Spatial and temporal variations of phytoplankton populations in Lake Bonney, Antarctica
by Nicole Lea Tursich

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Land Resources and Environmental Sciences
Montana State University

Abstract:
Quantitative comparisons of phytoplankton collected during the austral summers from 1989 to 2000 were conducted for the east and west lobes of Lake Bonney. The objectives of this research were to identify and enumerate the phytoplankton populations present and determine vertical and temporal differences. Phytoplankton identified in both the lobes of the lake included those observed in earlier analyses by previous investigators. Chlamydomonas subcaudata, Chroomonas sp., and Ochromonas sp. were the dominant phytoplankton genera in both lobes. These phytoplankton genera comprised >95% of the biomass and were located in distinct layers down the water columns. The biomass of Chlamydomonas subcaudata was significantly higher in the lower water column than in the upper water columns ($p>0.05$) in the lakes. The biomass of Chroomonas sp. was significantly higher in the upper water column than in the lower water column ($p>0.05$). Ochromonas sp. biomass was not significantly different between the upper and lower columns in the west lobe but was significantly higher in the lower water column in the east lobe ($p>0.05$). Certain physiological characteristics of the phytoplankton populations (i.e. ratios of phytoplankton carbon to chlorophyll a and to primary productivity) in the distinct layers also differed significantly between the upper and lower water columns of the lakes ($p>0.05$). Relationships between Lake Bonney’s phytoplankton carbon to primary production and chlorophyll a were not determined. Phytoplankton population shifts occurred in the lobes. Chroomonas sp. and Ochromonas sp. biomass changed from 1989 to 2000, whereas Chlamydomonas subcaudata biomass showed no significant changes from 1989-2000.

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of

Master of Science

in

Land Resources and Environmental Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 2003

APPROVAL

of a thesis submitted by

Nicole Lea Tursich

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

Dr. John C. Priscu John C Priscu 18 July 03
(Signature) Date

Approved for the Department of Land Resources and Environmental Sciences

Dr. Jon Wraith J M Wraith 7/18/03
(Signature) Date

Approved for the College of Graduate Studies

Dr. Bruce McLeod Bruce R. McLeod 7-28-03
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ACKNOWLEDGMENTS

During the course of this study, I depended on many people for their knowledge, experience, help, and understanding. I would like to thank everyone who contributed to the development of this thesis.

Special thanks to my advisor, Dr. John Priscu who was the driving force for the development of the project and product. Thank you for giving me the opportunity to study in Antarctica and be a part in the Long-Term Ecological Research network.

Dr. Christine Foreman you are a mentor and a friend. Your attention to details has assisted me enormously during the course of this study. I would not have been able to finish without your support and guidance.

Craig Wolf, thank you for sharing your knowledge of the lake ecosystems and developing the phytoplankton species database, without which the data would still be in notebooks scattered in the lab collecting dust.

Jill Mikucki, thanks for your support and understanding. Your novel ideas have helped my thesis come together. Thanks for being a great listener and friend.

I could not have finished my thesis without the support and understanding of friends and family. I am very grateful and indebted to my parents for their understanding, patience, support, interest, and love.

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ABSTRACT

Quantitative comparisons of phytoplankton collected during the austral summers from 1989 to 2000 were conducted for the east and west lobes of Lake Bonney. The objectives of this research were to identify and enumerate the phytoplankton populations present and determine vertical and temporal differences. Phytoplankton identified in both the lobes of the lake included those observed in earlier analyses by previous investigators. *Chlamydomonas subcaudata*, *Chroomonas sp.*, and *Ochromonas sp.* were the dominant phytoplankton genera in both lobes. These phytoplankton genera comprised >95% of the biomass and were located in distinct layers down the water columns. The biomass of *Chlamydomonas subcaudata* was significantly higher in the lower water column than in the upper water columns ($p>0.05$) in the lakes. The biomass of *Chroomonas sp.* was significantly higher in the upper water column than in the lower water column ($p>0.05$). *Ochromonas sp.* biomass was not significantly different between the upper and lower columns in the west lobe but was significantly higher in the lower water column in the east lobe ($p>0.05$). Certain physiological characteristics of the phytoplankton populations (i.e. ratios of phytoplankton carbon to chlorophyll *a* and to primary productivity) in the distinct layers also differed significantly between the upper and lower water columns of the lakes ($p>0.05$). Relationships between Lake Bonney's phytoplankton carbon to primary production and chlorophyll *a* were not determined. Phytoplankton population shifts occurred in the lobes. *Chroomonas sp.* and *Ochromonas sp.* biomass changed from 1989 to 2000, whereas *Chlamydomonas subcaudata* biomass showed no significant changes from 1989-2000.

CHAPTER 1

INTRODUCTION

The National Science Foundation established the McMurdo Dry Valleys' Long-Term Ecological Research (LTER) project in 1993 to assess physical and biological constraints on aquatic and terrestrial ecosystems on the planet's coldest, driest desert (MCM-LTER-Site-Review 2001). The McMurdo Dry Valleys are located near McMurdo Sound, Antarctica 77°00'S 162°52'E, and form the largest ice-free region (~4800 km^2) in Antarctica. Within the McMurdo Dry Valley ecosystems, confounding variables such as higher order plant vegetation and predators have no impact. Climate predominantly affects these ecosystems (Chinn 1993; Wharton, et al. 1993; Fountain, et al. 1999; Priscu, et al. 1999). A recent study on long-term (1989-2000) data collected by the LTER showed that the McMurdo Dry Valley ecosystems are highly sensitive to small variations in climate (Doran, et al. 2002).

This study investigates the phytoplankton populations present in perennially ice covered Lake Bonney. Lake Bonney is located in the Taylor Valley, one of the McMurdo Dry Valleys. Three main lakes located in the Taylor Valley include Lakes Fryxell, Hoare, and Bonney. A sill located 13 m below the surface of the water separates Lake Bonney into two lobes: an east lobe and a west lobe. Phytoplankton samples were collected from the east and west lobes of Lake Bonney during the austral summers (October-January) from 1989 to 1991 and during the LTER study from 1993 to 2000. Phytoplankton samples collected during 1993 were not used in this study since another investigator analyzed the data and no samples were available for comparisons. Previous studies on the phytoplankton populations in Antarctic lakes did not have the advantage of a long-term data set in which to study annual variations in phytoplankton populations. This study documents the phytoplankton populations present in the east and west lobes of Lake Bonney from 1989 to 2000.

Interrelations Among Chapters

Chapter 1 offers background and an introduction to material that will be presented in the following chapters. Chapter 1 describes the methods used for data collection by the LTER study. Chapters 2, 3, and 4 are assemblages of my research on Lake Bonney.

Chapter 2 highlights the taxonomic divisions significant to this study. Techniques on how the phytoplankton populations were identified are also presented in this chapter. Lastly, Chapter 2 determines the dominant taxa and their relevance in certain environments. Chapter 3 describes the vertical locations of the phytoplankton populations and discusses the characteristics of the phytoplankton populations relative to their vertical locations. Chapter 4 determines long-term changes in the phytoplankton populations. Chapter 5 summarizes all the conclusions generated from the data analyzed in this thesis and gives direction for continued research on the phytoplankton populations in the lobes of Lake Bonney, Antarctica.

Background

Few characteristics encompass all phytoplankton species, yet many attempts have been made at a concise definition for phytoplankton. Plankton refers to living suspended material. “Phyto” comes from Latin word “phyton” meaning tree, which insinuates that phytoplankton are autotrophic. However, not all phytoplankton species are autotrophic, which means they are able to convert CO_2 into usable forms of carbon for metabolism (Sournia 1978). Some phytoplankton species are capable of ingesting dissolved and particulate organic carbon for metabolism. This process of ingesting carbon for energy is referred to as mixotrophy. Mixotrophic species can photosynthesize, as well as use either osmotrophy or phagotrophy for sustenance. Osmotrophy is the ability of organisms to obtain dissolved organic carbon through their cell walls. Heterotrophic species exhibit both phagotrophy and osmotrophy. The definition of phytoplankton used in this study is the following: Phytoplankton species are suspended aquatic organisms that contain chlorophyll a, and are structurally less complex than land plants; they are non-vascular (Graham and Wilcox 2000).

Studies on phytoplankton species would not be possible today if it were not for the advent of several important discoveries. First was that of Anthony Van Leeuwenhoek who discovered marine microorganisms in 1676 (South and Whittick 1987). Two centuries later, Joseph Hooker examined green water on Antarctic ice in the Southern Ocean and realized that the green water contained plant-like organisms (South and Whittick 1987). Viktor Hensen coined the term "planktona" in 1887 and was the first to obtain quantitative estimates of phytoplankton (Morris 1980). During this same time, Forbes published "The Lake as a Microcosm" and described the roles phytoplankton populations play in freshwater lakes of Illinois (Forbes 1887). Einar Naumann, in 1919, introduced concepts of freshwater phytoplankton ecology (Fritsch 1931). By the middle of the 20th century, studies included the use of physiochemical parameters to investigate the features of phytoplankton ecology (Strickland and Parsons 1972). A major advance in the study of phytoplankton populations included the carbon-14 (^{14}C) method developed by Steeman Neilsen (1951) to measure phytoplankton photosynthesis (Banse 2002).

Background on Polar Systems

Polar systems include those environments in Arctic and Antarctic regions above 66° latitude. Low temperatures, minimal precipitation, and high winds define these extreme environments. Solar radiation, katabatic winds, and cloud cover have large effects on temperature. An increase in solar radiation during July and January in the Northern and Southern Hemispheres, respectively, generates annual temperature maxima. The temperature maxima in both Arctic and Antarctic systems rarely exceed 10°C (Stonehouse 1989). Polar systems annually receive about 40% as much solar radiation as equatorial regions. Of this small amount of solar radiation, 89-90% is reflected back into the atmosphere (Stonehouse 1989). This high percentage of reflectivity is a result of the polar system's ice and snow cover (Stonehouse 1989).

Despite certain similarities between the two polar regions there are several differences. One major difference between the Arctic and Antarctic is that Antarctica has remained cold for ~14 million years whereas the Arctic has remained cold for 3 million years (Wienke, et al. 1994). Another difference between the environments is their elevation. The mean elevation of Antarctica is ~2000 m, the highest mean elevation on the earth's surface of all the continents. This elevation difference contributes to the colder climate of Antarctica compared to the Arctic. Every 100 m rise in elevation causes air temperatures to fall approximately 1°C up to 2000 m, 1.27°C from 2000-3000 m, and at higher elevations there are greater rates of decreasing temperature (Stonehouse 1989). Antarctic systems are also distinct from Arctic systems because of the isolation of this continent from other landmasses (Stonehouse 1989).

Marine and Freshwater Polar Systems

Low irradiance, low temperatures, and high variability characterize marine environments in polar systems. The angle of the sun rarely exceeds 45° in polar systems (Stonehouse 1989). Light levels are determined by the vertical mixing of water columns, ice cover formation, and the vertical attenuation of light (Palmisano and Sullivan 1982; Gallegos, et al. 1983; Cota 1985). The ice covers fluctuate seasonally affecting the amount of irradiance reaching the organisms present under the ice cover and mixing depth. Polar marine environments have temperatures in the range of -1.8° to 2°C (Kirst and Wiencke 1995). The lower the mixing depth the greater the circulation of nutrients for the organisms present in the marine polar systems.

Melting glaciers in the polar environments and small amounts of precipitation create streams (Fountain, et al. 1998). These streams provide most of the freshwater in polar lakes and ponds (Fountain, et al. 1998). Polar lakes and ponds are partly or completely frozen and ice covered for most or all of the year. Large lakes maintain their surface ice cover for all or part of the year. Partial thawing does occur along the edges of the lakes; these areas are referred to as moats. Small ponds tend to thaw completely.

Background on the McMurdo Dry Valleys, Antarctica

The McMurdo Dry Valleys encompass the largest ice-free area on the continent (4800 km^2) (Figure 1.1) and are considered a cold desert environment. The average annual temperature is -20°C, and the mean annual precipitation is <10 cm yr^{-1} (Table 1.1). High winds create an even colder environment. The soil temperatures at 10 cm are widespread from the highest at 16.7°C to the lowest at -53.5°C. The mean soil temperature at Lake Bonney was recorded to be ~ -16.6°C and the soil is permanently frozen at 30 cm beneath the surface (Freckman and Virginia 1998).

Victoria, Wright, and Taylor are just a few of the McMurdo Dry Valleys that contain some of the most unique lakes in the world (Figure 1.2). The Taylor Valley in the McMurdo Dry Valley regions of Southern Victoria Land, Antarctica extends from McMurdo Sound to the end of the Taylor Glacier (Figure 1.2). Lakes Fryxell, Hoare, and Bonney are located in the Taylor Valley.

Characteristics of Lake Bonney

Lake Bonney is the largest ice covered lake in the Taylor Valley with an area of 4km^2. This lake is at the head of the Taylor Valley 77°43'S latitude, 162°23'E longitude. Lake Bonney is characterized by a long narrow depression at the western end of the Taylor Valley (Figure 1.3). A 12 to 13 m deep sill separates the deep waters of Lake Bonney into two lobes, east, and west. The east lobe of Lake Bonney encompasses an area of 3.3 km^2 and is ~37 m deep. The east lobe extends a length of 4.8 km with a maximum width of 0.9 km. The west lobe of Lake Bonney encompasses an area of 0.99 km^2 with a length of 2.6 km, width 0.9 km, and maximum depth of 40 m. The lobes of

Lake Bonney are characterized as closed basin lakes because of the absence of water outflow from the lakes.

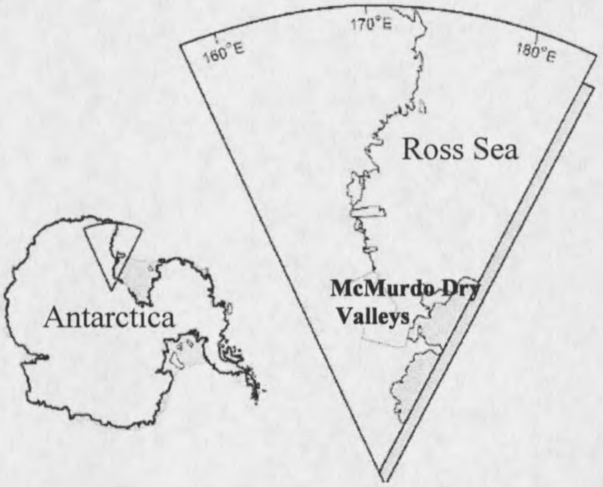


Figure 1.1 Locations of McMurdo Dry Valleys in Southern Victoria Land, Antarctica. The McMurdo Dry Valleys occupy the largest ice -free areas on the continent, encompassing an area of 4800 m^2. (Adapted from the National Science Foundation's color map of the McMurdo Dry Valleys (http://huey.colorado.edu/LTER))

Stratification

The permanent ice covers limit wind-induced mixing within the east and west lobes that, along with lake chemistry, help to stratify the lakes. Limited mixing occurs in the moat regions (Spigel and Priscu 1998). The moats are formed along the perimeters of the lakes where shallow areas have warmed enough during the austral summers to allow the melting of the ice covers. Currents generated by turbulence from stream inflows or density differences at the moat regions seldom disturb the vertical columns (Spigel and Priscu 1998). The salinity profiles in the lobes of Lake Bonney begin with freshwater values and increase down the water column to water 4 times saltier than the sea in the bottom depths. The increase in salinity down the water column creates chemoclines in the lobes of Lake Bonney.

Table 1.1 Climatic averages and extremes for Taylor, Wright, and Victoria Valley in Southern Victoria Land, Antarctica. The average soil temperature is –26.1° C, with widespread temperature ranges. (Data after Doran, et al. 1995)

McMurdo Dry Valleys	**Taylor**			**Wright**		**Victoria**
Air Temperature (°C)	Bonney	Hoare	Fryxell	Vanda	Brownsworth	Vida
Average mean annual	-17.9	-17.7	-20.2	-19.3	-20.9	-27.6
Absolute maximum	9.0	10.0	9.2	10.0	8.2	8.1
Absolute minimum	-47.9	-45.4	-60.2	-53.7	-51.9	-65.7
Soil temp @ 10 cm (°C)						
Average mean annual	-16.6	-18.8	-17.5	-19.6	-20.0	-25.4
Absolute maximum	16.7	4.2	7.0	7.8	8.2	5.2
Absolute minimum	-46.0	-37.8	-45.0	-48.5	-45.2	-53.5
Wind speed (m/s)						
Average mean annual	3.9	2.8	3.1	4.1	3.1	2.5
Maximum	35.6	36.3	37.8	35.3	32.0	32.3

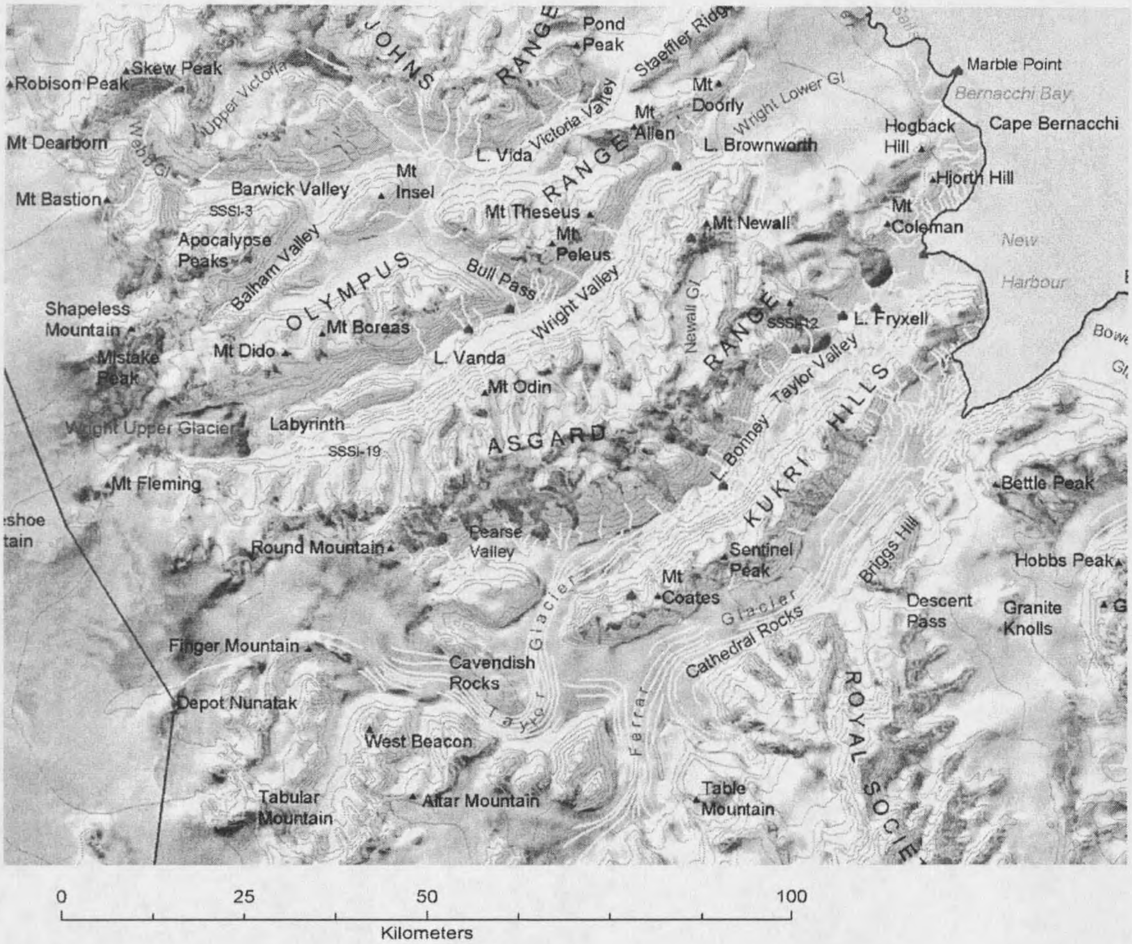


Figure 1.2 Map showing the locations of Victoria, Wright, and Taylor valleys within the McMurdo Dry Valleys in Southern Victoria land, Antarctica. Taylor Valley extends from the Taylor glacier to McMurdo Sound. Ice covered lakes are located within all three of these valleys. (Adapted from the National Science Foundations color map of the McMurdo Dry Valley region (http://huey.colorado.ledu/LTER))

Temperature

Temperature profiles do not influence the density stratification to the extnent that salts do in the east and west lobes of Lake Bonney (Spigel and Priscu 1998). Temperatures increase down the water column to a certain depth, then decrease again to the bottom of the lakes. Minimum temperatures have been recorded of -5°C in the bottom of the west lobe of Lake Bonney (Spigel and Priscu 1998). These low temperatures of water are possible due to the high amounts of salinity associated with the bottom waters. Annual temperatures remain relatively constant because of the ice cover, limiting heat loss and heat gain throughout the year.

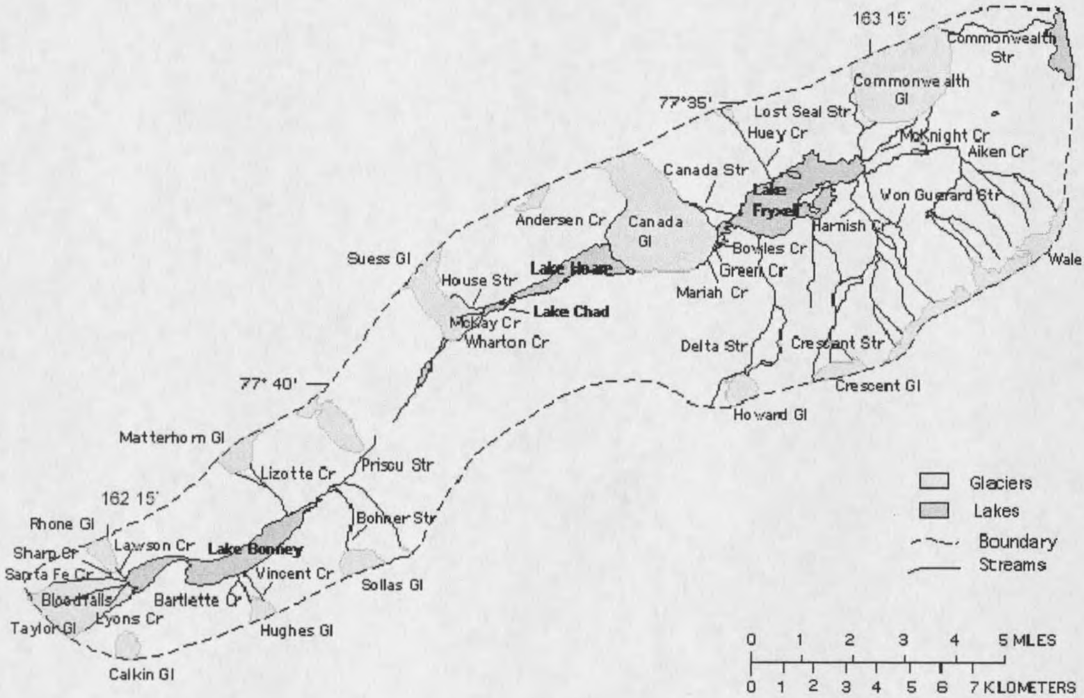


Figure 1.3 Image of the Taylor Valley showing the location of the lakes, streams, and glaciers present. Lake Bonney is the largest ice-covered lake in the Taylor Valley with an area of 4 km^2. This lake is located at the head of the Taylor Valley 77◦43'S latitude, 162◦23'E longitude (Adapted from Lyons et al. 1998)

Light

Incident irradiance in the east and west lobes of Lake Bonney is limited by the ice cover. The ice covers limit irradiance beneath the ice from 1-3% of incident irradiance

(Priscu 1991; Lizotte and Priscu 1992). Maximum irradiance in the ice cover on east lobe of Lake Bonney ranged from 1000 μmol photons m^{-2} s^{-1} at 1m to 40 μmol photons m^{-2} s^{-1} at 4m (Fritsen and Priscu 1999). Photosynthetically active radiation (PAR) is a measurement of the amount of solar radiation available for photosynthesis (400 nm to 700 nm) in the water column. The ice cover also selectively transmits wavelengths <500 nm (Lizotte and Priscu 1992). Usually, the highest penetration of incident irradiance occurs in the spring and again in the fall (Fritsen and Priscu 1999). Higher light penetration occurs in the spring and fall as a result of early and late season ice being more transparent to certain wavelengths of light because of the lack of snow on the ice and fewer ice bubbles (Fritsen and Priscu 1999). Maximum irradiance at 10 m in the water column reached only 6 μmol photons m^{-2} s^{-1} during November and February (1998) (Fritsen and Priscu 1999). In Lake Bonney, the maximum amount of PAR reached ~50 μmol photons m^{-2} s^{-1} beneath the surface of the ice (Priscu 1991; Lizotte and Priscu 1992).

Nutrients

Nitrogen and phosphorus concentrations are low in the upper water columns and increase at 15 m to the bottom of the lobes of Lake Bonney (Priscu 1995). The nutrients available for primary producers move up the chemocline by molecular diffusion to the upper depths (Priscu 1995). Phosphorus has been shown to be a limiting factor for phytoplankton growth in Lake Bonney (Priscu 1995; Dore and Priscu 2000). The influx of melt water also provides small amounts of nutrients to the lake (Lyons, et al. 1998).

Food Web

Phytoplankton are important in the food web dynamics in the east and west lobes of Lake Bonney. The lobes have a food web consisting of microbial organisms (Laybourn-Parry 1997). The microbial organisms include mixotrophic flagellates, heterotrophic flagellates, bactivorous ciliates, flagellate-feeding ciliates, and rotifers (Laybourn-Parry 1997) (Figure 1.4). Phytoplankton populations make up a large part of the microbial loop (Laybourn-Parry 1997). Phytoplankton populations as primary producers provide food webs with a major synthesis of organic carbon (Pomeroy 1974). Other sources of organic carbon for the dissolved organic carbon (DOC) pool in Lake Bonney include viruses (Laybourn-Parry, et al. 2001), stream flow (McKnight, et al. 1993), lake ice (Priscu 1998), benthic cyanobacteria mats (Hawes and Schwarz 1999), and legacy carbon (Lyons, et al. 2000). Few species of zooplankton are present that feed on phytoplankton; and fish and invertebrates do not exist in Lake Bonney (Parker and Simmons 1985). The lakes are relatively unproductive (Lizotte, et al. 1996). Respiration by heterotrophic bacteria exceeds photosynthesis indicating that this system is net heterotrophic and a carbon dioxide sink (Priscu, et al. 1999). Phytoplankton populations are important as carbon sources in the lobes of Lake Bonney.

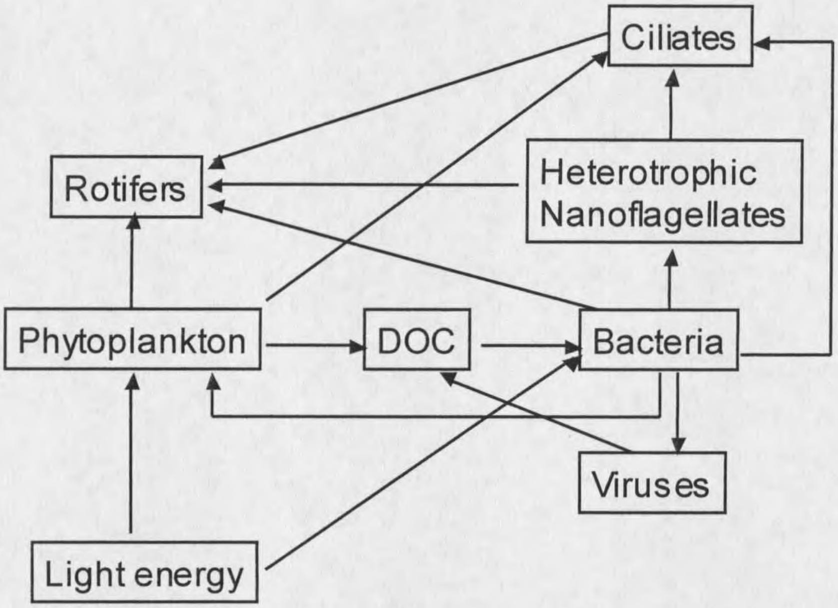


Figure 1.4 Diagram of the microbial food web present in the east and west lobes of Lake Bonney. Dissolved organic carbon pool (DOC) pool includes sources from populations of phytoplankton, bacteria, viruses, heterotrophic nanoflagellates, rotifers, and ciliates. (Adapted from Laybourne-Parry 1997)

Purpose of Study

The purpose of this study was to determine the spatial and temporal variations in the phytoplankton populations, the phytoplankton population's contributions to the carbon pool, and relationships between environmental variables and the phytoplankton populations using ~10 years of data for the east and west lobes of Lake Bonney.

