2.58×10^{-3}	2.76×10^{-4}	4.74×10^{-6}
Particulate fixation (M of $C/m^3/hr$)	8.41×10^{-6}	1.07×10^{-5}	0
ECP fixation [5] (M of $C/m^3/hr$)	3.95×10^{-6}	0	0
Total C fixation (M of $C/m^3/hr$)	1.24×10^{-5}	1.07×10^{-5}	0
Φ_A. [2]	0.0098	0.0799	0
Φ_B. [3]	0.0048	0.0390	0

1. Not determined
2. Total PAR absorbed at that depth
3. Data calculated assuming $k_c = 0.016$
4. Data calculated assuming $k_c = 0.0328$
5. Extracellular product fixation

Light Utilization Efficiencies and Energy Equivalent Quantum Yields

Table 8 shows the energy equivalents of PAR and primary productivity in calories, light utilization efficiencies and energy-equivalent quantum yields for the lakes studied. Values of ε were greatest at the greatest depth sampled as were values of Φ'. A value of 1.36% for ε was greatest at 8.5 m in Lake Fryxell and 0.006% was the least at 4 and 14 m in Lake Vanda. Values of Φ'_A and Φ'_B were the least at 4 m in Lake Vanda and the greatest at 20 m in Lake Vanda for all of the lakes studied.

Table 8. Photosynthetically active radiation, primary productivity, light utilization efficiencies, and energy equivalent quantum yields in the southern Victoria Land lakes. The data is from the same dates in Tables 3 through 7.

Depth	PAR ($cal/m^3/hr$)	1° Productivity ($cal/m^3/hr$)	ε %	$\Phi'_{A.}$ [1.] %	$\Phi'_{B.}$ [2.] %
Lake Hoare [3.]					
6 m	3.80×10^2	4.01×10^{-1}	0.11	3.96	1.94
12 m	2.24×10^1	1.83×10^{-1}	0.82	23.54	11.44
Lake Hoare [4.]					
6 m	1.12×10^3	1.39×10^0	0.12	2.16	1.06
12 m	1.67×10^2	1.20×10^0	0.72	17.58	8.58
Lake Bonney					
4 m	8.74×10^2	3.89×10^{-1}	0.04	2.27	1.10
14 m	1.67×10^2	2.07×10^{-1}	0.12	15.80	7.70
Lake Vanda					
4 m	3.85×10^3	2.40×10^{-1}	0.006	1.67	0.81
14 m	2.00×10^3	1.25×10^{-1}	0.006	5.68	2.77
20 m	5.36×10^2	2.60×10^{-1}	0.05	34.32	16.72
Lake Fryxell					
5 m	7.30×10^3	3.86×10^0	0.05	0.99	0.48
8.5 m	7.26×10^2	10.60×10^0	1.46	13.99	6.82

1. Data calcualted assuming $k_c = 0.016$
2. Data calculated assuming $k_c = 0.0328$
3. Data is from 11-19-1980
4. Data is from 1-15-1981

Species Composition of the Phytoplankton

Tables 9-15 lists the algal taxa found at each depth sampled, the percent of the total biovolume and the percent of the total number of algal units that each algal taxon represents.

In terms of biovolume, Chroomonas lacustris Pascher & Ruttner was the dominant species of the phytoplankton in Lakes Hoare (Tables 9, 10 and 15) and Bonney except at 14 m (Table 11). It was also the dominant in terms of algal units, except at 23 m in Lake Hoare (Table 9) where an unidentified species of Oscillatoria Vaucher was the dominant and at 14 m in Lake Bonney (Table 11) where it was codominant with an unidentified unicellular chlorophyte. C. lacustris was also found in the waters of Lake Fryxell where it was an important component of the phytoplankton community and it was sometimes the dominant in terms of algal units but not biovolume. Either of 2 unidentified flagellates labelled as C and D were usually dominant or codominant in terms of biovolumes (Table 13 and 14), except at 9 m on January 8, 1981. Flagellate C sometimes dominated in terms of algal units, while flagellate D never dominated. Ochromonas minuscula Conrad was the dominant in Lake Vanda (Table 12) with Monodus coccomyxa Pascher and an unidentified species of Ochromonas Wyssotzki being common.

Chlamydomonas subcaudata Wille occurred in samples from all of the Taylor Valley lakes. Chlorella vulgaris Beyernck was found in samples from all of the lakes. The only diatoms found were Pinnularia cymatopleura West & West and Navicula shackletoni West & West at 4 m in

Lake Bonney (Table 11). It is interesting to note that the vast majority of the algae enumerated were less than 20 μm in size and were mostly flagellated forms and filamentous bluegreens or small unicellular chlorophytes having a diameter of less than 10 μm.

Table 9. Algal taxa enumerated at the given depths for Lake Hoare on 11-04-1980. The percentages of each algal taxon in terms of total biovolume and the total number of algal units is also listed.

Algal Taxon	% of Biovolume	% of Algal Units
6 Meters		
Chroomonas lacustris Pascher & Ruttner	95.02	75.27
Unidentifiable ovoid algae	3.75	24.11
Chlamydomonas subcaudata Wille	1.22	0.31
Chlorella vulgaris Beyerinck	0.01	0.31
12 Meters		
Chroomonas lacustris Pascher & Ruttner	97.59	81.40
Oscillatoria sp. B Vaucher	2.04	12.52
Chlorella vulgaris Beyerinck	0.19	5.71
Chlorogonium tetragama Bohlin	0.18	0.37
24 Meters		
Chroomonas lacustris Pascher & Ruttner	65.50	19.18
Oscillatoria sp. B Vaucher	28.68	61.97
Chlamydomonas subcaudata Wille	3.60	0.34
Chlorella vulgaris Beyerinck	1.62	16.98
Green coccoid	0.60	1.53

Table 10. Alga taxa enumerated at the given depths for Lake Hoare on 11-19-1980. The percentages of each algal taxon in terms of total biovolume and the total number of algal units is also listed.

Algal Taxon	% of Biovolume	% of Algal Units
6 Meters		
Chroomonas lacustris Pascher & Ruttner	96.59	83.22
Flagellate A	2.21	13.86
Chloromonas alpina Wille	0.97	1.08
Chlorogonium tetragama Bohlin	0.18	0.38
Chlorella vulgaris Beyerinck	0.05	1.46
12 Meters		
Chroomonas lacustris Pascher & Ruttner	85.10	76.94
Oscillatoria amphigranulata Van Goor	12.09	4.76
Oscillatoria sp. B Vaucher	2.03	13.54
Chloromonas alpina Willie	0.49	0.58
Green coccoid	0.20	1.58
Chlorella vulgaris Beyerinck	0.08	2.59

Table 11. Algal taxa enumerated at the given depths for Lake Bonney on 12-05-1980. The percentages of each algal taxon in terms of total biovolume and the total number of algal units is also listed.

Algal Taxon	% of Biovolume	% of Algal Units
4 Meters		
Chroomonas lacustris Pascher & Ruttner	74.86	90.63
Thorakomonas feldmanii Bourrelly	13.09	3.59
Chlamydomonas subcaudata Wille	9.20	3.59
Pinnularia cymatopleura West & West	1.75	0.43
Navicula shackletoni West & West	0.87	0.43
Phormidium frigidum Fritsch	0.22	1.34
10 Meters		
Chroomonas lacustris Pascher & Ruttner	63.43	62.40
Chlamydomonas subcaudata Wille	20.22	6.41
Green coccoid	10.69	8.64
Thorakomonas feldmanii Bourrelly	5.01	1.11
Chlorella vulgaris Beyerinck	0.61	21.45
14 Meters		
Green coccoid	49.16	41.17
Chroomonas lacustris Pascher & Ruttner	48.33	49.29
Chlamydomonas subcaudata Wille	2.15	0.71
Chlorella vulgaris Beyerinck	0.20	7.42
Flagellate A	0.19	1.42

Table 12. Algal taxa enumerated at the given depths for Lake Vanda on 12-15-1980. The percentages of each algal taxon in terms of total biovolume and the total number of algal units is also listed.