Hypotheses and Objectives

Hypotheses

H1. The phytoplankton populations in Lake Bonney are vertically stratified. Each layer has distinct physiological characteristics, such as carbon to chlorophyll a ratios, and primary production to chlorophyll a ratios in response to environmental variables (stable water column, light, temperature, nutrients, and salinity).

H2. Temporal variation in phytoplankton carbon reflects changes in water column primary productivity and chlorophyll a.

H3. The percentage of phytoplankton carbon contributed to the carbon pool has remained constant over the past decade.

H4. The phytoplankton composition in Lake Bonney has remained constant over the past decade.

Objectives Corresponding to Hypotheses

H1. Identify and describe phytoplankton populations.

H1. Determine percentages of total phytoplankton carbon that each dominant phytoplankton population contributes in the vertical layers.

H1. Determine if ratios between phytoplankton carbon to chlorophyll *a* and primary productivity to chlorophyll *a* vary with depth.

H2. Evaluate decadal trends of phytoplankton carbon, primary production, chlorophyll *a*, and particulate carbon using photic zone integrated values (4.5-18 m in ELB and 4.5-20 m in WLB).

H3. Determine the percent of phytoplankton carbon that contributes to the carbon pool over time.

H4. Examine the temporal variation in the major phytoplankton divisions present in the lakes.

Methods

Lake Bonney Water Sample Collection

Lake Bonney water samples were collected from 1989 to 2000 between austral spring (late September to early October) and beginning fall (February). During this time, the lake was sampled usually every 20 to 30 days. However, samples collected from 1991 to 1992 and 1995 to 1996 field seasons were made more frequently. Collections were made near the deepest part of the lake through holes drilled in the ice. Holes were drilled using an ice auger and Jiffy ice auger power drill. Water samples were collected using a 5 l Niskin bottle at ~5 m intervals. Samples collected for measurements of chlorophyll *a*, particulate carbon and nitrogen, primary production, and phytoplankton were decanted into sampling bottles. Depths were read from the piezometric water level or water level within the sampling hole. Phytoplankton samples were collected in 500 ml dark high-density polyethylene (HDPE) bottles and preserved with acid-Lugol's solution (5 ml). The Lugol's solution contains iodine, a starch dying pigment that helps settle the algae faster by making the algae heavier. The Lugol's solution contains acetic acid, which helps preserve flagella, and formalin to preserve cell structure (APHA 1985). The samples were stored in a cold (4°C), dark incubator until analyzed.

Samples were settled to ensure all species in a sample were included in the analysis. This sedimentation process is a modification of the Utermöhl method (Utermöhl 1958). This method was developed to decrease clumping of phytoplankton cells while settling (Utermöhl 1958). One hundred mls of each sample were taken from the HDPE 500 ml bottles for quantitative analysis of phytoplankton biomass. The 100 ml sample was decanted into a graduated cylinder and covered with parafilm to eliminate wind mixing during sedimentation of the sample. Lund et al., (1958) experimentally determined relative settling time with respect to the size of the chamber that holds the water sample. For a 10 ml Utermöhl settling chamber, approximately three hours were sufficient time for sedimentation. However, a lake heavily laden with dissolved solids has a higher density than a lake without dissolved solids (Wetzel 2001), thus sedimentation time is longer for the samples from the east and west lobes of Lake Bonney.

Experiments were conducted to determine settling time for the east and west lobes of Lake Bonney using cell counts and time. Trial cell counts for 18 m and 13 m phytoplankton samples were set at 72 hr, 96 hr, 120 hr, and 144 hr. Cell number was plotted versus time (Figure 1.5). When the number of cells counted no longer increased with respect to time then complete sedimentation had been reached (Lund, et al. 1958). In Figure 1.5, the 13 m sample showed experiments determined that 120 hr was needed for complete sedimentation. For the 18 m sample, 144hr was needed for complete sedimentation (Figure 1.5). Based on the experiments each sample was settled for 144 hr in order to be consistent in the methods. Each 100 ml sample was siphoned from the top down using a pipette with a curved tip attached to a vacuum pump until 20 ml of the settled sample remained in the bottom of the graduated cylinder. The 20 ml sample was settled a second time in a 20 ml Utermöhl chamber for 1 day.

Phytoplankton Identification

A Nikon Diaphot inverted microscope with phase contrast was used to identify and enumerate the phytoplankton populations. The microscope was calibrated using a micrometer scale. The measurements of field of view, ocular micrometer, and whipple grid were calculated for all objectives used in this study (Table 1.2). Identifications took place with 100X oil immersion objective and a 10X eyepiece. Phytoplankton identifications were based on cell morphology. Some of the morphological features included cell size, storage products, chloroplast structure, and flagella characteristics. To remain consistent in the determination of the species, pictures of the dominant phytoplankton populations were stored in a database. Comparisons were made between the phytoplankton populations present in Lake Bonney to those present in Lake Fryxell. These comparisons were based on established records of known phytoplankton populations from Lake Fryxell (Seaburg, et al. 1979; Spaulding, et al. 1994; Roberts, et al. 2000). The record of phytoplankton populations taken by Sarah Spaulding in Lake Fryxell is archived in the MCMLTER website (http://huey.colorado.ledu/LTER), under

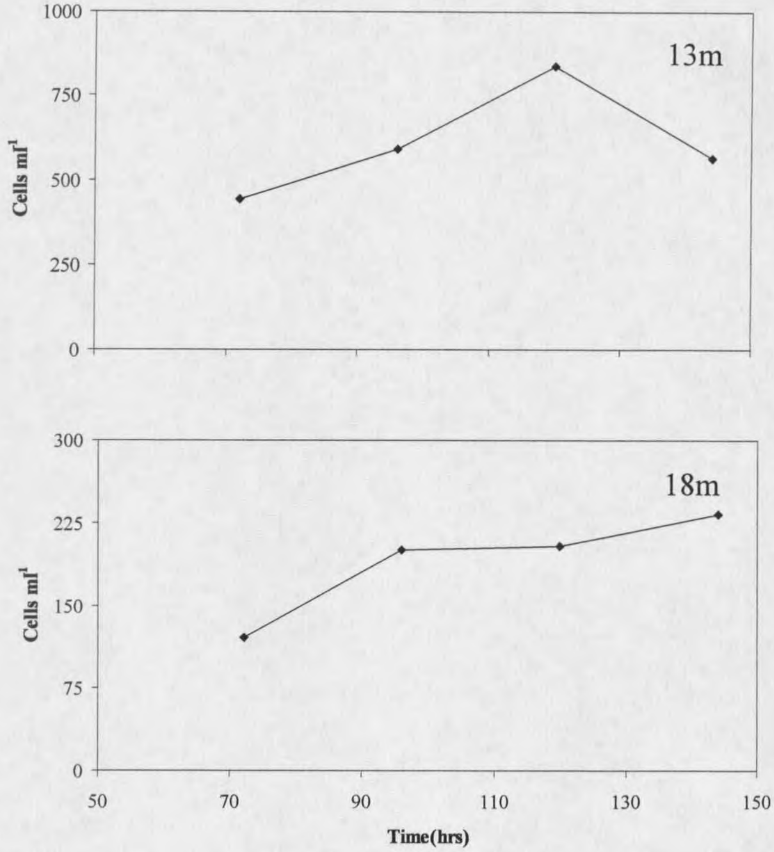


Figure 1.5 Experimental data from settling experiments. Experiments were based on phytoplankton samples collected from 13 m and 18 m from the east lobe of Lake Bonney. Four samples from each depth settled for 72 hr, 96 hr, 120 hr, and 144 hr. At 120 hr and 144 hr the 13 m and 18 m samples had reached complete sedimentation.

the direction of Dr. Diane McKnight. Phytoplankton species identifications were made using Seaburg et al. (1979), Prescott (1978), LTER website (http://huey.colorado.ledu/LTER), Klaveness (1985), and Whitford and Schumacher, (1984). The algal species that made up >90% of the total cell counts were included.

Table 1.2 Calibration table for the Nikon Diaphot inverted microscope

Objective	**Whipple disk (µm)**	**Whole field (µm)**	**Ocular Micrometer scale**
10X	L = 690	D = 1840	1 : 7.7 µm
	A = 373,738 μm^2	A = 2,657,696 μm^2	
20X	L = 350	D = 920	1 : 3.7 µm
	A = 96,162 μm^2	A = 664,424 μm^2	
40X	L = 175	D = 460	1 : 1.8 µm
	A = 24,040 μm^2	A = 166,106 μm^2	
100X +1.3 oil	L = 35	D = 190	1 : 0.77 µm
	A = 1225 μm^2	A = 28,338 μm^2	

Phytoplankton counts were made on an inverted microscope under 400X until 300 individual cells were counted. Measurements of the lengths and widths of cells were made under 1000X magnification. Measurements were taken from ten cells of each of the dominant phytoplankton populations. Abundance was calculated from the following formula:

$$cells \cdot ml^{-1} = \frac{C}{\# F} \cdot \frac{1F}{1U} \cdot \frac{1U}{V} \qquad \text{Eqn.1}$$

Where C is the number of cells counted, F is the fields used in counting, U is the Utermöhl chamber, and the volume of sample settled is V. The error estimates are based on the number of species counted determined by the following equation from Lund et al. (1958):

$$error_{\max} \pm 2\frac{100}{\sqrt{C}} \qquad \text{Eqn.2}$$

Where C is the number of cells counted. In this study, cells were counted until 300 cells of an individual species were examined giving an error estimate for counting of ±12%.

Biovolumes for phytoplankton cells were estimated from the individuals making up >90% of the total cell counts. The average of the dimensions were calculated and then applied to one of two equations based on the cell's geometric shape either round -shaped or rod -shaped (Hillebrand, et al. 1999).

Variations in the sizes of individual phytoplankton species create problems when using cell numbers in determining the contributions of these species to overall populations. For instance, the size difference between the dominant species *Ochromonas sp.* (Diameter = ~3 μm) and *Chlamydomonas subcaudata* (length = ~20 μm width = ~15 μm) is over an order of magnitude. These problems can be eliminated by calculating the carbon biomass. Obtaining the carbon biomass takes into account the biovolume of the species and the numbers of species present. The species that made up 1% of the total populations were measured for biovolume calculations. The biovolume data obtained was then converted into carbon biomass. Carbon biomass was estimated using the following formula (Mullin, et al. 1966):

$$\log_{10} N = 0.76 \cdot \log_{10} V - 0.29 \qquad \text{Eqn. 3}$$

Carbon biomass estimates were based on the number of cells per ml N and the average volume V of the cell determined from the length and width of ~10 species measurements.

Chlorophyll *a*

Chlorophyll *a* concentrations were determined by the fluorescence of extracts from filtered material measured on a Turner Fluorometer. One hundred ml of lake water was collected on combusted GF/F filters using vacuum filtration. Filtration was carried out in complete darkness to avoid degradation of chlorophyll *a*. Filters were frozen until further analysis at the McMurdo Station Crary labs. Extractions were performed in 20 ml scintillation vials using 10 ml of 90% acetone and dimethlysulfoxide (DMSO). After 12 hr in a cold dark environment, 4 ml of the extracts were placed in a Turner 10-AU fluorometer calibrated from known chlorophyll *a* standard. In order to correct for phaeophyton fluorescence, 0.2 ml of 3 N HCL was added to the sample and 4 ml of the acidified sample was placed in the fluorometer (Holm-Hansen, et al. 1965). Measurements from the acidified sample were subtracted from the original sample to obtain un-degraded chlorophyll *a* fluorescence.

Primary Production

Measurements of primary production were preformed using in-situ incorporation of ^{14}C over a 24 hr incubation (Priscu 1995). Lake water samples were collected in one dark and two clear 125 ml teflon screw-cap glass bottles, previously acid- washed and rinsed, then placed in a dark carrier box. Each sample was inoculated with ^{14}C-bicarbonate, a tracer to measure photosynthesis, using a pipette under a dark tarp. The sample bottles were then re-suspended in the water column to the depth from which they were collected. After incubation for 24 hr, the samples were returned to the dark box and vacuum filtered in the dark to collect the particles on combusted 25 mm Whatman GF/F filters. The filters were then placed in 10 ml scintillation vials with caps off and set on a heat block at 60°C. An Eppendorf repeater pipette was used to add 0.5 ml of 3 N HCL. Once the filters were dry they were transported to the lab at McMurdo Station in the capped scintillation vials. Ten ml of Cytoscint cocktail was added to each of the scintillation vials. Counts of the radioactive particles were performed using a calibrated Beckman LS 6000 scintillation counter. Calibrations were done using ^{14}C-toluene standards.

Particulate Carbon and Nitrogen

Particulate carbon and nitrogen measurements were determined from samples collected in 1000 ml amber Nalgene bottles. The samples were thoroughly mixed and 500 ml was decanted into a graduated cylinder. Samples were filtered through a pre-combusted 25 mm GF/F filter. Filter pressure was low (<0.3 atm). Filters were dried on aluminum weigh boats, stacked together, and frozen until further analysis. The samples were analyzed at Crary Lab using a Carlo Erba NA 1500 elemental analyzer. Flash combustion was used to convert carbon and nitrogen to combustion products of CO_2 and N_2. The gases were separated by gas chromatography and measured by a thermal conductivity detector.

Photosynthetically Active Radiation

PAR measurements at 10 m were obtained using a Li-Cor 193S 4π quantum sensor connected to a Li-Cor model LI-1000 data logger. Surface irradiance was logged contemporaneously with a 2π quantum sensor. PAR was logged during the incubation of the primary productivity samples. Measurements were recorded every 10 minutes.

Conductivity, Temperature, and Density

Conductivity temperature and density (CTD) measurements were made using a Sea-Bird Electronics (SBE) 25 data logger CTD. The CTD data logger was deployed using a hand operated winch through the drilled ice holes at speeds ranging from 0.2 to 0.5 m s^{-1}. Water is pumped through the instrument to eliminate noise from probe speed inconsistencies. Temperature and conductivity measurements are made on the same sample of water because the water is pumped through the duct that holds the temperature sensor, then through the conductivity cell. The CTD sensors used in this study are widely used and accurate (Spigel and Priscu 1998). The instrument is calibrated each season with the seawater and by the manufacturer.

Nutrients

Nitrate, nitrite, ammonium, and soluble reactive phosphorus were measured from samples collected in 1000 ml amber HDPE bottles. From thoroughly mixed 1000 ml samples, 100 ml of each sample was filtered through pre-combusted Whatman GF/F filters. Filtered water samples were frozen in acid-washed polyethylene-bottles until further analysis at Crary Lab. Analyses were performed using a spectrophotometer on a Lachat auto analyzer. Dissolved inorganic nitrogen was determined using the method by Parsons, et al. (1984). In samples where the salinity exceeded that of seawater, samples were diluted with deionized water to seawater levels. Soluble reactive phosphorus was measured using the molybdate/potassium antimonyl tartate method of Downes (1978).

CHAPTER 2

BASIS FOR PHYTOPLANKTON CELL IDENTIFICATIONS AND DESCRIPTION OF PHYTOPLANKTON POPULATIONS IN LAKE BONNEY, ANTARCTICA

Introduction

Identifications of phytoplankton populations are important in aquatic systems, especially those systems comprised entirely of microbial organisms. Phytoplankton populations are the main primary producers in most aquatic ecosystems (Hutchinson 1967). As primary producers, they provide food webs with a major synthesis of organic carbon (Pomeroy 1974). In the lobes of Lake Bonney, the aquatic system is comprised of microbial organisms. This chapter reviews the taxonomic divisions significant to this study and knowledge on how the taxa are distinguished. Techniques on how the phytoplankton taxa were identified in the lobes of Lake Bonney is documented. Lastly, the dominant taxa in Lake Bonney and their relevance in certain environments will be presented.

Background on Taxonomy

Identifications of organisms in the field or laboratory were made possible by the efforts of early taxonomists (i.e. Copeland 1956; Whittaker 1959). Taxonomists classify organisms based on characteristics such as morphology, genetic similarity, developmental patterns, behavior, metabolism, growth, and reproduction. Organisms with highly similar morphological characteristics with the ability to reproduce constitute a species. Groups of closely related species signify a genus. Carolus Linnaeus began the process of using binomial nomenclature to classify organisms. Using binomial nomenclature, the first part of an organism's name denotes genus the second part species. Growth of knowledge in biology amplified the range of traits used in Linnaeus's binomial nomenclature system. This system broadened to include, along with species and genus, families, orders, classes, divisions and, kingdoms. One of the first classification systems included only kingdoms that could be observed by sight, the kingdoms Plantae and Animalia. In the middle of the 19th century with the invention of the microscope, scientists distinguished bacteria and slime molds from plants and animals. A prominent difference between bacteria and other organisms was the absence of a nucleus. Edouard Chatton (1937) suggested that organisms lacking a nucleus be termed prokaryote and organisms with a nucleus called eukaryote (Margulis and Schwartz 1998). Whittaker's 5-kingdom classification scheme displays the separation of prokaryotes and eukaryotes into kingdoms (Whittaker 1959). The 5-kingdom include Monera, Protista, Plantae, Animalia, and Fungi. Prokaryotes are grouped into Monera, while the other four kingdoms encompass the eukaryotes. Margulis and Swartz (1998) revised Whittaker's scheme to include advances made in biology since the schemes development in 1959 (Figure 2.1).

Molecular data challenged the validity of the 5-kingdom classification system. Molecular sequencing is one of the greatest advances in science. This advancement created an accurate picture of the branching patterns of the tree of life. Carl Woese attested that molecular sequence comparisons provided evidence for a 3-domain system of life (Woese, et al. 1990). The three domains consist of Bacteria, Archaea, and Eucarya (Figure 2.2). Eucarya encompass four of the five kingdoms from Whittaker's classification system. Bacteria and Archaea have more differences and are further apart on the tree than the Kingdoms, Plantae, Fungi, and Animalia (Figure 2.2). The Protists are included with several kingdoms.

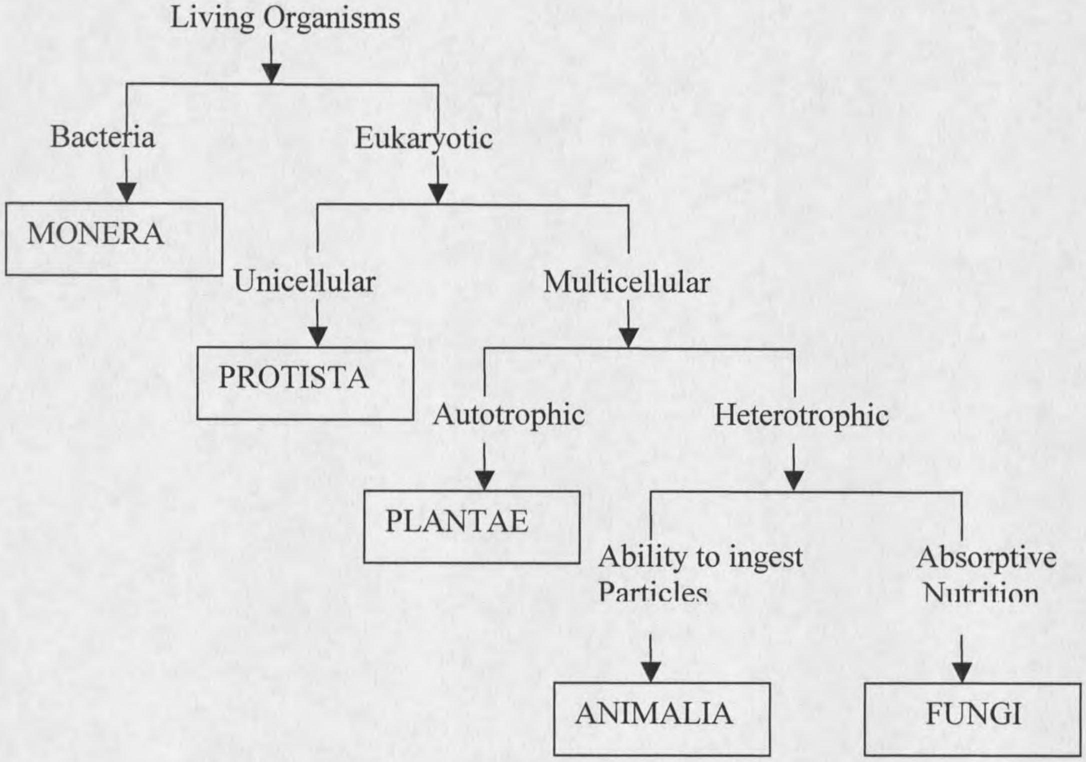


Figure 2.1 The five kingdom system proposed by Robert H. Whittaker (1959) revised by Margulis and Swartz, (1998) shows the location of the Monera and Protista in the five kingdom system and the difference between plants and animals. This scheme is no longer in use.

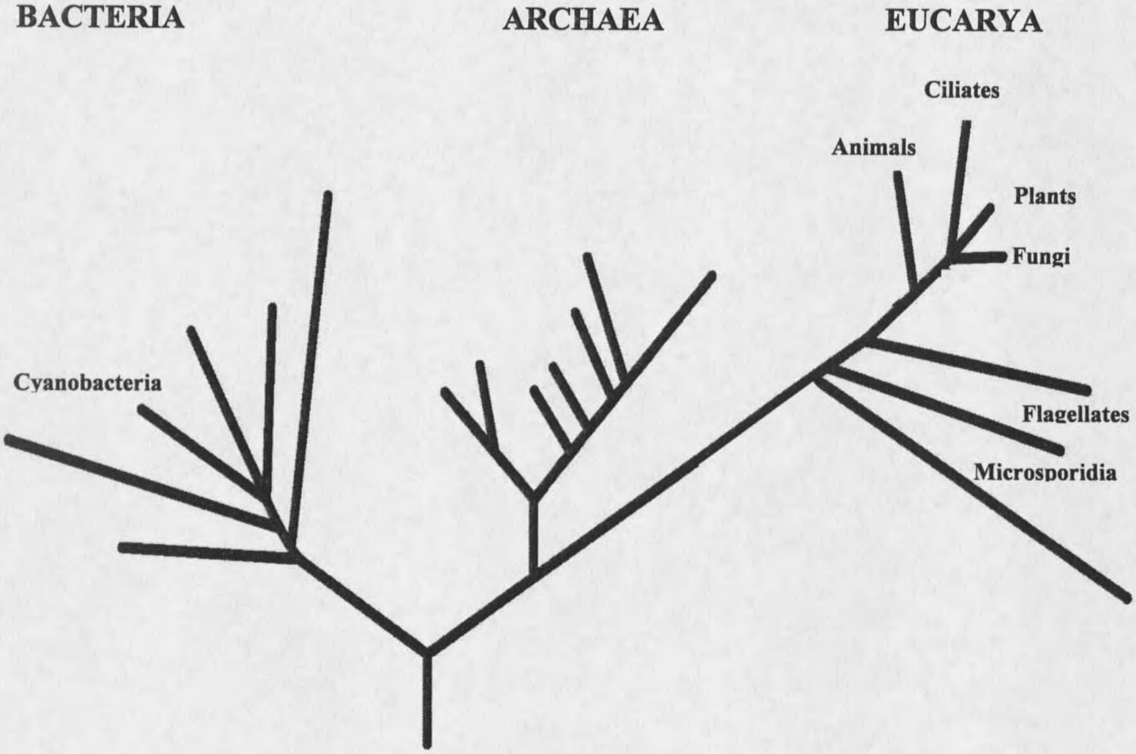


Figure 2.2 Phylogenetic tree, showing the domains Bacteria, Archaea, and Eucarya. The kingdoms Animalia, Plantae, and Fungi are in the domain Eukarya. Protists have been divided into additional kingdoms corresponding to major lineages. (Adapted from Woese et al. 1990)

Background on Phytoplankton Divisions

Currently, there are eleven different recognized phytoplankton divisions in the kingdom Protista (van-den-Hoek, et al. 1996). This study focuses on four divisions: Cyanophytes, Chlorophytes, Chrysophytes, and Cryptophytes. Pigment composition, types of storage products, the nature of the cell wall, reproductive differences, and locomotion mechanisms are examples of characteristics used to separate the phytoplankton cells into these divisions (Graham and Wilcox 2000). Of all the phytoplankton species divisions, the Cyanophytes are the only prokaryotic organisms. The nuclear material of Cyanophytes is not enclosed in a nuclear envelope, and plastids, mitochondria, golgi-bodies, and other membrane bound organelles are not present in Cyanophytes, thus they are considered bacteria. Although Cyanophytes are true bacteria, they are able to use water as an electron donor in photosynthesis, and they contain enzymatic pigments capable of photosynthesis. They are, therefore, considered phytoplankton in this study.

The morphology of Cyanophytes can be unicellular, colonial, or branched filaments. A thin membrane with a gelatinous peptidoglycan sheath usually covers the cell. The cells contain false vacuoles, nuclear material occurring in clusters, and chlorophyll *a* distributed throughout the entire cell usually in the peripheral region. Other pigments present may include phycocyanin, allophycocyanin, β-carotene, and xanthophylls. Food is mostly stored as cyanophytan starch (glycogen). Consequently, the iodine test for starch is negative (Prescott 1978). Some cells have the ability to fix nitrogen in specialized structures called heterocysts. The reproduction of Cyanophytes is usually by asexual binary fission, resulting in endospores. Orders in the Cyanophyte divisions include Pleurocapsales, Stigonematales, Chroococcales, Nostocales, and Oscillatoriales. *Anabaena sp.* is a species found in the order Oscillatoriaceae and family Nostocaceae. Common species from the order Oscillatoriales and family Oscillatoriaceae include *Oscillatoria sp.*, and *Phormidium sp.*

Chlorophytes, or green algae, have variable morphologies and can be unicellular, colonial, or filamentous. The cell wall, if present, is made of cellulose or pectose.

Chlorophyte cells contain pyrenoids, a nucleus, and chloroplasts, with pigments consisting of chlorophyll *a*, chlorophyll *b*, carotenoids, and some xanthophylls. If motile, the Chlorophytes usually have two flagella, but may sometimes have four or even eight flagella, all of equal lengths. The location of the flagella is in the anterior region of the cell. Iodine tests for starch are positive, since the storage products are mainly starch (Prescott 1978). The reproduction strategies by Chlorophytes are diverse and may occur sexually or asexually, although asexual reproduction by division of a vegetative cell is the most common. Some cells are monoecious; others are dioecious. A few taxa have a red eyespot present on the periphery of the cell. Chlorophytes have several orders including the Volvocales and Chlorococcales. Taxa found in the order Volvocales and family Chlamydomonas include *Chlamydomonas sp.*, *Chloromonas sp.*, and *Brachiomonas sp. Polytomella sp.* is also found in this order, but in the class Polyblepharidaceae. A phytoplankton cell similar to *Chlamydomonas sp.* in the Phacotaceae is called *Thorakomonas sp.* The familiar taxon, *Chlorella sp.* are found in the family Oostaceae.

Chrysophytes are the yellow-green or brown algae. Cells can be unicellular or colonial. Cell walls are thick and usually made of pectin, but can also be made of silicon (Graham and Wilcox 2000). In some cases, two scales overlapping in the mid-region make up the siliceous walls. In the chloroplasts, yellow-brown or golden-brown pigments predominate making the cells yellow, green, or brown. Pigments include chlorophyll *a*, chlorophyll *b*, chlorophyll *c*, carotenoids, and some xanthophylls. Motile cells usually contain two flagella of unequal length, or one flagellum. The storage product is mainly leucosin or some form of oil. The iodine test for starch is negative (Prescott 1978). Vegetative reproduction is usually by cell division.

Many species are found in the order Ochromonadales. One of the most usual species is *Ochromonas sp.* in the family Ochromonadaceae. Another widespread phytoplankton species found in the family Synuraceae is *Mallomonas sp.* Cryptophytes are present as solitary cells, which can be motile with two flagella, of unequal length. Flagella insertion can be lateral or sub-apical. The chloroplasts are large, brown, blue, or reddish. In some chloroplasts, pyrenoids may be present. Pigments located in the chloroplasts are chlorophyll *a*, chlorophyll *c*, phycocyanin, phycoerythrin, carotenes, and xanthophylls. Starch, the main storage product, is contained in granules in the cytoplasm. Cryptophytes cell walls are proteinaceous and contain a periplast beneath the plasma membrane. An opening may be present at the anterior end of some cells. This opening is called a gullet, a key taxonomic feature. Reproduction occurs as longitudinal cell division (Prescott 1978). Two common phytoplankton species, *Chroomonas sp.* and *Cryptomonas sp.*, are classified in the order Cryptomonadales and family Cryptomonadaceae.

Previous Studies on McMurdo Dry Valley Phytoplankton Populations

The lakes in the McMurdo Dry Valleys are ice covered year round. This permanent ice cover reduces light penetration and, along with lake chemistry, stratifies the water column. These conditions limit the amount and type of organisms present in the lakes. Previous studies on the McMurdo Dry Valley lakes have reported 90 algal taxa belonging to: Chlorophyceae, Xanthophyceae, Eustigmatophyceae, Bacillariophyceae, and Cyanophyceae (Goldman, et al. 1967; Koob and Leister 1968; Seaburg, et al. 1977). Seaburg et al. (1979) conducted an extensive study on the phytoplankton present in the McMurdo Dry Valley lakes. The phytoplankton compositions in the lakes varied considerably from one lake to another lake in separate valleys, but were similar from lake to lake in the same valley (Seaburg, et al. 1979). For example, the Taylor Valley lakes had high numbers (1000cells ml^{-1}) of a Cryptophyte called *Chroomonas lacustris* (Seaburg, et al. 1979). More recently, Spaulding, et al. (1994) also observed *Chroomonas lacustris* in Lake Fryxell more recently. Several species of Volvocales were also present in the lakes such as *Chlamydomonas subcaudata* and *Thorakomonas feldmannii* (Seaburg, et al. 1979). Species of Chlorococcales occurred in the lakes called Chlorella vulgaris (Seaburg, et al. 1979). Plankton cells from the family Bacillariophyceae were rarely seen in the dry valley lakes, although high numbers were reported in the glacial melt streams (Seaburg, et al. 1979). The Chyrsophyte division is represented in the lakes by *Ochromonas minuscule* and *Mallomonas sp.* (Seaburg, et al. 1979). The extreme cold, low light levels and isolation of the continent have resulted in low plankton biomass and low species diversity in Antarctic lakes (Laybourn-Parry, et al. 1992).

Purpose of Identifying Phytoplankton Populations

Taxonomic studies on the phytoplankton populations have been conducted in the McMurdo Dry Valley lakes, since the 1960s (Angino, et al. 1964; Goldman, et al. 1967; Koob and Leister 1968; Seaburg, et al. 1979; Vincent 1981; Spaulding, et al. 1994). However, these studies did not have the advantage of a long-term data set. This study uses data collected from the east lobe of Lake Bonney from 1989-1992 and 1994-2000 and 1989, 1992, 1994-2000 from the west lobe of Lake Bonney. Dominant phytoplankton cells were measured and enumerated. These characteristics used in classifying phytoplankton cells help identify the phytoplankton cells and ascertain the physical factors enabling the cells to survive or dominate the phytoplankton populations in certain environments (Reynolds, et al. 2002). The identifications are used to calculate diversity and dominance of a group of similar phytoplankton cells. One of the most common diversity indices is the Shannon and Wiener index (Pielou 1977). The index was used in this thesis because the index takes into account relative abundance and number of species and is used often in ecological studies (Wetzel 2001).

Methods

The methods used for phytoplankton identifications and enumerations are explained in Chapter 1. The Shannon Wiener index was used to calculate diversity. Shannon diversity indices are calculated using the following equation (Shannon and Weaver 1949):

$$H' = -\sum_{i=1}^{s} piLOG_2pi \qquad \text{Eqn. 2.1}$$

Where *pi* values were estimates of the proportional abundance of species. The proportional abundance of species is the abundance of one species over the total abundance of all species in the sample.

Results

Phytoplankton Identification

Few species of Cyanophytes have been found in the preserved samples of Lake Bonney's water column. The division of Cyanophytes is identified from other phytoplankton species by there cell's structure as prokaryotes and most contain phycobilin type pigments. Two taxa from the order Oscillatoriales were common in the lake water samples of Lake Bonney. *Phormidium sp.* was recognized by the cylindrical cells attached end to end to form long unbranched filaments (Figure 2.3). Heterocysts were not present and one trichome was contained in a thin sheath. The other Cyanophyta seen in the plankton called *Anabaena sp.* contained spherical shaped cells forming long filaments. Heterocysts were present in the non-tapering trichomes. A sheath covered only one filament and cells did not appear communal (Figure 2.4).

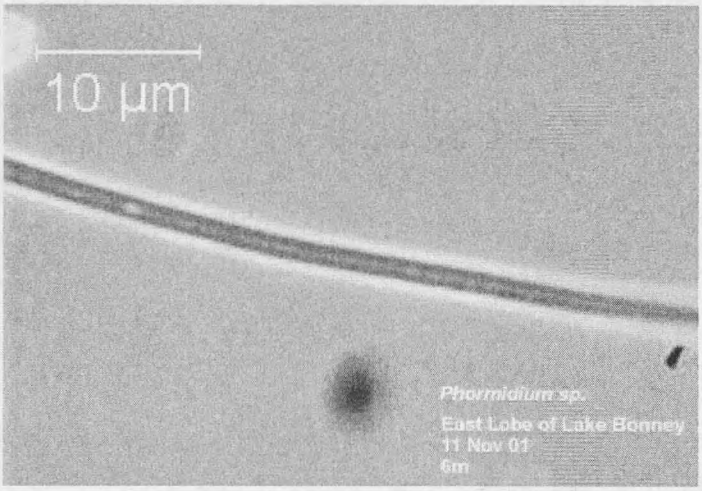


Figure 2.3 Digital image of *Phormidium sp.* Barrel shaped cells are attached end to end to form a long filament. The filaments vary in length.

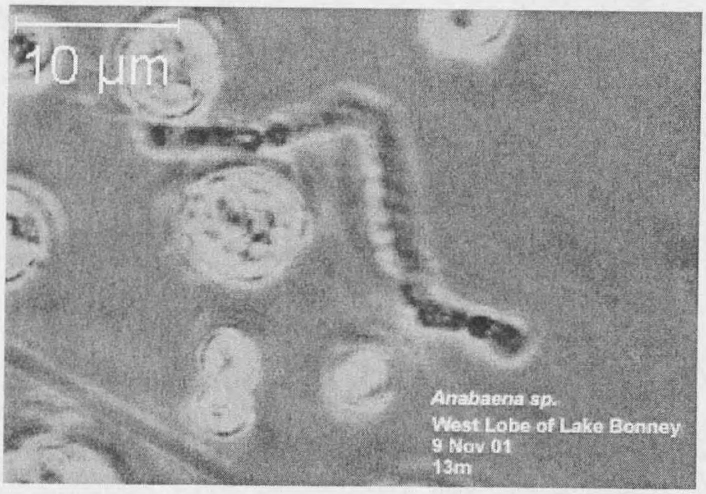


Figure 2.4 *Anabaena sp*. is made of prokaryotic phycobilin containing phytoplankton cells. These spherical cells are attached end to end to form a filament.

Chlorophytes were well represented among the phytoplankton present in Lake Bonney. Nineteen phytoplankton species from Lake Bonney's phytoplankton populations were classified in the division Chlorophyta, although, the majority were rare (<1% of total counts). One Chlorophyte that was not rare was *Chlamydomonas subcaudata*. These cells are placed in the order Volvocales and family Chlamydomonaceae. The genus *Chlamydomonas* was determined from the ovoid shape of the cell, the presence of a sheath covering the cell, location of the vacuoles near the base of 2 flagella of equal length, starch-storing pyrenoid, and cup shaped chloroplast (Figure 2.5a). The cells were identified to the species level by several characteristics. Firstly, the shape of the protoplast, which is pointed at one end; the larger size of the species (~25 µm by ~17 µm); the pyrenoid, which was large dark-stained located, and basally located; and the presence of 2 small contractile vacuoles located at the base of the flagella (Figure 2.5a).

The chloroplast extends around the cell. The nucleus is located between the arms of the chloroplast. The diagnosis was elucidated by the presence of mother cells exhibiting cell division into two, daughter cells (Figure 2.5b). *Chlamydomonas intermedia* cells were differentiated from *Chlamydomonas subcaudata* cells by the round shape of the posterior end of the cells, as well as the smaller sizes of the cells (15-25 µm long by 7-25 µm wide) (Figure 2.6). Several other phytoplankton cells classified in the family Chlamydomonaceae include *Chloromonas sp.* (Figure 2.7). *Chloromonas sp.* is similar to *Chlamydomonas subcaudata* except *Chloromonas sp.* lack the pyrenoid and stores starch in small granules dispersed in the chloroplast.

The *Chloromonas sp.* is smaller in size than both the *Chlamydomonas* sp. mentioned above (5-15 µm long and 3-10 µm broad). Another distinguishing characteristic of *Chloromonas sp.* is the pyrenoid is located on the periphery of the cell (Figure 2.7). *Brachiomonas sp.* are distinquished by their unique morphology of the cell. The cells are star- shaped, consisting of four protrusions and two flagella of equal length attached to one of the protrusions (Figure 2.8). The chloroplast fills the equatorial region and may extend into the protrusions.

Another phytoplankton taxa present in Lake Bonney in the family Chlamydomonaceae is a quadriflagellate called *Polytomella sp.* (Figure 2.9). The cell's flagella are shorter (3 to 4 µm) than the ovoid shaped cell (<9 µm long by <7 µm wide) and the nucleus is centrally located.

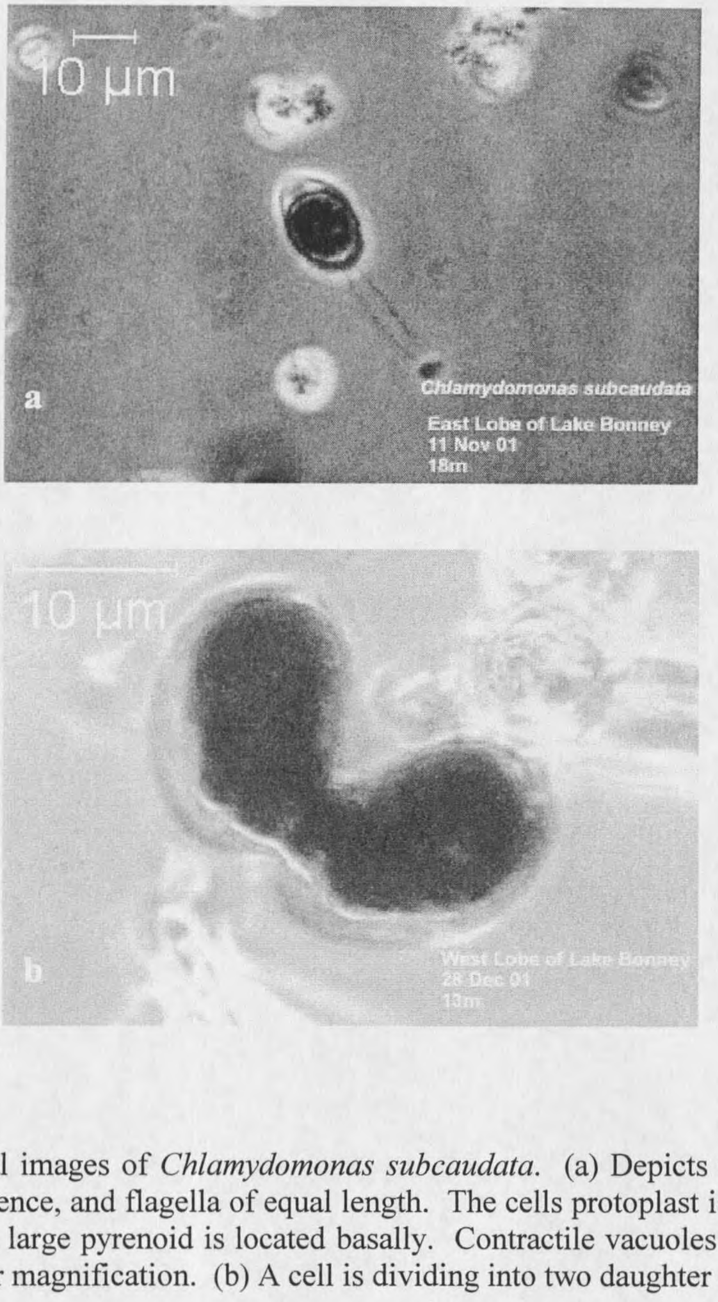


Figure 2.5 Digital images of *Chlamydomonas subcaudata*. (a) Depicts the cells ovoid shape, sheath presence, and flagella of equal length. The cells protoplast is pointed at the anterior end and a large pyrenoid is located basally. Contractile vacuoles are difficult to see without further magnification. (b) A cell is dividing into two daughter cells.

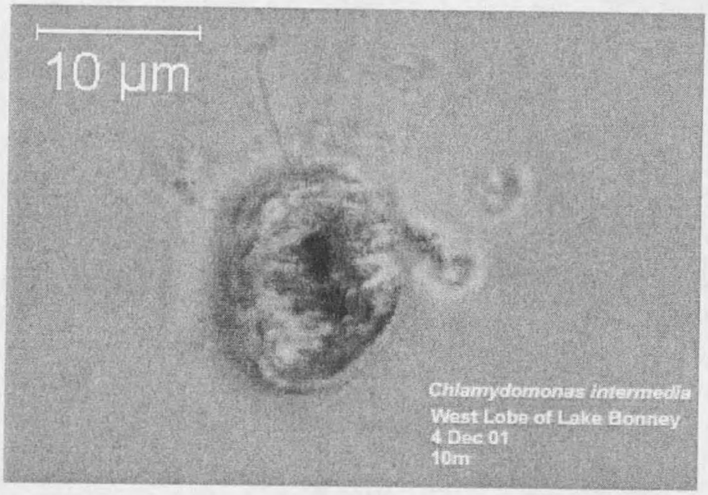


Figure 2.6 *Chlamydomonas intermedia* is similar to *Chlamydomonas subcaudata*. The cell has a rounded anterior end, two flagella of equal length, a smaller pyrenoid, and a nucleus located towards the anterior end of the cell.

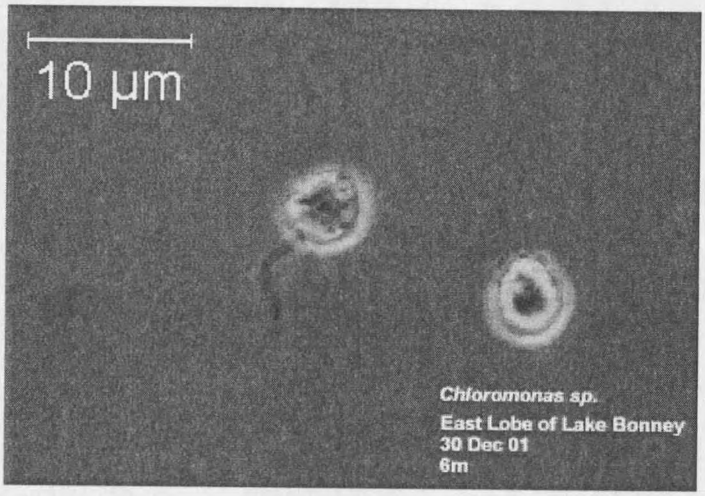


Figure 2.7 The distinguishing characteristics of the *Chloromonas sp.* include two flagella of equal length longer than the length of the cell, starch granules dispersed in the chloroplast and a cell diameter >10 µm.

Pyrenoids are lacking and sometimes the cells contain starch grains. *Thorakomonas sp.* is in the order Volvocales and family Phacotaceae. A protective covering, often mineralized, that surrounds cells is called a lorica. The irregular shape and dark brown color of *Thorakomonas sp.* lorica, which can be granular, are distinguishing factors in determining the genus of this species (Figure 2.10a). Cells range from 15 to 20 μm long by 10 to 15 μm broad. The *Thorakomonas sp.* have variable shaped protoplasts (Figure 2.10b). The last Chlorophyte cells identified frequently in Lake Bonney's phytoplankton populations are *Chlorella sp.* (Figure 2.11). *Chlorella sp.* is in the order Chlorococcales and family Oocystaceae. The taxon is identified by the spherical shaped cell and chloroplast a cup shape or girdle shape extending 3/4 of the cells periphery. Cells are tiny (~2 to 7 μm in diameter).

One member of the Chrysophytes was abundant in the phytoplankton populations in Lake Bonney. The *Ochromonas sp.*, in the class Chrysophyceae, order Ochromonadales, and family Ochromonadaceae, was a tiny cell with two flagella of unequal length. The long flagellum was ~3 times the length of the short. Chloroplasts were small with a flattened shape. Cell size and shape was variable, although the diameter never exceeded 6 μm (Figure 2.12). Another Chyrsophyte cell from the family Synuraceae, called *Mallomonas sp.*, was observed in the phytoplankton populations in Lake Bonney. It contained small spines projecting from the bottom half of the cell. Cells are large (~25 μm long and ~ 10 μm wide) and one flagellum extends from the anterior ends of the cells (Figure 2.13).

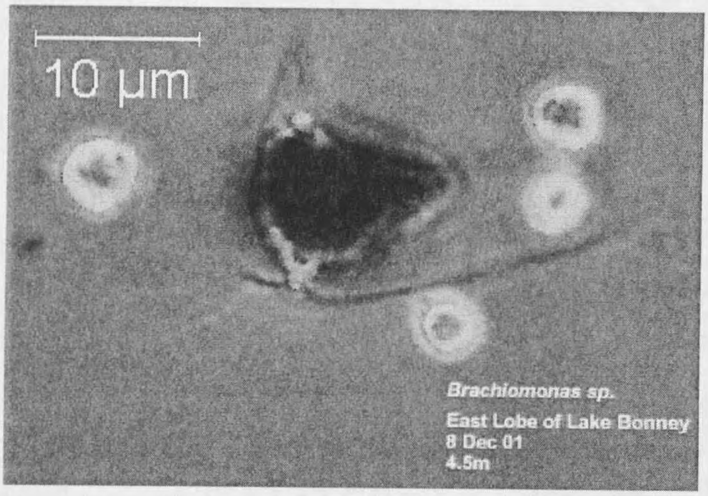


Figure 2.8 *Brachiomonas sp.*'s unusual cell shape made identifications of this genus relatively simple. Cell morphology is made of four projections and one projection has two flagella of equal length.

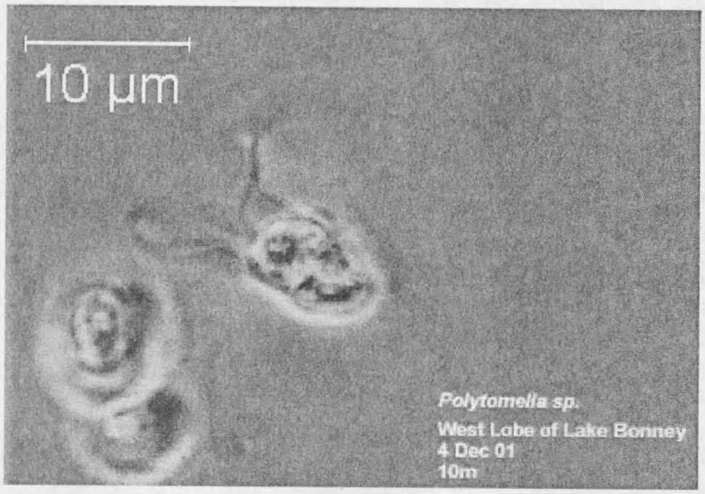


Figure 2.9 *Polytomella sp.* is unique in the plankton of Lake Bonney because it has four flagella of equal length and grainy cell constituents. The flagella are usually shorter than the cell, but this diagnostic feature is not seen in this picture.

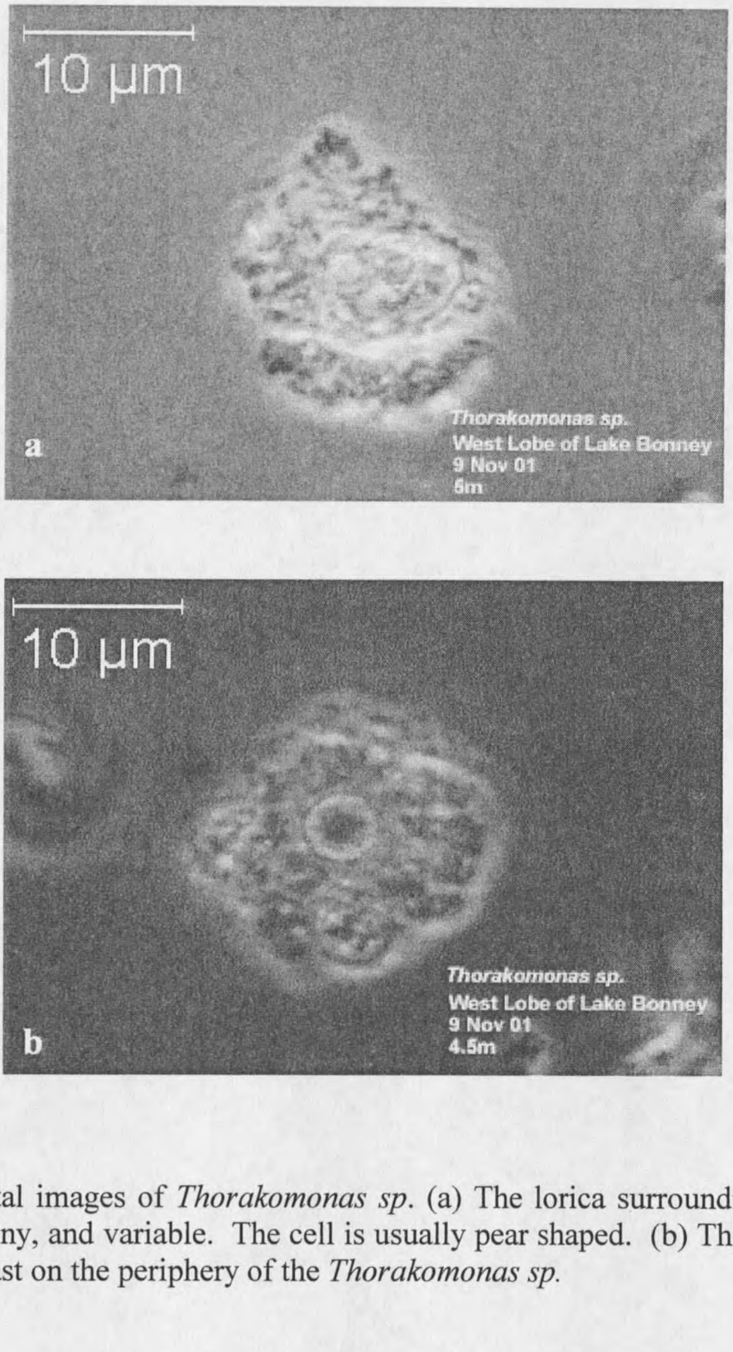


Figure 2.10 Digital images of *Thorakomonas sp*. (a) The lorica surrounding the cell is dark -colored, grainy, and variable. The cell is usually pear shaped. (b) This view shows a variable protoplast on the periphery of the *Thorakomonas sp.*

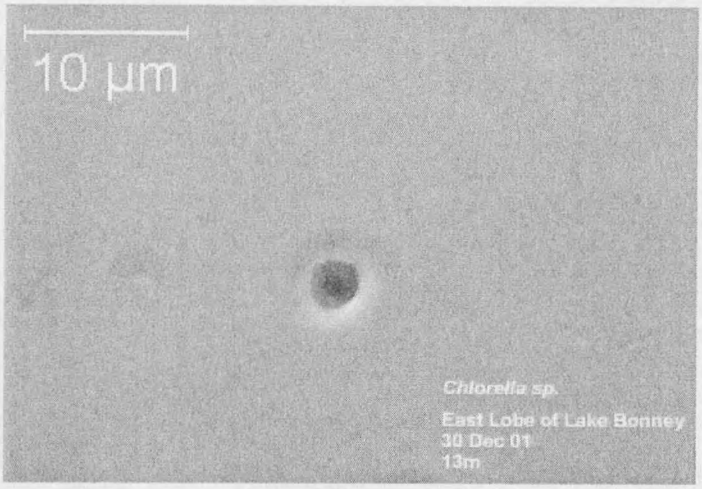


Figure 2.11 *Chlorella sp.* has a chloroplast extending ¾ around the periphery of the cell. The dark color of the cell is a result of the starch stored in the cells constituents.

Figure 2.12 *Ochromonas sp.* The unequal flagella and small cell morphology are distinguishing characteristics of this genus.

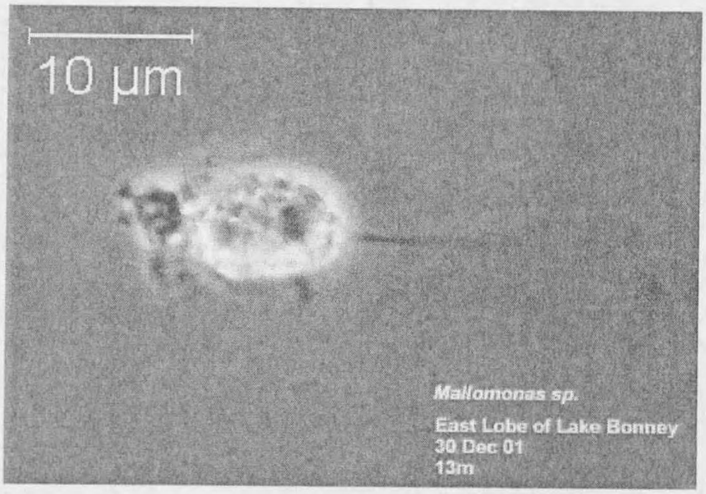


Figure 2.13 The long single flagellum is a unique feature of *Mallomonas sp*. Cell shape and location of cell's constituents are consistent with this genus.

Several taxa of Cryptophytes dominated the phytoplankton populations in Lake Bonney. The two common phytoplankton species were found in the order Cryptomonadales, family Cryptomonadaceae. The *Chroomonas sp.* was identified by the two flagella of almost equal length with sub-apical insertion (Figure 2.14a). Cells are pear shaped with the broadest end at the anterior of the cell. The cells size is 7-13 µm long by 5-12 µm wide. A pyrenoid was present and centrally located. Ejectosomes are small round structures in cells that can be discharged from the cell, and are located near the anterior end. Ejectosomes are found in *Chroomonas sp.* (Figure 2.14b). Chloroplasts are distinct and curved. The *Cryptomonas sp.* was distinguished from the *Chroomonas sp*. because of the larger cell size (>15 µm long by >5 µm wide). One of the cell's two flagellum is ~1/2 the length of the other (Figure 2.15a). A gullet is present at the anterior end of the cell and the pyrenoid is centrally located (Figure 2.15b).