Algal Taxon	% of Biovolume	% of Algal Units
4 Meters		
Ochromonas minuscula Conrad	73.48	87.10
Chroomonas lacustris Pascher & Ruttner	25.87	10.22
Chlorella vulgaris Beyerinck	0.91	2.68
14 Meters		
Ochromonas minuscula Conrad	43.31	45.44
Monodus coccomyxa Pascher	28.01	11.74
Chlorella vulgaris Beyerinck	12.27	32.08
Phormidium fragile (Meneghini) Gomont	8.53	2.12
Ochromonas sp. B Wyssotzki	4.64	1.62
Westella sp. de Wildemann	1.69	1.62
Oscillatoria sp. A. Vaucher	1.54	5.37
20 Meters		
Ochromonas minuscula Conrad	49.35	65.53
Ochromonas sp. B Wyssotzki	15.12	6.70
Monodus coccomyxa Pascher	14.96	7.94
Flagellate B	12.04	0.45
Chlorella vulgaris Beyerinck	2.81	9.30
Phormidium sp. Kutzing	1.96	0.45
Chlamydomonas acuta Korschikoff	1.87	2.49
Oscillatoria sp. A. Vaucher	1.52	6.70
Westella sp. de Wildemann	0.37	0.45

Table 13. Algal taxa enumerated at the given depths for Lake Fryxell on 12-28-1980. The percentages of each algal taxon in terms of total biovolume and the total number of algal units is also listed.

Algal Taxon	% of Biovolume	% of Algal Units
5 Meters		
Flagellate C	47.56	36.71
Flagellate D	41.00	10.47
Chroomonas lacustris Pascher & Ruttner	10.48	45.16
Chlamydomonas subcaudata Wille	0.42	0.81
Green coccoid	0.30	3.63
Flagellate A	0.04	1.61
Chlorella vulgaris Beyerinck	0.01	1.61
8.5 Meters		
Flagellate D	45.34	12.26
Flagellate C	43.60	35.62
Chroomonas lacustris Pascher & Ruttner	10.50	47.89
Chlamydomonas subcaudata Wille	0.38	0.77
Green coccoid	0.21	2.68
Chlorella vulgaris Beyerinck	0.01	0.77
9 Meters		
Flagellate C	84.48	34.61
Chroomonas lacustris Pascher & Ruttner	11.78	26.96
Green coccoid	3.61	23.13
Chlorella vulgaris Beyerinck	0.13	15.31

Table 14. Algal taxa enumerated at the given depths for Lake Fryxell on 1-08-1981. The percentages of each algal taxon in terms of total biovolume and the total number of algal units is also listed.

Algal Taxon	% of Biovolume	% of Algal Units
5 Meters		
Flagellate D	51.27	7.15
Chroomonas lacustris Pascher & Ruttner	29.92	70.41
Flagellate C	18.56	7.82
Chlorella vulgaris Beyerinck	0.10	12.24
Ochromonas sp. A Wyssotzki	0.10	1.35
Flagellate A	0.04	1.02
8.5 Meters		
Flagellate C	91.80	65.78
Chroomonas lacustris Pascher & Ruttner	7.24	28.95
Chlamydomonas subcaudata Wille	0.92	1.65
Flagellate A	0.03	1.30
Polytomella sp. Aragao	0.01	0.67
Chlorella vulgaris Beyerinck	0.01	1.65
9 Meters		
Chlamydomonas subcaudata Wille	55.85	10.52
Green coccoid	42.27	50.00
Chlorella vulgaris Beyerinck	1.88	39.47

Table 15. Algal taxa enumerated at the given depths for Lake Hoare on 1-15-1981. The percentages of each algal taxon in terms of total biovolume and the total number of algal units is also listed.

Algal Taxon	% of Biovolume	% of Algal Units
6 Meters		
Chroomonas lacustris Pascher & Ruttner	98.04	96.80
Chlamydomonas subcaudata Wille	1.44	0.46
Oscillatoria sp. B Vaucher	0.19	1.37
Chlorogonium tetragama Bohlin	0.15	0.46
Flagellate A	0.08	0.92
12 Meters		
Chroomonas lacustris Pascher & Ruttner	96.77	90.38
Oscillatoria amphigranulata Van Goor	2.17	0.88
Flagellate A	0.75	5.20
Oscillatoria sp. B Vaucher	0.27	1.86
Chlorella vulgaris Beyerinck	0.06	1.86

Total Organic Carbon and Dissolved Organic Carbon Concentrations

Table 16 shows TOC and DOC concentrations in Lakes Hoare and Fryxell. Table 17 shows the same for Lakes Bonney and Vanda. The greatest concentrations of TOC and DOC occurred at 23 m being 36.42 and 33.50 mg/l in Lake Hoare on November 4, 1980. The levels of TOC and DOC for Lakes Hoare and Fryxell were in the same range; the organic carbon concentrations were generally higher in Lake Fryxell. Total organic carbon and DOC were lower in Lake Bonney. Lake Vanda had the lowest TOC values. At 14 and 20 m in Lake Vanda TOC values were 4.21 and 3.81 mg/l.

Table 16. Total organic carbon (TOC) and dissolved organic carbon (DOC) in mg/l for Lake Hoare and Lake Fryxell on the dates shown.

Lake Hoare	11-04-1980		11-19-1980		1-15-1981	
Depth	TOC	DOC	TOC	DOC	TOC	DOC
6 Meters	19.60	17.86	18.49	-	19.89	18.41
12 Meters	18.03	-	16.49	15.91	-	16.16
24 Meters	36.42	33.50	14.20	11.10	-	-

Lake Fryxell	12-28-1980		1-08-1981	
Depth	TOC	DOC	TOC	DOC
5 Meters	22.73	17.36	16.96	13.88
8.5 Meters	27.99	22.67	-	32.93
9 Meters	29.35	25.67	30.43	25.78

Table 17. Total organic carbon (TOC) and dissolved organic carbon (DOC) in mg/l for Lake Bonney on 12-05-1980 and Lake Vanda on 12-15-1980.

	Lake Bonney		Lake Vanda	
Depth	TOC	DOC	TOC	DOC
4 Meters	5.73	-	7.55	-
10 Meters	10.69	9.48	-	-
14 Meters	15.72	15.35	4.21	-
20 Meters	-	-	3.81	-

Effect of Purging and Lyophilizing a Solution of Either Glycolate or Glucose

Table 18 shows the effect of bubbling a solution of glycolate or glucose with air. No loss of glycolate or glucose occurred due to purging the solutions for times up to 1 hr. Table 19 shows the effect of pH on the lyophilization of a glycolate solution. About 90% of the added glycolate was recovered when it was freeze dried at pH conditions ranging from 2.00 to 5.00. Table 20 shows the effect of pH on the lyophilization of a glucose solution. At a pH of 3.50, 85% of the added glucose was recovered, while recovery at the other pH conditions was greater except at the lowest pH tested. Table 21 shows the effect of time on the volatilization of $NaH^{14}CO_3$. All of the inorganic carbon was volatilized to CO_2 after only 2-4 hr in the presence of conc. HCl.

Table 18. Effect of bubbling a solution of either glycolate or glucose at a pH of 3.50 with air.

Glycolate		
Time in Minutes	Amount of Glycolate in cpm	% Recoverery
0	71187 ± 849	100.00 ± 1.19
5	72678 ± 297	102.09 ± 0.42
10	71528 ± 1861	100.47 ± 2.61
15	68941 ± 6115	96.84 ± 8.59
30	70429 ± 1991	98.93 ± 2.79
60	72086 ± 3845	101.26 ± 5.40

Glucose		
Times in Minutes	Amount of Glucose in cpm	% Recoverery
0	83384 ± 3588	100.00 ± 4.30
5	85920 ± 1173	103.04 ± 1.41
10	79693 ± 3629	95.57 ± 4.35
15	80407 ± 3162	96.43 ± 3.79
30	80206 ± 3243	96.19 ± 3.89
60	81194 ± 3895	97.37 ± 4.67

Table 19. Effect of pH on the lyophilization of glycolate.

Amount of glycolate added in cpm		123350 ± 337
pH	Amount Recovered in cpm	% Recoverery
1.25	107943 ± 1557	87.50 ± 1.26
2.00	114969 ± 504	93.20 ± 0.41
3.00	109726 ± 1671	88.96 ± 1.35
3.50	112540 ± 7149	91.24 ± 5.80
4.00	111626 ± 7154	90.50 ± 5.80
4.50	107823 ± 5534	97.41 ± 4.49
5.00	112200 ± 1249	90.96 ± 1.01
6.00	98482 ± 373	79.83 ± 0.30

Table 20. Effect of pH on the lyophilization of glucose.

Amount of glucose added in cpm	224627 ± 17630
pH	Amount Recovered in cpm	% Recoverery
1.25	171634 ± 2126	76.41 ± 0.95
2.00	205332 ± 1504	91.41 ± 0.67
3.00	196517 ± 1167	87.49 ± 0.52
3.50	192601 ± 683	85.74 ± 0.30
4.00	213381 ± 3822	94.99 ± 1.70
4.50	211877 ± 3984	94.32 ± 1.77
5.00	207363 ± 6743	92.31 ± 3.00
6.00	242073 ± 633	107.77 ± 0.28

Table 21. The effect of time on the volatization of a $NaH^{14}CO_3$ solution (pH of 9.0) in the presence of gaseous hydrochloric acid.

Time	Amount of $NaHCO_3$ in cpm
0	238414 ± 1085
2 hrs	917 ± 50
4 hrs	860 ± 38
8 hrs	851 ± 137
12 hrs	790 ± 32
24 hrs	732 ± 43
48 hrs	751 ± 43
96 hrs	659 ± 82
BKG[1].	760 ± 140

1. The background radioactivity of the $NaH^{14}CO_3$ solution was determined by acidifying the solution to a pH of 3.50 and bubbling with air for 2 hours.

Effect of Oxygen on Photosynthesis in *Chlamydomonas subcaudata* Wille

Table 22 shows the effect of DO and AIC on photosynthesis on *C. subcaudata*. Particulate carbon fixation and release of extracellular product increased with increasing AIC levels. Particulate carbon fixation was inhibited by ca. 2.5-3.5 x at the supersaturated level of DO. Percent extracellular release increased by ca. 2 x at supersaturated DO, while PER did not differ significantly with increasing levels of AIC. Chlorophyll a levels at saturated DO were 5.75, 5.64 and 5.54 µg/l, while at supersaturated DO, Chl a levels were 4.90 and 5.06 µg/l. Chlorophyll a values reported range from the lowest AIC concentration to the highest.

Table 22. Effect of oxygen and available inorganic carbon concentrations on photosynthesis in Chlamydomonas subcaudata Wille.

Available Inorganic Carbon (mg/l)		Dissolved Oxygen Concentration 12.05 ± 0.74 (mg/l)	Dissolved Oxygen Concentration 37.73 ± 3.95 (mg/l)
1.64	Particulate fixation (μg C/hr/μg Chl a)	$3.517 \times 10^{-1} \pm 1.422 \times 10^{-2}$	$9.645 \times 10^{-2} \pm 9.388 \times 10^{-3}$
	ECP fixation [1.] (μg C/hr/μg Chl a)	$3.200 \times 10^{-3} \pm 3.165 \times 10^{-4}$	$2.517 \times 10^{-3} \pm 3.183 \times 10^{-4}$
	PER [2.]	0.91 ± 0.09%	2.61 ± 0.33%
15.34	Particulate fixation (μg C/hr/μg Chl a)	$4.848 \times 10^{-1} \pm 7.365 \times 10^{-2}$	$1.923 \times 10^{-1} \pm 1.944 \times 10^{-2}$
	ECP fixation [1.] (μg C/hr/μg Chl a)	$5.866 \times 10^{-3} \pm 1.164 \times 10^{-3}$	$4.038 \times 10^{-3} \pm 5.384 \times 10^{-4}$
	PER [2.]	1.21 ± 0.24%	2.10 ± 0.28%
92.56	Particulate fixation (μg C/hr/μg Chl a)	$7.713 \times 10^{-1} \pm 1.186 \times 10^{-1}$	-
	ECP fixation [1.] (μg C/hr/μg Chl a)	$9.024 \times 10^{-3} \pm 1.388 \times 10^{-3}$	-
	PER [2.]	1.17 ± 0.18%	-

1. Extracellular product fixation

2. Percent extracellular release

DISCUSSION

Quantum yields determined for phytoplankton from the southern Victoria Land lakes are comparable to values for phytoplankton elsewhere (Tyler 1975; Dubinsky and Berman 1976, 1981; Morel 1978). Determinations of Φ are dependent upon the estimation of k_c. Other studies have reported values for k_c ranging from 0.005-0.021 (Dubinsky and Berman 1979; Atlas and Bannister 1980). Light quality (Dubinsky and Berman 1979; Atlas and Bannister 1980), differences in accessory pigments unique to each phytoplankton taxa (Bannister 1974; Dubinsky and Berman 1979; Atlas and Bannister 1980), physiological state (Dubinsky and Polna 1976; Welschmeyer and Lorenzen 1981), cell shape (Kirk 1975 a,b; Kirk 1976; Platt and Jassby 1976) and cell size (Kirk 1976; Jewson 1977) are factors that are thought to affect k_c. Small phytoplankton are more effective at trapping light, so that k_c is inversely proportional to cell size (Jewson 1977). Two values for k_c were used in the determination of Φ due to the variability of factors influencing k_c.

Algae adapt to low light intensities by increasing photosynthetic pigments relative to cell biomass (Falkowski 1981). Parker et al. (1982a) reported an increased ratio of Chl a to cell bivolume for the phytoplankton of seven southern Victoria Land lakes, including the four lakes in this study, in comparison to most lakes. The phytoplankton of these lakes are all small, having a diameter of less than 20 μm. The dominant phytoplankton are almost exclusively flagellates belonging to the Cryptophyceae, Chrysophyceae or Chlorophyceae. Previous investigators have reported similar findings in regards to the taxonomic composi-

ition of the phytoplankton of these southern Victoria Land lakes (Parker et al. 1977; Seaburg et al. 1979; Vincent 1981; Parker et al. 1982a). Therefore, the small size and increased Chl a content relative to cell biomass could explain the high empirical estimation of k_C = 0.0328.