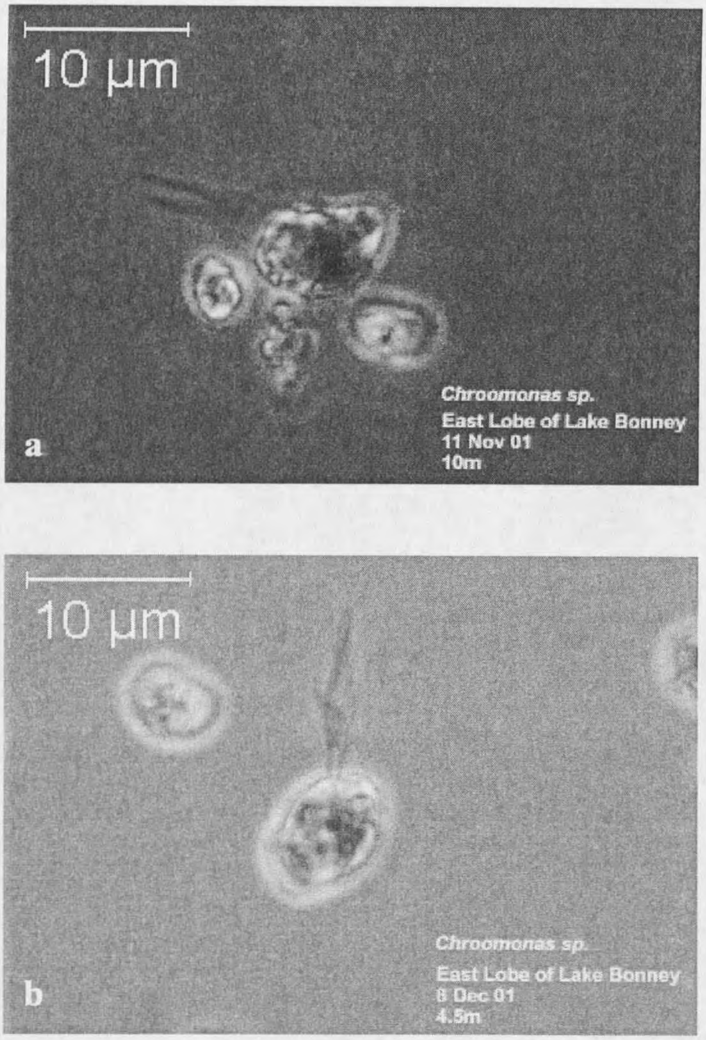


Figure 2.14 Images of *Chroomonas sp.* show (a) sub-apical insertion of flagella, which is a distinct characteristic of Cryptomonadaceae; the missing gullet shows that this species is *Chroomonas sp.* and (b) ejectosomes which are located at the base of the flagella and a pyrenoid located laterally.

Characteristics of the Phytoplankton Populations

The diversity of the phytoplankton populations in Lake Bonney's east and west lobes for samples collected from 1989-1992 and 1994-2001 varied from a diversity (>2) to (<0.2), based on the Shannon and Wiener diversity index. For instance, the maximum diversity found in the east lobe of Lake Bonney was 2.68 and for the west lobe 2.54. Minimum values for the east and west lobes were 0.18 and 0.06 (Table 2.1). The east lobe of Lake Bonney had a higher average diversity index than the west lobe, 1.36 and 1.16 respectively, although the west lobe of Lake Bonney had a wider range of values with a standard deviation of 0.54 compared to the east lobe of Lake Bonney at 0.48 (Table 2.1).

Table 2.1 Shannon diversity (H') indices and number of species for the lobes of Lake Bonney. Values determined using the Shannon and Wiener diversity index for the east and west lobes of Lake Bonney.

	East lobe of Lake Bonney (H')	West Lobe of Lake Bonney (H')	East Lobe # of species	West Lobe #of species
Mean	1.36	1.16	7	7
Standard deviation	0.48	0.54	2	2
Sample size	268	135	268	135
Minimum	0.18	0.06	3	2
Maximum	2.68	2.54	13	12

On average for both lobes of Lake Bonney, 7 species were present. The minimum number of species present was 2 in the west lobe of Lake Bonney while the maximum of 13 species was found in the east lobe of Lake Bonney (Table 2.1). Most of the phytoplankton cells present in Lake Bonney were phytoflagellates. In fact >90% of the population was made up of phytoflagellates. Phytoplankton cells from the divisions Cryptophytes, Chlorophytes, and Chyrsophytes made up over 90% of the phytoplankton population. Most of the species present in the samples included the ones identified above. A few rare species, that made up <1% of the total cells counts were mentioned in the identifications including *Mallomonas sp., Anabaena sp., Phormidium sp., Chlorella sp.*, and *Brachiomonas sp.*

Discussion

The identification of phytoplankton species in any environment is a long, arduous process. There are many instances where differences among taxonomists occur. However, in Lake Bonney's east and west lobes, cell numbers per ml of sample are relatively low. Thus, the identifications and quantification of phytoplankton species is less arduous. Results obtained in this long-term analysis of samples from 1989-1992 and 1994-2000 for the east lobe of Lake Bonney and 1989, 1992, 1994-2000 in the west lobe of Lake Bonney are consistent with results obtained from other taxonomic studies on Lake Bonney (Goldman, et al. 1967; Seaburg, et al. 1977; Seaburg, et al. 1979; Sharp 1993; Lizotte, et al. 1996). Differences among the studies were found with the results of Parker et al. (1979). Their results reported high numbers of the Chlorophyte species, *Chlorella sp.* in the plankton of Lake Bonney, whereas the long-term analysis reported few *Chlorella sp.* Priscu et al. (1998) noted that some cells are lost during the preservation process, and since some of the samples were 12 years old degradation of the samples are to be expected. On the other hand, the long-term analysis observed more *Ochromonas sp.* cells in the plankton of both lobes. Parker et al. (1979) observed these cells occurring in the plankton of Lake Bonney, but they were rare. Goldman et al. (1967) reported, similarly to the long-term analysis, *Ochromonas sp.* in the plankton of

Lake Bonney. Sharp (1993) also observed *Ochromonas sp.* occurring in the plankton. Parker et al. (1979) observed that phytoplankton populations in lakes within the same valley system, i.e. the Taylor Valley, contain similar populations.

The long-term analysis of samples shows that Cryptophytes also made up a large portion of the total phytoplankton populations in Lake Bonney. Several other species reported from other lakes in the Taylor Valley from previous studies were seen in this long-term study on Lake Bonney. Species of Volvocales were present in Lake Bonney, such as *Chlamydomonas subcaudata* and *Thorakomonas feldmannii*. These species were also seen in lakes Fyxell and Hoare (Seaburg, et al. 1979). Bacillariophyceae were rarely seen in Lake Bonney. They were rarely seen in any of the lakes in the Taylor Valley. If Bacillariophyceae were present, they were usually observed in the lower depths of the water column (15-20m). The Chrysophyte, *Mallomonas* unknown species, observed in Taylor Valley lakes from the Seaburg et al. (1979) study were also seen in the plankton of Lake Bonney. *Brachiomonas sp.* was only reported in Lake Vanda in the Wright Valley, however it was observed in the plankton of Lake Bonney during this analysis of the phytoplankton samples.

Characteristics of the Phytoplankton Populations

If more species are present, then diversity will be higher (Pielou 1977). Shannon diversity indices are reliable if at least 300 individuals per sample are identified and counted (Sournia 1978). Higher numbers of dominant species and the presence of rare species affect biodiversity indices (Pielou 1977). In this long-term study, over 300 individuals were counted. However, the abundances of some individuals were far greater. The east and west lobes of Lake Bonney had variable diversity although overall the Shannon diversity indices remained low. The east lobe had lower standard error than the west lobe of Lake Bonney probably because of the higher number of samples. These diversity measures are consistent for populations in harsh environments. Theinemann's explaination of diversity, in his second "biocoenotic laws", that the harsher the environment the fewer number of species will dominate in higher numbers coincides for both lobes of Lake Bonney (Lampert and Sommer 1997). For example, only seven species were present in a majority of the samples from the east and west lobes of Bonney, and the evenness index indicates that some of these species occur in higher numbers. This law is also intuitive since in extreme conditions one group of organisms increases while the other decreases due to unfavorable conditions for that organism. The diversity hypothesis does hold true for the phytoplankton populations in Lake Bonney because of the range in the diversity indices present in both lobes, however the problems of calculating diversity in a study are numerous and may affect results. Problems of calculating diversity indices occur when individuals are colonial and when species are of differing sizes, but the smallest species may not be dominant because of the smaller size. To eliminate these problems diversity indices can be based on biomass instead of cell numbers (Lampert and Sommer 1997). In Lake Bonney, the smaller species are almost 10X smaller than the largest species. The diversity index used here in cells per ml had to be performed because biovolumes of the rare species of cells were not measured.

Conclusions

The low diversity of phytoplankton species present in Lake Bonney is revealed in the few taxa of phytoplankton represented. Phytoplankton species present in Lake Bonney include those found in the divisions Cyanophytes, Chlorophytes, Chrysophytes, and Cryptophytes. Many species of Chlorophytes occur in the plankton including; *Chlamydomonas subcaudata, Chlamydomonas intermedia, Chloromonas sp., Thorakomonas sp., Brachiomonas sp.,* and *Polytomella sp.* The common species from Chrysophyte taxa includes *Ochromonas sp.* and *Mallomonas sp.* Lastly, one of the most common species seen in the phytoplankton populations in Lake Bonney was *Chroomonas sp.*, and less often *Cryptomonas sp.* These species have consistently been identified in studies conducted on Lake Bonney, as well as in many other lakes in the Taylor Valley before this long-term study. Phytoplankton species identified are from samples of the lake, and are subject to missing rare phytoplankton species present in the population.

CHAPTER 3

VERTICAL DISTRIBUTIONS OF DOMINANT PHYTOPLANKTON POPULATIONS IN LAKE BONNEY

Introduction

Spatial Heterogeneity of Phytoplankton Populations

Phytoplankton populations are as diverse as the ecosystems in which they are found. The phytoplankton species can be tolerant of their environments. Tolerant species include hyperthermophiles, organisms preferring high temperatures (maximum growth >80°C) and psychrophiles, organisms preferring colder environments (maximum growth <15°C) (Rothschild and Mancinelli 2001). Even within a freshwater lake, phytoplankton species can be selective in where they are located. Most freshwater lakes have horizontal layers separating the water columns. An upper layer (epilimnion) is the stratum of circulating waters and the lower layer (hypolimnion) is the layer of stable water (Wetzel 2001). A third layer called the metalimnion separates these layers and can be marked by thermal changes (Wetzel 2001). Halophyllic species of phytoplankton are selective, and prefer the metalimnion where higher amounts of dissolved solids are present (Hutchinson 1978). In some temperate oligotrophic lakes, certain species of phytoplankton are abundant in the hypolimnion (Tilzer, Paerl et al. 1977). Some of these phytoplankton species are adapted to lower irradiances present in the hypolimnion.

The water columns of Lake Bonney's east and west lobes are separated into an upper and lower layer by a chemocline. The dominant phytoplankton species present in the lobes of Lake Bonney are hypothesized to be evenly distributed between the upper and lower layers. The physiological characteristics of phytoplankton populations including phytoplankton carbon to chlorophyll *a* and primary productivity to chlorophyll *a* ratios are also hypothesized to be similar between the layers. The purpose of this chapter is to determine if differences in species present and their physiological characteristics are evident between the layers.

Methods of quantifying phytoplankton populations in a system are numerous. Some of the methods include identification and quantification (enumeration) of the phytoplankton species, measuring organic carbon, abundances of pigments, and determining primary production. Biomass is the mass of living material. Quantifying phytoplankton populations using parameters such as total carbon and pigments are impaired by the presence of detritus (Wetzel 2001). Enumeration affords the benefit of identifying the phytoplankton species and differentiating the phytoplankton from detritus. Counts are usually reported as abundance, or cells per unit volume. However, enumeration may overestimate or underestimate the biomass because of the differences in cell size. To better approximate biomass, measurements of the phytoplankton species are determined for the majority of species present (species making up >1% of the total phytoplankton counts). The species counts per unit volume times the average of the measurements can then be converted to phytoplankton carbon (Mullin, et al. 1966).

Characteristics of Phytoplankton Species

The main pigment that all algae contain is chlorophyll *a*. Chlorophyll *a* pigments associated with the antenna and the reaction centers for photosynthesis. Various phytoplankton species possess accessory pigments in addition to the chlorophyll *a* pigments. The amount and types of pigments can be signatures for different phytoplankton species in a population. Accessory pigments extend the ability to harvest light for photosynthesis. Photosynthesis is the process of converting light energy into chemical energy. Two photosystems are part of the process, photosystem I and photosystem II. When a pigment absorbs photons of light, electrons are promoted to higher orbital shells. Energy obtained is passed from pigment molecule to pigment molecule. The photolysis of water donates an electron to photosystem II. Electrons are then transferred to photosystem I and used to create NADPH or ATP. This energy is then passed to the Calvin cycle to convert CO_2 into sugars.

Primary production to pigment ratios and different rates of primary production can determine different phytoplankton species' responses to environmental conditions (Wetzel 2001). Primary production is related to the increase in biomass of phytoplankton populations because it is the quantity of organic matter produced or stored during photosynthesis (Wetzel 2001). A widely used method of determining primary production includes the direct measurement of ^{14}C contained in light and dark bottles. This method results in values close to net production. Gross primary production is respiration added to net primary production (Wetzel 2001).

Environmental Constraints on Phytoplankton Populations

Light, temperature, and nutrients affect phytoplankton populations. Photosynthetically active radiation (PAR) is the amount of solar radiation available for photosynthesis (400 nm-700 nm) in the water column. If light is low the photochemical reactions will limit photosynthesis. Phytoplankton can adjust to low light levels by changing the amount of pigment per cell (Steeman-Neilsen and Jorgensen 1968). Phytoplankton adjustments may also include changing the rate of photosynthesis (Wetzel 2001). Temperature tolerances vary for the phytoplankton species. The minimum temperature at which photosynthesis can occur for some species is approximately 15°C (Ragotzkie and Likens 1964). Nitrogen and phosphorus are the two most important nutrients for phytoplankton species. Useable forms of inorganic nitrogen include ammonium-nitrogen (NH_4^+-N), nitrite–nitrogen (NO_2^--N), and nitrate-nitrogen (NO_3^{2-}-N). These forms are used in amino acid synthesis and other organic nitrogenous compounds. Usually nitrogen compounds are prevalent in freshwater systems. Phosphorus in lake environments is of interest because it is often the limiting nutrient in freshwater systems (Wetzel 2001). Phosphorus is required for energy transformation during photosynthesis (Rao 1997). The most useable form is soluble reactive phosphorus (SRP) and (PO_4^{3-}) (Wetzel 2001). Phytoplankton species can become dominant if the conditions are conducive to their physiological requirements (Lampert and Sommer 1997). Dominance of phytyoplankton species can be observed by changes in direct counts, phytoplankton carbon, changes in the amounts and types of pigments, changes in the primary production values, and changes in the ratios of these parameters to one another. These changes are usually related to the changes in the environmental conditions. Even though phytoplankton species have distinct physiological requirements, the coexistence of rare with dominant species can occur. Competitive exclusion theoretically should be taking place instead of the high diversity of the phytoplankton species observed in certain environments. Hutchinson (1961) referred to this as the "paradox of the plankton." There are varieties of explanations for the rejected competitive exclusion theory. Most explanations include reference to the dynamic environments these species inhabit. Nutrients, light availability, temperatures, and salinities, affect phytoplankton species' abundance. Most of these factors will vary with small changes in the climate.

Within lakes of the McMurdo Dry Valleys, the environments are stable. The ice-covers limit mixing to localized regions and helps with lake chemistry to stratify the lakes (Spigel and Priscu 1998). Previous studies have documented the stratified phytoplankton populations in the lakes, but these studies did not have the benefit of a long-term data set. This study will use long-term data to determine the extent of phytoplankton stratification in Lake Bonney from the lake's water samples collected from 1989 to 1991 and 1994 to 2000. A sill located at 13 m separates Lake Bonney into two lobes. The lobes are referred to as the east lobe and west lobe. This study investigates both lobes of the lake. In the east lobe of Lake Bonney long-term data collected from 1989 to 1991 and 1994 to 2000 will be used to determine the extent of phytoplankton stratification in Lake Bonney. Data collected from 1989, 1992, and 1994-2000 will be investigated for the west lobe of Lake Bonney. Characteristics of the populations determined from Chapter 2 including the diversity indices and species' numbers will be depicted by depth. The physiological differences amount of chlorophyll *a* per phytoplankton carbon unit and per primary productivity unit will also be compared by depth.

Physiochemical Characteristics of Lake Bonney

Vertical gradients of conductivity as well as nutrients and oxygen help to stratify the lakes in the McMurdo Dry Valleys (Angino, et al. 1964; Koob and Leister 1968; Spigel, et al. 1991; Sharp 1993; Spigel and Priscu 1998). Conductivity is a measurement of the concentration of ions dissolved in waters (Wetzel 2001). Lake Bonney is one of the most highly stratified lakes in the Taylor Valley. Conductivity measurments in the lobes of Lake Bonney begin with freshwater values and increase down the water column to near 3 times that of seawater (Spigel and Priscu 1998). Conductivity measures the resistance of a solution to electrical flow. An increase in ions results in declining resistance and increasing conductance. In the lobes of Lake Bonney, the conductivity increases further down the water column (Figure 3.1). The west lobe of Lake Bonney follows the same conductivity profile as the east lobe (Figure 3.1). Conductivity profiles of the lakes also show the division of the water column into an upper layer, similar to the epilimnion in less stratified lakes, (5-10 m) and a lower layer, (13-~40 m) (Figure 3.1). The layers are separated by a chemocline (10-13 m). The chemocline is the layer with rapid increases in conductivity (Figure 3.1). Temperatures are so cold in the lake that the density difference is minimal (Figure 3.1). In the lobes of Lake Bonney, the temperatures increase down the water column to ~20m, then decrease to the bottom waters. Coldest temperatures can be below zero in the bottom waters of the lakes. The high conductivity keeps the lakes from freezing in the lower layer (Figure 3.1).

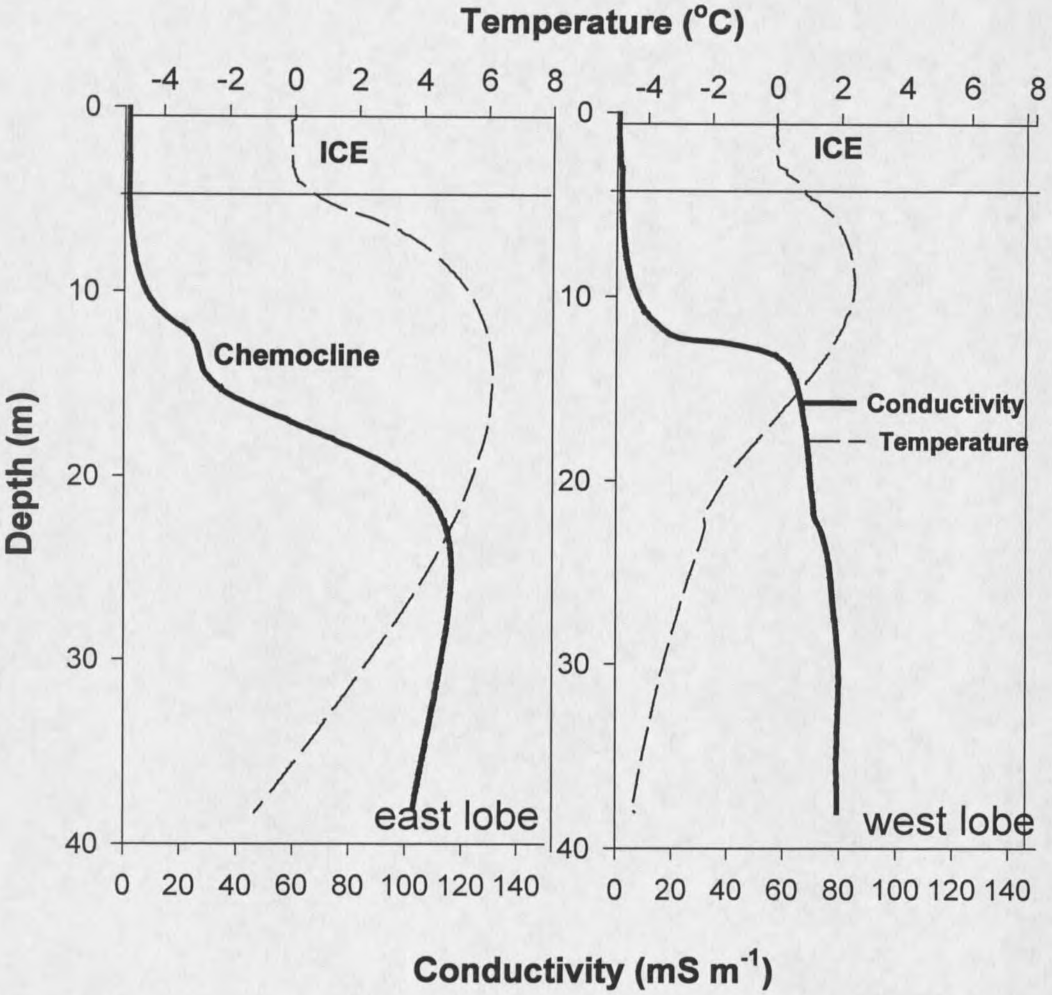


Figure 3.1 Conductivity and temperature profiles for the east (ELB) and west (WLB) lobes of Lake Bonney during November 1998.

Profiles of nitrogen and phosphorus show the location of the chemocline present in the lakes (Figure 3.2). Chemoclines separate the nutrient rich bottom depths from the upper depths. Chemoclines are the areas of increasing conductivity (Wetzel 2002). The upper layer has extremely low nutrient concentrations where as the bottom waters provide a nutrient sink. Nutrients available for primary producers move from bottom waters up through the chemocline by molecular diffusion to the upper layer (Neale and Priscu 1995). The influx of melt water provides small amounts of nutrients for the upper waters (Lyons, Welch et al. 1998).

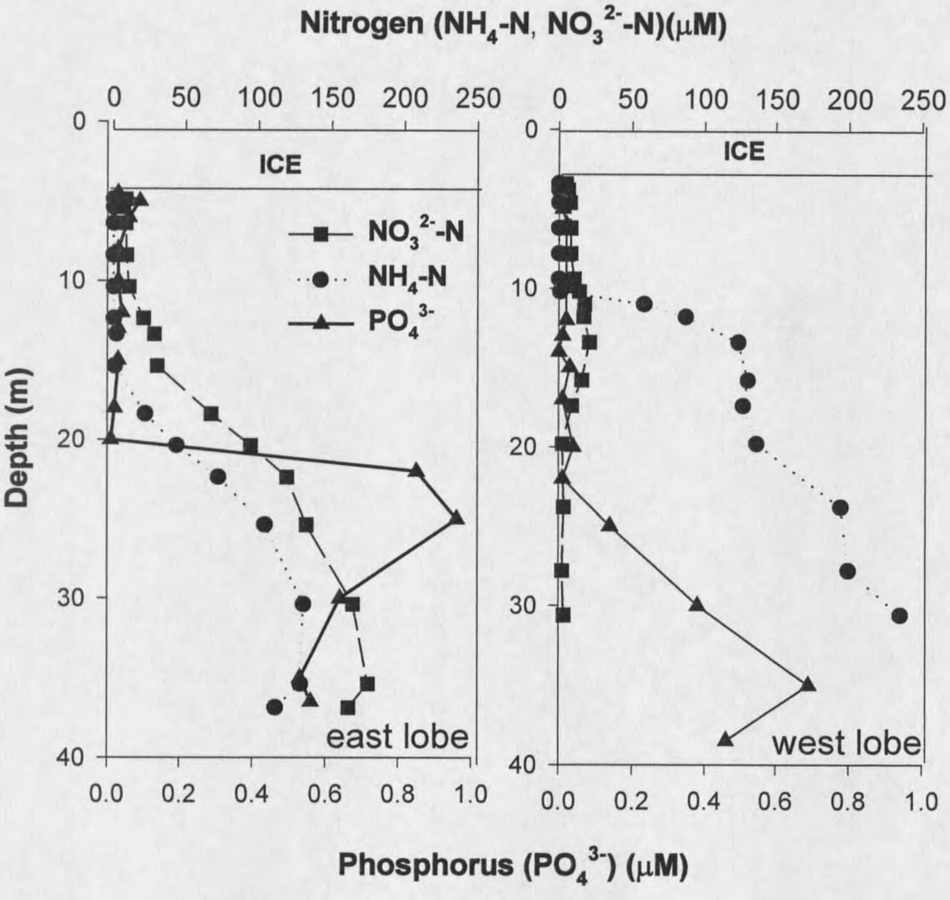


Figure 3.2 Nutrient profiles show the difference between the nutrient rich bottom waters and nutrient deficient upper waters. Data were taken from November 1999 samples.

The ice covers on the lobes of Lake Bonney limit irradiance beneath the ice from 1-3% of incident irradiance (Priscu 1991; Lizotte and Priscu 1992). These ice covers also selectively transmit wavelengths of light <500 nm (Lizotte and Priscu 1992). Photosynthetically active radiation (PAR) is a measurement of the amount of solar radiation available for photosynthesis (400 nm-700 nm) in the water column. In Lake Bonney, the maximum amount of PAR is <50 umol photons m^{-2} d^{-1} (Priscu 1991; Lizotte and Priscu 1992). PAR is attenuated down the water column so that phytoplankton populations further down the water column receive less amounts of PAR than those under the surface of the ice (Figure 3.3). At 13 m, less than 1% of PAR is available for photosynthesis in the lakes. Seasonal changes in PAR are not significant. Nutrients, temperature, conductivity, and PAR measurements vary down the water column creating distinct environments for phytoplankton populations in both lobes of Lake Bonney. Three distinct layers are present in the lakes: the upper layer (5-10 m), chemocline (10-13 m), and the lower layer (13-40 m).

Characteristics of Phytoplankton Populations in Lake Bonney

The phytoplankton species in Lake Bonney occur in stratified layers (Koob and Leister 1968; Vincent 1981). Studies on the east lobe of Lake Bonney show the lake is stratified with distinct physiological and biological differences at each layer (Seaburg, et al. 1983; Lizotte and Priscu 1992; Sharp 1993; Lizotte and Priscu 1998). Phytoplankton species present contain varying amounts of chlorophyll *a*. Distinct chlorophyll *a* peaks in the water columns signify the locations of phytoplankton populations. In previous studies, the peaks were located at ~ 4-5 m, and further down the water column at ~10-13m and again at ~17-20 m in the east lobe of Lake Bonney (Lizotte and Priscu 1998).

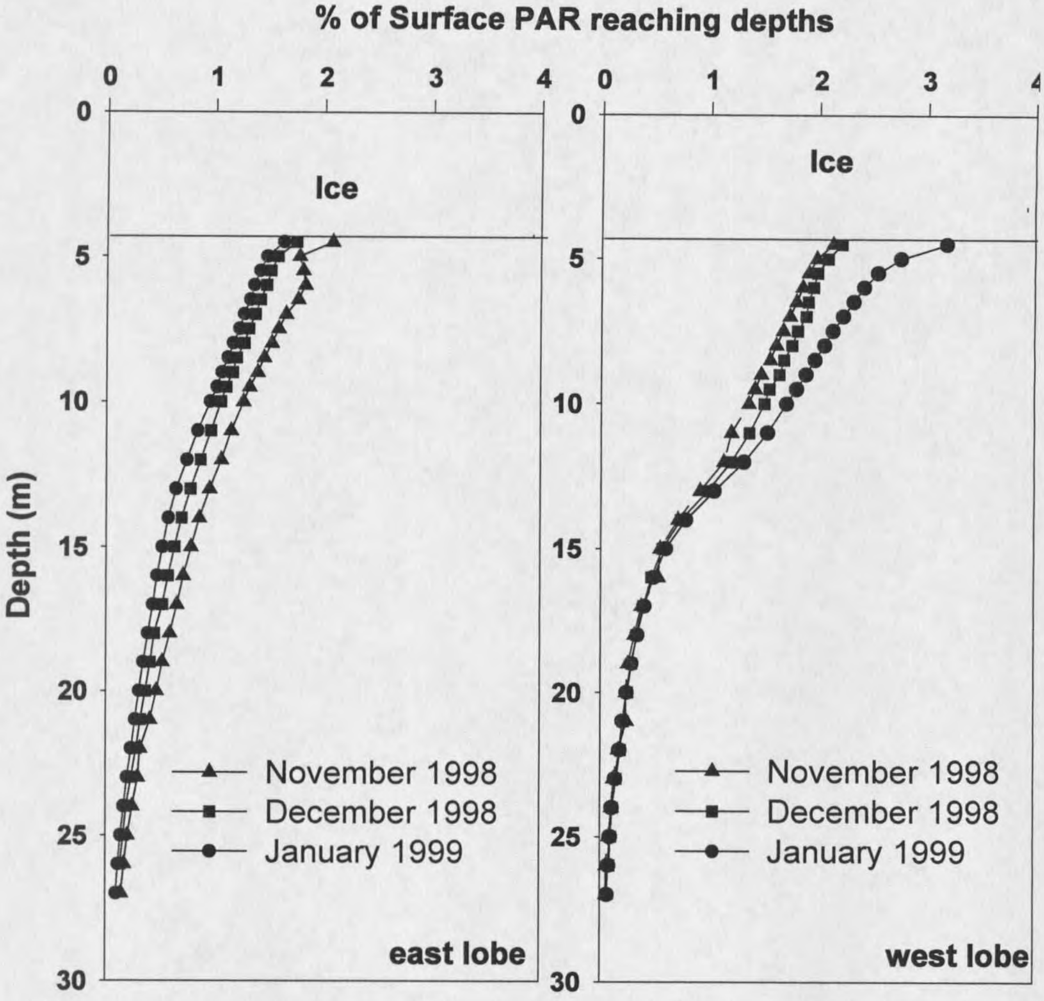


Figure 3.3 Photosynthetically active radiation (PAR) attenuation profiles. Data were from 1998-1999 season.