Nevertheless, it could be erroneous to assume that k_C is constant for the phytoplankton of these lakes, since it is known that k_C varies with algal taxon, depth and water color (Atlas and Bannister 1980). Another possible error is the effect of other light absorbing components of the water column which are not fully accounted for by the regression of E_{PAR} versus Chl a, resulting in an overestimation of k_C. Yet, the use of K_C = 0.16 as suggested by Bannister (1974) probably is an underestimation, because Φ_A should not exceed the theoretical maximum of Φ = 0.125 (Rabinowitch and Govindjee 1969). Φ_A was estimated to be 0.156 at 20 m in Lake Vanda, assuming k_C = 0.016.

Overall, the ratio of Chl a to cell bivolume increased with depth in each lake except in Lake Hoare on 11-04-1980. Vincent (1981) reported an increased amount of accessary pigments from deep-living phytoplankton in comparison to the shallow water phytoplankton of Lake Fryxell. In the relatively stable environment of these lakes which allows for maximal chromatic adaptation by the phytoplankton, it is quite probable that the phytoplankton are so well adapted that k_C would differ at each discrete depth within each lake.

Quantum yields increased from lower values at shallow depths to maximum values at greater depth in the southern Victoria Land lakes. In other aquatic ecosystems Φ increased with depth to a maximal value near

the bottom of the photic zone (Tyler 1975; Dubinsky and Berman 1976, 1981; Morel 1978). As light intensities decrease with depth, Φ should approach a constant maximum value at subsaturating intensities since Φ is the slope of the line that is formed by plotting the rate of photosynthesis versus the rate at which PAR is absorbed by the algae. Another explanation for variation in Φ is that vertical mixing prevents the phytoplankton from acclimating completely to ambient light conditions so that they never completely optimize their light trapping mechanisms (Morel 1978). Tilzer and Schwartz (1976) and Tilzer and Goldman (1978) showed that only under conditions of thermal stratification can there be maximum adaptation of the phytoplankton community to ambient light conditions. In the completely stratified conditions of the southern Victoria Land lakes, no passive movement or vertical circulation of phytoplankton occurs. These motile phytoplankton can maintain their own position within the water column (Vincent 1981) so that maximum acclimation to their light environment seems likely.

Energy equivalent quantum yield (Φ') (Dubinsky Berman 1976) is closely related to Φ. Energy equivalent quantum yield is the ratio of the energy content of PAR absorbed by the phytoplankton to the energy content of the photosynthate produced by the phytoplankton. Assuming that $\Phi' = 2.2\ \Phi$ (Dubinsky and Berman 1976), under optimal conditions $\Phi' = 2.2\ (0.125)$ or 27.5%. The range of Φ' for the phytoplankton of southern Victoria Land lakes are comparable to values reported for the phytoplankton of Lake Kinneret, Israel (Dubinsky and Berman 1976, 1981).

Light utilization efficiencies (ε) calculated for the phytoplank-

ton of the southern Victoria Land lakes are among the lowest ε values reported from aquatic ecosystems (Dubinsky and Berman 1976, 1981; Morel 1978). The low values of ε are due to the low biomass of the phytoplankton of these antarctic lakes. Morel (1978) and Dubinsky and Berman (1981) found ε dependent upon phytoplankton biomass; that is greater values of ε occurred at sites or at times of greater phytoplankton biomass. In Lake Kinneret, the difference between the values of ε and Φ' decreased when phytoplankton abundance was high (Dubinsky and Berman 1981). Light utilization efficiencies in comparison to Φ' in the southern Victoria Land lakes are very low, being approximately an order of magnitude lower. The difference between ε and Φ' indicates that environmental conditions in the southern Victoria Land lakes are limiting to their respective phytoplankton communities. The environmental conditions that have been indicated as limiting to varying degrees the communities of each of these lakes are the low levels of PAR penetrating the ice covers (Goldman 1964; Goldman et al. 1967; Parker et al. 1980; Seaburg et al. 1981; Vincent 1981; Parker et al. 1982a; Seaburg et al. in press), the low temperature of the lake waters (Goldman 1964; Goldman et al. 1967; Vincent 1981; Parker et al. 1982a; Seaburg et al. in press), nutrient limitations (Goldman et al. 1967; Vincent 1981; Parker et al. 1982a; Seaburg et al. in press), photorespiration due to supersaturation of the lake waters with oxygen and often low concentrations of AIC (Parker et al. 1977; Parker et al. 1980; Parker et al. 1982a) and hypersalinity (Goldman et al. 1967; Parker et al. 1982a).

Algal biomass and rates of carbon fixation were low in these

lakes. Previous investigators reported sparse phytoplankton communities (Goldman et al. 1967; Koob and Leister 1972; Parker et al. 1977; Vincent 1981; Cathey et al. 1981; Parker et al. 1982a) and low rates of primary production (Goldman 1964; Goldman et al. 1967; Koob and Leister 1972; Parker et al 1977; Vincent 1981; Vincent et al. 1981; Parker et al. 1982a) in these lakes. Maximum rates of primary production or algal biomass often occurred at intermediate depths or deeper in these lakes (Goldman 1964; Goldman et al. 1967; Koob and Leister 1972; Parker et al. 1977; Vincent 1981; Vincent et al. 1981; Parker et al 1982a; Figures 4 and 6). Parker et al. (1982a) found that maximum algal biomass as measured by Chl a occurred at depths of maximum water temperature within the photic zone of the lakes studied except for Lake Vanda. Vincent (1981) reported a similar occurrence in Lake Fryxell. Other investigators reported maximum rates of primary production at the depth of greatest water temperature within the photic zone of Lake Vanda (Goldman 1964; Goldman et al. 1967; Vincent et al. 1981). In contrast, at other times, maximum rates of primary production or algal biomass were positively correlated with available PAR in Lakes Hoare (Figures 3 and 8), Bonney (Figure 5) and Vanda (Goldman 1964).

Vincent (1981) concluded that available nutrients such as nitrogen and phosphorus are the major factors controlling phytoplankton biomass in these antarctic lakes instead of water temperature or ambient levels of PAR. Nutrient deficiency was most acute in the shallower waters of Lake Fryxell (Vincent 1981). The phytoplankton communities are at times limited by phosphorus (Seaburg et al. in press). Maximum concentrations of nutrients probably occurred at the chemoclines of Lakes

Fryxell (9-10 m), Bonney (11-15 m) and Vanda (> 50m). Within these chemoclines, maximum water temperatures were also found. Nutrient concentrations were at their lowest in the waters just under the ice covers of Lakes Fryxell, Hoare and Bonney (Torii et al. 1975; Hoehn et al. 1977; Vincent 1981) and the shallower waters of Lake Vanda, < 50m deep (Torii et al. 1975; Vincent et al. 1981). The low nutrient conditions of these lakes were preserved by the loss of nutrients due to sedimentation and algal mat lift off (Simmons et al. 1979; Parker et al. 1980; Parker and Simmons 1981; Parker et al. 1982b). In certain areas of these lakes, the benthic microbial mats lift off the lake bottom, float to the water-ice interface and become entrapped in the lake's ice cover. These microbial mats pass through the ice cover to the surface, resulting in the removal of nutrients from the lake environment (Simmons et al. 1979; Parker et al. 1980; Parker and Simmons 1981; Parker et al. 1982b).

Percent extracellular release was higher in the shallower waters of Lakes Fryxell and Hoare and very high ($\geq$ 90%) in the shallow waters of Lake Vanda. These shallower waters were more brightly illuminated, supersaturated with oxygen and had low concentrations of nutrients. Such conditions are among those environmental conditions that are thought to favor photorespiration in algae (Tolbert 1974; Harris 1980). Photorespiration in algae can result in either a decrease in the rate of photosynthesis, an increase in the rate of excretion of extracellular products or both, causing an increase in PER.