Types of phytoplankton species and the spatial variability of a phytoplankton population can be determined from the locations of pigments in the water column using a High Performance Liquid Chromatography (HPLC) pigment analysis. Lizotte and Priscu (1998) performed HPLC analysis on Lake Bonney. Stratification of phytoplankton species were determined in the HPLC analysis (Lizotte and Priscu 1998). For example, alloxanthin found in Cryptophytes dominated the upper waters just below the surface of the ice-cover of the east lobe of Lake Bonney (Lizotte and Priscu 1998). Where as fucoxanthin, found in Chrysophytes, and chlorophyll *b*, found in Chlorophytes, dominated the deeper depths (Lizotte and Priscu 1998).

Photosynthesis irradiance curves are frequently used when modeling primary productivity to determine the physiology of the primary producers present (Henley 1993). The hyperbolic tangent function is one of many modeling equations used to fit measured production data to incident irradiance (Henley 1993). Lizotte and Priscu (1992) used photosynthesis irradiance curves to determine physiological characteristics of the phytoplankton present in Lake Bonney relative to *in situ* PAR. Four depth zones were selected (5 m, 6 m, 10 m and 17 m) in the east lobe of Lake Bonney. The zones were based on locations of chlorophyll *a* peaks from chlorophyll *a* profile graphs. Photosynthetic rates for Lake Bonney were low in the upper depths and higher further down the water column, indicating adaptation to low levels of PAR (Lizotte and Priscu 1992). Photosynthetic efficiencies from the 10 m and 17 m depths were higher than the value determined from the 5 m depth. These results indicated phytoplankton populations in the deeper depths were more efficient at utilizing PAR (Lizotte and Priscu 1992).

Methods

Limnological sampling and analysis methods are reported in Chapter 1 and will not be repeated in this Chapter. The null hypothesis being tested is that the percent phytoplankton carbon contributed by the dominant phytoplankton taxa is the same for the upper and lower layers of the water columns. Paired t-tests were performed on the log-transformed values of phytoplankton species carbon for the dominant species in the layers since the samples were taken from the same water column. These layers correspond to the trophogenic zone or zone where enough light is present for photosynthesis. In the east lobe of Lake Bonney the trophogenic zone extends from under the ice cover ~5 m to ~18 m. In the west lobe of Lake Bonney the zone is from under the ice cover ~5 m to 20 m. Chlorophyll *a* to carbon ratios and primary production to carbon ratios were also hypothesized to be the same in the upper and lower water columns. This hypothesis was tested using paired t-tests between the layers. Values were numerically integrated into layers using the trapezoidal rule. Layers for the east and west lobes of Lake Bonney included the upper layer (5-10 m), the chemocline (10-13 m), and the lower layer (13-18 m). The west lobe of Lake Bonney had a lower layer extended further down the water column to ~20 m. Grouping of layers corresponds with the chemical and biological characteristics of the lakes observed in the profile plots (Figures 3.1, 3.2, 3.3, 3.4, 3.5, and 3.6). Values were transformed using the natural log. This resulted in the best normal distribution of the phytoplankton carbon.

Results

Depth profiles of chlorophyll *a*, primary production, and phytoplankton carbon from the lake's water samples. Profiles of primary productivity for the east and west lobes of Lake Bonney are similar to the chlorophyll *a* profiles (Figure 3.4 and 3.5). Peaks in primary production occur in the east lobe of Lake Bonney in the upper layer in November 1998 and at 13 m in December 1998. In the west lobe of Lake Bonney a peak is prominent at 13 m. The peak in the upper layer at 5 m is very small compared to the 13 m peak. The primary production, chlorophyll *a* and phytoplankton carbon profiles for the west lobe of Lake Bonney are more than two times greater than the east lobe's profile plots. Phytoplankton carbon profiles resemble the chlorophyll *a* and primary production profile plots (Figure 3.6). Peaks were located in the upper layer in November 1998 and in the lower layer at about 13 m in December 1998 in the east lobe of Lake Bonney. Total phytoplankton carbon in the west lobe of Lake Bonney was nearly three times the phytoplankton carbon in the east lobe of Lake Bonney. Peaks in phytoplankton carbon for the west lobe were very prominent at 13 m. The data used for the plots were taken from the 1998-1999 field season.

Spatial Distribution of Phytoplankton Species

The species for the east lobe of Lake Bonney that made up >90% of the total phytoplankton counts included *Chlamydomonas subcaudata*, *Chlorococcum sp.*, *Chloromonas sp.*, *Chlamydomonas intermedia*, *Pyramimonas sp.*, *Thorakomonas sp.*, *Chrysococcus sp.*, *Ochromonas sp.*, *Cryptomonas sp.*, and *Chroomonas sp.* (Appendix A). For the west lobe of Lake Bonney species making up over 90% of the population included *Chlamydomonas subcaudata*, *Chloromonas sp.*, *Chlamydomonas intermedia*, *Pyramimonas sp.*, *Thorakomonas sp.*, *Chrysococcus sp.*, *Ochromonas sp.*, *Cryptomonas sp.*, and *Chroomonas sp.* (Appendix A). *Chroomonas sp.*, *Cryptomonas sp.*, *Ochromonas sp.*, *Chlamydomonas subcaudata*, and *Chlamydomonas intermedia* made up ~90% of the total cell counts and total phytoplankton carbon in both lobes of Lake Bonney (Figure 3.7 and Figure 3.8). *Ochromonas sp.* made up a large portion of the total abundance.

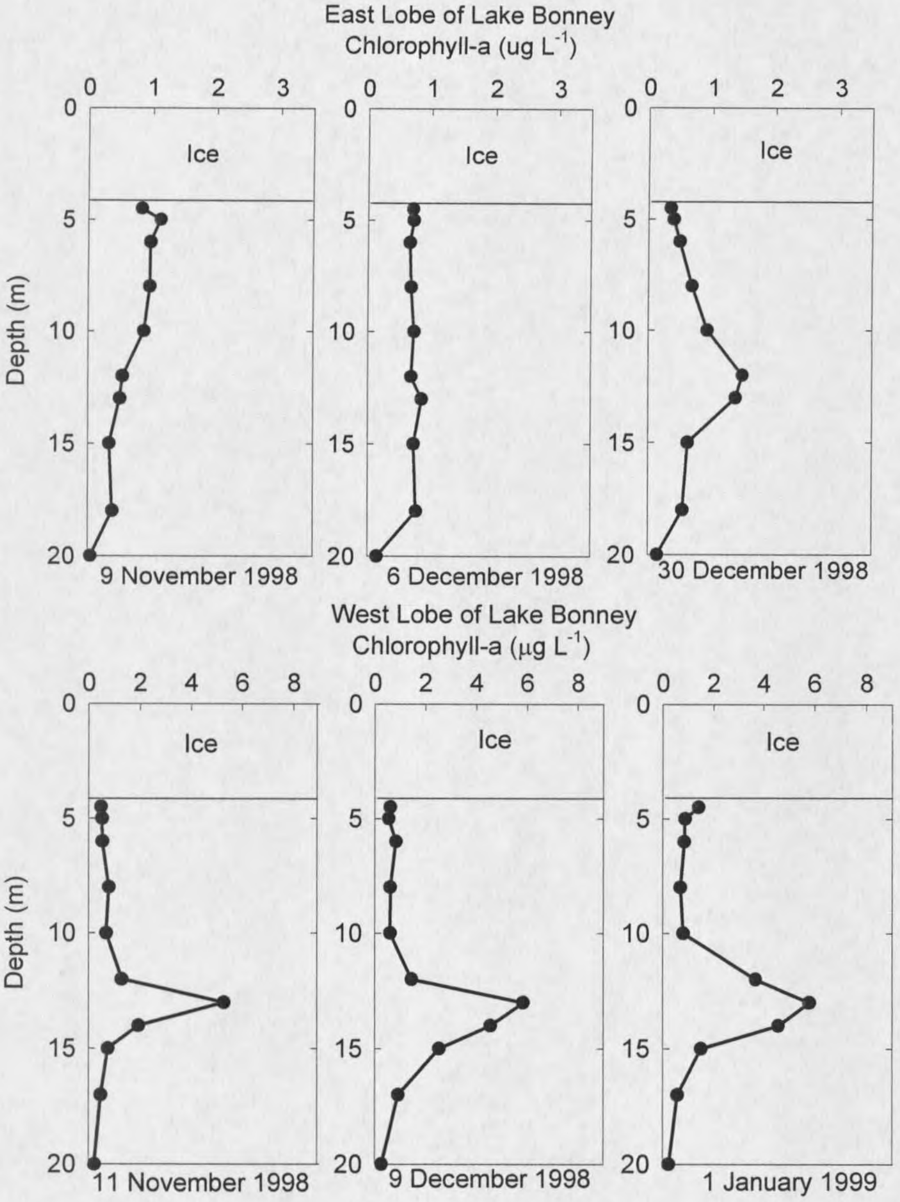


Figure 3.4 Chlorophyll *a* profiles for the east and west lobes of lake Bonney correspond to regions where phytoplankton populations are found.

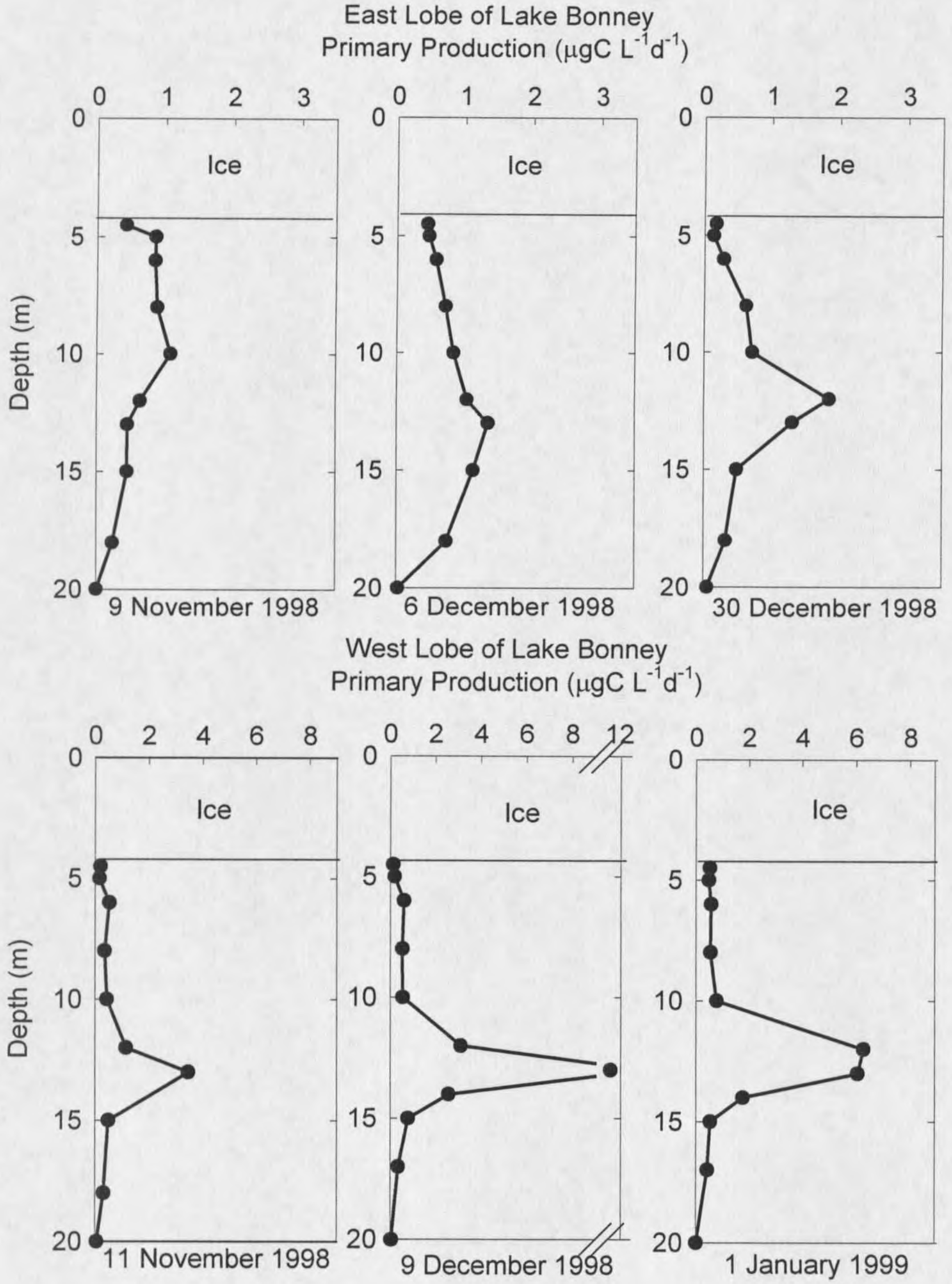


Figure 3.5 Primary productivity profiles for the east and west lobes of Lake Bonney. Note the difference in axes between the east and west lobes.

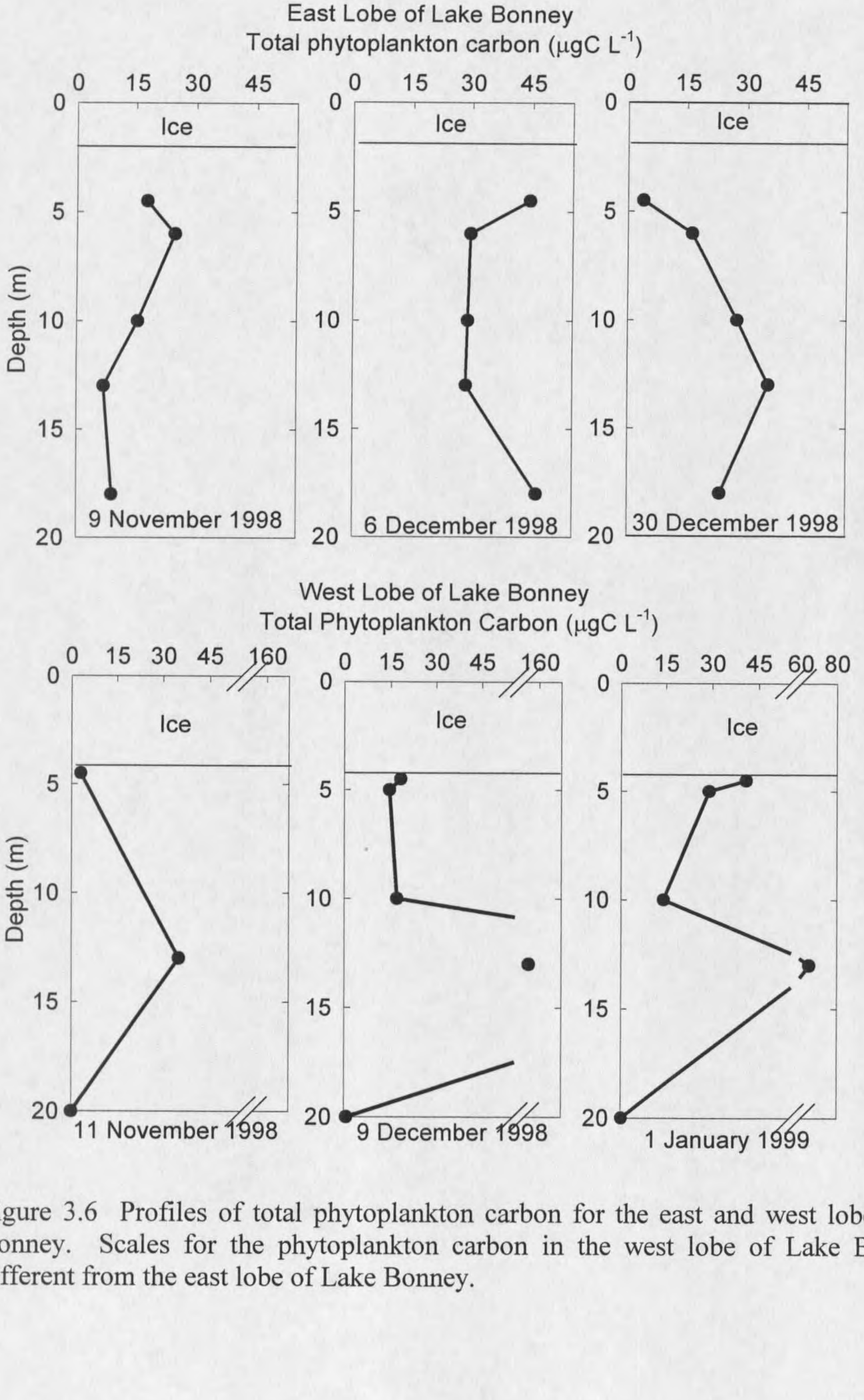


Figure 3.6 Profiles of total phytoplankton carbon for the east and west lobes of Lake Bonney. Scales for the phytoplankton carbon in the west lobe of Lake Bonney are different from the east lobe of Lake Bonney.

However, because of its small size, it contributed far less to the total phytoplankton carbon in the east lobe of Lake Bonney (Figure 3.7). In December 1998, the dominance of *Chlamydomonas subcaudata* is exclusive to the lower layer in the east lobe of Lake Bonney (Figure 3.7).

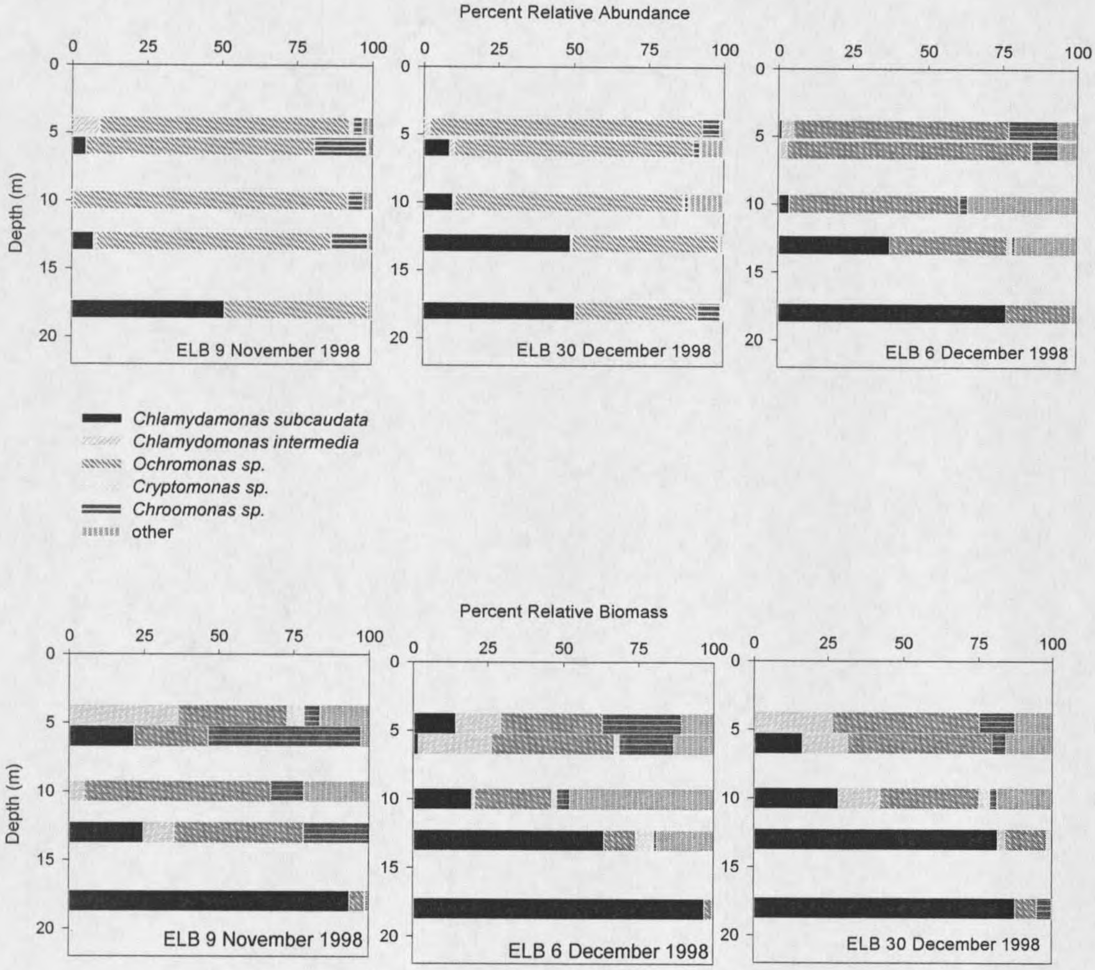


Figure 3.7 (a) Relative phytoplankton abundance and (b) relative phytoplankton biomass from the east lobe of Lake Bonney.

In the west lobe of Lake Bonney the species that tends to dominate in both abundance and total phytoplankton carbon is *Ochromonas sp.* (Figure 3.8). Populations of *Ochromonas sp.* are distributed throughout the water column. The majority of the populations of *Chlamydomonas subcaudata* was found in the lower layer (Figure 3.8).

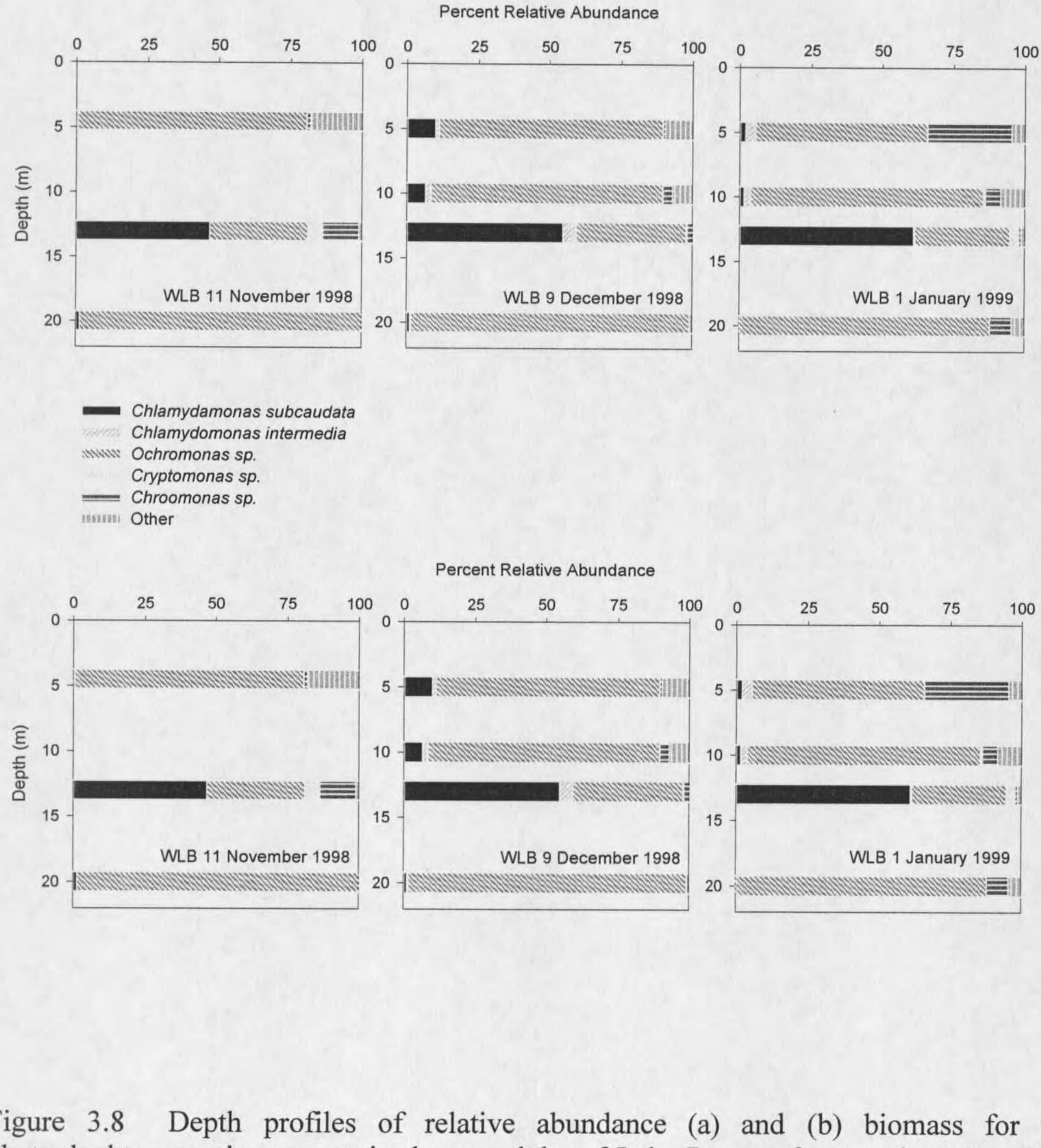


Figure 3.8 Depth profiles of relative abundance (a) and (b) biomass for the phytoplankton species present in the west lobe of Lake Bonney for samples taken from 1998-1999.

Phytoplankton carbon values for the dominant taxa and total phytoplankton carbon were integrated over depth using trapezoidal integration. The layers included; the upper layer (5-10 m), chemocline (10-13 m), and the lower layer (13-20 m). The upper and lower layers contained the majority of the phytoplankton cells whereas phytoplankton cell counts in the chemocline were low. Thus, the chemocline was not included in further analyses. Single missing values were linearly interpolated from the values above and below. If multiple missing values occurred, then the average for all data points was used.

Data were normalized by dividing the value of each dominant taxon by the total phytoplankton carbon. Paired t-tests determined that *Chroomonas sp.* biomass was significantly greater in the upper layer than in the lower layer for the east and west lobes of Lake Bonney ($P<0.001$) (Table 3.2). Paired t-tests also revealed that *Chlamydomonas subcaudata* biomass was greater at the lower layer than at the upper layer for the lakes ($P<0.001$) (Table 3.2). However, the biomass of *Ochromonas sp.* in the west lobe was not significantly greater at the upper or lower layers ($P=0.262$) (Table 3.2).

Physiological differences of the vertically stratified phytoplankton in Lake Bonney Primary production, chlorophyll *a*, and phytoplankton carbon values were depth integrated using trapezoidal integration for separation of the values into layers the upper layer (5-10 m), chemocline (10-13 m), and the lower layer (13-20 m) as described above for the phytoplankton carbon data. Missing values were determined similarly to the interpolations for single and missing values already discussed. One data point on 19

Table 3.1 Results from t-tests on the location of the dominant phytoplankton species for the east and west lobes of Lake Bonney. Data included all phytoplankton samples analyzed from 1989-01. Data were converted to phytoplankton biomass (μgC l^{-1}) and integrated for the depth zones using the trapezoidal integration (mgC m^{-2}). The data were divided into the total phytoplankton carbon to determine the percent each species contributed to the carbon.

East Lobe of Lake Bonney	*Mean (%) 5-10m*	*Mean (%) 13-18m*	*Degrees freedom*	*t-statistic*	*Probability*
Chroomonas sp.	74.54	11.88	34	12.45	>0.001
Ochromonas sp.	54.53	21.17	34	7.02	>0.001
C. subcaudata	21.04	53.06	34	-4.41	>0.001

West Lobe of Lake Bonney	*Mean (%) 5-10m*	*Mean (%) 13-18m*	*Degrees freedom*	*t-statistic*	*Probability*
Chroomonas sp.	59.06	23.48	29	3.96	>0.001
Ochromonas sp.	42.24	34.17	29	1.14	0.262
C. subcaudata	9.17	52.36	29	-8.29	>0.001

September 1995 was an outlier for the phytoplankton carbon to chlorophyll *a* values in the layers 5-10 m and 13-18 m, as well as the primary productivity values to chlorophyll *a* values. It was assumed that the chlorophyll *a* value determined at this point was not accurate. Outliers were omitted from further analysis.