There are several studies that show increased PER at shallower depths (Fogg et al. 1965; Watt 1966; Thomas 1971; Allen 1973; Watanabe

1980) and under conditions of photoinhibition of photosynthesis (Fogg et al. 1965; Nalewajko 1966; Watt 1966; Watanabe 1980). Harris and Lott (1973) reported a decrease in photosynthesis at high light intensities due to photorespiration. Other investigators reported increased PER under conditions of nutrient deficiency (Ignatiades 1973; Ignatiades and Fogg 1973; Berman 1976; Harris 1980; Watanabe 1980). The higher values of PER from the shallower waters of Lakes Hoare, Fryxell and Vanda could be due to photorespiration.

Photosynthesis in C. subcaudata was inhibited by supersaturated O_2 under light, temperature and pH conditions that mimic the aquatic environment of the studied lakes. This inhibition of photosynthesis by O_2 is probably due to photorespiration. Other studies have reported O_2 inhibition of photosynthesis in algae and attributed this phenomenon to photorespiration (Bunt 1971; Pope 1975; Beardall and Morris 1975; Black et al. 1976; Burris 1977; Coleman and Colman 1980). Birmingham et al. (1982) reported an increase in the rate of CO_2 evolution with increased levels of O_2 due to photorespiration.

Percent extracellular release by C. subcaudata was approximately twice as high under supersaturated O_2 in comparison to saturated O_2. Burris (1977) also reported an increase in PER with higher concentrations of O_2. Percent extracellular release was unaffected by AIC concentrations, being nearly constant. Nalewajko (1966) reported PER to be nearly constant at different concentrations of AIC except at very low concentrations where PER was greatest, while in another study PER decreased with increasing concentrations of AIC (Smith and Wiebe 1976). Release of extracellular product increased with AIC concentrations and

was also independent of O_2 concentrations. Smith and Wiebe (1976) reported release of extracellular product to be constant at several concentrations of AIC in marine phytoplankton, while Nalewajko (1966) reported the release of extracellular product to increase with increasing AIC concentrations and photosynthesis. Burris (1977) reported the effect of O_2 on the amount of extracellular release was variable in the algae studied. Several algae exhibited an increase in the rate of extracellular release under increased O_2 tensions while, in other algae the amount of extracellular release was independent of O_2 (Burris 1977).

Percent extracellular release by C. subcaudata was low. Other investigators have reported that PER was low (<5%) in log phase algal cultures subjected to increased O_2 concentrations (Pope 1975; Burris 1977; Birmingham et al. 1982). The low PER exhibited by C. subcaudata is not due to any loss of extracellular product due to treatment of the sample. No loss of either glycolate or glucose occurred (Table 18) due to acidification and purging. Anderson and Zuetschel (1970) reported only a small loss (< 2%) of a variety of organic compounds due to acidification and purging. Lyophilization of glycolate (Table 19) and glucose (Table 20) resulted in a loss of $\leq$ 15% of either compound and McKinley et al. (1977) reported a loss of ca. 10% of either glycolate or glucose due to lyophilization. Any residual $NaH^{14}CO_3$ absorbed by the filters would be volatilized to $^{14}CO_2$ in the presence of HCl for 2 hrs (Table 21). Thus the low PER by C. subcaudata is not due to residual $NaH^{14}CO_3$ retained in the particulate fixation.

One might speculate that PER would be higher for stationary phase

cultures of C. subcaudata under nutrient limiting conditions in addition to those that were used to mimic the aquatic environment of these antarctic lakes. Percent extracellular release was higher in stationary phase algal cultures and declining phytoplankton populations (Hellebust 1965; Huntsman 1972; Ignatiades 1973). Several investigators have reported increased values for PER in algal cultures (Ignatiades and Fogg 1973) and in natural populations (Ignatiades 1973; Berman 1976; Harris 1980; Watanabe 1980) under conditions of nutrient limitation.

In these oligotrophic lakes, concentrations of TOC and DOC were higher than in most temperate lakes of similar trophic state (Wetzel 1975). The concentrations of TOC and DOC in this study fall within the range of values reported by previous investigators (Parker et al. 1974; Parker et al. 1977; Allnutt et al. 1981). Parker et al. (1974) and Parker et al. (1977) concluded that the high levels of TOC and DOC in Lake Bonney were due to the production of organic matter by the algal community of Lake Bonney and not from sources outside of the lake.

CONCLUSIONS

In conclusion, the values of Φ for the phytoplankton of the southern Victoria Land lakes are comparable to values reported elsewhere. Determinations of Φ based upon $k_C = 0.0328$ show that the phytoplankton of these dimly lit lakes are among the most efficient at trapping PAR, while calculations of Φ using $k_C = 0.016$ would lead to the conclusion that the phytoplankton of these lakes are among the most efficient algae yet studied at converting PAR into carbon compounds. Other data indicate the phytoplankton were chromatically adapted to their low light environments. This would support the idea the the algae were more efficient at trapping PAR and that the use of $k_C = 0.0328$ for the calculations of Φ in these southern Victoria Land lakes is a more valid choice. The comparison of values of Φ' to ε indicate that environmental conditions are limiting the phytoplankton communities of these lakes.

Percent extracellular release was higher in the shallower waters of Lakes Fryxell and Hoare and very high in the shallow waters of Lake Vanda. The shallow waters of these lakes are brighter, supersaturated with oxygen and probably nutrient deficient. These conditions favor the occurrence of photorespiration in algae and photorespiration could account for the high values of PER measured in the shallower waters. It is not known if these values of PER are due to inhibition of photosynthesis, increased rates of extracellular release or a combination of both. Photosynthesis in C. subcaudata, which occurred in all of the Taylor Valley lakes, was inhibited by oxygen under conditions that

mimic the aquatic environments of the southern Victoria Land lakes. Percent extracellular release was higher under supersaturated oxygen but was lower than observed *in situ*. The inhibition of photosynthesis could not be attributed to an increase in the release of extracellular product by log phase cultures of a planktonic alga *C. subcaudata*. The occurrence of higher values of PER in the shallower waters of the studied lakes and the inhibition of photosynthesis in *C. subcaudata* by supersaturated oxygen supports to some extent the hypothesis that photorespiration does occur in antarctic lake phytoplankton. The occurrence of photorespiration may even inhibit the development of the phytoplankton communities of these lakes at times.

LITERATURE CITED

Allen, H. A. 1973. Production and utilization of dissolved organic carbon during *in situ* phytoplankton photosynthesis measurements. Int. Rev. ges. Hydrobiol. 58: 843-849.

Allnutt, F. C. T., B. C. Parker, K. G. Seaburg, and G.M. Simmons, Jr. 1981. *In situ* nitrogen (C_2H_2) fixation in lakes of southern Victoria Land, Antarctica. Hydrobiol. Bull. 15: 99-109.

Anderson, G. C., and R. P. Zeutschel. 1970. Release of dissolved organic matter by marine phytoplankton in coastal and offshore areas of the North-East Pacific Ocean. Limnol. Oceanogr. 15: 402-407.

Angino, E. A., K. B. Armitage, and J. C. Tash. 1962. Chemical stratification in Lake Fryxell, Victoria Land, Antarctica. Science (Wash.) 138: 34-35.

_____, _____, and _____. 1964. Physico-chemical limonology of Lake Bonney, Antarctica. Limnol. Oceanogr. 9: 207-217.

Anonymous. 1976. Standard methods for the examination of water and wastewater. American Public Health Association.

Armitage, K. G., and H. B. House. 1962. A limnological reconnaissance in the area of McMurdo sound, Antarctica. Limnol. Oceanogr. 7: 36-41.

Atlas, D., and T. T. Bannister. 1980. Dependence of mean spectral extinction coefficient of phytoplankton on depth, water color and species. Limnol. Oceanogr. 25: 157-159.

Bannister, T. T. 1974. Production equations in terms of chlorophyll concentration, quantum yield and upper limit to production. Limnol. Oceanogr. 19: 1-12.

Beardall, J., and I. Morris. 1975. Effects of environmental factors on photosynthesis in *Phaeodactylum tricornutum* (Bacillariophyceae). II. Effect of oxygen. J. Phycol. 11: 430-434.

Bell, R. A. I. 1967. Lake Miers, South Victoria Land, Antarctica. N. Z. J. Geol. Geophys. 10: 540-556.

Benoit, R., R. Hatcher, and W. Green. 1971. Bacteriological profiles and some chemical characteristics of two permanently frozen antarctic lakes, p. 281-295. In J. Cairns, Jr. (ed.). The structure and function of fresh-water microbial communities. V. P. I. and S. U.

Berman, T. 1976. Release of dissolved organic matter by photosynthesizing algae in Lake Kinneret. Freshw. Biol. 16: 13-18.

Bidwell, R. G. S. 1977. Photosynthesis and light and dark respiration in freshwater algae. Can. J. Bot. 55: 809-818.

Birmingham, B. C., J. R. Coleman, and B. Colman. 1982. Measurement of photorespiration in algae. Plant Physiol. 69: 259-262.

Black, C. C., Jr., J. E. Burris, and R. G. Everson. 1976. Influence of oxygen concentration on photosynthesis in marine plants. Aust. J. Plant Physiol. 3: 81-86.

Boswell, C. R., R. R. Brooks, and A. T. Wilson. 1967 a. Trace element content of antarctic lakes. Nature 213: 167-168.

_____, _____, and _____. 1967 b. Some trace elements in lakes of McMurdo oasis, Antarctica. Geochim. Cosmochim. Acta. 31: 731-736.

Bourrelly, P. 1966. Les algues d'eau douce. Algues vertes. Boubee and Cie.

_____. 1968. Les algues d'eau douce. Les algues jaunes et brunes. Boubee and Cie.

_____. 1970. Les algues d'eau douce. Eugleniens, Perideniens, algues rogues et algues bleues. Boubee and Cie.

Bunt, J. S. 1971. Levels of dissolved oxgen and carbon fixation by marine microalgae. Limnol. Oceanogr. 16: 564-566.

Burris, J. E. 1977. Photosynthesis, photorespiration and dark respiration in eight species of algae. Mar. Biol. 39: 371-379.

Bydder, E. L., and R. Holdsworth. 1977. Lake Vanda (Antarctica) revisted. N.Z. J. Geol. Geophys. 20: 1027-1032.

Campbell, P.J. 1978. Primary productivity of a hypersaline antarctic lake. Aust. J. Mar. Freshw. Res. 29: 717-724.

Cathey, D., B. C. Parker, G. M. Simmons, Jr., W. Yongue, and M. Van Brunt. 1981. The microfauna of algae mats and artificial substances in southern Victoria Land lakes of Antarctica. Hydrobiologia 85: 3-15.

_____, G. M. Simmons, Jr., B. C. Parker, W. Yongue, and M. Van Bunt. 1982. Protozoan colonization of artificial substances in two antarctic lakes. Trans. Amer. Microsc. Soc. 101: 353-367.

Cheng, K. H., and B. Colman. 1974. Measurements of photorespiration in some microscopic algae. Planta 115: 207-212.

Coleman, J. R., and B. Colman. 1980. Effect of oxygen and temperature on the efficiency of photosynthetic carbon assimilation in two microscopic algae. Plant Physiol. 65: 980-983.

Dubinsky, Z., and T. Berman. 1976. Light utilization efficiencies of phytoplankton in Lake Kinneret (Sea of Galilee). Limnol. Oceanogr. 21: 226-230.

_____, and _____. 1979. Seasonal changes in the spectral composition of downwelling irradiance in Lake Kinneret (Israel). Limnol. Oceanogr. 24: 652-663.

_____, and _____. 1981. Light utilization by phytoplankton in Lake Kinneret (Israel). Limnol. Oceanogr. 26: 660-670.

_____, and M. Polna. 1976. Pigment composition during a Peridinium bloom in Lake Kinneret (Israel). Hydrobiologia 51: 239-243.

Ettl, H. 1976. Die gattung Chlamydomonas Ehrenberg. Beih. Nova. Hedwigia.

Falkowski, P. G. 1981. Light shade adaptation in marine phytoplankton, p. 99-119. In P. G. Falkowski (ed.), Primary productivity in the sea. Plenum Press.

Findenegg, G. R., and K. Fischer. 1978. Apparent photorespiration of Scenedesmus obliquus: Decrease during adaptation to low CO_2 level. Z. Pflanzenphysiol. 89: 363-371.

Fogg, G. E. 1971. Extracellular products of algae in freshwater. Arch. Hydrobiol. Beih. Engeb. Limnol. 5: 1-25.

_____, and A. J. Horne. 1970. The physiology of antarctic freshwater algae, p. 632-638. In M. W. Holdgate (ed.), Antarctic ecology, V. 2. Academic Press.

_____, C. Nalewajko, and W. D. Watt. 1965. Extracelllar products of phytoplankton photosynthesis. Proc. R. Soc. Lond. Ser. B. 162: 517-534.

_____, and D. F. Westlake. 1953. The importance of extracellular products of algae in freshwater. Verh. Int. Verein. Limnol. 12: 219-232.

Goldman, C. R. 1964. Primary productivity studies in antarctic lakes. p. 291-299. In R. Carrick, M.W. Holgate and J. Pre'vost (eds.), Biologie antartique. Hermann.

_____, D. T. Mason, and J. E. Hobbie. 1967. Two antarctic desert lakes. Limnol. Oceanogr. 12: 295-310.

_____, _____, and B. J. B. Wood. 1963. Light injury and inhibition in antarctic freshwater phytoplankton. Limnol. Oceanogr. 8: 313-322.

Harris, G. P. 1980. The measurement of photosynthesis in natural populations of phytoplankton, p. 129-185. In I. Morris (ed). The physiological ecology of phytoplankton. Blackwell Scientific Publications.

_____, and J. N. A. Lott. 1973. Light intensity and photosynthetic rates in phytoplankton. J. Fish. Res. Bd. Can. 30: 1771-1778.

Hellebust, J. A. 1965. Excretion of some organic compounds by marine phytoplankton. Limnol. Oceanogr. 10: 192-206.

_____. 1974. Extracellular products, p. 838-865. In W. P. D. Stewart (ed.), Algal physiology and biochemistry. Blackwell Scientific Publications.

Henry, C. H., A. T. Wilson, K. B. Popplewell, and D. A. House. 1977. Dating of geochemical events in Lake Bonney, Antarctica, and their relation to glacial and climate changes. N. Z. J. Geol. Geophyrs. 20: 1103-1122.

Hoare, R. A. 1968. Thermocline convection in Lake Vanda, Antarctica. J. Geophys. Res. 73: 607-612.

_____, K. B. Popplewell, D. A. House, R. A. Henderson, W. M. Prebble, A. T. Wilson. 1965. Solar heating of Lake Fryyell, a permanently ice-covered antarctic lake. J. Geophys. Res. 70: 1555-1558.