Normal distributions were obtained by transforming the data using the natural log. To determine if the populations above the chemocline have different ratios of phytoplankton carbon to chlorophyll *a* and primary productivity to chlorophyll *a* from populations of phytoplankton below the chemocline, paired t-tests were performed.

Paired t-tests showed that phytoplankton populations in the upper layer differed in ratios of chlorophyll *a* to phytoplankton carbon for both lobes of Lake Bonney. However, primary production to chlorophyll *a* ratios for the west lobe of Lake Bonney did not reveal a significant difference between the upper and lower layers.

Table 3.2 Results from t-tests between two sample means. The means were from ratios of phytoplankton carbon (Total phytoplankton) to chlorophyll *a* and primary productivity (PPR) to chlorophyll *a*. Data were transformed to a normal distribution using the natural log before tests were performed.

Lake Bonney	Degrees freedom	T-statistic	Probability
East lobe Total phytoplankton/chlorophyll *a*	28	8.56	>0.001
East lobe Primary production/chlorophyll *a*	28	9.02	>0.001
West lobe Total phytoplankton/chlorophyll *a*	21	-4.75	>0.001
West lobe Primary production/chlorophyll *a*	21	1.57	0.13

Discussion

Spatial Distribution of Phytoplankton Species in Lake Bonney

The east and west lobes of Lake Bonney have distinct vertical layers separated by a chemocline into an upper and lower layer with distinct microbial populations. In general, meromictic lakes have two distinct microbial populations. The populations are found in the upper and in lower layers (Bell and Laybourn-Parry 1999). Roberts et al. (2000) found in Lake Fryxell that the biomass was greatest around the chemocline separating the layers. In the spatial analyses of the lobes of Lake Bonney, phytoplankton populations were located in the upper layer and below the chemocline in the lower layer. Phytoplankton populations of the dominant taxa at 11 and 12 m were fewer than populations found in the upper and lower layers. The chemocline, similar to the metalimnion in temperature stratified lakes, is the area of increased ion and nutrient content. However, low amounts of PAR are available for photosynthesis in this layer. In the east and west lobes of Lake Bonney, chlorophyll *a*, primary production, and phytoplankton carbon peaks were prominent in the lower layer below the chemocline for most samples analyzed from 1989-01. The *Chlamydomonas subcaudata* populations correspond with the locations of these peaks in the lower layer in both lobes of Lake Bonney. Less prominent peaks in chlorophyll *a*, primary production, and phytoplankton carbon are found in the upper layer. These peaks correspond with high abundances and biomass of *Chroomonas sp.* for both lobes of Lake Bonney. In the upper layer of the east lobe of Lake Bonney, populations of *Ochromonas sp.* are found in higher numbers than in the lower layer. However, populations of *Ochromonas sp.* in the west lobe of Lake Bonney are ubiquitous and occur in both the upper and lower layers. The upper layers of the east and west lobes of Lake Bonney are deficient in nutrients (Priscu 1995). Nutrients available for primary producers move from the nutrient rich bottom waters up through the chemocline by molecular diffusion to the upper layer (Neale and Priscu 1995). The influx of melt water and aeolian transported material that moves down through the ice provides nutrients for the upper waters (Howard-Williams, et al. 1989; Priscu 1995; Lyons, et al. 1998). This influx of melt water creates a fluctuating environment for the phytoplankton species inhabiting the upper layer that are nutrient limited (Priscu 1995). The upper layer favors smaller phytoplankton species with greater surface areas for nutrient absorption. *Ochromonas sp.* and *Chroomonas sp.* are smaller than *Chlamydomonas subcaudata* and both of these species are found in the upper layer.

Physiological Characteristics of Phytoplankton Species

Previous studies determined that photosynthetic rates for Lake Bonney were low in the upper layer and higher further down the water column, indicating adaptation to low levels of PAR and efficient use of light (Lizotte and Priscu 1992). Chlorophyll *a* peaks are present in the upper hypolimnion of many oligotrophic arctic lakes (Tilzer, et al. 1977; Vincent 1981; Vincent and James 1996). Phytoplankton species present have adapted to low levels of light. Adaptations of phytoplankton are specific to the species and may include decreasing carbon to chlorophyll *a* ratios, increasing accessory pigments, or adjusting the rate of photosynthesis.

Phytoplankton populations in the lobes of Lake Bonney are physiologically distinct with respect to their carbon to chlorophyll *a* ratios and primary production to chlorophyll *a* ratios (Wetzel 2001). Chlorophyll *a* peaks are more prominent in the lower layers of the east and west lobes of Lake Bonney. *Chlamydomonas subcaudata* cells found primarily in the lower layers of both lakes efficiently use light with wavelengths of 500nm by increasing their accessory pigments, specifically chlorophyll *b* (Neale and Priscu 1995). In later studies, *Chlamydomonas subcaudata* was reported to be adapted to the low light levels by high ratios of photosystem II pigments over photosystem I, and are locked in this state because of the stable environment (Morgan, et al. 1998). These findings are consistent with the physiological characteristics of the species in the lower layer.

Conclusion

In the east and west lobes of Lake Bonney, the dominant phytoplankton species are located in distinct vertical layers. *Chroomonas sp.* is primarily located in the upper layers of both lobes and *Chlamydomonas subcaudata* is primarily located in the lower water columns of both lobes. These species are physiologically distinct from one another, which are also shown in the differences between the physiological characteristics between the populations.

CHAPTER 4

TEMPORAL VARIATIONS IN PHYTOPLANKTON POPULATIONS IN LAKE BONNEY, ANTARCTICA

Introduction

Organic Carbon in Aquatic Systems

Most organic carbon in aquatic systems is comprised of dissolved organic carbon and particulate organic carbon (Fisher and Likens 1973). The difference between particulate and dissolved organic carbon is functionally based on the sizes of the particles of carbon. Dissolved organic carbon is usally defined as particles <0.2 μm. Sources of carbon in aquatic systems are diverse and include allochthonous, or out of lake sources, and autochthonous, within lake sources (Wetzel 2001). Particulate and dissolved detritus is more abundant than live particulate carbon in many of these systems (Fisher and Likens 1973). Live particulate carbon includes phytoplankton, bacterioplankton and zooplankton.

Phytoplankton in Aquatic Systems

The evaluation of phytoplankton species is important in aquatic ecosystems because phytoplankton populations are the primary producers of organic carbon (Odum 1983). Phytoplankton populations can be evaluated using measured biomass, chlorophyll *a*, primary production, and particulate carbon from samples of aquatic environments. Phytoplankton biomass is the total weight of all living phytoplankton organisms present in a unit area at a certain time. Chlorophyll *a* is necessary for photosynthesis and is present in most algal species. Measurements of chlorophyll *a* in an aquatic system are a manageable way of estimating the phytoplankton biomass. However, measurements of chlorophyll a are impaired by the presence of detritus (Hallegraeff 1977) which affect the differences in chlorophyll *a* to carbon ratios for species of phytoplankton (Steele and Baird 1961; Steele and Baird 1962).

Primary production analysis has also been used to quantify phytoplankton populations (Strickland 1960; Strickland and Parsons 1972; Wetzel and Likens 2000). Primary production is a rate of photosynthesis. The most effective way of determining species contributions to total particulate carbon in an aquatic system is to identify and quantify (enumerate) the phytoplankton populations. Enumerations of phytoplankton species afford the benefit of identifying the phytoplankton species and differentiating the phytoplankton from detritus (Wetzel 2001). Counts are usually reported in abundance, or carbon per unit volume. These enumerations may overestimate or underestimate the phytoplankton biomass because of the differences in cell size. To better approximate phytoplankton biomass, measurements of the phytoplankton species are determined for the majority of species present (species making up >1% of the total phytoplankton counts). The species counts per unit volume times the average of the measurements can then be converted to phytoplankton carbon (Mullin, et al. 1966).

Phytoplankton Species Shifts

Phytoplankton populations have the ability to adapt to changing environments in a number of ways. One is by changing the amount of carbon production per unit biomass. A second is by shifting the phytoplankton species composition. The word succession is usually restricted to events, in a series, of species replacements resulting from preceding replacements (Reynolds 1980). The term shift can be used to describe a phytoplankton species' direct response to environmental factors. Phytoplankton species shifts will be used to refer to changes in phytoplankton populations with time instead of species succession. With turnover rates being only a few weeks in duration, phytoplankton species shifts can occur in a matter of months (Reynolds 1980). Species shifts result from conditions becoming more or less conducive to the phytoplankton species in a population (Reynolds 1980). Light and nutrient levels can contribute to these changes.

Photosynthetic active radiation (PAR) is a measurement of the amount of solar radiation available for photosynthesis (400 -700 nm) in the water column. The amount of PAR in the water columns can change. Nitrogen and phosphorus are the two most important nutrients for phytoplankton species. Nutrients were discussed in chapter 3 and will not be repeated.

McMurdo Dry Valleys Aquatic Systems

The McMurdo Dry Valleys are the largest ice-free areas on the Antarctic Continent. Within the Valleys, there are ice covered lakes where the aquatic organisms are dominated by microorganisms (Laybourn-Parry, et al. 1992; Laybourn-Parry 1997; Laybourn-Parry, et al. 2001). Studies on lakes of the Taylor Valley, one of the McMurdo Dry Valleys, have been conducted since the early 1900s (Scott 1905). These studies offered the first descriptions of the lakes. Later studies used quantitative measurements to document physical, chemical, and biological properties of the lakes (Angino and Armitage 1963; Angino, et al. 1964; Goldman 1964; Goldman, et al. 1967; Goldman 1970). These studies determined that the McMurdo Dry Valley lakes offer the opportunity to study phytoplankton populations in a simplified environment. For instance, in most aquatic systems, phytoplankton populations are affected by complex interactions of many physical, chemical, and biotic environmental factors varying in intensity and frequency (Reynolds 1989). However, in the McMurdo Dry Valleys, few predators of phytoplankton species are present in the lakes, and the aquatic systems are stable (Parker and Simmons 1985). The microbial plankton dominates this system (Laybourn-Parry 1997). Phytoplankton species are important in aquatic ecosystems because they are the primary producers of organic carbon (Odum 1983). Pomeroy (1974) alluded to the important contribution of carbon by phytoplankton species into the food web as part of the microbial loop. In the McMurdo Dry Valleys, the phytoplankton species populations are even more essential because of the low allochthonous carbon inputs into the lakes.

Lakes in the Taylor Valley include lakes Bonney, Fryxell, and Hoare. The focus of this study is on Lake Bonney. A sill present at 13 m separates Lake Bonney into two lobes (east and west). Thus, the upper waters of the lobes are connected above 13m. The west lobe of Lake Bonney is located at the head of the Taylor Glacier. Glacial melt water from the Taylor, Calkin, Hughes, Sollas, LaCroix, Matterhorn and Rhone glaciers flow into Lake Bonney between November and March (Heywood 1984). Permanent lake ice-covers and high chemical gradients help limit mixing of the water column and stabilize the environment (Spigel and Priscu 1998). Previous studies on Lake Bonney show lower amounts of nutrients, including phosphorus and nitrogen, are present in the upper water columns (5-10 m), and nutrients increase down the water columns (Priscu 1995).

Phytoplankton in the upper water columns are severely nutrient deficient in both phosphorus and nitrogen (Priscu 1995).

Lake Bonney phytoplankton populations are separated into vertical layers consisting of distinct physiological and biological differences in the water column (Lizotte and Priscu 1992). This separation was documented in Chapter 3. Photosynthetic efficiencies from the 10 m and 17 m depths were higher than the values determined from the 5 m depth, indicating highly efficient use of PAR at deeper depths (Lizotte and Priscu, 1992). This chapter addresses the temporal changes in the phytoplankton populations in the water column from 1989 to 1992 and 1994 to 2000 in the east lobe of Lake Bonney and from 1992 and 1994-2000 in the west lobe of Lake Bonney. It also addresses the physical constraints on the phytoplankton populations of individual species in the distinct layers.

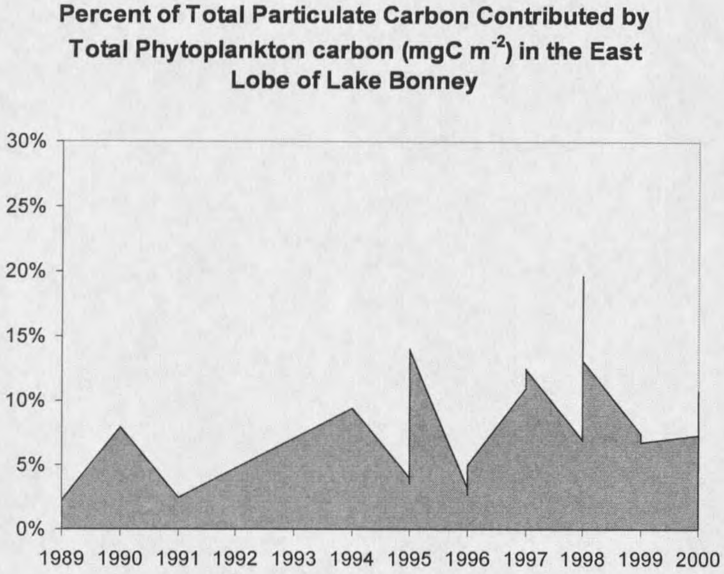
Methods

To assess the amount of particulate carbon that was phytoplankton carbon, numerical integrations were performed on the distinct layers in the east and west lobes of Lake Bonney. The photic zone of the east and west lobes of Lake Bonney are from 5-18 m and 5-20 m respectively. Measurements of particulate carbon, chlorophyll *a*, primary production, and phytoplankton carbon in the layers were also numerically integrated over depth in each layer. The layers included upper layer (5-10 m), chemocline (10-13 m), lower layer (13-18 m), and the total water column (5-18 m). The lower layer and total water column for the west lobe of Lake Bonney extended down to 20 m which corresponds to the trophogenic zone explained in Chapter 3. The interpolation of missing values was discussed in Chapter 3. Primary production, chlorophyll *a*, and total phytoplankton carbon values for integration of the trophogenic zone 5-18 m in the east lobe of Lake Bonney and 5-20 m in the west lobe of Lake Bonney were plotted with time. Analysis of variance (ANOVA) was used to determine if the dominant phytoplankton species changed during the period of this study from 1989 to 2000. ANOVA was performed using SYSTAT 10. Phytoplankton cell numbers from September and October will not reflect cell numbers from samples collected in November and December. Only November and December values are used in the plots and in all statistical analyses for both lobes of Lake Bonney.

Results

Particulate Carbon in Lake Bonney

Phytoplankton species contribute carbon to the total amount of carbon in the lobes of Lake Bonney, although the phytoplankton populations' contributions are small. The phytoplankton populations in the east lobe of Lake Bonney make up <10% of the total carbon. In the west lobe of Lake Bonney, the phytoplankton populations made up almost three times the total carbon as found in the east lobe of Lake Bonney although still only <30% (Figure 4.1). The contributions of phytoplankton populations to the particulate carbon pool in the east lobe of Lake Bonney were similar year to year from 1989-1992 and 1994-2000. However, in the west lobe of Lake Bonney, this year to year input of phytoplankton to particulate carbon decreased from 1994-2000 (Figure 4.1).



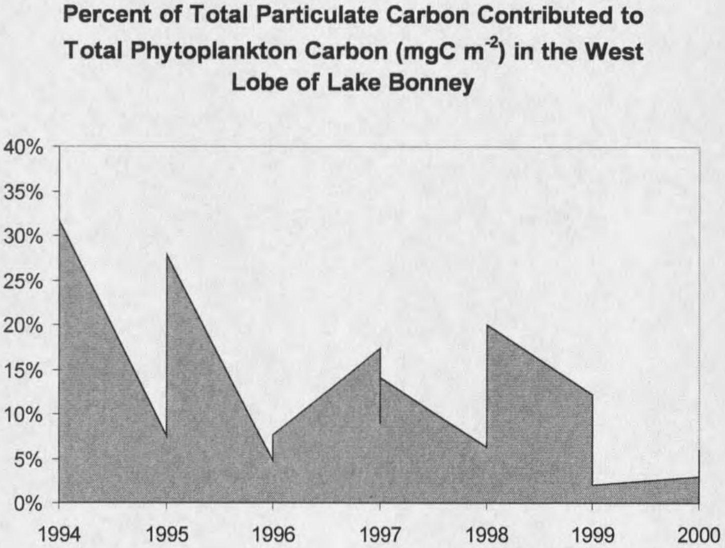


Figure 4.1 Graphs of the integrated values (5-18 m) of total phytoplankton carbon divided by the integrated total particulate carbon (5-18 m). The values are from November and December for the east and west lobes of Lake Bonney.

Phytoplankton biomass assessment in Lake Bonney

Winter sampling in the McMurdo Dry Valleys is constrained by logistics. Most of the sampling occurs in the austral summer and ends in late January, although trends are still evident from the data obtained annually. The trophogenic zones of the east and west lobes of Lake Bonney are the zones where phytoplankton productivity is occuring. Zones in the east and west lobes of Lake Bonney extend to ~18 m and ~20 m respectively. At 20 m there is no light available for photosynthesis in the east lobe of Lake Bonney. The light data is shown in Chapter 3. Values for primary production, chlorophyll *a* and phytoplankton carbon were integrated throughout the photic zone to show temporal variations. Priscu et al. (1999) reported a lag in chlorophyll *a* following increases in primary production in photic zone integrated data from 1989-1997. This lag is also shown in Figure 4.2 for the east lobe of Lake Bonney, and Figure 4.3 for the west lobe of Lake Bonney, except the data is extended to include 1997, 1998, and 1999 sampling years. The west lobe of Lake Bonney was only sampled during 1989, 1992, 1993, and 1994-2000. Phytoplankton carbon samples were obtained during the sampling of the primary production and chlorophyll *a* measurements. However, long-term trends in the total phytoplankton carbon, chlorophyll *a*, or primary production data were not evident for the east or west lobes of Lake Bonney (Figure 4.2, 4.3).

Primary production showed evidence of a possible linear relationship with phytoplankton carbon for the west lobe of Lake Bonney (p=0.05) (Figure 4.4). However, this relationship is showing non constant variance in the data thus the relationship is suspect. No other linear relationships are detectable (Figure 4.4).

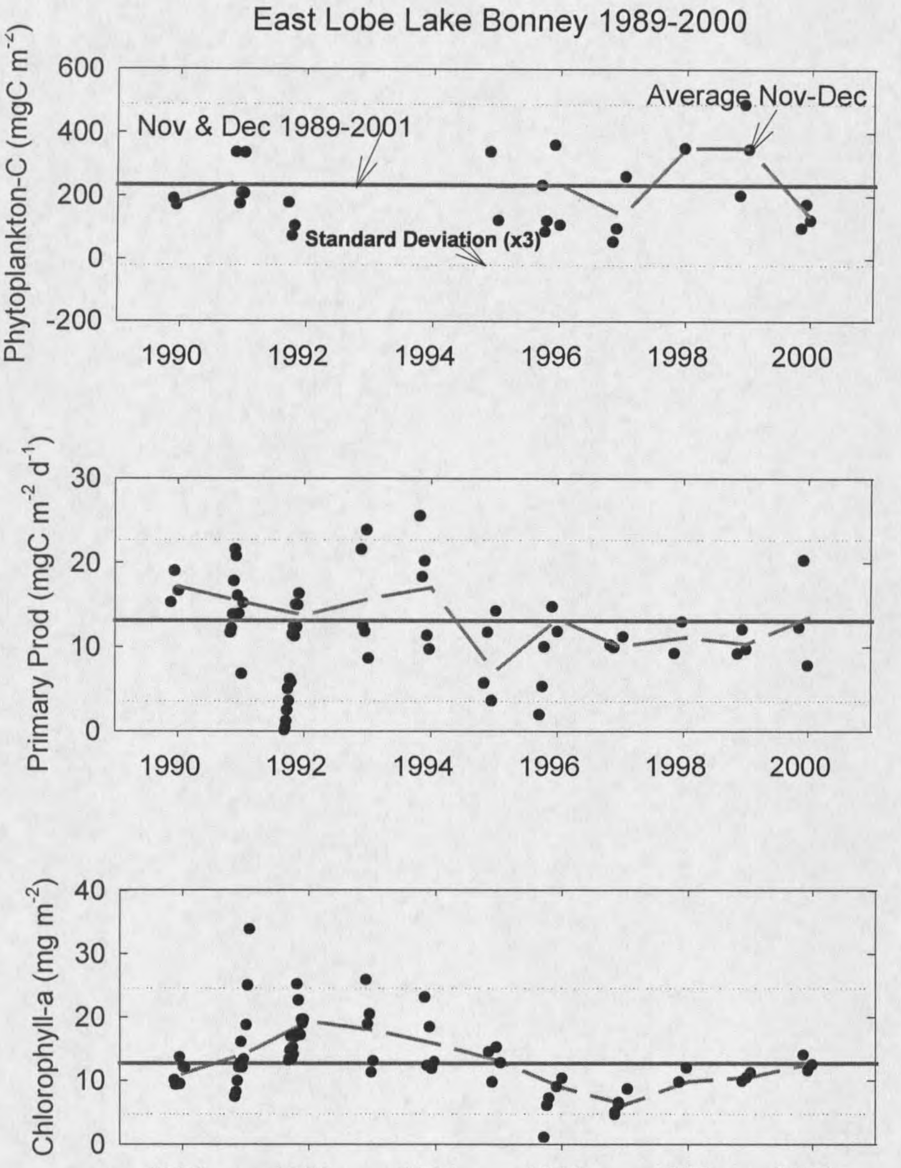


Figure 4.2 Integrated values (5-18 m) of total phytoplankton carbon, primary production (PPR), and chlorophyll *a* through time for the east lobe of Lake Bonney. The dash line is the average for November and December values for each year and the solid line is the running average from November and December 1989-2000 the dotted lines are showing 3 standard deviations away from the mean.

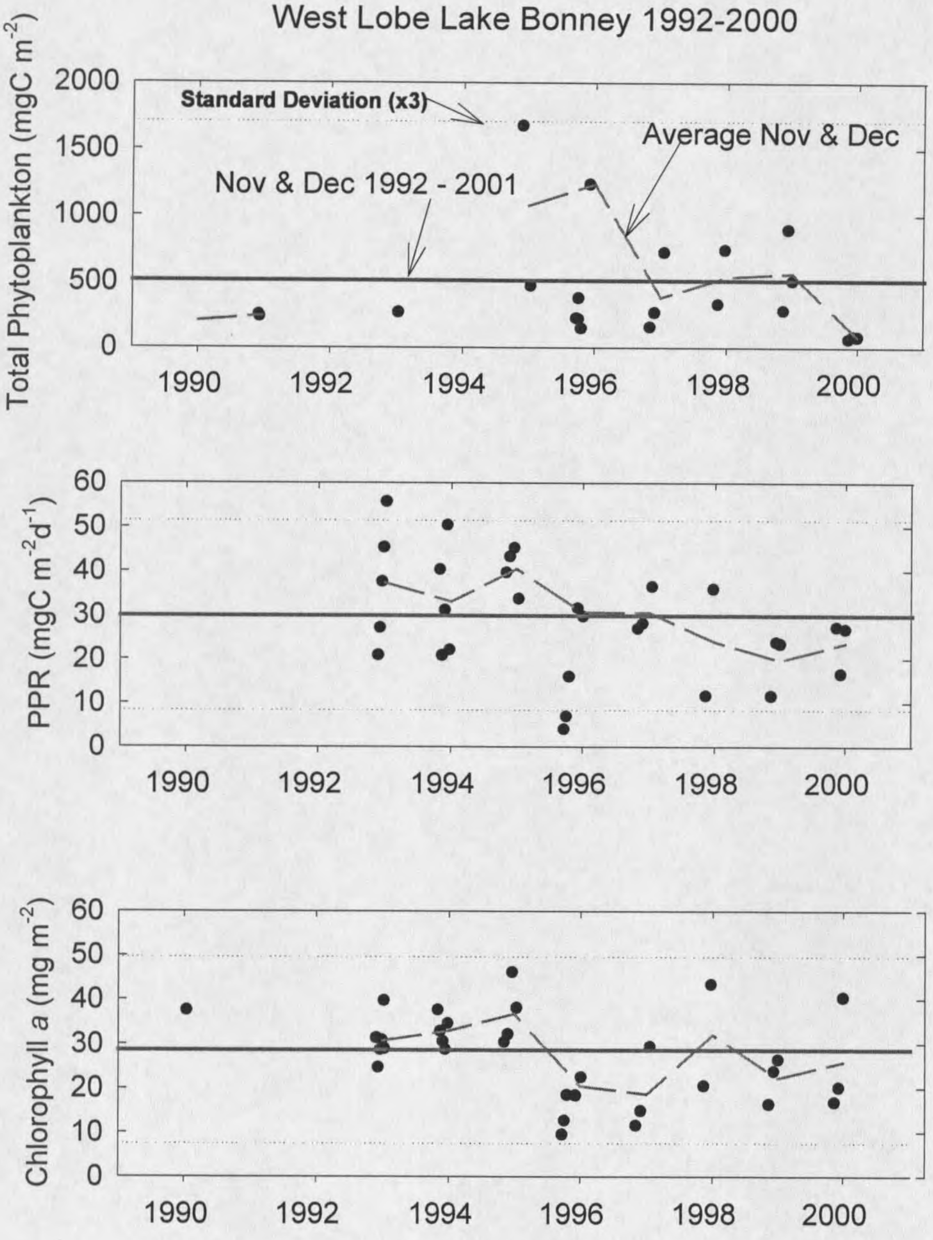


Figure 4.3 Integrated values (5-18 m) of total phytoplankton carbon, primary production (PPR), and chlorophyll *a* through time for the west lobe of Lake Bonney. The dash line is the average for November and December values for each year and the solid line is the running average from November and December 1989-2000 the dotted lines are showing 3 standard deviations away from the mean.

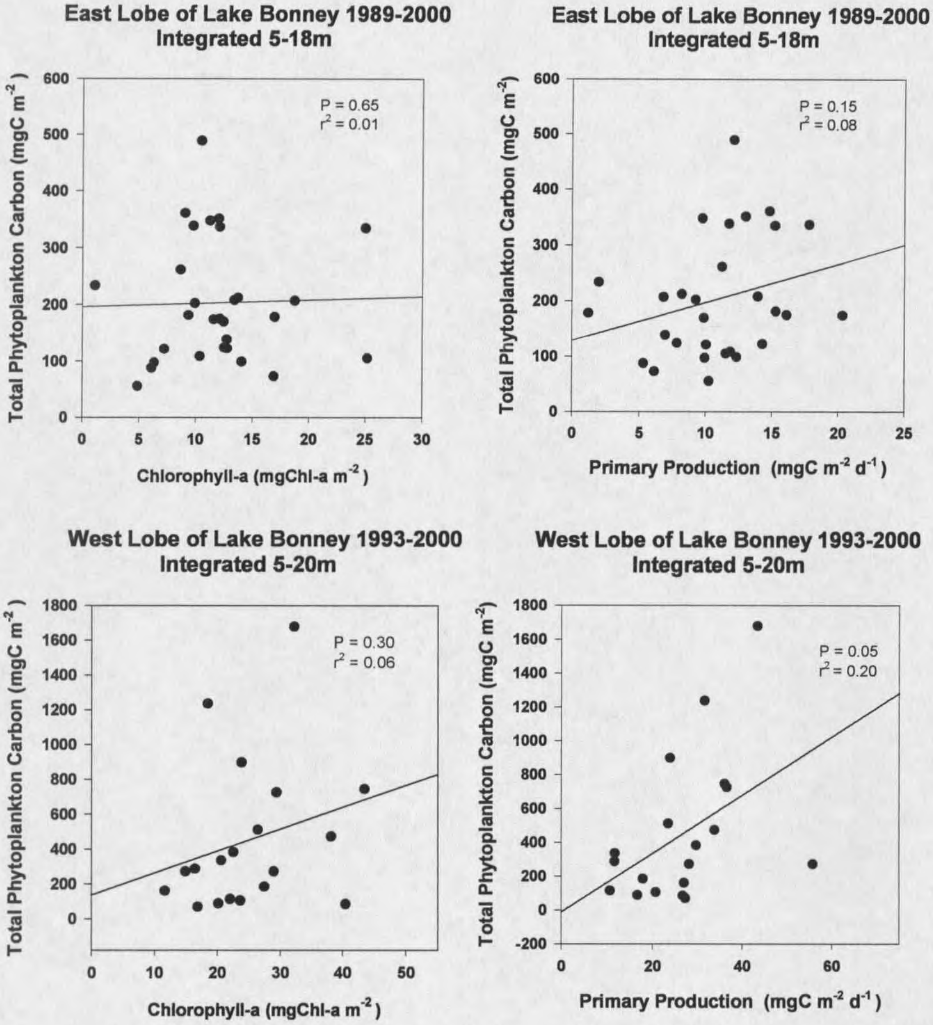


Figure 4.4 Linear regressions between phytoplankton carbon and primary production and between phytoplankton carbon and chlorophyll *a* for the east lobe of Lake Bonney and the west lobe of Lake Bonney. Values used in analysis were taken from November and December sampling dates for the integrated values in the lobes.

ANOVA determined that *Chlamydomonas sp.* do not vary significantly for the east and west lobes of Lake Bonney from 1989-2000 (p=0.107, 0.652 respectively) (Table 4.1). *Chroomonas sp.* significantly changed from 1989 to 2000 in both lobes of Lake Bonney (P=0.019, 0.001 respectively) (Table 4.1). ANOVA of November and December photic zone integrated values for *Ochromonas sp.* changed significantly from 1994-2000 for only the east lobe of Lake Bonney (p=0.001) (Table 4.1).

Table 4.1 Results from Analysis of Variance on dominant taxa from 1989 to 2000 in the east lobe and west lobes of Lake Bonney. Data used in analysis was transformed using the log of the values of numerically integrated carbon biomass (mgC m^{-2}). Only November and December data were used in the analysis.

East lobe of Lake Bonney	*Chlamydomonas sp.*	*Chroomonas sp.*	*Ochromonas sp.*
r^2	0.545	0.699	0.799
n	23	23	23
f-ratio	2.100	3.541	6.937
p-value	0.107	0.019	0.001
West lobe of Lake Bonney	*Chlamydomonas sp.*	*Chroomonas sp.*	*Ochromonas sp.*
r^2	0.652	0.881	0.598
N	21	21	21
f-ratio	0.763	9.056	1.816
p-value	0.652	0.001	0.174

The least squares means obtained from the ANOVA results were plotted to determine the significant changes in the data. *Ochromonas sp.* and *Chroomonas sp.* biomass integrated over the trophogenic zone increased biomass changed from 1989 to 2000 in the east lobe of Lake Bonney. The west lobe of Lake Bonney showed similar trends as the east lobe of Lake Bonney in that *Chroomonas sp.* biomass also changed from 1989 to 2000. To verify the changes observed in the plots pairwise comparisons were generated (Figure 4.5). Pairwise comparisons for the east lobe of Lake Bonney showed that the most significant change for *Ochromonas sp.* and *Chroomonas sp.* occurred between 1989 and 1996 and between 1990 and 1999 respectively (Figure 4.5, Appendix B). In the west lobe of Lake Bonney the most significant change for *Chroomonas sp.* occurred between 1998 and 2000 (Figure 4.6, Appendix B).

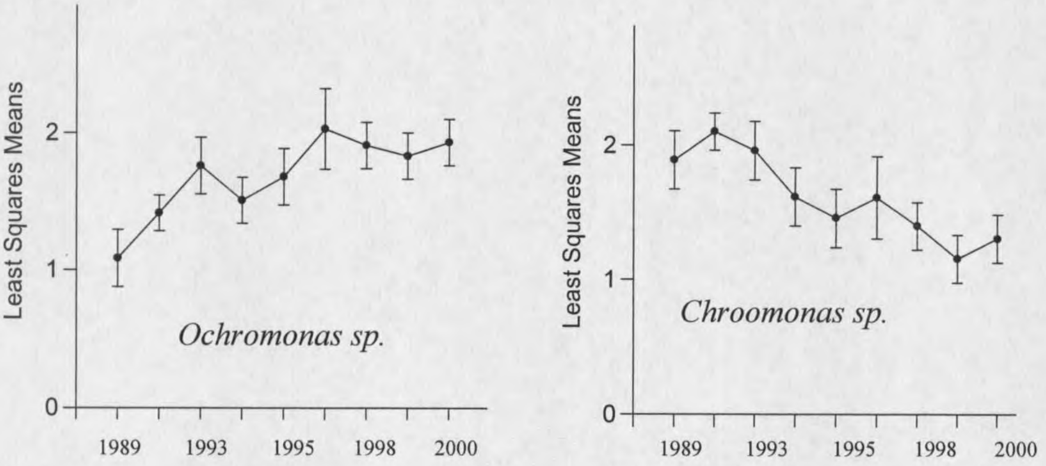


Figure 4.5 Plots of least squares means obtained from ANOVA on dominant phytoplankton taxa with time for the east lobe of Lake Bonney. *Ochromonas sp.* and *Chroomonas sp.* has changed from 1989-2000 in μgC m^{-2}. Data were log transformed values of integrated carbon biomass from the dominant species.

Discussion

In Lake Bonney, most of the carbon is autochthonous since no carbon comes from allochthonous inputs because of the lack of plant-life in the Antarctic (Wetzel and Likens

2000). Although <10% of the carbon is phytoplankton carbon in the east lobe of lake Bonney and <30% in the west lobe of Lake Bonney. Most of the carbon stored in the lakes is not phytoplankton carbon. This result is consistent with previous studies, which found that the sinking of organic carbon in the trophogenic zone exceeds the new carbon production by four times (Priscu, et al. 1999). Carbon stores in the bottom of the lakes provide carbon to the upper depths (Lyons, et al. 2000). The source of the carbon is not known, although evidence suggests that this source has been developing over the past 10,000 years (Lyons, et al. 1998; Lyons, et al. 2000).

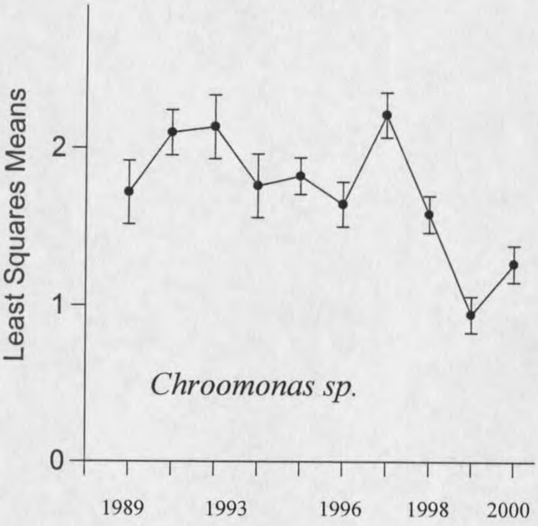


Figure 4.6 Plots of least squares means obtained from ANOVA on dominant phytoplankton taxa with time for the west lobe of Lake Bonney. *Chroomonas sp.* is changing in μg C m^{-2} from 1989 to 2000. Data were log transformed values of integrated carbon biomass from the dominant species.

Phytoplankton populations were evaluated using measured biomass, chlorophyll *a*, and primary production estimates from the east and west lobes of Lake Bonney. Measurements of chlorophyll *a* were not related with measurements of phytoplankton carbon in either of the lobes. This measurement of phytoplankton could be affected by the high amount of dead particulate carbon in these lakes since chlorophyll *a* measurements do not distinguish between live phytoplankton species and dead particulate carbon (Hallegraeff 1977). Measurements of chlorophyll *a* are also affected by the differences in chlorophyll *a* to carbon ratios for different species of phytoplankton (Steele and Baird 1961). Previous studies determined the ratios of fixed CO_2 per unit photon absorbed by photosynthetic pigments, and determined that this ratio increased with depth in Lake Bonney (Neale and Priscu 1995). Primary production was also not related to phytoplankton carbon in the east and west lobes of Lake Bonney. Similarly to chlorophyll *a,* primary production is affected by the different ratios of primary production to carbon for the phytoplankton species. The higher amounts of phytoplankton carbon in the west lobe of Lake Bonney may contribute to the discrepancy between primary production and phytoplankton carbon. A better way to study the phytoplankton populations has been shown to study the different populations, since the total phytoplankton carbon, chlorophyll a, and primary production values do not distinguish between the different populations.

Phytoplankton population changes were seen in the phytoplankton populations present in the lobes of Lake Bonney during the long-term analysis. *Ochromonas sp.* a tiny phytoplankton species and *Chroomonas sp.* changed in concentration significantly from 1989 to 2000 in the east lobe of Lake Bonney. *Chroomonas sp.* also changed significantly from 1989 to 2000 in the west lobe of Lake Bonney, although *Ochromonas sp.* did not show a significant change in the west as well as from 1989, 1992, 1994-2000 in the west lobe of Lake Bonney. In previous studies of ice covered Lake Bonney it was hypothesized that phytoplankton species located further down the water column (13-18 m) are more affected by PAR because PAR is more limiting at deeper depths (Lizotte and Priscu 1992; Fritsen and Priscu 1999). Studies also determined that phytoplankton species at 13-18 m are less affected by limiting nutrients because they are closer to the chemocline (Priscu 1995; Fritsen and Priscu 1999). ANOVA did not reveal a significant change in the populations of *Chlamydomonas subcaudata* for either of the lobes of Lake Bonney. These results are what are expected in this environment. The phytoplankton populations located in the upper water columns are significantly changing while the phytoplankton located in the lower water columns and not. The upper water column is more susceptible to change since it is affected by the inflow of meltwater supplying nutrients to the phytoplankton populations. Whereas the lower water column is a stable environment for the phytoplankton populations.

Conclusion

In the lobes of Lake Bonney, one of the dominant taxa *Chroomonas sp.* located in the upper water columns significantly decreased from 1989 to 2000 similarly in both lobes. *Ochromonas sp.* increased significantly in the east lobe of Lake Bonney. Temporal analysis of the biomass of *Chlamydomonas subcaudata* did not reveal any changes from 1989 to 2000 in either the west lobe or the east lobe of Lake Bonney.

CHAPTER 5

CONCLUSIONS

This study was the first to identify and quantify all phytoplankton species present and determine the spatial and temporal trends in a long –term data set collected from the east and west lobes of Lake Bonney, Antarctica. The earliest studies on the phytoplankton in Lake Bonney resulted in a broad base of the organisms present (Goldman et al. 1967, Parker et al. 1979, Vincent 1983). Later studies began to include quantitative measurements of the phytoplankton species present, although most of the later studies were conducted on Lake Fryxell (Sharp 1993, Lizotte et al. 1995, Laybourn-Parry et al. 1992, Spaulding et al. 1994, Roberts et al. 2000, Laybourn-Parry et al. 2002). This study allowed for the quantitative comparisons of Lake Bonney's phytoplankton species found in the austral summers from as early as 1989 to 2000.

The low diversity of phytoplankton species present in Lake Bonney is revealed in the few divisions of phytoplankton represented. Phytoplankton species present in Lake Bonney include those found in the divisions Cyanophytes, Chlorophytes, Chrysophytes, and Cryptophytes. Many species of Chlorophytes occur in the plankton including; *Chlamydomonas subcaudata, Chlamydomonas intermedia, Chloromonas sp., Thorakomonas sp., Brachiomonas sp.,* and *Polytomella sp.* The common species from Chrysophyte taxa includes *Ochromonas sp.* and *Mallomonas sp.* Lastly, one of the most common species seen in the phytoplankton populations in Lake Bonney was *Chroomonas sp.* and less often *Cryptomonas sp.* These species have consistently been identified in studies conducted on Lake Bonney as well as in many other lakes in the Taylor Valley before this long-term study.

The east and west lobes of Lake Bonney have strong vertical gradients of conductivity, temperature, nutrients, and PAR. In conjuction with these distinct gradients the phytoplankton are located in distinct layers within the water columns. The distribution of *Chlamydomonas sp.* showed that these species were significantly higher in number in the lower water column than in the upper water column ($p>0.05$). Whereas, *Chroomonas sp.* were significantly higher in the number in the upper water column than in the lower water column ($p>0.05$). *Ochromonas sp.* was distributed throughout the water columns of the west lobe but located in the lower water column in the east lobe ($p>0.05$). Physiological characteristics of the species in the distinct layers were also compared and were significantly different between the upper and lower water columns of the lakes.

The phytoplankton carbon estimated from the total phytoplankton species abundances were compared with other widely used measurements of phytoplankton populations in the lobes of Lake Bonney. Measurements of phytoplankton populations included chlorophyll *a* and primary production measurements. However, no relationships were evident between primary production and chlorophyll *a* to phytoplankton carbon; which implies that in these environment phytoplankton populations should be studied separately since they are distinct.

The phytoplankton populations located in the upper water columns of the east and west lobes of Lake Bonney are significantly changing. Biomass estimates of

Chroomonas sp. changed from 1989-2000 for the east and west lobes of Lake Bonney. These species are located in the upper water column of the lobes of Lake Bonney. In the west lobe of Lake Bonney, *Ochromonas sp.* is not located primarily in the upper water column and in fact is located in the lower water column as well. *Ochromonas sp.* has not changed significantly from 1989-2000. However, *Chroomonas sp.* which is primarily located in the upper water column has shown significant changes from 1989-2000.

The omission of data collected during the winter months makes the role of phytoplankton populations restricted to only a few months out of a year. All the analysis in this thesis was on November and December data and still trends in the data were detectable. The role of phytoplankton populations in Lake Bonney would be greatly elucidated by inclusion of samples collected during the winter.

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APPENDICES

APPENDIX A

TOTAL PHYTOPLANKTON COUNTS

East Lobe Collection Date	Depth (m)	Brachiomonas sp	Chlamydomonas subcaudata	Chlorococcum sp.	Chloromonas sp.	Chloromonas alpina	Chlamydomonas intermedia	Polytomella sp.	Pyramimonas sp.	Thorakomonas sp.	Thorakomonas sp.2	Chrysococcus sp.	Mallomonas sp.
21-Nov-89	5		1				1		4				
21-Nov-89	8		6	2									
21-Nov-89	13		12	19		23	36	4	31	4		9	5
21-Nov-89	17		4	10			146	4	48	3			4
21-Nov-89	19		7	69				5	39	11			
7-Dec-89	5	1	85					3	3	10	13		
7-Dec-89	17	1	157		4				4			2	
17-Nov-90	4									7			1
17-Nov-90	5		3		4				1	7			3
17-Nov-90	6		10		7					9			
17-Nov-90	8		13		2					11			
17-Nov-90	10		2		9					6			1
17-Nov-90	13				76		31			8			
17-Nov-90	15		1		70		104			6			
17-Nov-90	16		5		57		128	2	1	1			
17-Nov-90	17		1		19		125						
17-Nov-90	18		15		28		40		80	1			
17-Nov-90	20		4		24		10		105	1			
17-Nov-90	23		2		73		6	2	94	1	31		
17-Nov-90	25		2		15		3	1	4	10	20		
17-Nov-90	30		17		46			8			33		
17-Nov-90	35		3		25		12	4	78		15		
23-Nov-90	15		5						1				1
24-Nov-90	4.5		1				15		2	14			
24-Nov-90	6				2		19			20		2	
25-Nov-90	10		6				17	1	3	19			
25-Nov-90	17		213		4			3				5	
10-Dec-90	4.5		6				18	1	1	17			2
10-Dec-90	6				2		15		12	7			
10-Dec-90	10		7				32		5	8			4
10-Dec-90	13		203		3		25	2					
10-Dec-90	17	1	231						11	12		67	
18-Dec-90	4		4		5		4	1	2	12	1		
18-Dec-90	5		5						2	6			
18-Dec-90	6		1				26	1	12	9			
18-Dec-90	8		2		2		13		17	2			
18-Dec-90	10		17				15	1	13	2			
18-Dec-90	12		2				2			1			
18-Dec-90	13		205				1	2	3	5			

East Lobe Collection Date	Depth (m)	Navicula sp.	Tabellaria sp.	Ochromonas sp.	Achnanthes sp.	Anabaena sp.	Chroococcus sp.	Lyngbya sp.	Oscillatoria sp.	Phormidium sp.	Phormidium frigidum	Cryptomonas sp.	Chroomonas sp.
21-Nov-89	5			26								4	310
21-Nov-89	8			129						6		6	170
21-Nov-89	13			143						1		4	7
21-Nov-89	17			80				1				5	
21-Nov-89	19		3	101								13	17
7-Dec-89	5	2		165									211
7-Dec-89	17			201						1		2	102
17-Nov-90	4			30								12	304
17-Nov-90	5			124						2		11	171
17-Nov-90	6			58									291
17-Nov-90	8			161						2		1	136
17-Nov-90	10			103						1		16	289
17-Nov-90	13			176								5	35
17-Nov-90	15			104								5	2
17-Nov-90	16			117								1	3
17-Nov-90	17			162						3			
17-Nov-90	18			136						2			
17-Nov-90	20			166								4	1
17-Nov-90	23			117									3
17-Nov-90	25			138									4
17-Nov-90	30			182								4	9
17-Nov-90	35			146									
23-Nov-90	15			272					23	8		3	12
24-Nov-90	4.5			34									209
24-Nov-90	6			46									182
25-Nov-90	10			167						6			205
25-Nov-90	17			70								2	
10-Dec-90	4.5			114									198
10-Dec-90	6			136						1		1	218
10-Dec-90	10			212									130
10-Dec-90	13			46						1		7	7
10-Dec-90	17			83									
18-Dec-90	4			69						8		3	199
18-Dec-90	5			204									64
18-Dec-90	6			162						1			201
18-Dec-90	8			198						2		2	114
18-Dec-90	10			226						6		1	143
18-Dec-90	12			48						1		17	216
18-Dec-90	13			180									21

East Lobe Collection Date	Depth (m)	Brachiomonas sp.	Chlamydomonas subcaudata	Chlorococcum sp.	Chloromonas sp.	Chloromonas alpina	Chlamydomonas intermedia	Polytomella sp.	Pyramimonas sp.	Thorakomonas sp.	Thorakomonas sp.2	Chrysococcus sp.	Mallomonas sp.
18-Dec-90	15		219						9	7			
18-Dec-90	16	3	16					1	3				4
18-Dec-90	17		55					2	8	1			
18-Dec-90	18		167		2				2	1			
18-Dec-90	20		20		1		1			2			4
18-Dec-90	23		3				1			29			7
18-Dec-90	25		56		12			1		5			3
18-Dec-90	30		5		3		1	1		80			10
18-Dec-90	35	2	63		4		4	1		13	19		
4-Jan-91	4.5		1							1			
4-Jan-91	6									3			
4-Jan-91	10							3		16			
4-Jan-91	12		2				1		7	4			
4-Jan-91	17		7							7			1
9-Jan-91	4									4			
9-Jan-91	5									2			
9-Jan-91	6									4			1
9-Jan-91	8				5			1	14				1
9-Jan-91	10				10		1	3	14				5
9-Jan-91	12		5				2	1		3			
9-Jan-91	13		4						13				
9-Jan-91	15		2					2		7		3	2
9-Jan-91	16		37		5		5	2		6		5	
9-Jan-91	17		4	46	41				23				6
9-Jan-91	18		64	6	66		2	1	19				
9-Jan-91	19		12	41	37	1	4		1				3
9-Jan-91	20		3		8				9	8		75	
9-Jan-91	21				2					21		91	
9-Jan-91	22		1							16		99	
9-Jan-91	23		1	62	1				15	10			14
9-Jan-91	25			125					47	34		1	6
9-Jan-91	30			43			35			26			13
14-Sep-91	6						34						
14-Sep-91	8						9		20				
14-Sep-91	16						116		17			3	
14-Sep-91	16						78			2		12	
14-Sep-91	18		21				67	5					
19-Sep-91	5	29						3	8	1			4
19-Sep-91	6		45					1					

East Lobe Collection Date	Depth (m)	Navicula sp.	Tabellaria sp	Ochromonas sp.	Achnanthes sp.	Anabaena sp.	Chroococcus sp.	Lyngbya sp	Oscillatoria sp.	Phormidium sp.	Phormidium frigidum	Cryptomonas sp.	Chroomonas sp.
18-Dec-90	15			119						2		1	21
18-Dec-90	16			75					1	5		9	216
18-Dec-90	17			126					7	12			206
18-Dec-90	18			290					4	5			24
18-Dec-90	20	1		281						1			8
18-Dec-90	23			293						3		1	1
18-Dec-90	25			294		2			8				7
18-Dec-90	30			298				1	6				4
18-Dec-90	35	1		324				1	1				
4-Jan-91	4.5			31		3							287
4-Jan-91	6			81						4		10	219
4-Jan-91	10			193						1		12	116
4-Jan-91	12			94						2		6	250
4-Jan-91	17			202								19	66
9-Jan-91	4			48									249
9-Jan-91	5			46									259
9-Jan-91	6			136								6	165
9-Jan-91	8			165								8	160
9-Jan-91	10			172						4		15	160
9-Jan-91	12			159								34	84
9-Jan-91	13			174								17	192
9-Jan-91	15			188								9	112
9-Jan-91	16			163						4		13	53
9-Jan-91	17			144		1						3	12
9-Jan-91	18			117		3						7	4
9-Jan-91	19			138						3		1	10
9-Jan-91	20			145						3			4
9-Jan-91	21			192						2			15
9-Jan-91	22			165									21
9-Jan-91	23			118						3		6	5
9-Jan-91	25			71		1				1		1	7
9-Jan-91	30	1		128						1		3	73
14-Sep-91	6			32								44	151
14-Sep-91	8			319						3		3	182
14-Sep-91	16			8									
14-Sep-91	16			49								6	75
14-Sep-91	18			70						1		39	
19-Sep-91	5			20								16	245
19-Sep-91	6			82								17	153

East Lobe Collection Date	Depth (m)	Brachiomonas sp.	Chlamydomonas subcaudata	Chlorococcum sp.	Chloromonas sp.	Chloromonas alpina	Chlamydomonas intermedia	Polytomella sp.	Pyramimonas sp.	Thorakomonas sp.	Thorakomonas sp.2	Chrysococcus sp.	Mallomonas sp.
19-Sep-91	8	9					1	8	1				1
19-Sep-91	8						1	1	9	1			1
19-Sep-91	10		2				169		1				
19-Sep-91	10		4				133		4			1	
19-Sep-91	13				8	4	4	3					
19-Sep-91	13		12	29			39		39	7			
19-Sep-91	15						31		22			11	
19-Sep-91	15						14	1	2			40	
19-Sep-91	16						67					3	
19-Sep-91	16						45					4	
19-Sep-91	17						58	22	9				
19-Sep-91	18						70		47				
19-Sep-91	18		2				67		27				
19-Sep-91	20						82		30	1		25	
19-Sep-91	20						97			1		16	
19-Sep-91	20							1		1			
10-Oct-91	3.9							2					
10-Oct-91	4.5								1	4			
10-Oct-91	6									3			
10-Oct-91	8									1			
10-Oct-91	10		2				1		2	2			
10-Oct-91	13		7		2		1		1	3			
10-Oct-91	15						3		4			87	
10-Oct-91	16		1				80		7	2			
10-Oct-91	17			56	3		11		3				
10-Oct-91	18			80					3				
10-Oct-91	20		1	133				6	2				
17-Oct-91	11		1		1				1				
17-Oct-91	12												2
17-Oct-91	14		199							5			3
17-Oct-91	20		5				8		1	5			9
24-Oct-91	3.9		11				1	2		2			
24-Oct-91	4.5		6					1		2			
24-Oct-91	6		4						2	2			1
24-Oct-91	8		16										
24-Oct-91	10		1						2	1			
24-Oct-91	12		1		18		13	5	2	12			
24-Oct-91	16		2	69	15								
24-Oct-91	17		10	61					18	1			

East Lobe Collection Date	Depth (m)	Navicula sp.	Tabellana sp.	Ochromonas sp.	Achnanthes sp.	Anabaena sp	Chroococcus sp.	Lyngbya sp.	Oscillatoria sp.	Phormidium sp	Phormidium frigidum	Cryptomonas sp.	Chroomonas sp.
19-Sep-91	8			133						1		5	150
19-Sep-91	8			199						4		7	129
19-Sep-91	10			59									2
19-Sep-91	10			62									7
19-Sep-91	13			196								10	108
19-Sep-91	13			116			7			1			70
19-Sep-91	15			58			2			15			12
19-Sep-91	15			16						3		14	15
19-Sep-91	16			101									6
19-Sep-91	16			101		1			1				52
19-Sep-91	17			89					1	1		5	32
19-Sep-91	18			84									47
19-Sep-91	18			68						2			27
19-Sep-91	20			68						11			4
19-Sep-91	20			134									
19-Sep-91	20		1	114					5				
10-Oct-91	3.9			61								6	266
10-Oct-91	4.5			128								2	173
10-Oct-91	6			124						8		9	197
10-Oct-91	8			117						3		17	197
10-Oct-91	10			198						9		3	82
10-Oct-91	13			261						1		11	41
10-Oct-91	15			193								7	2
10-Oct-91	16			243						2		1	6
10-Oct-91	17			237									
10-Oct-91	18			223			2						
10-Oct-91	20			199									5
17-Oct-91	11			69					1				251
17-Oct-91	12			21					4			3	216
17-Oct-91	14			33					6				
17-Oct-91	20			260						5			1
24-Oct-91	3.9			42						1		3	250
24-Oct-91	4.5			66								2	264
24-Oct-91	6			166						4		6	173
24-Oct-91	8			160						3		5	169
24-Oct-91	10			167						2		1	131
24-Oct-91	12			192						3			77
24-Oct-91	16			260								4	4
24-Oct-91	17			184						3			2

East Lobe Collection Date	Depth (m)	Brachiomonas sp.	Chlamydomonas subcaudata	Chlorococcum sp.	Chloromonas sp.	Chloromonas alpina	Chlamydomonas intermedia	Polytomella sp.	Pyramimonas sp.	Thorakomonas sp.	Thorakomonas sp.2	Chrysococcus sp.	Mallomonas sp.
24-Oct-91	18		2	41			3		24				
24-Oct-91	20		4	150			21	4	5	1			
2-Nov-94	30		1							2			
3-Nov-94	30		2		9					52			
23-Nov-94	5		6				16		1	11			
23-Nov-94	6								6	2			1
23-Nov-94	8		1										
23-Nov-94	10												
23-Nov-94	13		23				68		19	5			
23-Nov-94	13		5				1	1	50				
23-Nov-94	13		6				66		2				
23-Nov-94	13		1	10				1				19	
23-Nov-94	15	1	127	2	28		2			1			
23-Nov-94	18		20	13			136		2				
23-Nov-94	18		34				8		37				
23-Nov-94	18		17	9				3	1				1
23-Nov-94	18		6				18	1					
23-Nov-94	22									13			
10-Jan-95	5			5				1	3	7			3
10-Jan-95	6				1				5	9			2
10-Jan-95	8								4	3			2
10-Jan-95	10							2		4			
10-Jan-95	13		3				4			3		20	
10-Jan-95	15		2	1						3		23	
10-Jan-95	18		31							8		47	
10-Jan-95	22							4				64	
10-Jan-95	25				1					14		150	
10-Jan-95	30		1							14		92	7
19-Sep-95	4.3		3				34			3			1
19-Sep-95	5		1				12		1	1			
19-Sep-95	8						6						
19-Sep-95	10		11	5			1						
19-Sep-95	12		7	13									
19-Sep-95	13		63									9	
19-Sep-95	15		132										
19-Sep-95	18		178				3						
19-Sep-95	20			6			7						
19-Sep-95	22	1	48									1	
19-Sep-95	25						35					208	