Hoehn, R. C., B. C. Parker, R. D. Fortner, B. L. Weand, J. A. Craft, L.S. Lane, R. W. Stavros, H. G. Sugg, and J. T. Whitehurst. 1977. Nitrogen and phosphorus availability to plankton and benthic communities in Lake Bonney, southern Victoria Land, Antarctica, p. 859-872. In G. A. Llano (ed.), Adaptations within antarctic ecosystems. Gulf Publishing.

Huntsman, S. A. 1972. Organic excretion by Dunaliella tertiolecta. J. Phycol. 8: 59-63.

Ignatiades, L. 1973. Studies on the factors affecting the release of organic matter by Skeletonema costatum (Greville) Cleve. in field conditions. J. Mar. Biol. Ass. U.K. 53: 923-935.

_____, and G. E. Fogg. 1973. Studies on the factors affecting the release of organic matter by Skeletonema Costatum (Greville) Cleve. in culture. J. Mar. Biol. Ass. U. K. 53: 937-956.

Jewson, D. H. 1977. Light penetration in relation to phytoplankton content of the euphotic zone of Lough Neagh (Northern Ireland). Oikos 28: 74-83.

Jones, L. M., and G. Faure. 1967. Origin of the salts in Lake Vanda, Wright Valley, southern Victoria Land, Antarctica. Earth Planet. Sci. Lett. 3: 101-106.

_____, and _____. 1968. Origin of the salts in Taylor Valley. Antarct. J. U.S. 3: 177-178.

Kerry, K. R., D. R. Grace, R. Williams, and H. R. Burton. 1977. Studies on some saline lakes of the Vestfold Hills, Antarctica, p. 839-858. In G. A. Llano (ed.), Adaptations within antarctic ecosystems. Gulf Publishing.

Kirk, J. T. 1975 a. A theoritical analysis of the contribution of algal cells to the attenuation of light within natural waters. 1. General treatment of pigmented cells. New Phytol. 75: 11-20.

_____. 1975 b. A theoritical analysis of the contribution of algal cells to the attenuation of light within natural waters. 2. Spherical cells. New Phytol. 75: 21-36.

_____. 1976. A theoritical analysis of the contribution of algal cells to the attenuation of light within natural waters. 3. Cylindrical and spheroidal cells. New Phytol. 77: 341-358.

Kok, B. 1960. Efficiency of photosynthesis, p. 563-633. In W. Ruhland (ed.), Hanbuch der pflanzenphysiologie, v. 5, p. 1. Springer.

Koob, D. D., and G. L. Leister. 1972. Primary productivity and associated physical, chemical and biological characteristics of Lake Bonney, a perennially ice-covered lake in Antarctica, p. 51-68. In G.A. Llano (ed.), Antarct. Res. Ser. 20. American Geophysical Union.

Lane, L. S. 1977. Microbial community fluctuations in a meromictic, antarctic lake. Hydrobiologia 55: 187-190.

Lee, K., and C. Nalewajko. 1978. Photosynthesis, extracellular release and glycolic acid uptake by plankton: fractionation studies. Verh. Int. Verein. Limnol. 29: 257-262.

Light, J. J. 1977. Production and periodicity of antarctic freshwater phytoplankton, p. 829-837. In G.A. Llano (ed.), Adaptations within antarctic ecosystems. Gulf Publishing.

_____, J. C. Ellis-Evans, and J. Priddle. 1981. Phytoplankton ecology in an antarctic lake. Freshw. Biol. 11: 11-26.

Lloyd, N. D. H., D. T. Canvin, and D. A. Culver. 1977. Photosynthesis and photorespiration in algae. Plant Physiol. 59: 936-940.

Love, F. G., G. M. Simmons, Jr., R. A. Wharton, Jr., B. C. Parker, and K. G. Seaburg. 1983. Modern Conophyton - like algal mats discovered in Lake Vanda, Antarctica. Geomicrobiol. J. 3: 33-48.

MacNamura, E. E. 1970. Some limnological observations from Enderby Land, Antarctica. Limnol. Oceanogr. 15: 768-775.

Matsubaya, O., H. Sokai, T. Torii, H. Burton, and K. Kerry. 1979. Antarctic saline lakes - stable isotopic ratios, chemical compositions and evolution. Geochim. Cosmochim. Acta. 43: 7-25.

McKinley, K. R., A. K. Ward, and R. G. Wetzel. 1977. A method for obtaining more precise measures of excreted organic carbon. Limnol. Oceanogr. 22: 570-573.

Menzel, D. W., and R. F. Vaccaro. 1964. The measurement of dissolved organic and particulate carbon in sea water. Limnol. Oceanogr. 9: 138-142.

Midell, A. T., B. C. Parker, and G. M. Simmons, Jr. 1984. Response of an antarctic lake heterotrophic community to high dissolved oxygen. Appl. Environ. Microbiol. 47: 1062-1066.

Morel, A. 1978. Available, usable, and stored radiant energy in relation to marine photosynthesis. Deep-Sea Res. 25: 673-688.

Nalewajko, C. 1966. Photosynthesis and excretion in various plankton algae. Limnol. Oceanogr. 11: 1-10.

_____, and D. R. S. Lean. 1972. Growth and execretion in planktonic algae and bacteria. J. Phycol. 8: 361-366.

_____, and L. Marin. 1969. Extracellular production in relation to the growth of four planktonic algae and of phytoplankton populations from Lake Ontario. Can. J. Bot. 47: 405-413.

_____, and D. W. Schindler. 1976. Primary production, extracellular release and heterotrophy in two lakes in the ELA northwestern Ontario. J. Fish. Res. Bd. Can. 33: 219-226.

Nauwerck, A., 1963. Die beziehungen zwischen zooplankton and phytoplankton in see erken. Symb. Bot. Ups. 11: 11-26.

Nichols, H .W. 1973. Growth media-freshwater, p. 7-24. In J. R. Stein (ed.), Handbook of phycological methods. I. Culture Methods and Growth Measurements. Cambridge University Press.

Parker, B. C., and G. M. Simmons, Jr. 1981. Biogeochemical cycles in antarctic oasis lakes. Trends in Biochemistry 6: 3-4.

_____, and R. A. Wharton, Jr., 1985. Physiological ecology of bluegreen algal mats (modern stromatolites) in antarctic oasis lakes. Archiv. Hydrobiol. 71: 331-348.

_____, J. T. Whitehurst, and R. C. Hoehn. 1974. Observations of in situ concentrations and production of organic matter in an antarctic meromictic lake. Virg. J. Sci. 25: 136-140.

_____, G. M. Simmons, Jr., K. G. Seaburg, and R. A. Wharton, Jr. 1980. Ecosystem comparisons of oasis lakes and soils (ECOLS). Antarct. J. U. S. 15: 167-170.

_____, _____, F. G. Love, K. G. Seaburg, and R. A. Wharton, Jr. 1981. Modern stromatolites in antarctic dry valley lakes. Bioscience 31:656-661.

_____, _____, K. G. Seaburg D. D. Cathey, and F. C. T. Allnutt. 1982 a. Comparative ecology of plankton communities in seven antarctic oasis lakes. J. Plank Res. 4: 271-286.

_____, _____, R. A. Wharton, Jr., K. G. Seaburg, and F. G. Love. 1982 b. Removal of organic and inorganic matter from antarctic lakes by aerial escape of bluegreen algal mats. J. Phycol. 18: 72-78.

_____, R. C. Hoehn, R. A. Paterson, J. A. Craft, L. S. Lane, R. W. Stavros, H. G. Sugg, J. T. Whitehurst, R. D. Fortner, and B. L. Weand. 1977. Changes in dissolved organic matter, photosynthetic production and microbial community composition in Lake Bonney, southern Victoria Land, Antarctica, p. 873-890. In G. A. Llano (ed.), Adaptations within antarctic ecosystems. Gulf Publishing.