East Lobe Collection Date	Depth (m)	Navicula sp.	Tabellaria sp.	Ochromonas sp	Achnanthes sp.	Anabaena sp.	Chroococcus sp.	Lyngbya sp.	Oscillatoria sp.	Phormidium sp	Phormidium frigidum	Cryptomonas sp.	Chroomonas sp
24-Oct-91	18			270						3		2	
24-Oct-91	20	1		211									1
2-Nov-94	30			239									4
3-Nov-94	30			355						2			5
23-Nov-94	5			129									346
23-Nov-94	6			249						3		18	141
23-Nov-94	8			233						6			79
23-Nov-94	10			223						2		7	56
23-Nov-94	13			187									
23-Nov-94	13			222								11	36
23-Nov-94	13			209									37
23-Nov-94	13			289								19	58
23-Nov-94	15			529					3	7		6	31
23-Nov-94	18			149						1			
23-Nov-94	18			108								57	47
23-Nov-94	18			81									89
23-Nov-94	18			95			50						120
23-Nov-94	22			376								3	5
10-Jan-95	5			219						2		9	76
10-Jan-95	6			175						3		19	117
10-Jan-95	8			291						3		4	51
10-Jan-95	10			228						3		1	69
10-Jan-95	13			240								11	60
10-Jan-95	15			237						2		4	68
10-Jan-95	18			215						3			43
10-Jan-95	22			181			64					4	27
10-Jan-95	25			137									47
10-Jan-95	30			123									57
19-Sep-95	4.3			630						3		6	211
19-Sep-95	5			467						3		8	180
19-Sep-95	8			338						11			113
19-Sep-95	10			458						2			13
19-Sep-95	12			299									8
19-Sep-95	13			419					8	2		2	5
19-Sep-95	15			435					3	5		1	11
19-Sep-95	18			517									7
19-Sep-95	20			293						5			4
19-Sep-95	22			26						3			9
19-Sep-95	25	1		50						1			3

East Lobe Collection Date	Depth (m)	Brachiomonas sp.	Chlamydomonas subcaudata	Chlorococcum sp	Chloromonas sp.	Chloromonas alpina	Chlamydomonas intermedia	Polytomella sp.	Pyramimonas sp.	Thorakomonas sp.	Thorakomonas sp.2	Chrysococcus sp.	Mallomonas sp.
19-Sep-95	30		37	9				7		1		73	
6-Oct-95	4.5		2						1	1			
6-Oct-95	4.5						11		1	1			
6-Oct-95	6									1			
6-Oct-95	6				2			2	2	3			
6-Oct-95	10			8	3			1					
6-Oct-95	10				2								
6-Oct-95	13		1	21	10		1		3				
6-Oct-95	18						6		3	5		52	
6-Oct-95	18			56									
6-Oct-95	25		2				1	2		5	16	113	
6-Oct-95	25			160						2			
17-Oct-95	4.3			1					1	2			
17-Oct-95	6												2
17-Oct-95	10		4		5				2				
17-Oct-95	13		7	83					1	2			
17-Oct-95	18		16	107			4						
17-Oct-95	25		23	119			2	2		3			
1-Dec-95	4.5						6			2			
1-Dec-95	6						4	2	1				
1-Dec-95	10		37						2				
1-Dec-95	13		79				2						
1-Dec-95	18		241		1								
1-Jan-96	4.5							2	13				
1-Jan-96	6		8						2	1			2
1-Jan-96	10		1						9			63	
1-Jan-96	13		10	13	4							38	
1-Jan-96	18		11							2		76	
1-Jan-96	25		24	11				3				75	
3-Nov-96	4.5		3							5			
3-Nov-96	6	1	4				13	3	2	26			
3-Nov-96	10		5					5		19	1		
3-Nov-96	13	4	2				31	1	4	7			
3-Nov-96	18		31				3			129			
3-Nov-96	25		2						4	1			
24-Nov-96	4.5		1				27		6	7			1
24-Nov-96	6		1				11		19	2			9
24-Nov-96	10		2				3		3	1			
24-Nov-96	13		29						5				

East Lobe Collection Date	Depth (m)	Navicula sp.	Tabellaria sp.	Ochromonas sp.	Achnanthes sp.	Anabaena sp.	Chroococcus sp.	Lyngbya sp	Oscillatoria sp.	Phormidium sp.	Phormidium frigidum	Cryptomonas sp.	Chroomonas sp.
19-Sep-95	30			406						1			1
6-Oct-95	4.5			377						6		13	70
6-Oct-95	4.5			236						6		2	30
6-Oct-95	6			258						1		5	46
6-Oct-95	6			242				1		6		2	59
6-Oct-95	10			255						3		3	1
6-Oct-95	10			308				2		10			13
6-Oct-95	13			282				1				3	7
6-Oct-95	18			317						2			1
6-Oct-95	18			242				1				4	8
6-Oct-95	25			117									
6-Oct-95	25			108						3			9
17-Oct-95	4.3			253								8	108
17-Oct-95	6			266						1		2	69
17-Oct-95	10			311						5		4	25
17-Oct-95	13			356						2			28
17-Oct-95	18			205									2
17-Oct-95	25			123						1		11	
1-Dec-95	4.5			308						4		4	315
1-Dec-95	6			370									163
1-Dec-95	10			403						7			43
1-Dec-95	13			514						12		7	9
1-Dec-95	18			295						1			28
1-Jan-96	4.5			162						1		30	234
1-Jan-96	6			279					2	3		18	44
1-Jan-96	10			227								5	18
1-Jan-96	13			363								5	3
1-Jan-96	18			188									7
1-Jan-96	25			220									11
3-Nov-96	4.5			105				2		1		62	166
3-Nov-96	6			9				1		1		153	68
3-Nov-96	10			121						16		19	102
3-Nov-96	13	1		38				1		2		21	171
3-Nov-96	18			60								48	31
3-Nov-96	25			18					30	5			193
24-Nov-96	4.5			62								4	202
24-Nov-96	6			102									214
24-Nov-96	10			201					1	26		1	32
24-Nov-96	13			232					7			18	10

East Lobe Collection Date	Depth (m)	Chlamydomonas acuta	Chlamydomonas subcaudata	Chlorococcum sp.	Chloromonas sp.	Chloromonas alpina	Chlamydomonas intermedia	Polytomella sp.	Pyramimonas sp.	Thorakomonas sp.	Thorakomonas sp.2	Chrysococcus sp.	Mallomonas sp.
24-Nov-96	18		4										
24-Nov-96	25												
15-Jan-97	4.5		12					1		1			
15-Jan-97	6		11					1	4				
15-Jan-97	10		47				6	1		1			
15-Jan-97	13		60				1					11	
15-Jan-97	18		54				9		1			70	
15-Jan-97	25		18	232			2					13	
20-Dec-97	6		7							1			
20-Dec-97	10		4						3				
20-Dec-97	13		181						29	3			1
20-Dec-97	18		64										
20-Dec-97	20									5			
20-Dec-97	37		2		8			3		17			
09-Nov-98	4.5						42			13			
09-Nov-98	6		21							5			1
09-Nov-98	10						2			8			
09-Nov-98	13		29				4						
09-Nov-98	18		334							1			
09-Nov-98	30		97					6				292	
06-Dec-98	4.5		5	1	27		19			3			
06-Dec-98	6		2		21		9	1		2			
06-Dec-98	10		20		201		1			3			
06-Dec-98	13		300		161					1			
06-Dec-98	18		358		5			1					
06-Dec-98	25		245				16						
30-Dec-98	4.5						7			5			
30-Dec-98	6		46		40		8						
30-Dec-98	10		45		49		4			1			
30-Dec-98	13		325		3		4						
30-Dec-98	18		305		2								
30-Dec-98	25		149				19						
06-Nov-99	4.5						5						
06-Nov-99	6		2				4						
06-Nov-99	10		1				1						
06-Nov-99	13		305				1			1			
06-Nov-99	18		181				1			5			
06-Nov-99	30	1	5	309			8	1					
03-Dec-99	4.5				3			2					

East Lobe Collection Date	Depth (m)	Navicula sp.	Tabellaria sp	Ochromonas sp.	Achnanthes sp.	Anabaena sp.	Chroococcus sp.	Lyngbya sp.	Oscillatoria sp.	Phormidium sp.	Phormidium frigidum	Cryptomonas sp.	Chroomonas sp.
24-Nov-96	18			195									8
24-Nov-96	25												36
15-Jan-97	4.5			233						1		5	52
15-Jan-97	6			251								4	88
15-Jan-97	10			262						9		6	12
15-Jan-97	13			354								21	
15-Jan-97	18			190									
15-Jan-97	25			109									
20-Dec-97	6			294									73
20-Dec-97	10			200						3		1	14
20-Dec-97	13			197								14	4
20-Dec-97	18			200						18			
20-Dec-97	20			231		1							1
20-Dec-97	37	4		327		1			6				32
09-Nov-98	4.5			377						1		5	14
09-Nov-98	6			342						2			78
09-Nov-98	10			340						2	1		19
09-Nov-98	13	1		307						3			48
09-Nov-98	18			311					1			1	5
09-Nov-98	30	4		395									
06-Dec-98	4.5			339									78
06-Dec-98	6			307								1	33
06-Dec-98	10			314						1	1	2	14
06-Dec-98	13			314						1	4	13	8
06-Dec-98	18			102						2			1
06-Dec-98	25			350						1			7
30-Dec-98	4.5			317									20
30-Dec-98	6			416						2			11
30-Dec-98	10			346						3		2	6
30-Dec-98	13			322						4		2	2
30-Dec-98	18	1		245						1			46
30-Dec-98	25			348						2			9
06-Nov-99	4.5			314	2					1			18
06-Nov-99	6			316									29
06-Nov-99	10			295						1			3
06-Nov-99	13			136	2	1				1			5
06-Nov-99	18	1		292						5	33		6
06-Nov-99	30	5		38					2				7
03-Dec-99	4.5			343						1			67

East Lobe Collection Date	Depth (m)	Chlamydomonas subcaudata	Chlorococcum sp.	Chloromonas sp.	Chloromonas alpina	Chlamydomonas intermedia	Polytomella sp.	Pyramimonas sp.	Thorakomonas sp.	Thorakomonas sp 2	Chrysococcus sp.	Mallomonas sp.
03-Dec-99	6			18		14			1			
03-Dec-99	10			14		3						
03-Dec-99	13	109	4	1								
03-Dec-99	18	299		7		10						1
03-Dec-99	30	178				16						
28-Dec-99	4.5	43				7			5			
28-Dec-99	6	4				8		1	2			
28-Dec-99	10	4				1						
28-Dec-99	13	159				3			3			
28-Dec-99	18	310							6			
28-Dec-99	30	276				14			2			
29-Oct-00	4.5	3		7		2						
29-Oct-00	6	1				10			1			
29-Oct-00	10	5						3				
29-Oct-00	13	47										
29-Oct-00	18	245				1		2	1			
29-Oct-00	30	196				17						
25-Nov-00	4.5					8			1			
25-Nov-00	6	1				6		1				
25-Nov-00	10	5		47								
25-Nov-00	13	62				1						
25-Nov-00	18	285										
25-Nov-00	30	237				6			1			
22-Dec-00	4.3											
22-Dec-00	6								1			
22-Dec-00	10	3				10						
22-Dec-00	13	178							1			
22-Dec-00	18	261		4								
22-Dec-00	30	155				17			2			

East Lobe Collection Date	Depth (m)	Navicula sp.	Tabellaria sp.	Ochromonas sp.	Achnanthes sp.	Anabaena sp.	Chroococcus sp.	Lyngbya sp	Oscillatoria sp.	Phormidium sp.	Phormidium frigidum	Cryptomonas sp.	Chroomonas sp.
03-Dec-99	6			334						1	1		10
03-Dec-99	10			363						1			6
03-Dec-99	13			246									1
03-Dec-99	18	1		182					4				69
03-Dec-99	30	2		81					3	2			6
28-Dec-99	4.5	1		346									8
28-Dec-99	6			362						1			31
28-Dec-99	10			339									11
28-Dec-99	13			269						2			5
28-Dec-99	18			243						11		1	22
28-Dec-99	30	2		72						5			7
29-Oct-00	4.5	5	2	357	32	1			6			2	40
29-Oct-00	6	1		335	3					3			53
29-Oct-00	10			372	1					4			12
29-Oct-00	13	3		318	8					2		1	5
29-Oct-00	18	1		307	4					1			32
29-Oct-00	30	7		304	1					7			60
25-Nov-00	4.5	1		312					1	2		5	11
25-Nov-00	6			376		1					1	7	26
25-Nov-00	10			325									1
25-Nov-00	13			322									12
25-Nov-00	18	1		224	1					1			42
25-Nov-00	30			289						9		1	17
22-Dec-00	4.3			312					1	3		12	43
22-Dec-00	6			308						2	3	5	42
22-Dec-00	10			391						2		1	20
22-Dec-00	13		1	316						2		3	4
22-Dec-00	18	1		312						3			47
22-Dec-00	30			297						3			19

West Lobe Collection Date	Depth (m)	Brachiomonas sp.	Chlamydamonas acuta	Chlamydomonas subcaudata	Chlamydomonas sp.	Chlorococcum sp.	Chloromonas sp.	Chlamydomonas intermedia	Duniella sp	Polytomella sp.	Pyramimonas sp.	Thorakomonas sp.	Thorakomonas sp.2
28-Nov-89	5			1				28			49	17	
28-Nov-89	8				2			29			29	15	3
28-Nov-89	10			2	2			96			67	1	
28-Nov-89	14	1		7	10		3			1			
28-Nov-89	16												
28-Nov-89	18	1		9	1							28	
28-Nov-89	20			112		3						17	
1-Dec-90	4	2					5	43		4		12	1
1-Dec-90	6		1					24			2	10	
1-Dec-90	8						1				2	3	
1-Dec-90	10				4			59			13	8	2
1-Dec-90	13		1					29				7	5
6-Dec-90	8							31			32	6	
6-Dec-90	10			7	35			163		3	62	2	
6-Dec-90	12			3	17						3		
6-Dec-90	13			26	2							19	
6-Dec-90	15												
7-Jan-93	4											1	
7-Jan-93	5	3		23				2				14	
7-Jan-93	6			23				1				10	
7-Jan-93	8			7							38		
7-Jan-93	10			41							87	8	2
7-Jan-93	12			44				68		3	1	5	
7-Jan-93	13			7								1	
7-Jan-93	14			8							3	5	17
7-Jan-93	15			2								9	
7-Jan-93	17	2		4				20			2	9	
7-Jan-93	20			27						1		15	
7-Jan-93	22												
7-Jan-93	25											12	
7-Jan-93	30			2								7	
7-Jan-93	35			8							8	7	
25-Nov-94	5							13			5	1	
25-Nov-94	10			2			25	13				6	
25-Nov-94	10							12			1		
25-Nov-94	13			5									
25-Nov-94	20			4		3	2	2		4		3	
25-Nov-94	20												
12-Jan-95	5			1				11				1	

West Lobe Collection Date	Depth (m)	Chrysococcus sp.	Ochromonas sp.2	Mallomonas sp.	Navicula sp.	Ochromonas sp.	Synedra sp.	Achnanthes sp.	Anabaena sp.	Oscillatoria sp.	Phormidium sp.	Cryptomonas sp.	Chroomonas sp.
28-Nov-89	5					106							200
28-Nov-89	8					200					4		84
28-Nov-89	10					214	1						98
28-Nov-89	14	1				2							178
28-Nov-89	16												
28-Nov-89	18	82				190							33
28-Nov-89	20					193	1						2
1-Dec-90	4					125	1					2	172
1-Dec-90	6					116							204
1-Dec-90	8					12							227
1-Dec-90	10			1		110					3	1	200
1-Dec-90	13	1		1		120					4		174
6-Dec-90	8					178					1		89
6-Dec-90	10	1				188					5		185
6-Dec-90	12					28						21	223
6-Dec-90	13					4							94
6-Dec-90	15												
7-Jan-93	4					84							254
7-Jan-93	5			6		89							226
7-Jan-93	6			1		137						36	164
7-Jan-93	8			8		146							126
7-Jan-93	10			1		144					3		90
7-Jan-93	12					144						5	97
7-Jan-93	13	1				113						7	237
7-Jan-93	14			1		87						24	292
7-Jan-93	15					180						1	179
7-Jan-93	17	3				219							38
7-Jan-93	20	7				177							110
7-Jan-93	22	207				82							
7-Jan-93	25	8				199						1	118
7-Jan-93	30	41				153						5	77
7-Jan-93	35	32				156							65
25-Nov-94	5					212					2	2	205
25-Nov-94	10			1		438							53
25-Nov-94	10	4				546				10	8	1	42
25-Nov-94	13					378				4	1	16	
25-Nov-94	20					29					6		5
25-Nov-94	20					13							3
12-Jan-95	5					211					3	2	101

West Lobe Collection Date	Depth (m)	Brachiomonas sp.	Chlamydamonas acuta	Chlamydomonas subcaudata	Chlamydomonas sp.	Chlorococcum sp.	Chloromonas sp.	Chlamydomonas intermedia	Duniella sp.	Polytomella sp.	Pyramimonas sp.	Thorakomonas sp.	Thorakomonas sp.2
12-Jan-95	10			6			3	11			2		
12-Jan-95	13			104								7	
12-Jan-95	20											7	
21-Sep-95	4.3						1					4	
21-Sep-95	5			2			1	9			1	5	
21-Sep-95	10			1								2	
21-Sep-95	13			14				7				2	
21-Sep-95	20			3								2	
21-Sep-95	25			1									
21-Sep-95	35			9				2				1	
4-Oct-95	4							12			5	7	
4-Oct-95	5			2				25			1		
4-Oct-95	10			1				4			1	2	
4-Oct-95	13			13				3					
4-Oct-95	20								4			1	
4-Oct-95	35			8					2				
19-Oct-95	4.5									1		2	
19-Oct-95	5											5	
19-Oct-95	10					1		1		1		6	
19-Oct-95	13			5		49	76			1	3		
19-Oct-95	20												
3-Dec-95	4.5			2			1	30			2	1	
3-Dec-95	5						6	42			4	9	
3-Dec-95	10							25				1	
3-Dec-95	13			129				1					
3-Dec-95	20												
3-Jan-96	4.5									2	3	6	
3-Jan-96	5			2		2						5	
3-Jan-96	13			6								2	
3-Jan-96	20						8						
3-Jan-96	35										5		
1-Nov-96	4.5			2				16		10	1	10	
1-Nov-96	5				3			26			2	17	2
1-Nov-96	10			15				15				29	
1-Nov-96	13			2				4					
1-Nov-96	20			3								3	
26-Nov-96	4.5			5			1		2		4	3	2
26-Nov-96	5						1	12		1	19	8	4
26-Nov-96	10			8							36	2	

West Lobe Collection Date	Depth (m)	Chrysococcus sp.	Ochromonas sp.2	Mallomonas sp	Navicula sp.	Ochromonas sp	Synedra sp.	Achnanthes sp.	Anabaena sp.	Oscillatoria sp.	Phormidium sp.	Cryptomonas sp.	Chroomonas sp.
12-Jan-95	10	2				252					7		52
12-Jan-95	13					207					1	4	18
12-Jan-95	20					207					1	1	1
21-Sep-95	4.3					254			4		4	16	306
21-Sep-95	5					300	1				1		297
21-Sep-95	10		8			370					19	7	30
21-Sep-95	13					398				2	1	29	
21-Sep-95	20			2		44						5	
21-Sep-95	25					5							1
21-Sep-95	35					17					1	3	6
4-Oct-95	4					182							339
4-Oct-95	5					140					1		311
4-Oct-95	10					331					7	3	30
4-Oct-95	13					373							66
4-Oct-95	20					6							6
4-Oct-95	35					9							4
19-Oct-95	4.5					54					2	15	309
19-Oct-95	5					89					1	15	284
19-Oct-95	10					245					16	12	41
19-Oct-95	13					152					2	9	12
19-Oct-95	20					163							
3-Dec-95	4.5		4			338				2	8		284
3-Dec-95	5			1		146					9		292
3-Dec-95	10	1				513					16		18
3-Dec-95	13					385				1		4	10
3-Dec-95	20												
3-Jan-96	4.5			1		193					4	10	116
3-Jan-96	5					131						7	175
3-Jan-96	13					475					1	4	16
3-Jan-96	20					285							3
3-Jan-96	35					25							
1-Nov-96	4.5										1	1	269
1-Nov-96	5	4				25					3	3	198
1-Nov-96	10					99	5			1	13	47	
1-Nov-96	13										4	4	249
1-Nov-96	20											2	9
26-Nov-96	4.5					34						5	216
26-Nov-96	5			2		84					2	6	203
26-Nov-96	10					202				3	17	8	26

West Lobe Collection Date	Depth (m)	Brachiomonas sp.	Chlamydamonas acuta	Chlamydomonas subcaudata	Chlamydomonas sp.	Chlorococcum sp	Chloromonas sp.	Chlamydomonas intermedia	Duniella sp	Polytomella sp	Pyramimonas sp.	Thorakomonas sp.	Thorakomonas sp.2
26-Nov-96	13			226								1	
26-Nov-96	18											5	
26-Nov-96	20			1									
17-Jan-97	4.5			12							2	1	
17-Jan-97	5			11						2	1		
17-Jan-97	10			10				43				4	
17-Jan-97	13			18				180			2		
17-Jan-97	20												
11-Nov-97	4.5											2	
11-Nov-97	5						1				4	1	
11-Nov-97	10						1						
11-Nov-97	13			5							3	4	
11-Nov-97	20			1									
20-Dec-97	4.5							1					
20-Dec-97	5			5							7	2	
20-Dec-97	10			10			4				10		
20-Dec-97	13			217		2							
20-Dec-97	20												
11-Nov-98	4.5			2					41			22	
11-Nov-98	13			306								2	
11-Nov-98	20			3									
9-Dec-98	4.5			1			51	37		1			
9-Dec-98	5			52			48	6				1	
9-Dec-98	10			25			26	7					
9-Dec-98	13			417				35					
9-Dec-98	20			5				2				2	
1-Jan-99	4.5			12				43					
1-Jan-99	5		1	12			23	19			2		
1-Jan-99	10			7			33	9					
1-Jan-99	13			377				3				1	
1-Jan-99	20												
11-Nov-99	4.5			8		1							
11-Nov-99	5			6			22						
11-Nov-99	10			1				7				1	
11-Nov-99	13			91				21				2	
11-Nov-99	20			7				1	5	1			
5-Dec-99	4.5			1				4					
5-Dec-99	5							2					
5-Dec-99	10			1		1							

West Lobe Collection Date	Depth (m)	Chrysococcus sp	Ochromonas sp.2	Mallomonas sp	Navicula sp.	Ochromonas sp.	Synedra sp.	Achnanthes sp.	Anabaena sp.	Oscillatoria sp.	Phormidium sp.	Cryptomonas sp.	Chroomonas sp.
26-Nov-96	13					78				1	1	9	5
26-Nov-96	18					366					4	3	2
26-Nov-96	20					145				1		1	
17-Jan-97	4.5					158						6	148
17-Jan-97	5					158					1		183
17-Jan-97	10					204						6	70
17-Jan-97	13					159					2	27	8
17-Jan-97	20					305							2
11-Nov-97	4.5					154			2	1	1	27	225
11-Nov-97	5					141				1		26	217
11-Nov-97	10					237					1	17	88
11-Nov-97	13					272				3	1	18	24
11-Nov-97	20					10							2
20-Dec-97	4.5			1		212						11	114
20-Dec-97	5			1		99					6	6	236
20-Dec-97	10					223					1		20
20-Dec-97	13					309					4	11	5
20-Dec-97	20					21			2		2		
11-Nov-98	4.5					301					2		5
11-Nov-98	13					223				2		33	84
11-Nov-98	20					200							
9-Dec-98	4.5					319				3	3		
9-Dec-98	5					406					1		5
9-Dec-98	10					308					1		13
9-Dec-98	13					293						2	14
9-Dec-98	20					398					1		
1-Jan-99	4.5	4			1	326							151
1-Jan-99	5					341						1	168
1-Jan-99	10					333						3	22
1-Jan-99	13	2				206			2		1	19	6
1-Jan-99	20				2	80				1			7
11-Nov-99	4.5					311							2
11-Nov-99	5					325					2		11
11-Nov-99	10				3	325		1			2		40
11-Nov-99	13				1	245					1		40
11-Nov-99	20					222					1		29
5-Dec-99	4.5					322							24
5-Dec-99	5					330					1		9
5-Dec-99	10					325					1		2

West Lobe Collection Date	Depth (m)	Brachiomonas sp.	Chlamydamonas acuta	Chlamydomonas subcaudata	Chlamydomonas sp.	Chlorococcum sp.	Chloromonas sp.	Chlamydomonas intermedia	Duniella sp.	Polytomella sp.	Pyramimonas sp.	Thorakomonas sp.	Thorakomonas sp.2
5-Dec-99	13			140					1			33	
5-Dec-99	20			1									
30-Dec-99	4.5			4				2					
30-Dec-99	5			1				2				2	
30-Dec-99	10							12				7	
30-Dec-99	13			153				1				29	
30-Dec-99	20			3			1					4	
1-Nov-00	4.5							3	1			1	
1-Nov-00	5			8				2				1	
1-Nov-00	10			1				2					
1-Nov-00	13			17				2					
1-Nov-00	20			42				1	2		1	1	
28-Nov-00	4.5			2				1					
28-Nov-00	5							1			1		
28-Nov-00	10			3				5					
28-Nov-00	13			62				4					
28-Nov-00	20			126				11	6				
27-Dec-00	4.5			13				6	2				
27-Dec-00	5			5				5	1		1		
27-Dec-00	10			6				1				2	
27-Dec-00	13			95				3	1				
27-Dec-00	20							7					

West Lobe Collection Date	Depth (m)	Chrysococcus sp.	Ochromonas sp 2	Mallomonas sp.	Navicula sp.	Ochromonas sp.	Synedra sp	Achnanthes sp.	Anabaena sp.	Oscillatoria sp.	Phormidium sp.	Cryptomonas sp.	Chroomonas sp.
5-Dec-99	13					302					1		4
5-Dec-99	20					315							4
30-Dec-99	4.5					329							32
30-Dec-99	5			1		299							60
30-Dec-99	10					326					3		19
30-Dec-99	13					295					1		15
30-Dec-99	20					293							2
1-Nov-00	4.5					324					1	1	136
1-Nov-00	5					381						2	25
1-Nov-00	10					325					3		4
1-Nov-00	13				1	310					1	8	9
1-Nov-00	20					386							14
28-Nov-00	4.5					323		2			1	4	54
28-Nov-00	5					364					1	2	25
28-Nov-00	10					338		4			1		4
28-Nov-00	13				1	299		1	10		4		6
28-Nov-00	20					410		2			1		12
27-Dec-00	4 5					307		19			2	2	70
27-Dec-00	5					342		6				1	41
27-Dec-00	10				1	292		1				5	21
27-Dec-00	13					318		1	1			7	4
27-Dec-00	20					179						4	9

APPENDIX B

MATRICES OF PAIRWISE MEAN DIFFERENCES

East Lobe of Lake Bonney *Ochromonas sp.*

	1989	1990	1994	1995	1996	1997	1998	1999	2000
1989	0								
1990	0.329	0							
1994	0.675	0.346	0						
1995	0.800	0.471	0.125	0					
1996	0.595	0.266	-0.080	-0.205	0				
1997	0.945	0.616	0.270	0.145	0.350	0			
1998	0.825	0.496	0.150	0.025	0.230	-0.120	0		
1999	0.748	0.419	0.073	-0.052	0.153	-0.197	-0.077	0	
2000	0.848	0.519	0.173	0.048	0.253	-0.097	0.023	0.100	0

East Lobe of Lake Bonney *Chroomonas sp.*

	1989	1990	1994	1995	1996	1997	1998	1999	2000
1989	0								
1990	0.212	0							
1994	0.070	-0.142	0						
1995	-0.245	-0.487	-0.345	0					
1996	-0.435	-0.647	-0.505	-0.160	0				
1997	-0.280	-0.492	-0.350	-0.005	0.155	0			
1998	-0.493	-0.705	-0.563	-0.218	-0.058	-0.213	0		
1999	-0.737	-0.949	-0.807	-0.462	-0.302	-0.457	-0.243	0	
2000	-0.587	-0.799	-0.657	-0.312	-0.152	-0.307	-0.093	0.150	0

West Lobe of Lake Bonney *Chroomonas sp.*

	1989	1990	1992	1994	1995	1996	1997	1998	1999	2000
1989	0									
1990	0.379	0								
1992	0.416	0.037	0							
1994	0.044	-0.335	-0.372	0						
1995	0.0106	-0.273	-0.310	0.062	0					
1996	-0.073	-0.452	-0.489	-0.117	-0.179	0				
1997	0.493	0.114	0.078	0.450	0.388	0.566	0			
1998	-0.135	-0.514	-0.551	-0.179	-0.241	-0.062	-0.629	0		
1999	-0.773	-1.152	-1.189	-0.817	-0.879	-0.700	-1.267	-0.638	0	
2000	-0.449	-0.828	-0.865	-0.493	-0.493	-0.376	-0.943	-0.314	0.324	0