Platt, T., and A. D. Jassby. 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. J. Phycol. 12: 421-430.

Pope, D. H. 1975. Effects of light intensity, oxygen concentration and carbon dioxide concentration on photosynthesis in algae. Microbial Ecol. 2: 1-16.

Rabinowitch, E. I., and R. Govindjee. 1969. Photosynthesis. John Wiley.

Ragotzkie, R. A., and G. E. Likens. 1964. The heat balance of two antarctic lakes. Limnol. Oceanogr. 9: 412-425.

Samsel, G. L., Jr., and B. C. Parker. 1971. Comparisons of two antartic lakes with different trophic states. Virg. J. Sci. 22: 177-182.

_____, and _____. 1972. Limnological investigations in the areas of Anvers Island, Antarctica. Hydrobiologia 40: 505-511.

Saunders, G. W., F. B. Trama, and R. W. Bachmann. 1962. Evaluation of a modified ^{14}C technique for shipboard estimation of photosynsynthesis in large lakes. Publ. Great Lakes Res. Div. 8. Univ. Mich.

K. G. Seaburg, B. C. Parker, G. W. Prescott, and L. A. Whitford. 1979. The algae of southern Victoria Land, Antarctica. J. Cramer.

_____, _____, and G. M. Simmons, Jr. 1981. Temperature-growth responses of algal isolates from antarctic oasis. J. Phycol. 17: 353-360.

_____, _____, _____., R. A. Wharton, Jr., and M. Kaspar. In press. Phosphorus-A major limiting nutrient for antarctic dry valley lakes. Polar Biol.

Sharp, J. H. (1977). Excretion of organic matter by marine phytoplankton. Do healty cells do it? Limmol. Oceanogr. 22: 381-399.

Shoaf, W. T., and B. W. Lium. 1976. Improved extraction of chlorophyll a and b from algae using dimethyl sulfoxide. Limnol. Oceanogr. 21: 926-928.

Simmons, G. M., Jr., R. A. Wharton, Jr., B. C. Parker, and D. T. Andersen. 1983. Chlorophyll a and adenosine triphosphate levels in antarctic and temperate lake sediments. Microbiol Ecol. 9: 123-135.

_____, B. C. Parker, F. C. T. Allnutt, D. P. Brown, D. D. Cathey, and K. G. Seaburg. 1979. Ecosystem comparisons of oasis lakes and soils. Antarct. J. U. S. 14: 181-183.

Smith, D. F., and W. J. Wiebe. 1976. Constant release of photosynthate from marine phytoplankton. Appl. Environ. Microbiol. 32: 75-79.

Talling, J. F., R. B. Wood, M. V. Prosser, and R. M. Baxter. 1973. The upper limit of photosynthetic productivity by phytoplankton: evidence from Ethiopian soda lakes. Freshw. Biol. 3: 53-76.

Thomas, J. P. 1971. Release of dissolved organic matter from natural populations of marine phytoplankton. Mar. Biol. 11: 311-323.

Tilzer, M. M., and C. R. Goldman. 1978. Importance of mixing, thermal stratification and light adaptation for phytoplankton productivity in Lake Tahoe (California-Nevada). Ecology 59: 810-821.

_____, and A. J. Horne. 1979. Diel pattern of phytoplankton productivity and extracellular release in ultraoligotrophic Lake Tahoe. Int. Revue ges. Hydrobiol. 64: 157-176.

_____, and K. Schwartz. 1976. Seasonal and vertical patterns of phytoplankton light adaptation in a high mountain lake. Arch. Hydrobiol. 77: 488-504.

_____, C. R. Goldman, and E. Amezaga. 1975. The efficiency of photosynthetic light energy utilization by lake phytoplankton. Verh. Int. Verein. Limnol. 19: 800-807.

Tolbert, N. E. 1974. Photorespiration, p. 474-504. In W. P. D. Stewart (ed.), Algal physiology and biochemistry. Blackwell Scientific Publications.

Tominago, H. 1977. Photosynthetic nature and primary productivity of antarctic freshwater phytoplankton. Jap. J. Limnol. 38: 122-130.

Torii, T., N. Yamagata, S. Nakaya, S. Murata, T. Hashimoto, O. Matsubaya, and H. Sakai. 1975. Geochemical aspects of the McMurdo saline lakes with special emphasis on the distribution of nutrient matters, p. 5-29. In T. Torii (ed.) Geochemical and geophysical studies of dry valleys, Victoria Land, Antarctica. National Institute of Polar Research, Japan.

Tyler, J. E. 1975. The in situ quantum efficiency of natural phytoplankton populations. Limnol. Oceanogr. 20: 976-980.

Utermohl, H. 1958. Zur vervollkommung der quantitative phytoplanktonmetodik. Mitt. Int. Ver. Limnol. 9: 1-38.

Vincent, W. F. 1981. Production strategies in antarctic inland waters: phytoplankton eco-physiology in a permanently ice-covered lake. Ecology 62: 1215-1224.

_____, M. T. Downes, and C. L. Vincent. 1981. Nitrous oxide cycling in Lake Vanda, Antarctica. Nature 292: 618-620.

Watanabe, Y. 1980. A study of the excretion and extracellular products of natural phytoplankton in Lake Nakanuma, Japan. Int. Revue. ges. Hydroiol. 65: 809-834.

Watt, W. D. 1966. Release of dissolved organic material from the cells of phytoplankton populations. Proc. R. Soc. Lond. Ser. B. 164: 521-551.

Welschmeyer, N. A., and C. J. Lorenzen. 1981. Chlorophyll-specific photosynthesis and quantum efficiency at subsaturating light intensities. J. Phycol. 17: 283-293.

Wetzel, R. G. 1975. Limnology. W. B. Saunders.

_____, and G. E. Likens. 1979. Limnological analysis. W. B. Saunders.

Wharton, R. A., Jr., B. C. Parker, and G. M. Simmons, Jr. 1983. Distribution, species composition, and morphology of algal mats (stromatolites) in antarctic dry valley lakes. Phycologia 22: 355-365.

_____, _____, _____, K. G. Seaburg and F. G. Love. 1982. Biogenic calcite structures forming in Lake Fryxell, Antarcitca. Nature 295: 403-405.

Wiebe, W. J., and D. F. Smith. 1977. ^{14}C-Labeling of the compounds excreted by phytoplankton for employment as a realistic tracer in secondary productivity measurements. Microbiol Ecol. 4: 1-8.

Williams, P. J. Le B. and C. S. Yentsch. 1976. An examination of photosynthetic production, excretion of photosynthetic products, and heterotrophic utilization of dissolved organic compounds with reference to results from a coastal subtropical sea. Mar. Biol. 35: 31-40.

Wilson, A. T. 1979. Geochemical problems of the antarctic dry areas. Nature 280: 205-208.

_____, and D. W. Wellman. 1962. Lake Vanda: an antarctic lake. Nature 196: 1171-1173.

Wodehouse, E. B., and B. C. Parker. 1981. Atmospheric ammonia-nitrogen: The cause of eutrophication of fresh-water antarctic ecosystems. Antarct. Res. Ser. 30: 155-167. American Geophysical Union.

Wright, R. T. 1964. Dynamics of a phytoplankton community in an ice-covered lake. Limnol. Oceanogr. 9: 163-178.

Yentsch, C. S., and D. W. Menzel. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res. 10: 221-231.

The vita has been removed from the scanned document